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A first look at the phylogeny of the Myrmarachninae, with rediscovery and redescription of the type species of *Myrmarachne* (Araneae: Salticidae)

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Abstract

Myrmarachne melanocephala MacLeay, 1839, type species of the genus *Myrmarachne* MacLeay, 1839, is rediscovered and redescribed, and a neotype is here designated. Five **new synonyms** of *M. melanocephala* are proposed: *M. contracta* (Karsch, 1880) [lectotype here designated], *M. providens* (Peckham & Peckham, 1892), *M. ramosa* Badcock, 1918, *M. albicrurata* Badcock, 1918, and *M. lateralis* Badcock, 1918. *Myrmarachne melanocephala* is shown to be a widespread species in southern Asia that mimics the ant *Tetraponera rufonigra* (Jerdon). *Myrmarachne christae* (Prószyński, 2001) and *Myrmarachne galianoae* (Prószyński, 2001) are transferred from *Damoetas*, **new combinations**. The latter results in a homonym with *Myrmarachne galianoae* Cutler, 1981: we rename the species *Myrmarachne mariaelenae* Edwards & Benjamin, **replacement name**. Further characterization of the species groups of *Myrmarachne* is presented, related genera are discussed, and a preliminary phylogeny of the Myrmarachninae is given.

Key words: Myrmarachninae, new combination, new name, new synonym, phylogeny, species groups, *Belippo, Bocus, Damoetas, Judalana, Ligonipes, Panachraesta, Rhombonotus*

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Introduction

It might be expected that the type genus of a subfamily would be well known, and the type species of that genus well defined. That has not been the case in this instance. The ant-mimicking genus *Myrmarachne* MacLeay[1], 1839, is one of the most speciose genera of Salticidae, containing over 200 nominal species naturally distributed over five continents and numerous tropical islands (Prószyński 2009; Platnick 2009). Yet, due to the loss of the holotype (the only known specimen) of the type species (*Myrmarachne melanocephala* MacLeay, 1839), whose description was published in the same paper as the genus description, and due to mistakes in the literature as to its type locality, the identity of this species has remained a mystery. MacLeay (1839) published a paper describing five new species of spiders from a diversity of families. Four of these species were described from Cuba. The fifth, *M. melanocephala*, was described from 'Bengal.' According to various sources (*e.g.*, Majumdar, 1943), Bengal consisted of what is now the state of West Bengal in eastern India (at times of local rule, it also sometimes included parts of neighboring states), and East Bengal which is now Bangladesh. Unfortunately, Lucas (1857) mistakenly mentioned this species in a paper that discussed Cuban natural history, which apparently led subsequent cataloguers (Petrunkevitch 1911; Lutz 1915; Mello-Leitão 1933; Roewer 1954; Bonnet 1957) to list this species from Cuba. Galiano (1969), attempting to remedy this error, reported that the correct type locality for *M. melanocephala* was 'Bengala' (not 'Bengal' as reported by MacLeay, although probably her spelling was simply due to her writing in Spanish). Nevertheless, this is misleading, because old maps for 'Bengala' seem to indicate that these two are not synonymous. 'Bengala' appears to include Burma (aka Myanmar) as well as Bangladesh and India (*i.e.*, the countries bordering the Bay of Bengal), including but not exclusive to East and West Bengal. Therefore, it seems safe to state that 'Bengal' as defined above (essentially the state of West Bengal in India and Bangladesh combined) is the correctly designated origin for the type of *M. melanocephala*.

Fortuitously, we have been able to match *Myrmarachne melanocephala* with its junior synonyms, some of which are fairly well known (see below). It is redescribed herein, giving a firmer basis to subsequent discussion of *Myrmarachne* and related genera. One topic these genera have in common is the propensity of their constituent species to mimic ants, and we take this opportunity to add a few notes on that subject. For the most part, though, we review the present status of the Myrmarachninae, take a first look at overall phylogenetic relationships in the subfamily using various analytical techniques, further examine the species groups in *Myrmarachne*, and discuss all the myrmarachnine genera, how they appear to be related, and problems that still need to be resolved.

It should be noted that some basic assumptions in our analyses follow the pioneering work of Maddison and Hedin (2003) on jumping spider phylogeny using molecular data. This paper defined the clade Salticoida (essentially, the 'modern' salticids) but not enough taxa were represented to resolve the clade. Subsequently, Maddison *et al.* (2008) largely resolved the Salticoida. To summarize this resolution, the amycoids were shown to be sister to the rest of the salticoids, and the remaining salticoids were split into two diverse lineages. One of these two lineages is represented here by *Chinattus parvulus* (Banks), which is the most distant outgroup included here and roots our phylogenetic tree. The remaining species in this study belong to the other lineage.

Materials and methods

Types and some other specimens were borrowed from the following institutions: Museum of Comparative Zoology (MCZ), Cambridge, Massachusetts; Museum für Naturkunde (ZMB), Berlin; British Natural History Museum (BNHM), London; U.S. National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.; Museum d'Histoire Naturelle (MHNG), Geneve, Switzerland; and the California Academy of Sciences (CAS), San Francisco.

Methodology for the description follows Benjamin (2004). Digital images were taken with a Nikon

DXM1200F camera. Images were edited using an AutoMontage software package. Left structures are depicted unless otherwise stated. Setae are usually not depicted in the final palp drawings. All measurements are given in millimeters (range from smallest to largest, with neotype measurements in parentheses) and were made with a compound microscope equipped with a 10x ocular and an ocular micrometer scale. Morphological abbreviations: CO = copulatory opening, contained within translucent "window-like" atria; RTA = retrolateral tibial apophysis. Literature citations follow the format used by Platnick (2009).

For convenience, we refer to the sclerotized part of the spermathecal ducts plus the anteriorly placed, variously developed spermathecae containing the fertilization ducts as the spermathecal complex. This is also due to the fact that at this time, for some species, illustrations are not available to document the border between the spermathecae and the sclerotized ducts. In addition, in order to be properly studied, the membranous ducts between the elongate spermathecal complex and the copulatory openings must be stained. The staining technique used by Prószyński (*e.g.,* 2008) with Chlorazol Black E has proven useful in this regard.

The 38 characters chosen for the phylogenetic analysis are predominately the most obvious genitalic and somatic characters, including those proposed in the literature (see Appendix A for a list of characters and states, and Table 1 for the data matrix).

A total of 29 species were included. At least two species (if available) from each proposed species group of *Myrmarachne* and some species unassigned to groups, known from both male and female, were chosen as representatives (in some cases, this prevented the nominal species of a group from being chosen, as it is known from only one sex). Most species were coded by observing specimens directly. Some species were coded based on published descriptions and illustrations in order to have sufficient representatives of the most species groups for the analysis [two from Davies and Zabka (1989), indicated by DZ; several from Wanless (1978a, b)].

In total, 17 species of *Myrmarachne* were chosen for analysis. Eight additional myrmarachnine species were included: *Belippo ibadan* Wanless, 1978, *Belippo milloti* (Lessert, 1942), *Bocus excelsus* Peckham and Peckham, 1892, *Damoetas galianoae* Prószyński, 2003, *Damoetas nitidus* (L. Koch, 1879), *Ligonipes* sp., *Judalana lutea* Rix, 1999, and *Rhombonotus gracilis* L. Koch, 1879. Four of these species are type species for the genus (*B. excelsus, D. nitidus, J. lutea,* and *R. gracilis*). Four species (the two *Belippo* spp., *Bocus excelsus,* and *D. galianoae*) we considered *a priori* to be of questionable association. Four outgroups to the Myrmarachninae were also included: *Chinattus parvulus* (Banks, 1895) [Hasarieae]*, Mantisatta longicauda* Cutler and Wanless, 1973 [Ballinae]*, Neon nelli* Peckham and Peckham, 1888 [representing the most basal genus in Astioida], and *Orthrus bicolor* Simon, 1900 [Astioida]. These four genera bracket myrmarachnines to various extent, based on the molecular phylogeny of Salticidae published in Maddison *et al.* (2008), from which we use *Chinattus parvulus* to root our phylogenetic tree.

Parsimony and Bayesian methods were utilized to complete the phylogenetic analyses. Parsimony analyses were conducted using both PAUP* 4.0b10 (Swofford 2002) and TNT 1.1 (Goloboff *et al.* 2008). The Bayesian analysis was done by MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck 2003).

In Parsimony analysis, all character states were treated as unordered (one step for any state change). In PAUP, heuristic searches were initially implemented with 200 random addition sequence replicates, each saving at most five trees using tree bisection reconnection (TBR) branch swapping. The second round of TBR branch swapping on the most parsimonious trees from the first round was then performed without constraint except by MAXTREES of 100,000. In TNT, the traditional search mode was used with 100 random addition sequence replicates, and the TBR swapping algorithm saving 100 trees per replication. Trees were enhanced in Winclada (Nixon 2002) in slow optimization mode.

Non-parametric bootstrap analysis (Felsenstein, 1985) was conducted in PAUP* 4.0b10 (Swofford, 2002) to assess clade support, with 300 replicates using heuristic searches (10 random addition sequence replicates, each saving at most 100 trees) and TBR branch swapping.

In Bayesian analysis, two independent analyses were performed with four Markov chains across

50,000,000 generations, sampling every 1000th generation. We used the Mk model developed by Lewis (2001) with the variation in rates following the gamma distribution. The first 25% of samples were considered as burn-in and the others were used to calculate the clade credibility. From two runs during the last 37,500,000 generations, 75,000 trees were sampled, examined and input for the majority rule consensus.

TABLE 1. Data matrix corresponding to Appendix 1. Dashes (-) indicate inapplicable characters. * Original name of species, herein renamed *Myrmarachne mariaelenae*.

Characters:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
Species:																																						
Chinattus parvulus	0	0	1	0	-	-	0	0	3	5	-	-	-	0	0	1	1	-	0	1	-	4	1	0	5	0	0	0	0	0	0	3	0	0	0	1	2	0
Mantisatta longicauda	0	0	1	0	-	-	1	0	1	-	-	0	-	3	-	2	1	-	0	-	-	3	0	1	5	0	0	0	0	0	0	3	0	0	0	2	0	0
Neon nellii	1	0	1	0	-	-	2	0	4	0	-	4	0	3	-	1	1	-	1	1	-	5	0	3	4	0	4	0	0	0	0	3	0	0	0	0	1	0
Orthrus bicolor	0	2	1	0	-	0	1	0	0	1	-	0	1	4	0	1	0	0	-	0	-	0	0	1	5	0	5	0	0	2	0	0	0	2	1	1	1	0
Damoetas nitidus	6	2	0	0	2	0	0	1	2	1	2	1	1	0	0	3	0	2	0	0	0	0	0	3	3	0	0	0	0	0	0	3	0	0	0	1	0	1
Rhombonotus gracilis	6	2	0	0	2	0	1	1	2	1	2	1	1	3	-	3	0	2	3	0	3	0	0	3	3	0	0	0	0	0	0	3	0	0	0	0	0	1
Ligonipes DZ	6	2	0	0	2	1	1	1	4	1	2	1	1	0	0	3	0	2	3	0	3	3	0	3	3	0	1	1	0	0	0	3	0	0	0	1	0	1
Judalana lutea	6	2	0	0	2	0	1	1	4	1	2	1	1	3	-	3	0	2	3	0	3	0	0	3	3	0	1	0	0	0	0	3	3	0	0	1	0	1
Belippo ibadan	0	2	0	0	1	0	1	1	5	4	0	3	1	2	1	3	0	3	0	0	0	2	0	1	1	1	3	4	0	1	0	2	0	1	1	1	2	1
Belippo milloti	0	2	0	0	1	1	1	1	5	4	0	3	1	2	1	3	0	3	0	0	0	2	0	1	1	1	3	4	0	1	0	2	1	1	1	1	2	1
Myrm Australia DZ	0	2	0	0	1	1	1	1	5	1	2	2	1	0	0	3	0	3	1	0	0	2	0	0	0	0	0	3	0	1	1	0	0	0	1	1	3	1
Myrm grossa	6	2	0	0	1	1	0	1	5	1	2	2	1	0	1	3	0	3	1	0	0	2	0	2	1	0	0	3	0	1	0	0	0	2	1	2	3	1
Myrm gigantea	5	2	0	5	1	0	0	1	5	0	4	2	1	0	0	3	0	3	1	0	0	2	0	2	1	0	0	1	0	1	1	0	0	0	1	2	3	1
Bocus excelsus	0	2	0	0	0	1	1	1	5	0	0	2	1	0	1	3	0	3	1	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	1	2	3	1
Myrm plataleoides	2	2	0	0	1	1	1	1	5	0	0	2	1	0	1	3	0	3	4	1	2	1	0	1	1	0	0	0	0	1	2	0	0	0	1	2	2	2
Myrm turriformis	0	2	0	0	4	0	1	1	5	3	0	2	1	0	1	3	0	3	3	0	0	2	0	1	1	0	0	0	0	1	1	0	0	0	1	1	3	1
Myrm panamensis	4	2	0	0	0	1	0	1	5	0	1	2	1	0	0	3	0	3	0	0	0	2	0	1	1	0	0	0	0	1	1	0	0	0	1	1	2	1
Myrm parallela	4	2	0	0	0	1	0	1	5	0	1	2	1	0	0	3	0	3	0	0	0	2	0	1	1	0	0	0	0	1	1	0	0	0	1	1	1	1
Damoetas galianoae*	6	2	0	1	0	0	1	1	5	0	0	2	1	1	1	3	0	3	1	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	1	1	1	1
Myrm eumenes	6	2	0	1	0	0	1	1	5	0	0	2	1	0	1	3	0	3	2	0	0	1	0	1	1	0	0	0	0	1	0	0	2	0	1	2	3	3
Myrm eugenei	6	2	0	1	3	0	1	1	5	0	0	2	1	0	0	3	0	3	2	0	0	2	0	1	1	0	0	0	0	1	0	0	1	0	0	2	0	1
Myrm peckhami	6	2	0	1	3	0	1	1	5	0	0	2	1	0	1	3	0	3	2	0	0	2	0	1	1	0	0	0	0	1	0	0	1	0	1	2	1	1
Myrm kilifi	3	2	0	0	0	1	0	1	5	0	1	2	1	0	1	3	0	3	1	0	0	2	0	2	1	0	1	0	0	1	0	1	0	2	1	1	2	1
Myrm laurentina	3	2	0	0	0	1	0	1	5	0	0	2	1	0	1	3	0	3	1	0	0	2	0	1	1	0	0	1	0	1	0	1	1	2	1	1	1	1
Myrm formicaria	6	2	0	3	0	0	0	1	5	2	3	2	1	0	0	3	0	3	1	0	0	1	0	0	2	0	1	2	0	1	0	0	0	3	1	1	1	1
Myrm kiboschensis	6	2	0	3	0	0	0	1	5	2	3	2	1	0	1	3	0	3	1	0	1	2	0	0	1	0	1	0	0	1	0	0	0	3	1	1	2	1
Myrm melanocephala	6	2	0	2	0	0	0	1	5	0	0	2	1	2	1	3	0	3	1	0	1	2	0	1	1	0	2	2	1	1	0	0	0	2	1	1	3	2
Myrm foenisex	6	2	0	2	0	1	0	1	5	2	3	2	1	2	1	3	0	3	1	0	1	1	0	0	1	0	2	2	1	1	2	0	0	0	1	1	3	2
Myrm tristis	6	2	0	2	0	1	0	1	5	2	3	2	1	2	1	3	0	3	1	0	1	1	0	0	1	0	2	2	1	1	0	0	0	2	1	1	3	1

