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The lace web spiders (Araneae, Phyxelididae) of Madagascar: phylogeny, biogeography and taxonomy

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We briefly review the potential history of Madagascar as either a Darwinian or a Wallacean island, summarize the phylogenetic evidence regarding the biogeography of Madagascar spiders, examine the dispersal history of the Madagascar Phyxelididae, and monograph the family in Madagascar. Molecular phylogenetic analyses for 32 Malagasy phyxelidid exemplars, nine confamilial outgroup taxa, and seven other more distant outgroups are performed for three nuclear markers and one mitochondrial genetic marker (28S, 18S, H3 and COI) utilizing Bayesian, maximum-likelihood and parsimony methods. These analyses suggest that there are 14 species of Phyxelididae that may be recognized from Madagascar, that these may be divided into three genera, and that the Malagasy phyxelidids form a monophyletic group, probably resulting from a single invasion of the island by an ancestor from Africa. Two new genera, ten new species, and two new combinations are proposed: ***Manampoka atsimo*** **gen. nov., sp. nov.**; ***Rahavavy*** **gen. nov.**, including ***R. ida*** **sp. nov.** and ***R. fanivelona*** (Griswold, 1990) **comb. nov.** and ***R. malagasyana*** (Griswold, 1990) **comb. nov.**; and ***Ambohima andrefana*** **sp. nov.**, ***A. antsinanana*** **sp. nov.**, ***A. avaratra*** **sp. nov.**, ***A. maizina*** **sp. nov.**, ***A. ranohira*** **sp. nov.**, ***A. vato*** **sp. nov.**, ***A. zandry*** **sp. nov.** and ***A. zoky*** **sp. nov.**

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ADDITIONAL KEYWORDS: Darwinian islands – dispersal – vicariance – Wallacean islands.

INTRODUCTION

Madagascar's biota has long been recognized for its richness, high proportion of endemics, and, at least for vertebrates, its disharmony (Carlquist, 1965). For vertebrates, Madagascar preserves iconic relicts that are largely extinct elsewhere in the world, i.e. Madagascar's famous and diverse lemurs, and lacks many taxa that are common in nearby Africa; for example, there are no vultures, woodpeckers, hornbills, larks or turacos, and no deadly snakes. Although continental in origin, the great age of Madagascar's isolation, estimated to be from 80 (Krause *et al.*, 1997) to 140 Mya (Rabinowitz, Coffin & Falvey, 1983), makes the study of the island's biota and their origin particularly intriguing. Gillespie & Roderick (2002) recognize two kinds of islands. 'Darwinian' islands are ones that have arisen de novo later than the barrier separating them from other areas and are sometimes also referred to as 'oceanic'. 'Fragment' islands are ones that were in existence before a barrier appeared and are sometimes also referred to as 'continental'. We prefer to think of the latter as 'Wallacean' islands,

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*Corresponding author. E-mail: cgriswold@calacademy.org commemorating the work of Alfred Russell Wallace who recognized these dramatic contrasts in island biotas (Wallace, 1880). For Malagasy endemics, is Madagascar a Darwinian or Wallacean island? In other words, did they arrive there by dispersing across a pre-existing barrier, or do they pre-date and were they isolated by the formation of that barrier?

Spiders, like other Madagascan organisms, exhibit remarkable richness and endemism (Griswold, 2003). Although there are only just over 525 species known from Madagascar (Platnick, 2011), the rate of new species discovery suggests that the total may be much higher. In a comprehensive study of the Madagascar spider fauna, Griswold (2003) found that 29% of the 207 genera and 85% of the 459 described species or subspecies known at that time are endemic to Madagascar. Notably, the spider fauna is not disharmonic and contains most of the families found in Africa or Asia. The spider fauna known to Griswold (2003) showed a strong affinity to Africa (19 species and 22 genera shared exclusively by Africa and Madagascar), and much weaker affinity to Asia and the Indo-Pacific.

The Phyxelididae, commonly referred to as 'lace web weavers' (Jocqué & Dippenaar-Schoeman, 2006), occur in South East Asia, in Africa from the Mediterranean to the Cape of Good Hope, and in Madagascar (Griswold, 1990). All are cribellate and incorporate complex, multistrand capture lines into lacey funnel or sheet webs (Fig. 2A). Adults of both sexes have a set of modified setae along the inner margin of the palpal femur (Fig. 51D), which probably represents part of a stridulatory mechanism, and males of most species have mate clasping mechanisms on their first (and sometimes second) legs (Figs 1, 42, 43, 44A–I, 51H, I), a morphology rarely seen in araneomorph spiders. The world fauna, comprising 53 species, was monographed and subject to a quantitative phylogenetic analysis of morphological characters (Griswold, 1990). That sudy described the first phyxelidids from Madagascar, all members of the tribe Phyxelidini, including the genus *Ambohima* and two species attributed to the primarily African genus *Phyxelida*. The cladogram proposed by that study suggested three sets of relationships for the Malagasy fauna: *Ambohima* (with two species) is related to the *Malaika* group from Africa (Griswold, 1990: fig. 13), and the two Malagasy *Phyxelida* species, *P. malagasyana* and *P. fanivelona*, are each related to different sections of the African fauna of *Phyxelida* (Griswold, 1990: fig. 81). Within Africa phyxelidids are confined to cool temperate forests in South Africa and to comparable habitats scattered among mountains and in caves in the tropics. Such a disjunct distribution has been termed 'afromontane' (White, 1978, 1983) and phyxelidids are considered typical afromontane organisms (Griswold, 1991). That study and also Griswold (2000) suggested that there are also afromontane spiders in Madagascar, and that they probably originated through no fewer than seven dispersals, three of these by phyxelidids. Extensive spider prospecting in Madagascar over the last 15 years has revealed a large fauna of phyxelidids (at least 14 species). This new collection, coupled with tissues from potential African relatives and the putative outgroup family (Titanoecidae), has enabled a reassessment of the origin, distribution, and monophyly of Madagascar phyxelidids, and has provided data sufficient to test the hypothesis of multiple invasions of Madagascar by these spiders.