Taxonomy

Family Salticidae

Genus *Myrmarachne* MacLeay, 1839

Type species: *Myrmarachne melanocephala* MacLeay, 1839

(Figs 1A–H, 2A–D, 3A–D, 4A–E, 5A–D, 6)

Myrmarachne melanocephala MacLeay, 1839: 11, fig. 4 (Dm).
Salticus contractus Karsch, 1880: 396 (Dm). **New synonymy**.
Salticus providens Peckham and Peckham, 1892: 34 (Dmf); **New synonymy**.
Myrmarachne providens Simon, 1901: 500; Pocock, 1908: 259; Narayen, 1915: 399.
Myrmarachne ramosa Badcock, 1918: 303, fig. 8 (Dm); Edmunds and Prószyński, 2003: 301–304, figs 8–29. **New synonymy**.
Myrmarachne albicrurata Badcock, 1918: 306, fig. 9a (D imm. f). **New synonymy**. Synonymized by Edmunds and Prószyński (2003) with *M. ramosa*.
Myrmarachne lateralis Badcock, 1918: 310, fig. 9b (Df). **New synonymy**. Synonymized by Edmunds and Prószyński (2003) with *M. ramosa*.
Myrmarachne contracta Sherriffs, 1931: 539.

Type material: Holotype of *M. melanocephala*: male from "Bengal" (modern day India: West Bengal State plus Bangladesh) (originally kept in MacLeay collection: apparently lost). As this species was described only from the holotype and is the type species of the genus, it is necessary to designate a neotype to clarify the taxonomic status of the species. Conditions satisfying ICZN Article 75.3 are given below and in the Acknowledgments.

Neotype of *M. melanocephala* (herewith designated): **INDIA:** ***West Bengal:*** Calcutta, Calcutta Botanical gardens, 22° 34' N, 88° 24' E, 25 July 1973, leg. Ginter Ekis (USNM 2049842), examined. According to ICZN Article 76.3, the locality of the neotype becomes the type locality.

Syntypes of *Salticus contractus*: one male from Ceylon (now Sri Lanka), leg. Hoffmann (ZMB 1538), no more data given, examined, herewith designated as the **lectotype** (Figs 1D–F, 4D); and one badly damaged male from Bintang Island, Indonesia, leg. Böttger (ZMB 1537), no more data given, examined, herewith becoming the **paralectotype** (Figs 1G–H).

Syntypes of *Salticus providens*: one male and one female from Ceylon, leg. E. Simon (MCZ 22768), no more data given, examined (Figs 1A–C, 4A–C, 5A).

Holotype of *Myrmarachne ramosa*: male, from "Malay States," leg. N. Annandale and H. C. Robinson, 1901–1902, no more data given, examined.

Other material examined. SRI LANKA: ***Ratnapura district:*** 1 male, Gilimale, Induruwa Jungle, 13–15 March 1979, leg. K. V. Krombein, T. Wijesinghe, S. Siriwardana, L. Jayawickrama (USNM). ***Colombo district:*** 1 male, Labugame, 25 May 1975, leg. D. H. Messersmith, G. I. Williams, P. B. Karunaratne (USNM). ***Anuradapura district:*** 1male 1juv, Padaviya, 19 May 1976, leg. "K. V. K." (Krombein?) (USNM). ***Ampara district:*** 1 female, Ekgal Aru Sanctuary Jungle, 9–11 March 1979, leg. K. V. Krombein, T. Wijesinghe, S. Siriwardana, L. Jayawickrama (USNM). ***Kandy district***: 1 female, Udawattakelle sanctuary, 510–580m, 26–30 July 1978, leg. K. V. Krombein (USNM). ***North Western Province:*** 1 male 1 female, Kurunagala district, Kurunagala, Ethagala Mountains, ca. 300m, 11 October 2008, leg. Ziyard Jaleel (MHNG). **INDIA:** ***Uttar Pradesh:*** 1 male, 1 female, 2 juveniles, 1 ant (*Tetraponera rufonigra*), 5 miles SW Dehra Don, 600m, 9 November 1961, leg. E. S. Ross and D. Q. Cavagnaro (CAS).

Diagnosis. Other Indian and Sri Lankan *Myrmarachne* generally do not resemble *M. melanocephala* in appearance (see Remarks below). Only *M. prava* (Karsch, 1880), described in the same publication as *M. melanocephala* (sub *M. contracta*) could be confused with *M. melanocephala*, as both species have black females. However, *M. prava* can be easily separated by the overall black color of the male, very much shorter pedicel, slanted dorsal surface of the chelicerae, oval opisthosoma, and by the tapering, straight RTA, quite different from the male of *M. melanocephala* (from which this species was described).

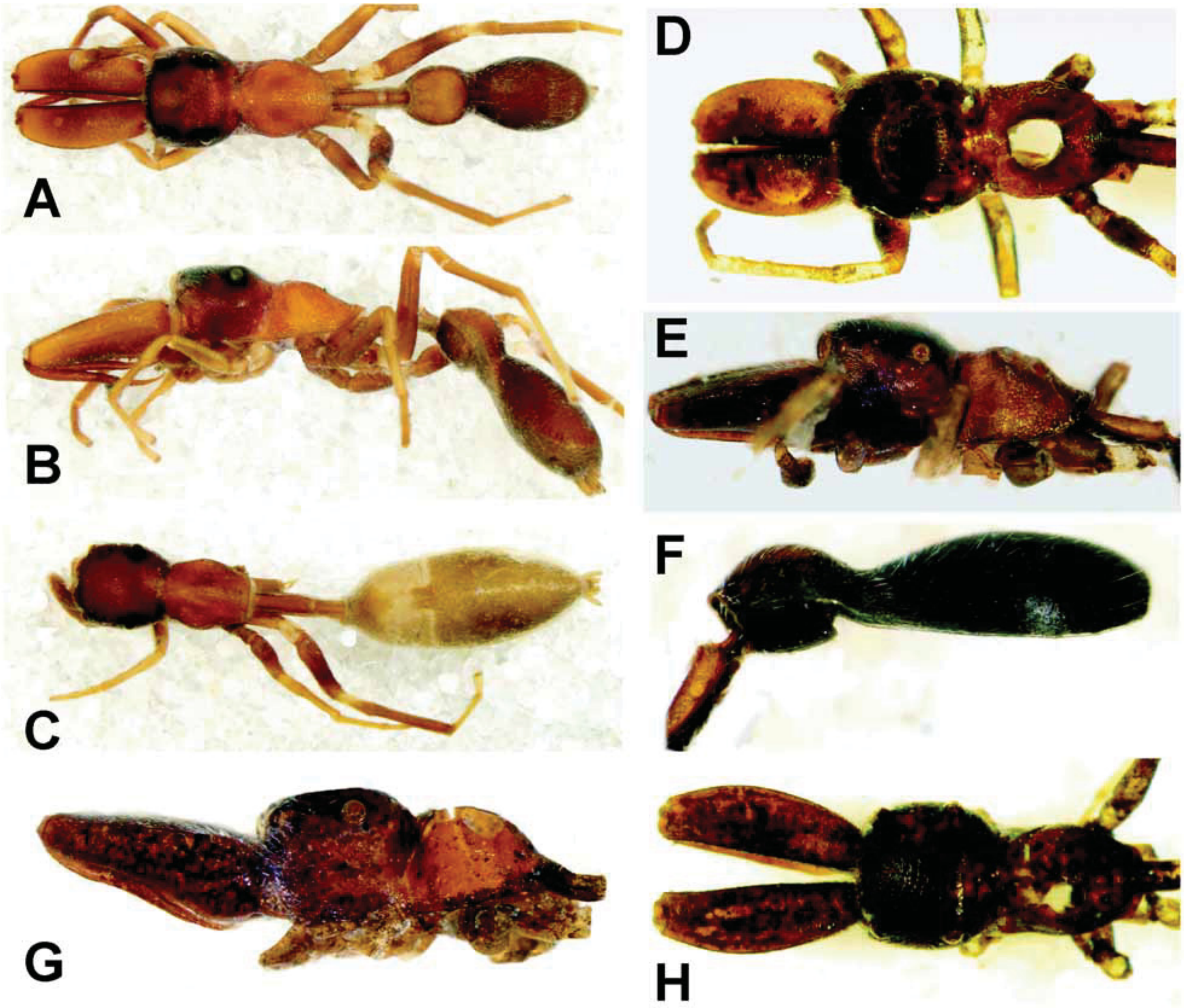

FIGURE 1. *Myrmarachne melanocephala*. A–C *M. providens* syntypes from MCZ 22768; D–F *M. contracta* lectotype from ZMB 1538; G–H *M. contracta* paralectotype from ZMB 1537 (A dorsal view of male, B lateral view of male, C dorsal view of female, D male prosoma dorsal view, E male prosoma lateral view, F male opisthosoma dorsal view, G male prosoma lateral view, H male prosoma dorsal view; A–F from Sri Lanka, G–H from Bintang Island, Indonesia.)

Description. Male: Total length: 7.2 (7.7) 12.4; prosoma length: 4.0 (4.1) 6.4, width: 1.2 (1.3) 1.6. Leg I: femur 1.6, patella 0.8, tibia 1.6, metatarsus 0.8, tarsus 0.4. Prosoma elongated with a constriction at the 50% point, anterior half black, posterior half red/brown. Opisthosoma elongated with a constriction at the anterior 25% margin, anterior 25% red/brown, posterior 75% black (Figs 2A–D, 3A). All legs red/brown with black and white rings. Chelicerae enlarged, brown/black, dorsally flattened, median margin parallel. Teeth: neotype with 13 longer teeth on outer margin distributed full length of chelicera, 9 tiny teeth on inner margin not distributed to either end of chelicera, spacing of teeth more sparse in middle and rows closer together from middle to proximal end, both rows sinuate, spacing of teeth not quite symmetrical between two chelicerae; other specimens similar, some with a few more teeth in same general pattern. Leg formula 4132. Leg I spination: 5 pair on venter of tibia, 2 pair on venter of metatarsi. Palps as in Figs 4A–E. Cymbium oval, as long as the palpal tibia. RTA a hook-shaped flattened spiral (although it is somewhat less flattened in the Malaysian specimens), mostly covered by the base of the cymbium, with its tip projecting outwards. Tegulum rounded and small, with sperm duct showing on ventral surface with a half loop immediately after the sperm reservoir. Embolus begins in distal retrolateral region right after sperm duct half loop, broad and appressed around proximal side of tegulum, then tapering and becoming free of tegulum on prolateral side, making a more ventral smaller spiral inside the diameter of the basal revolution, altogether forming about two spiral revolutions around the tegulum.

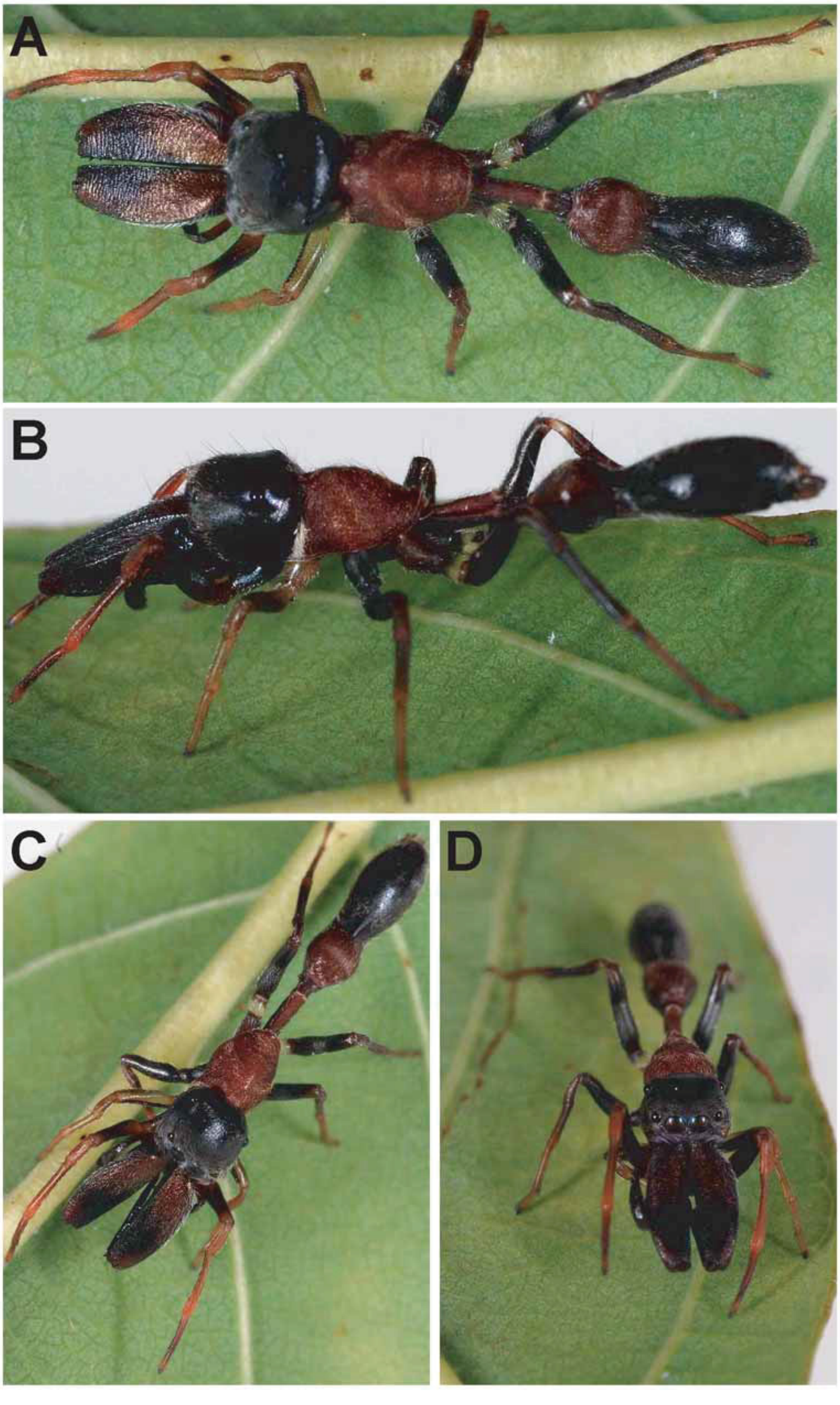

FIGURE 2. Photographs of *Myrmarachne melanocephala* male from Kurunagala, Sri Lanka. A, C, D dorsal view, B lateral view.

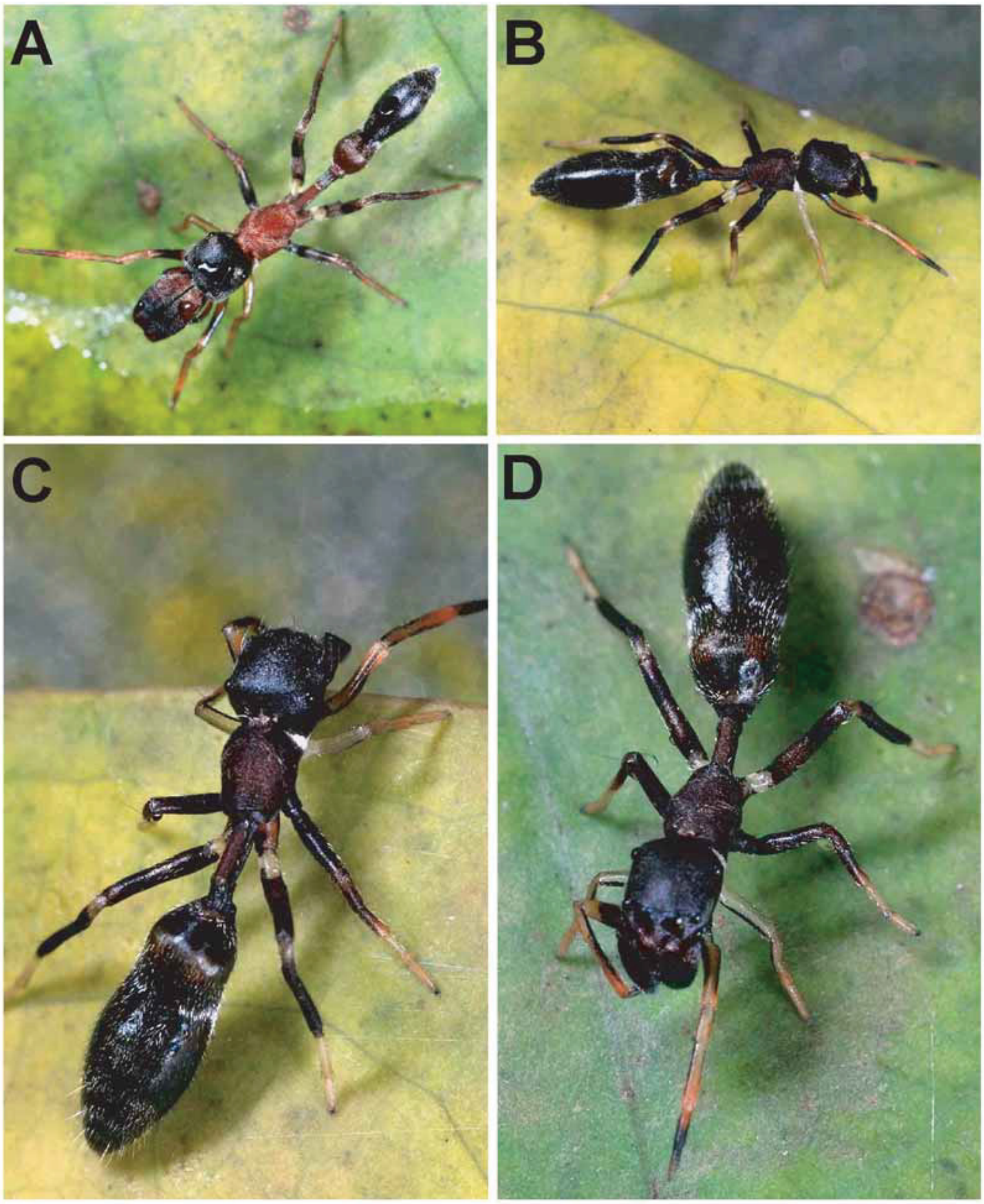

FIGURE 3. Photographs of *Myrmarachne melanocephala* from Kurunagala, Sri Lanka. A male; B–D female (A, B dorsal view, C, D lateral view).

Female: Total length: 7.4–7.6; prosoma length: 3.1–3.2, width: 1.2. Leg I: femur 1.2, patella 0.8, tibia 1.2, metatarsus 0.8, tarsus 0.4. Females lack red/brown patches and appear darker, shape as in male except for the compact vertical chelicerae (Figs 4B**,** D). Leg formula 4132. Leg I spination as in male. Epigyne and vulva as in Figs 5A–D. CO large, two laterally-oriented pockets between CO and epigastric furrow. Each CO leads to an inverted "C" shaped duct that lead to an oval spermatheca.

Variation. Color of chelicerae and fang are variable; some fangs are black, others red/brown. Some specimens are a bit darker than others. Juvenile females lack the red/brown pigmentation and are thus black.

Distribution. Pakistan to Indonesia. Narayen (1915) reported the record from Pakistan. There are no recent records to confirm this; however, the record from India below is in the northwest part of the country, so a record from Pakistan does not seem unlikely. The natural distribution of the model ant *Tetraponera rufonigra* (Jerdon) is Pakistan to Java (Ward 2001), completely overlapping the reported distribution of its spider mimic.

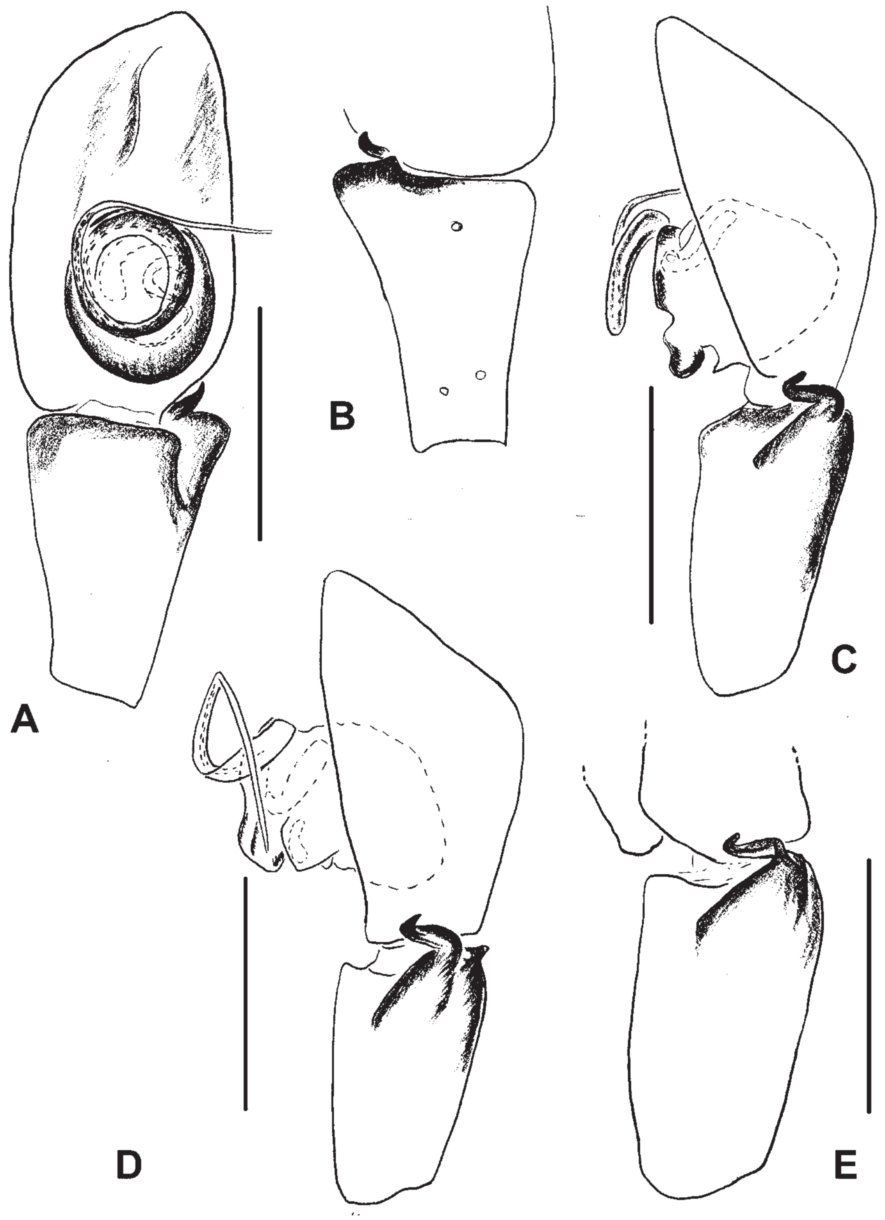

FIGURE 4. *Myrmarachne melanocephala* male palp. A–C MCZ 22768; D ZMB 1538; E Padaviya, Sri Lanka (A ventral view, B dorsal view, C–E retrolateral views). Scale bars = 0.2 mm.

Natural History. As observed by Pocock (1908: 259), *M. melanocephala* is associated with the ant *Tetraponera* [reported as *Sima*] *rufonigra*. He states, "In the Oriental Region there is a common red-and-black tree-ant, *Sima rufo-nigra*. It is pugnacious and fearless… On human beings the effects of its bite are both painful and lasting. Wherever these insects occur in any numbers, a species of spider [*Myrmarachne providens*], one of the Salticidae, is to be found running about amongst them. The spider closely resembles the ant in form and colour. It appears to be on the most friendly footing with its formidable associates, moving quickly here and there in their company and copying their busy, hurried actions." Further confirmation for this relationship is provided by one of the records listed above. Pocock's comments indicate that *M. providens*, described from Sri Lanka (formerly Ceylon), and here shown to be a synonym of *M. melanocephala*, was considered a widespread species more than a century ago.

Remarks. The male of *M. contracta* from Bintang Island is so badly damaged that illustrating its genitalia was not attempted. Its general outline matched other examined *M. melanocephala* specimens (as in Figs 1G–H; chelicerae dorsally flattened, prosoma constricted at the centre).

A species recently redescribed from Peninsular Malaysia and Singapore, strikingly similar to *M. melanocephala,* is *M. ramosa* Badcock, 1918 (Edmunds and Prószyński 2003; Platnick 2009). The type of *M. ramosa* has been compared with the neotype of *M. melanocephala* (by GBE) and found to be a junior synonym, therefore the type species has been recently well illustrated. Bintang Island is very close to Singapore, and represents the southeastern most record for this species. We agree with the synonyms *M. albicrurata* and *M. lateralis* for *M. ramosa* as proposed by Edmunds and Prószyński (2003), which become synonyms of *M. melanocephala*.

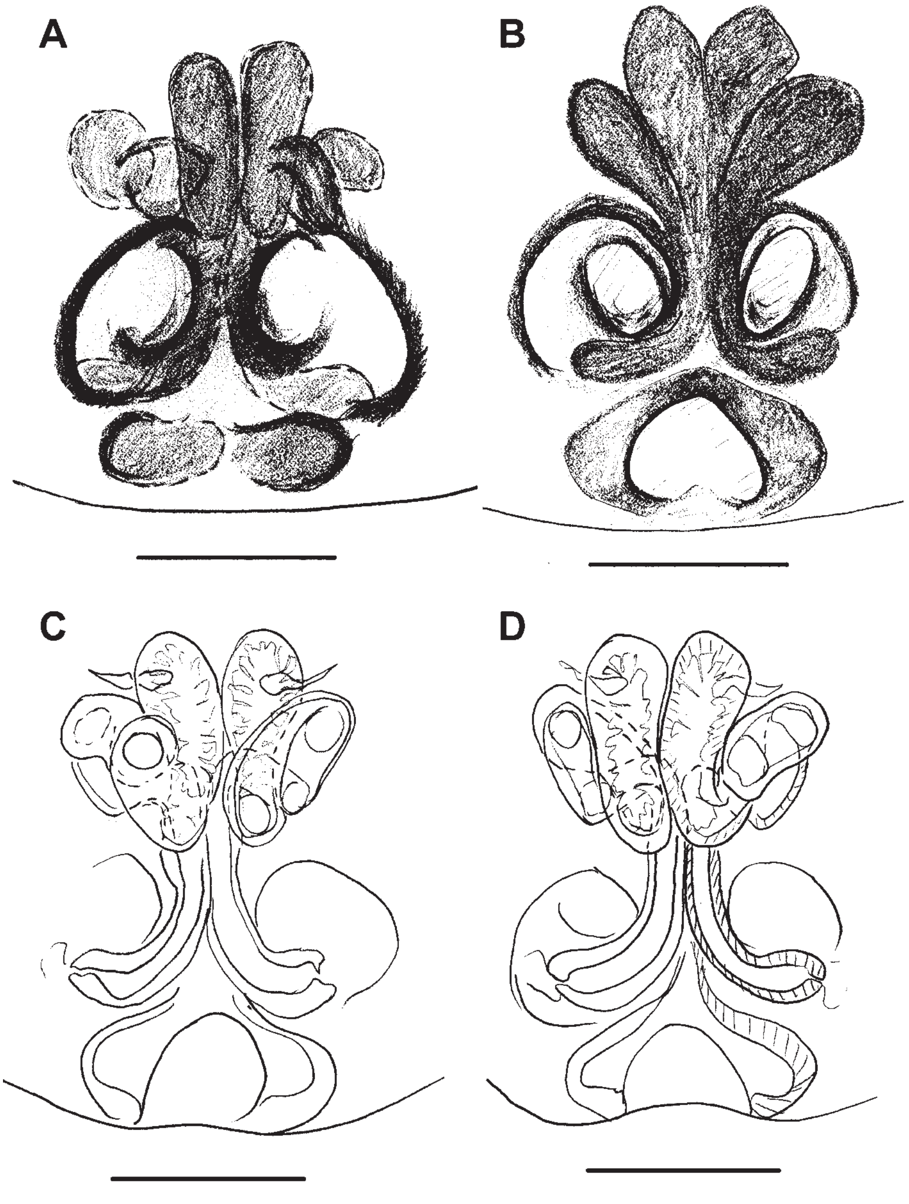

FIGURE 5. *Myrmarachne melanocephala*. A MCZ 22768; B–D Ekgal Aru Sanctuary (A, B epigyne ventral view, C vulva ventral view cleared, D vulva dorsal view). Scale bars = 0.2 mm.

Although many species of *Myrmarachne* have distinctive body shapes, final determination to species, like in most other entelegyne spiders, generally depends on the structure of the genital organs, especially when body shapes and color patterns among related species are similar. On the other hand, many well known species are easily recognized by their overall habitus, and we are of the opinion that this is true for *M.*

melanocephala as well. It is instructive to note that Wanless (1978a: 21) clearly states, "…in *Myrmarachne*…the structure of the genitalia cannot always be relied upon to separate the species." Comparison of the color plate (Fig. 6) of *M. melanocephala* in the original description (MacLeay, 1839) with *M. contracta* Karsch, 1880, from Sri Lanka, part of a study of Sri Lankan *Myrmarachne* currently in progress (SPB, in prep.) showed virtually no difference in the habitus of the two species. We believe they are conspecific and that the problem of the type species of *Myrmarachne* has been resolved. A neotype for *M. melanocephala* is designated above from Calcutta, West Bengal State, India, the only specimen presently known in collections that is from the area where the original specimen was described. In the same study of the *Myrmarachne* of Sri Lanka, SPB has found 11 species of *Myrmarachne*, seven of which are described (four of these are shared with India), plus four undescribed species. India has an additional 16 described species (not counting overlapped species with Sri Lanka; Prószyński 2009). No other species of similar color, or somatic or genital morphology, is present in Sri Lanka. This is also true for species known from India (the fauna of which, however, is less well known than the Sri Lankan *Myrmarachne* fauna, as at this time, data on undescribed species from India is incomplete, although SPB notes that no undescribed Indian species he is familiar with are similar in appearance to *M. melanocephala*). Therefore, we are reasonably certain that we have correctly identified *M. melanocephala* from among the species known from Sri Lanka and the Indian subcontinent.

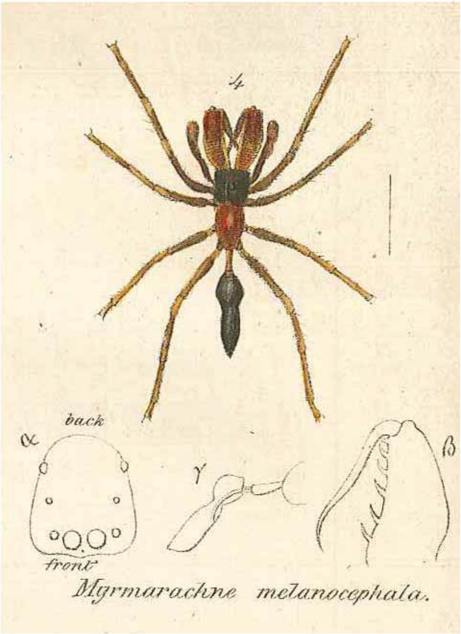

FIGURE 6. *Myrmarachne melanocephala*, replica of original plate (MacLeay, 1839).

Further Notes on Mimicry

Species of *Myrmarachne* are Batesian ant mimics. The species that have been looked at in detail seem to be species-specific (*i.e.*, the spider mimics one, or very few similar, species of ants), and Wanless (1978a: 21) gives a list of known ant models. However, he also states that some species seem to be generalized ant mimics, but could this simply be due to lack of study of these species? Edmunds (1978), in a study on *Myrmarachne*/ant associations published in the same year, documented that *Myrmarachne* tend to be associated with the dominant ant in an area and/or a species with a particularly virulent bite or sting, which implies that they are largely species-specific. Several more recent papers have documented various *Myrmarachne* species and their specific ant models (*e.g.*, Nelson *et al.* 2005; Edmunds 2006; Ceccarelli 2008;

Jackson *et al.* 2008). Ceccarelli and Crozier (2007) found that evidence for mimickry in species of *Myrmarachne* was indicative of adaptive radiation by the mimic, rather than co-evolving with their models as expected of Batesian mimics. Perhaps this accounts for the great number of *Myrmarachne* species that have so far been described.

Prószyński (2001) suggested that other genera related to *Myrmarachne* are not necessarily ant-like. However, even Peckham and Peckham (1892: 8–11) listed *Damoetas nitidus* and *Rhombonotus gracilis* as ant-like spiders. Davies and Zabka (1989) refer to, "The 4 plurident ant-mimics *Ligonipes, Rhombonotus, Myrmarachne* and *Damoetas*…" Rix (1999) reported that *Judalana lutea* specimens "strongly resemble" the formicine ant *Opisthopsis rufithorax* Emery, with both species occurring on *Acacia* bushes. Interestingly, in the same paper, Rix (1999) noted that there is a species of *Myrmarachne* that mimics the same ant species on the same bushes.

There is considerable variation in the types of ants (and other arthropods) that salticid spiders mimic; if the model is not apparent to an observer, the mimicry may be overlooked. For example, in the New World, there are salticid genera that mimic a diversity of distinctive ants, and some that mimic beetles (e.g., Richman 2008). One genus that mimics both is *Synemosyna* Hentz, 1846, where most known species are excellent mimics of individual species of the slender ants in the genus *Pseudomyrmex* (Galiano 1966; Reiskind 1977), a few species mimic *Crematogaster* ants, and one species (*S. ubicki* Cutler) mimics a staphylinid beetle (the spider might mistakenly be thought not to be a mimic, since it is not an ant mimic). A different case is that of some species of *Bellota* Peckham and Peckham, 1892 (Galiano 1972), that seem to mimic flat cephalotine ants, which are morphologically very different from the models in the previous example. All of these examples have been observed by GBE and colleagues in the Neotropics.

Review of the Myrmarachninae

The species of *Myrmarachne* and related genera have variable and unusual development of the spermathecae and attached ducts that might be unique in the Salticidae. All these genera have a basic distinctive shape of the epigyne, with a sclerotized, elongate spermathecal complex (consisting of the anteriorly placed spermathecae with sclerotized ducts extending posteriorly) connected by membranous ducts to the copulatory openings. While the male palps are also reasonably distinctive, there is not a single characteristic about them that is as notable as the spermathecal complex in the female epigyne. This group would be considered the Myrmarachninae, established by Simon (1901) as Myrmarachneae, changed to Myrmarachninae by Petrunkevitch (1928), and recognized in part by Davies and Zabka (1989) for the Australian fauna. The oldest included genus (*Myrmarachne*) was designated by Simon (1901) as the type genus of the subfamily. The other included genera presently considered valid are *Belippo* Simon, 1910*, Bocus* Peckham and Peckham, 1892*, Damoetas* Peckham and Peckham, 1886, *Ligonipes* Karsch, 1878, *Judalana* Rix, 1999, *Panachraesta* Simon, 1900, and *Rhombonotus* L. Koch, 1879. The monophyly of Myrmarachninae was supported by the molecular analysis of Maddison *et al*. (2008), who included two species of *Myrmarachne* and one species of *Ligonipes*.

Belippo was revised by Wanless (1978a) and distinguished from *Myrmarachne* by a movable palpal tibial apophysis in the male and presence of secondary spermathecae in the female. Wanless (1978a) considered *Myrmarachne* to have only one set of spermathecae, whereas *Belippo* he considered to have two sets of spermathecae (primary and secondary) joined by a sclerotized duct. Some illustrations and text, especially for *Belippo milloti* (*e.g.,* Wanless 1978a: 13-14, fig. 7K; "…the appearance of the secondary spermathecae is inconsistent…") seem to dispute this. It is apparent to us that only the anterior distinctive swelling in the sclerotized part is a true spermatheca (the presence of an illustrated fertilization duct on each anterior spermatheca supports this supposition). The opposite end of the sclerotized part of the duct is where the membranous part of the duct attaches, which happens to be near where the duct in *Belippo* is swollen. If this area is not a true spermatheca, which seems to be the case, it would negate one of the two differences proposed between *Belippo* and *Myrmarachne*. Furthermore, swelling in the sclerotized duct at its posterior end is variable in *Myrmarachne*, and may correlate with the diameter of the membranous part of the duct at that point. Another possibility is that the swelling may correspond with a glandular area, as, *e.g.,* seems to be the case in *M. grossa* (Edmunds and Prószyński 2003; see Fig. 7), as was previously suggested by Prószyński (2001). Four of the seven species of *Belippo* were originally described as *Myrmarachne* (see Wanless 1978a).

Bocus, a genus previously thought to be endemic to the Philippines (Wanless 1978c), was more recently found in Borneo (Deeleman-Reinhold and Floren 2003). It is distinguished by the structure of the sternum and coxal plates and the elongate thoracic area of the cephalothorax. However, the genital structure of the three known species is similar to various species groups of *Myrmarachne*, leading to a supposition that *Bocus* may be only a morphological variant within *Myrmarachne*.

Similarly, Bornean species of *Damoetas* (but not the Australian type of the genus, *D. nitidus*), while appearing a bit more compact in body and cheliceral form than typical for many *Myrmarachne*, have epigynes that would seem to correspond to the *volatilis* species group of *Myrmarachne*.

Davies and Zabka (1989) synonymized *Discocnemius* Thorell, 1881, and *Haterius* Simon, 1900, with *Ligonipes*, but resurrected *Rhombonotus* from *Ligonipes*. Of the described *Ligonipes* species, three (including the type, *L. illustris* Karsch, 1878) are known from Queensland (Australia), with one species each from New Guinea, Norfolk Is., and Sumatra. These species are only known from females and have *Myrmarachne*-like genitalia. A male, reportedly of this genus, was illustrated by Davies and Zabka (1989); its palp closely resembles that of *Judalana* and *Rhombonotus* (both also from Queensland), which also have *Myrmarachne*-like female genitalia, although the structure of the palp, while having some basic similarities, is different from that of *Myrmarachne*.

Panachraesta paludosa Simon, 1900, from Sri Lanka, is only known from the female; little is known about it, other than it too appears to have a typical myrmarachnine spermathecal complex, and we have not included it in any analyses here.

Simon (1901) synonymized several generic names that have rarely been used since. Other generic names more recently used within the Myrmarachninae are listed with their type species and their present assignment: *Emertonius exasperans* Peckham and Peckham, 1892: 53 (represents a new species group of *Myrmarachne* according to Wanless 1978b); *Hermosa volatilis* Peckham and Peckham, 1892: 54 (*volatilis* group); *Iola cowanii* Peckham and Peckham, 1892: 75 (*formicaria* group); *Bizone longiventris* Simon, 1903 (*Bizone* preoccupied, replaced by *Bizonella* Strand, 1929) (*volatilis* group). All of these generic names were synonymized with *Myrmarachne* by Wanless (1978a, b). Several of the earliest described species were placed in the genus *Salticus* Latreille; however, the type species of this genus, *S. scenicus* (Clerck), the type species for the family Salticidae, is not closely related to *Myrmarachne* (Maddison *et al.* 2008).

Results and taxonomic implications of phylogenetic analysis

The PAUP and TNT analyses resulted in the same 24 most parsimonious trees of length 175 and an identical strict consensus tree (Fig. 8; with seven collapsed nodes). PAUP bootstrap values are shown in Figs 8 and 9. The posterior probability values from Bayesian analysis are shown in Figs 8 and 9 as well. Two cladograms are shown (Figs 9, 10). All other trees were slight variations of these two examples. These variations consisted of rearrangements of some of the species within three individual clades (*Ligonipes* clade, Australasian clade, and Western clade, as can be deduced from the strict consensus tree, Fig. 8). In the *Ligonipes* clade, *Damoetas nitidus* is always sister to some combination of *Judalana, Ligonipes,* and *Rhombonotus*; the latter three genera take turns being sister to the other two combined. A similar situation exists in the Australasian clade, where *Myrmarachne turriformis* is sister to all the remaining species, *M. plataleoides* is always paired with *Bocus excelsus*, and the other three *Myrmarachne* species in the clade can be together in a variety of combinations among themselves (e.g., Fig. 9), or *M. gigantea* can be sister to the other two plus the *M. plataleoides/Bocus* pair (e.g., Fig. 10). Rarely do any of these combinations have a synapomorphy supporting them. The Western clade is restricted to the two variations shown, but note that the species of the *formicaria* group, when placed with the *tristis* group, do not form their own distinct group. Also, the *laurentina* and *parallela* groups show up as sister groups only in one of the two configurations.

The apparent relationship of the outgroups *Mantisatta* Warburton, 1900, and *Neon* Simon, 1876 (Figs 8-10), is not well supported (with both bootstrap value and posterior probability lower than 50%), with no synapomorphy. *Mantisatta* is a member of the Ballinae (Benjamin 2004) and *Neon*, like *Myrmarachne*, is close to the base of the Astioida, although neither *Mantisatta* nor *Neon* was particularly stable in the molecular analysis of Maddison *et al.* (2008). This analysis continues that instability by placing *Neon* outside the remaining species studied here, which are all astioids.

The remaining astioids (with four synapomorphies), the myrmarachnines (with four synapomorphies), the *Ligonipes* clade (with four synapomorphies), and the *Belippo* + *Myrmarachne* clade (with six synapomorphies) all seem well supported. Both bootstrap values and posterior probability values for these branches are over 70%, with posterior probability values over 90% for the astioids and myrmarachnines (Fig. 8).

Belippo is very well supported, with seven synapomorphies and 100% bootstrap and posterior probability values. However, *Myrmarachne* is so poorly supported as a single entity that this branch collapsed and formed a polytomy with *Belippo* in the majority rule consensus tree from Bayesian analysis (the one major difference between the strict consensus tree of Parsimony analysis and the majority rule consensus tree from Bayesian analysis). In the latter tree, the Australasian clade completely collapsed, the Western clade collapsed to its constituent species groups (which individually are mostly well-supported; Fig. 8), and only the trans-Indian Ocean clade was supported in its entirety (by a posterior probability value of 71%). The *laurentina* species group was supported by a posterior probability value of 72%, whereas the *electrica* group, the *parallela* group, and the *tristis* group, as well as the relationship between the *tristis* group and the species included in the *formicaria* group (although the latter was not supported as a group in the Bayesian majority rule consensus tree) were supported by posterior probability values of 95% or greater.

The monophyly of the trans-Indian Ocean clade seems clear given the characters analyzed. As a result, the Bornean species *Damoetas galianoae* Prószyński, 2001 (and by homology in the epigyne, the closely related *D. christae* Prószyński, 2001, even though the latter is only known from the female), are shown to be misplaced, therefore these two species are transferred to *Myrmarachne* (new combinations). The primary basis for this is the presence in both species of a single ventral loop in the spermathecal complex shared with the *volatilis* and *electrica* groups, along with several other character states which agree more with *Myrmarachne* than with *Damoetas*. Like *Myrmarachne* in general, the carapace of these two Bornean *Damoetas* is raised anteriorly (not monoplanar between the cephalic and upper thoracic areas), and for *D. galianoae*, the male chelicerae are extended forward, the sperm duct on the bulbus is typical of *Myrmarachne*, and the embolus has 2 full spirals. The embolus has 1.5 spirals in *Damoetas nitidus, Rhombotus, Judalana,* and *Ligonipes,* which all also have a more elongate bulbus (surrounded by a more elongate, more sinuous, broader embolus), a different duct shape, no clear differentiation on the dorsum of the carapace between the cephalic and upper thoracic parts, vertical chelicerae in the male, and an unmodified spermathecal complex.

Transferral of *D. galianoae* Prószyński, 2001, to *Myrmarachne* results in a homonym: *Myrmarachne galianoae* Cutler, 1981, has precedence. To maintain the connection with Maria Elena Galiano, we rename the species in her honor, *Myrmarachne mariaelenae* Edwards and Benjamin, replacement name. We nevertheless labelled the species *D. galianoae* in Figs 8–10 to emphasize its generic misplacement.

Since the type species of *Bocus*, *B. excelsus*, groups with the Australasian clade of *Myrmarachne*, the validity of this genus might be questioned as well. However, as discussed below, this ‘clade’ is almost completely unresolved, and *Bocus* might yet prove to be a valid genus and the immediate sister group to *Myrmarachne*.

Discussion

Species groups of *Myrmarachne*

Prószyński (in litt. to GBE 2008) noted that the composition of species groups in *Myrmarachne* has been difficult to diagnose because the membranous internal structure of the epigyne has not been sufficiently illustrated for many described species. This may be true; other structural details of the epigyne certainly seem important in species group determination. Wanless (1978a), using an assortment of other characters, defined some species groups of *Myrmarachne* based largely on the 58 species of the Ethiopian region. These groups, named after an included species, are the *electrica, formicaria, lesserti, nubilis, tristis,* and *volatilis* groups. He also included a number of "*species solae*," spaced throughout the paper, near what he thought were their closest relatives. More recent papers, such as those by Zabka (1985) from Vietnam, Barrion and Litsinger (1995) from the Philippines, Berry *et al*. (1996) from the Pacific Islands, Edmunds and Prószyński (2003) from Malaysia, and the thesis of Huang (2004) from Taiwan, have provided further information on Oriental and Pacific *Myrmarachne*. Galiano (1969, 1974) had previously revised the Neotropical species. We draw on these references to enhance the species group classification proposed by Wanless (1978a).

Characters used by Wanless (1978a) to define groups included: RTA shape, RTA flange development, cymbium modification, embolus shape, and epigyne posterior pocket shape. We have tried to include as many of Wanless' characters as possible given that in some cases, we are using drawings and text descriptions to fill the data matrix. A useful character distinguishing some groups is the shape of the spermathecal complex. Unfortunately, what may be most pertinent about the shape of the spermathecal complex is what at present cannot be diagnosed from most published illustrations. The problem is distinguishing the actual extent of a spermatheca, given the multitude of shapes present in the spermathecal complex of various *Myrmarachne* species. Illustrations by Prószyński (2009; Fig. 7) comparing representatives of species groups clearly show spine-like internal spermathecal structures. These are restricted to the area inside normally-shaped (*e.g.*, spherical, ovoid) spermathecae, but in cases where the spermathecae become more irregular or duct-like, these spine-like structures are present to a variable extent, including in some cases in part of the transverse lateral diversion of the duct. In these cases, the spermathecae appear to be C , J or L shaped. Future analysis will need to address this problem, but for now (since this character has only been documented for relatively few species), we can only analyze the overall shape of the spermathecal complex. Even so, this seems to be one of the more useful characters for delimiting species groups.

It is clear that the richest group diversity in *Myrmarachne* occurs in the Ethiopian and Oriental Regions. Two new groups (*plataleoides, grossa*) are defined based primarily on the Oriental fauna, and probably more exist. The cladograms indicate that the African and Australasian faunas are largely separated, although possibly this is an artifact of the low percentage of *Myrmarachne* species studied. Only one group (*parallela* group, newly designated) is represented in Central and South America. Interestingly, it seems to be embedded among the primarily mainland African species groups (see below), which together we call the Western Clade. Otherwise, diversity and distribution in the genus is more scattered, with a few species known in Australia and the Pacific Islands, and a single species found in western Europe, *M. formicaria* (De Geer), recently introduced to the United States of America (Bradley *et al.*, 2006).

As presently diagnosed, there are ten species groups of *Myrmarachne* (*electrica, formicaria, grossa, laurentina, lesserti, nubilis, parallela, plataleoides, tristis, volatilis*), of which the *formicaria* and *tristis* groups are the largest in species composition and possibly grade into one another (Figs 7, 10). These ten species groups, based on the relationships demonstrated in the cladograms, are assigned to three main clades of *Myrmarachne*, tentatively designated the ‘Australasian clade’ (southern Asia to Australia), the ‘trans-Indian Ocean clade’ (Madagascar and Borneo), and the ‘Western clade’ (mainland Africa with outliers in Eurasia, and the Neotropics]. The latter two clades apparently are sister groups; although tree support for this is limited, there are at least three apparent synapomorphies noted in the discussion of the various clades.

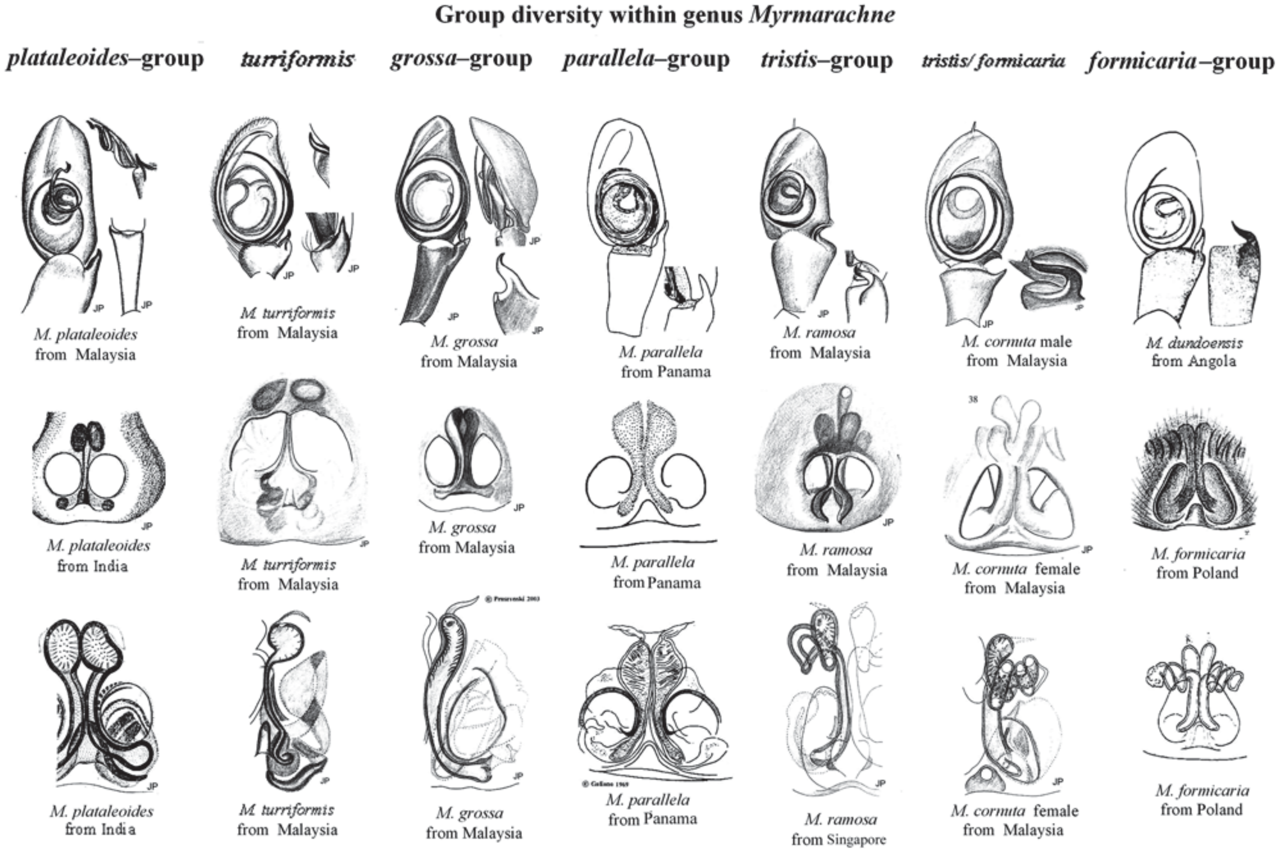

FIGURE 7. Comparison of some representatives of *Myrmarachne* species groups. Courtesy of J. Prószyński. Top row, male palps; middle row, female epigynes, ventral view; bottom row, female epigynes cleared.

Australasian 'Clade'

Unlike the other two clades, there is no synapomorphy supporting this 'clade', so at this time, what we have, based on the strict consensus (Fig. 8), is a group of species with mostly undifferentiated or unsupported relationships. Apparently the selection of species was insufficient, and almost every species represents a different group. This is a real possibility, as unlike the African fauna (Wanless 1978a), the species from this part of the world have not been previously sorted into groups, and the species chosen as representatives of this fauna were chosen for their distinctive characteristics. Nevertheless, given that there are a lot more species than were represented in the analysis, we give a provisional list of some mainland groups and their species, and discuss possible relationships therein. This also is necessary for later discussion of the genus *Bocus*.

The ***plataleoides*** **group** is characterized in females by a very narrow spermathecal complex terminating in front of the atria and small oval spermathecae (see Fig. 7). Each sclerotized duct medially curves to a somewhat extended posterolateral transverse component. In most groups, by contrast, the anterior termination of the spermathecae is not sharply delimited, but the end of the duct is gradually dilated and otherwise modified to varying degrees. In male *M. plataleoides,* the initial coil of the embolus is distinctly shorter and broad in the proximal half of the bulbus, with an even shorter elevated terminal coil, which gives the embolus a cork-screw appearance. The embolus tip is recurved and truncate, unique to this species. The tibial apophysis is nearly straight, recurved distally, without a ventral flange. Other species have a similar short second coil of the embolus, such as found in *M. russellsmithi* of Nigeria (Wanless 1978a: 93) (only known from the male and not analyzed here), but in other respects, this species is similar to the *formicaria* group, where it is placed. Another species with a short second coil is *M. melanocephala* in the *tristis* group. In all other groups, usually the second coil of the embolus is longer and directly overlays the bulbus and appressed first coil.

Provisional list of species of this group: *M. aureonigra* Edmunds and Prószyński, *M. hispidacoxa* Edmunds and Prószyński, *M. malayana* Edmunds and Prószyński, *M. plataleoides* (O. P.-Cambridge), *M. turriformis* Badcock. Note that the last species comes out near but not with *M. plataleoides* in any of the cladograms. Since these were the two species representatives of this group in the analysis, the group is not supported at this time. *Bocus excelsus* Peckham and Peckham, 1892, has a similar slender spermathecal complex.

The *grossa* group has the spermathecal complex simple, duct-like, gently bent, and slightly dilated anteriorly. In males, the cymbium and bulbus are distinctly broader than the tibia, with a broad reservoir, following internally the edge of the bulbus at least 2/3 of its circumference (Fig. 7).

Provisional list of species of this group: *M. cuneata* Badcock, *M. grossa* Edmunds and Prószyński, *M. hirsutipalpi* Edmunds and Prószyński, *M. magna* Saito. *Myrmarachne gigantea* Zabka may belong here or represent yet another group. Unlike the members of the *electrica* and *volatilis* groups, the single loop in its spermathecal complex is on the dorsal, not the ventral side. Note that most of these species have an elongate thoracic part of the carapace. This group too is not yet well supported, although *M. gigantea* and *M. grossa* appeared together as sister species in some of the 24 most parsimonious trees. *Bocus philippinensis* Wanless, 1978, has a similar palp and body form to this group.

Trans-Indian Ocean Clade

Members of this clade seem to consist of three species groups from Madagascar, and a small subgroup from Borneo, based on epigynal characters. The *nubilis* group is included, even though not analyzed here, because the species included in this group have posterior spirals in the spermathecal complex (although less extensive than in the *electrica* group).

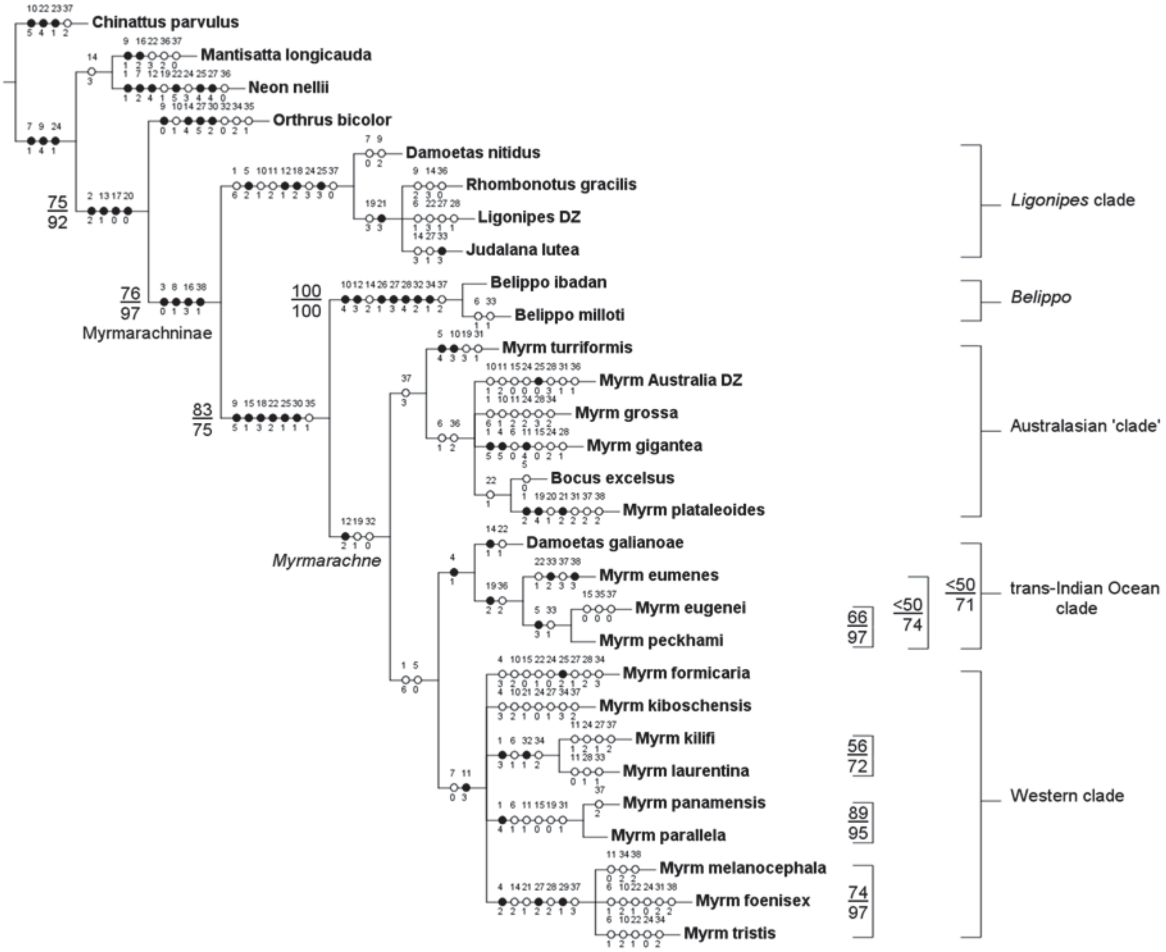

FIGURE 8. Strict consensus tree of Parsimony analysis of Myrmarachninae, with synapomorphies indicated as black circles, character above symbol, state below. Main myrmarachnine groups labelled. Bootstrap values (above line) and posterior probabilities (below line) also given for branches in which at least one of these values was over 50%.

The spermathecal complex in these species groups has a lateral transverse detour in the anterior third. After the detour, the duct continues in the original direction towards the anterior, and ends in a broader terminal part, usually with internal spines, which is the actual spermatheca. The most simple form of the detour can be seen in *M. volatilis* from Madagascar, just an angulate ventral loop. Species included by Wanless (1978a) into the *electrica* group have the same condition of the spermathecal complex, but the copulatory channel makes a number of small spiral coils posteriorly before joining the spermathecal complex. It is not clear yet whether these are membranous or sclerotized, but not all species associated with this clade have such a developed series of spiral coils (*e.g. M. eumenes*, a *species sola* of Wanless 1978a). In the *nubilis* group, the detour in the spermathecal complex resembles the *formicaria* group but is turned anteriorwards, parallel to the termination of the spermathecae.

The male bulbus contains a very characteristic additional anterior half loop of the sperm duct, apart from the usual wide semi-circular reservoir, following internally the edge of the bulbus. Males in the *electrica* group have the apical end (embolus tip) of the embolus filamentous and generally wavy, the sperm reservoir elongate as in the *grossa* group, and the tibial apophysis straight.

The transverse diversion in the spermathecal complex, presence of subposterior epigynal pockets, and the half loop in the palpal sperm duct are similar to most of the species groups in the Western Clade, which is why we consider these clades to be sister groups.

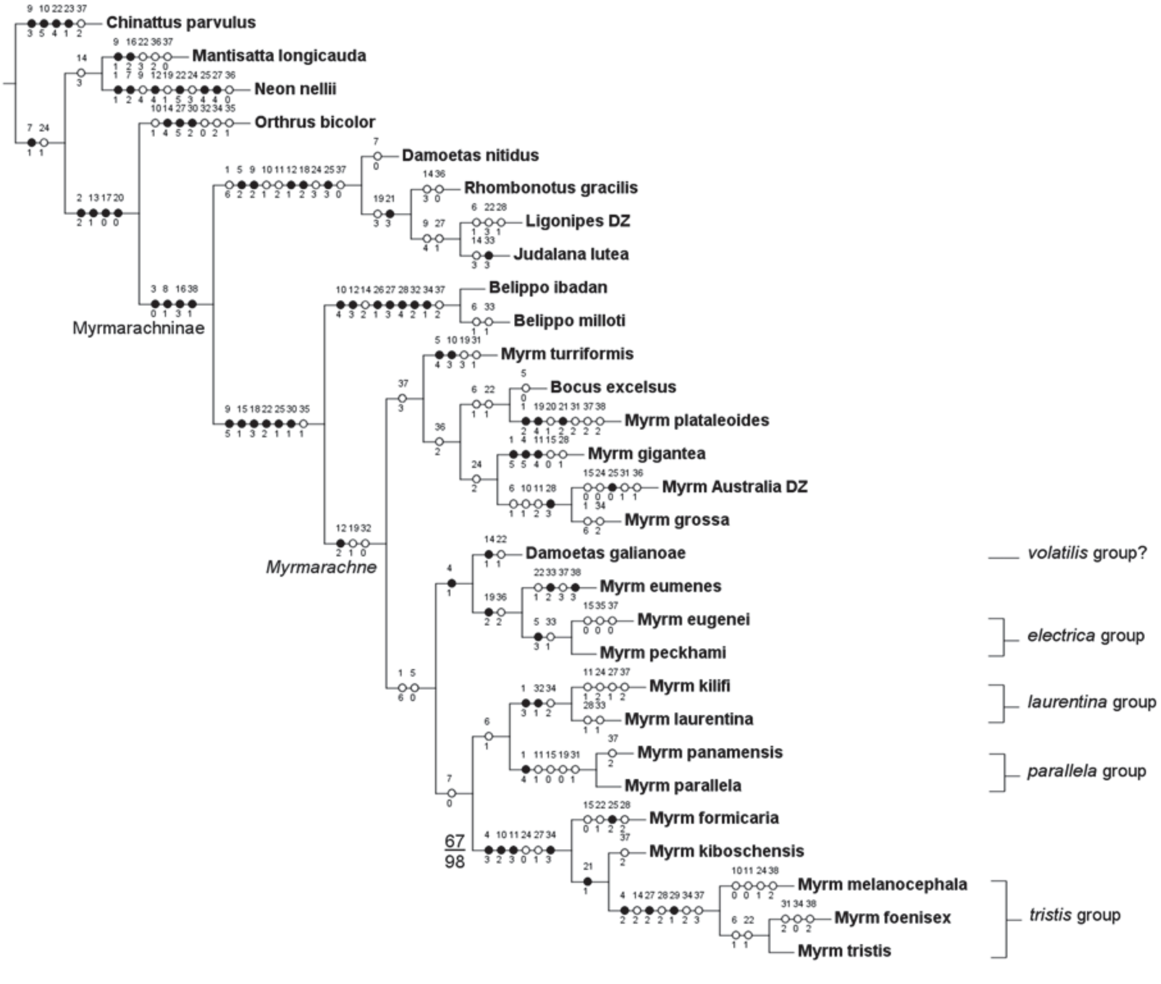

FIGURE 9. Representative most parsimonious tree of Myrmarachninae, with synapomorphies as in Fig. 8. This configuration is similar to the Majority Rule tree in TNT. One set of bootstrap and posterior probability values given here (see Fig. 8). Supported species groups of *Myrmarachne* labelled.

Provisional list of species of these groups:

***electrica* group:** *M. andringitra* Wanless, *M. electrica* (Peckham and Peckham), *M. eugenei* Wanless, *M. eumenes* (Simon), *M. peckhami* Roewer. The members of this group are restricted to Madagascar.

***nubilis* group:** *M. mahasoa* Wanless, *M. nubilis* Wanless. Only known from females described from Madagascar, not included in present phylogenetic analysis.

***volatilis* group:** *M. christae* (Prószyński) n. comb., *M. galianoae* (Prószyński) n. comb., *M. longiventris* (Simon), *M. volatilis* (Peckham and Peckham). Only known so far from Madagascar and Borneo.

Although *Damoetas galianoae* comes out near the *electrica* group in the present phylogenetic analysis, it lacks the posterior spirals in the ducts characteristic of that group, therefore we include it (and *D. christae*) in the *volatilis* group. *Myrmarachne eumenes*, a '*species sola*' of Wanless (1978a) and presently placed with the *electrica* group, might also belong here.

Western Clade

African Species Groups

The use of 'African' for these groups is something of a misnomer in the sense that it is used primarily because the majority of the species represented in the analysis are from Africa. The two largest groups (*formicaria* and *tristis* groups) are much more widespread into Eurasia. Nevertheless, given the relationships demonstrated here, the name may be appropriate as the center of diversity for most and perhaps all of the species groups represented in this clade is in Africa. As with the species groups from Madagascar (trans-Indian Ocean Clade), these species groups mostly have been characterized by Wanless (1978a) and will be summarized here. In most groups in this clade, females are characterized by a lateral transverse detour of the spermathecal complex in its apical third, just anterior to the atria (exception: the *laurentina* group lacks the detour). In the *tristis* group the detour consists of a single lateral, usually twisted, loop. The spermathecal complex in the *formicaria* group is more developed, *i.e.*, the detour is in the form of several loops twisted around a transverse duct (possibly part of the spermatheca). Another feature of the African groups is that in most species, the median pocket is in a subposterior position, *i.e.*, it is somewhat anterior to the epigastric furrow. In the *tristis* group, the subposterior median pocket is split into two opposing parts.

Like the trans-Indian Ocean clade, the male bulbus contains an additional anterior half loop of the sperm duct and a wide semi-circular reservoir. The tibial apophysis in the *tristis* group is a spiral hook and fits into a depression on the lateral wall of the cymbium, often fringed with short setae. In the *formicaria* group, the RTA is more or less straight, but there are intermediate forms, slightly inclined, or wavy, and the tip is usually recurved. In *M. cornuta,* the epigyne is typical for the *formicaria* group, while the male RTA resembles the *tristis* group (perhaps the sexes are mismatched; see Fig. 7).

Provisional list of species of these groups:

***laurentina* group:** *M. andrewi* Wanless, *M. globosa* Wanless, *M. kilifi* Wanless, *M. laurentina* Bacelar. A new group, formerly part of the *volatilis* group, restricted to mainland Africa. Separated from the *volatilis* group by the lack of a ventral loop in the spermathecal complex and also distinguished by the presence of a distal ventral lobe on the male chelicerae.

***lesserti* group:** *M. albosetosa* Wanless, *M. lesserti* Lawrence. Only known from males from South Africa, not included in the present phylogenetic analysis. Wanless (1978a) suggested this group may be related to the species groups from Madagascar, herein placed in the trans-Indian Ocean clade, but we leave it here as it is a mainland African group and we would like to see further evidence from females before reassigning it.

***formicaria* group:** *M. cornuta* Badcock, *M. cowani* (Peckham and Peckham), *M. dundoensis* Wanless, *M. edentata* Berry, Beatty and Prószyński, *M. edwardsi* Berry, Beatty and Prószyński, *M. foreli* Lessert, *M. formicaria* (De Geer), *M. formosana* (Saito), *M. inflatipalpis* Wanless, *M. kiboschensis* Lessert, *M. kitale* Wanless, *M. leleupi* Wanless, *M. lugubris* (Kulczynski), *M. nigeriensis* Wanless, *M. pisarskii* Berry, Beatty and Prószyński, *M. russellsmithi* Wanless, *M. solitaria* Peckham and Peckham, *M. topali* Zabka, *M. uelensis* Wanless, *M. uvira* Wanless, *M. vanessae* Wanless. *Bocus angusticollis* Deeleman-Reinhold and Floren, 2003, has a spermathecal complex similar to this group. Widespread.

***tristis* group:** *M. annamita* Zabka, *M. bamakoi* Berland and Millot, *M. collarti* Roewer, *M. confusa* Wanless, *M. edentula* (Peckham and Peckham), *M. elongata* Szombathy, *M. evidens* Roewer, *M. foenisex* Simon, *M. formosicola* Strand, *M. gisti* Fox, *M. hesperia* (Simon), *M. ichneumon* (Simon), *M. iridescens* Banks, *M. lawrencei* Roewer, *M. legon* Wanless, *M. lulengana* Roewer, *M. lulengensis* Roewer, *M. marshalli* Peckham and Peckham, *M. melanocephala* MacLeay, *M. militaris* Szombathy, *M. naro* Wanless, *M. richardsi* Wanless, *M. rufisquei* Berland and Millot, *M. tristis* (Simon). Widespread. Even though this group includes the type species, *M. melanocephala*, we retain the name of the group as it was first designated.

FIGURE 10. Representative most parsimonious tree of Myrmarachninae, showing equally parsimonious alternate configuration, with synapomorphies as in Fig. 8. Supported species groups of *Myrmarachne* labelled.

Neotropical Species Group

The *parallela* group contains Central and South American species, studied by Galiano (1969, 1974). Females of these species have gently bent sclerotized ducts, dilated anteriorly into hemispherical spermathecae, lacking the transverse diversion seen in most African species groups (but resembling the *laurentina* group; given the position of these two groups, this may be a synapomorphic character state reversal). The bulbus of males has an additional small anterior half loop of the sperm duct, resembling the African groups. Tibial apophyses are straight without a flange. The apparent derivation of this group from the African groups, probably near the *laurentina* group, deserves further study.

Provisional list of species of this group: *M. brasiliensis* Mello-Leitão, *M. centralis* (Peckham and Peckham), *M. chickeringi* Galiano, *M. galianoae* Cutler, *M. guaranitica* Galiano, *M. mocamboensis* Galiano, *M. panamensis* Galiano, *M. parallela* (Fabricius), *M. penicillata* Mello-Leitão, *M. sumana* Galiano.

One correction on distribution needs to be made concerning *M. parallela*. The type locality is 'América Central: Antillas' (Galiano, 1969), which apparently lead Platnick (2009) to list this species from the West Indies. Most specimens in collections are known from Panama; there is also a record from Nicaragua (Platnick, 2009). While 'Antillas' is frequently considered an alternative spelling to 'Antilles,' in this case it seems to be an actual locality, since, although Central America and the West Indies (*i.e.*, Greater and Lesser Antilles) cover overlapping latitudes, they are not synonymous and usually not used together as a collection locality, as one indicates the mainland, the other a series of islands. It is possible that the Antilles could be considered a subset of Central America, but in this case, since almost all other specimens are known from Panama, it seems highly unlikely. The National Geospatial-Intelligence Agency GEOnet online lists several alternatives for Antillas, some of which are in or near what is normally considered Central America. For example, there is a Mar de las Antillas in Panama (in which case, Antillas might indicate that the specimen was collected along the seashore in the vicinity of this named sea), and also an Antillas in Colombia, Estado Huila. Panama and Colombia were at one time considered a single territory. No modern records are known to us establishing that any *Myrmarachne* species are found in the West Indies. Therefore, based on the available evidence, 'West Indies' (*e.g.,* as in Platnick, 2009) should be removed from the distribution of *M. parallela*, and the type locality for this species redesignated as Panama.

Phylogenetic Relationships of the Myrmarachninae

As noted earlier, support within *Myrmarachne* is problematic. The genus as a whole is not strongly supported (only one synapomorphy in the strict consensus tree, for a character in which the states could be considered semi-continuous). The two initial subdivisions lack strict consensus synapomorphies, although the analysis supports many of the existing (if included) and one proposed new species group given the limited representation of each group. The clade from mainland Africa and the Neotropics (the Western Clade) is also supported by one synapomorphy with semi-continuous states. Only the trans-Indian Ocean Clade (Madagascar and Borneo) has a distinctive synapomorphy, the presence of a ventral loop (in some species, it is clear that the spermatheca forms a major part of this loop) in the anterior of the spermathecal complex.

Myrmarachne mariaelenae (the former *Damoetas galianoae*) comes out close to the *electrica* group in the present analysis, but also shares epigynal characters with the *volatilis* group. A problem with phylogenetic resolution seems to be caused by the fact that both *volatilis* group members in Madagascar are only known from females, therefore neither is analyzed here. These are *M. volatilis* and *M. longiventris*, both of which have a single ventral loop in the spermathecal complex. The other species assigned by Wanless (1978a) to the *volatilis* group, all from mainland Africa, lack the ventral loop and have males with shorter chelicerae that have a distal, ventral lobe. The true *volatilis* group appears to belong with the Madagascan *M. eumenes* and some Asian species, all of which have the ventral loop. They also seem related to the *electrica* group, which shares the presence of the single ventral loop in the spermathecal complex and also occurs in Madagascar. This would mean the mainland African species likely belong to a different group, here designated the *laurentina* group based on its oldest included species, *M. laurentina* Bacelar, 1953. This also would suggest that *M. mariaelenae* and/or *M. eumenes* are the most likely representatives of the *volatilis* group in the present analysis. It is important to note that in the phylogeny of the Myrmarachninae, only *Myrmarachne* as presently understood has modifications to the anterior part of the spermathecal complex, therefore by definition, any myrmarachnine with such a modified spermathecal complex belongs in *Myrmarachne*.

Based on the last conclusion, there remains the question of what to do with *Bocus.* There are three described species of *Bocus*: type species *B. excelsus* Peckham and Peckham, 1892, *B. philippinensis* Wanless, 1978c, and *B. angusticollis* Deelemann-Reinhold and Floren, 2003. Both *B. excelsus* and *B. angusticollis* have fused ventral cephalothoracic sclerites, apparently unlike other myrmarachnines. The former species has a spermathecal complex similar to the *plataleoides* group, while the latter species has an anterolateral diversion in the spermathecal complex reminiscent of the *formicaria* group (therefore, based on the above argument, should be in *Myrmarachne*). The palp of *B. philippinensis* has an elongate broad duct on the bulbus as in the *grossa* group, the carapace shape is also similar to *M. grossa* (as is true of the two other species of *Bocus*), and the ventral sclerites are not fused; unfortunately the female is unknown. There should be further study of the ventral cephalothoracic sclerites (not analyzed here because the data was not available for some *Myrmarachne* species included in the present study) and any other characters which serve to define *Bocus*, as it seems in many respects that this genus is merely a slightly atypical form of *Myrmarachne*. Compared with genital characters used to establish species groups in *Myrmarachne*, the species of *Bocus* do not even belong to the same species groups. If it is possible to define *Bocus* in such a way as to make it a phylogenetically meaningful taxon, a re-evaluation of the characters used for defining the genus will need to be made. As a potential sister group to *Myrmarachne*, *Bocus* could be a genus with similar variation in genitalic conformation as occurs in *Myrmarachne*. If that is the case, *Bocus* would have to be defined based on somatic characters. Perhaps the place to start would be to compare the members of *Bocus* to the *grossa* group of *Myrmarachne*, which contains species of similar appearance.

Our initial discussion of *Belippo* suggested that it might end up as a species group of *Myrmarachne*, especially since one of the two synapomorphies distinguishing *Belippo* suggested by Wanless (1978a) appeared to be discredited. However, our analysis shows in fact seven synapomorphies for this genus. *Belippo* therefore seems to be a valid genus, and sister to *Myrmarachne sensu lato* based on six other synapomorphies (Fig. 8). One of us (GBE) has examined specimens of the *Belippo* species analyzed here, and confirmed a membranous hinge at the base of the elongate part of the RTA. Although the manner in which the RTA functions has not yet been determined, possibly it is inserted into the longitudinal median groove formed by a narrow deep depression in the epigyne (where the median septum between the atria would be in *Myrmarachne*). Pressure on the RTA would cause it to fold against its rough base, perhaps forming a clamp. Detailed analysis will be required to fully understand how this structure functions.

With more than 200 described species, *Myrmarachne sensu lato* is a large, diverse, and cumbersome genus. The confirmation of *Belippo* as a valid genus prevents an even larger and more diverse conglomeration. Could *Myrmarachne* be split in a meaningful way? The type species, *M. melanocephala*, falls within the *tristis* group of the Western clade, so at least this clade belongs in *Myrmarachne sensu stricto*. The trans-Indian Ocean clade, should it be split off, has a valid name, as *M. volatilis* was originally described in the genus *Hermosa* Peckham and Peckham, 1892, now considered a synonym of *Myrmarachne*. However, this clade shares several character states with the Western clade, which presently seems to preclude a separate genus for it. The Australasian clade, although not supported as a single entity at this time, does contain the type species of *Bocus* and species of similar morphology in the *grossa* group. Also, Wanless (1978b) considered *Myrmarachne exasperans* (Peckham and Peckham) from Java and the Philippines as not belonging to any existing group (by default, it would be the *exasperans* group), and it needs further investigation.

The close relationship of the type of *Damoetas*, *D. nitidus*, to the species of *Judalana, Ligonipes,* and *Rhombonotus* brings up the question of how many valid genera exist in this clade. The genitalic and somatic shared similarities among them seem more numerous and significant than the differences. Conceivably, at one extreme, there could be one genus with two to four species groups. The discussion by Davies and Zabka (1989) on three of these genera (all except *Judalana*) would dispute this; however, with the removal of the two Bornean species from *Damoetas*, the genera other than *Ligonipes* are now all monotypic (*Damoetas, Judalana,* and *Rhombonotus*). Unfortunately, the oldest name, *Ligonipes* Karsch, 1878 (hence the *Ligonipes* clade), has no known males among its described species. Further study will be needed to resolve the relationships within this group.

One aspect of this analysis is that four synapomorphies are identified for the entire subfamily Myrmarachninae, including the spermathecal complex as defined above, the shape of which was previously noted by Prószyński (2001). Overall, though, the conclusions reached here are the opposite of those hypothesized by Prószyński (2001). He suggested that the "basic stock" of the myrmarachnine body shape was similar to that represented by the species from Borneo that he described in *Damoetas*. While we agree that the genital structures of myrmarachnines are unique and help define a relationship among these genera, our data suggest that: (1) the basic genitalic features (especially the development of a spermathecal complex) arose prior to (or perhaps concurrent with) ant mimicry, (2) sexually-dimorphic (in the context of cheliceral structure) species-specific ant mimicry arose within one lineage of myrmarachnines and subsequently diversified, and (3) anterior modifications to the spermathecal complex only arose in the lineage leading to *Myrmarachne*, and possibly only in *Myrmarachne* itself (pending the resolution of *Bocus*). Prószyński's '*Damoetas galianoae*' from Borneo (for which we previously listed a number of *Myrmarachne*-like character states) ends up in a terminal position among the species of *Myrmarachne*, rather than in a basal position, which fits well with our hypotheses.

A more thorough analysis with additional characters and species will be necessary to fully understand the relationships of the more than 200 species in the Myrmarachninae. The analysis published here is but a first step toward looking at the validity of proposed species groups of *Myrmarachne*, and resolution of generic and suprageneric relationships within the subfamily.

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Appendix A. Characters and character states coded for Myrmarachninae analysis

1. **Spermatheca shape:**
   0. spherical
   1. semispherical–*transverse orientation*
   2. ovoid–*longitudinal in orientation*
   3. semi-spiral–*sphere starting to unwind*
   4. hemispherical–*somewhat ovoid, flat on median side*
   5. cylindrical–"*sausage-like*" *but distinctly wider than duct*
   6. duct-like–*slightly dilated, no obvious external distinction from duct*

2. **Spermatheca longitudinal position:**
   0. posterior
   1. medial
   2. anterior

3. **Spermatheca to duct position:**
   0. direct in line with orientation of duct
   1. lateral to orientation of duct

4. **Median sclerotized duct shape:**
   modifications to duct immediately posterior to spermatheca.
   0. unmodified–*straight or curved*
   1. ventral loop–*spermatheca J or C shaped*
   2. lateral loop–*may be twisted into figure 8*
   3. extended lateral loop–*duct diverted laterally, then spiraling back on itself multiple times*
   4. extended anterior loop–*duct extended laterally then anteriorly, then spiraling multiple times around or ventrally to itself*
   5. dorsal loop

5. **Posterolateral sclerotized duct shape:**
   0. abbreviated–*not extending past most posterior part of atrial area*
   1. extended laterally–*extending to outer edge of atrial area*
   2. extended lateroanteriorly–*extending to outer edge of atrial area then bent anteriorly 1/4 to 1/2 median duct length*
   3. spiral extended–*extending posterolaterally as multiple spirals* (*possibly not sclerotized*)
   4. spiral abbreviated

6. **Sclerotized duct posterior end:**
   0. not swollen
   1. swollen

7. **Sclerotized duct width:**
   0. normal
   1. very slender
   2. broad

8. **Ducts with membranous section between copulatory opening and spermathecal complex:**
   0. absent
   1. present

9. **Copulatory opening position:**
   0. anteromedial
   1. anterolateral
   2. subanterolateral
   3. mediolateral
   4. subposteromedial
   5. submedial

10. **Epigyne atrial composition:**
    converging or diverging posteriorly.
    0. two more or less circular atria
    1. two converging elliptical atria
    2. two diverging elliptical atria
    3. two diverging angulate atria
    4. one common atrium
    5. lost

11. **Atria size:**
    0. small circular, anterior to posterolateral branch of spermathecal complex–*no more than half distance between spermathecae and posterior edge*
    1. large circular, not including posterior spermathecal ducts
    2. large elongate, not including posterolateral part of spermathecal complex
    3. large elongate, including posterolateral branch of spermathecal complex
    4. large circular, including posterior spermathecal ducts

12. **Atrial rim position:**
    primary position, may be partially in other areas.
    0. absent
    1. medial
    2. anterior
    3. lateral
    4. most of circumference–*except for variable posterior gap*

13. **Epigyne atrial depth:**
    0. noticeably depressed
    1. superficial, not noticeably depressed

14. **Median pocket shape:**
    0. simple, hood-like
    1. hood-like, bilateral depressions internally
    2. split into two opposing pockets
    3. lost, not apparent
    4. posterior lobe crossing epigastric furrow

15. **Median pocket position:**
    0. posterior–*close to epigastric furrow*
    1. subposterior

16. **Embolus primary position:**
    0. distal median
    1. distal prolateral
    2. distal retrolateral
    3. ventral

17. **Embolus rotation (left palp):**
    0. clockwise
    1. counterclockwise

18. **Embolus ventral rotations clockwise (left palp):**
    0. 0
    1. 1
    2. 1.5
    3. 2

19. **Embolus tip:**
    0. short, narrow
    1. elongate, narrow

2. wavy, filamentous
3. elongate, broader, not very slender, hooked at tip
4. short, wavy, truncate

20. Embolus proximal area:

0. slender–*slight taper throughout length*
1. broad proximally–*broad attachment to tegulum, narrows considerably to tip*

21. Embolus distal spiral:

0. overlapping basal spiral
1. inside basal spiral, nearly monoplanar
2. inside basal spiral, corkscrew
3. outside basal spiral

22. Bulbus (functional tegulum):

0. longitudinally elliptical
1. longitudinally oval
2. circular
3. lobed proximally retrolateral side
4. lobed proximally prolateral side
5. subtriangular

23. Tegular 'shoulder':

0. absent
1. present

24. Visible bulbal duct length/ bulbus circumference:

not including small half loop

0. 1/3 or less
1. between 1/3 and 2/3
2. 2/3 or more
3. duct not on circumference, more medial

25. Bulbus ventral duct form:

0. wide without half loop
1. wide with one half loop
2. narrow with two half loops
3. medial, half loop only
4. medial with 2 half loops in transverse arrangement
5. along retrolateral side

26. Tibial apophysis attachment:

0. fixed
1. moveable

27. Tibial apophysis shape:

0. nearly straight–*tip slightly recurved*
1. bent ventrally–*bent toward venter with tip noticeably recurved*
2. spiral–*very bent toward venter with tip turned retrolaterally in a spiral curve*
3. elongate, hooked ventrally
4. bifid
5. truncate

28. RTA basal flange:

0. absent
1. ventral
2. distal, poorly developed

3. distal, well developed
4. distal, well developed with mucros

29. Cymbium retrolateral proximal excavation:
0. absent
1. present

30. Male chelicerae position:
0. vertical
1. horizontal–*extended greater than 45 degrees*
2. porrect–*distally* (*from ventral position*) *tilted forward, much less than 45 degrees*

31. Male chelicerae length/carapace length:
0. less than
1. about equal (+ or - 10%)
2. greater than

32. Male cheliceral teeth position:
0. throughout length
1. on anterior ventral lobes
2. anterior side of mid-ventral lobe
3. on medial side of truncated end–*distal to medial excavation, if present*

33. Male retrolateral cheliceral denticle:
0. absent
1. 1 present–*more or less at midpoint of dorsal retrolateral edge of chelicera*
2. 2 present–*one at midpoint and one subproximal away from edge*
3. mastidion on distal anterior cheliceral face

34. Fang tooth:
0. absent
1. fang swollen just posterior to middle
2. a narrow ventral swelling that is pointed
3. well-developed extended tooth-like projection–*fang apophysis*

35. Carapace proportional height:
0. cephalic equal to anterior thoracic–*may be depression between*
1. cephalic higher than thoracic

36. Carapace section proportional length:
0. cephalic >10% longer than thoracic
1. cephalic about equal to thoracic
2. thoracic >10% longer than cephalic

37. Carapace profile:
0. flat–*continuous, no difference in cephalic and anterior thoracic dorsum*
1. anterior thorax elevated continuously–*thoracic part slopes continuously upward toward but below cephalic part, may flatten out shortly before PLE*
2. anterior thorax level–*well below cephalic height, flattens out well behind PLE*
3. anterior thorax depressed–*thoracic part depressed immediately behind cephalic part, associated with constriction*

38. Pedicel length/ thoracic part of carapace:
0. not visible in dorsal view
1. much shorter than
2. over half as long as
3. much longer than