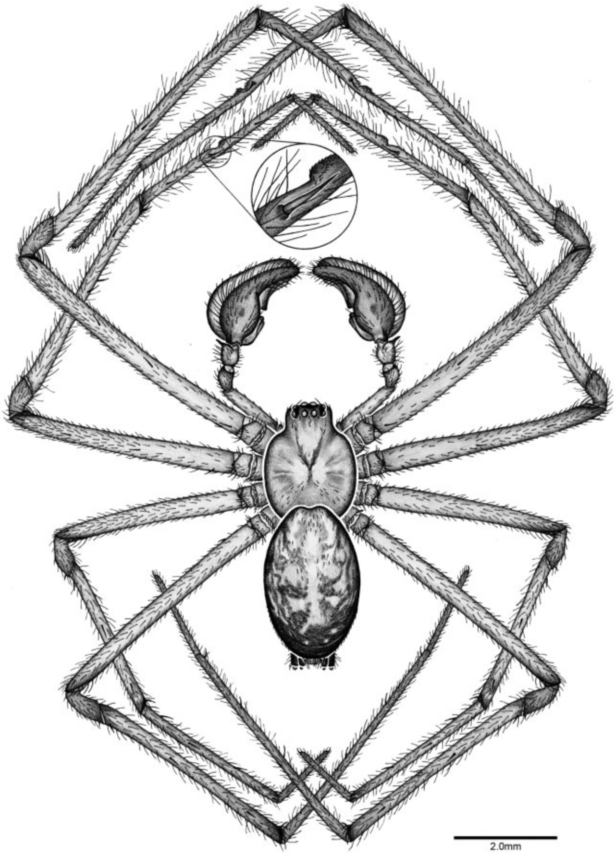

Figure 1. Habitus of *Ambohima sublima* male from Ambohimanga, CASENT9016199; inset shows metatarsus II prolateral clasping spine. Illustration by JS.

In this paper we briefly review the potential history of Madagascar as either a Darwinian or a Wallacean island, summarize the phylogenetic evidence regarding the biogeography of Madagascar spiders, examine the dispersal history of the Madagascar Phyxelididae,

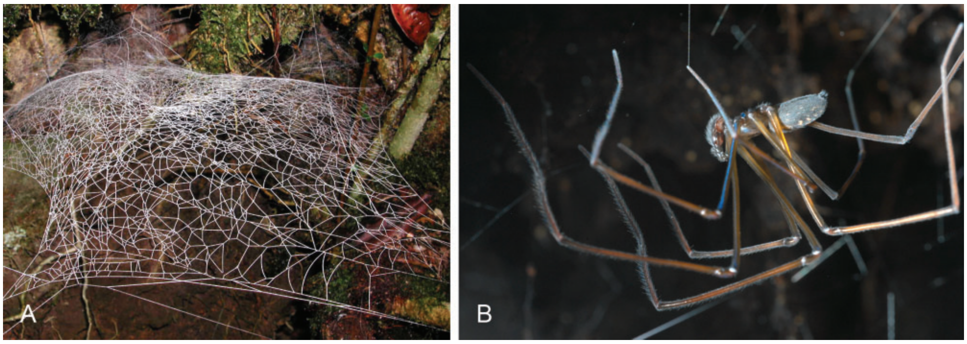

Figure 2. *Ambohima sublima*. A, web from Andranomay (Joel Ledford photo). B, male from Talatakely (Jeremy Miller photo).

Figure 3. Dorsal habitus of *Ambohima* males. A, *A. ranohira* from Ranohira, CASENT9005938. B, *A. sublima* from Anjozorobe, CASENT9004080.

and, based on 239 adult specimens, monograph the family in Madagascar.

MATERIALS AND METHODS

Measurements (in millimetres) were taken using a reticule in Olympus SZH, Leica MZ12.5 or Leica MZ16 stereomicroscopes; carapace length and width were taken in dorsal view, and carapace height (from lower margin to dorsal midline) was taken in lateral view; leg articles were measured in lateral view along the dorsal margin. Macrosetae are reported for the dorsal (d), prolateral (p), retrolateral (r), and ventral (v) surfaces of the legs and are listed from proximal to distal ends of each segment.

Measurements are given based on one specimen of each sex, where available: this specimen is listed at the beginning of the description. Variation for each sex is reported separately.

Data for all vouchers are presented in the Appendix.

Photographs of somatic morphology and female genitalia were taken with a Nikon DXM 1200 digital camera mounted on a Leica MZ16A stereomicroscope. Multiple images were combined with software from Syncroscopy. Photographs of the epigynum in dorsal view were taken with the specimen cleared in lactic acid. Some very small preparations were slide mounted for manipulation as described by Grandjean (1949) and Coddington (1983). Illustrations of male genitalia were sketched using a camera lucida mounted on a Leica MZ12.5 stereomicroscope, rendered on coquille board, scanned, and finished in Adobe Illustrator (version CS3). Illustrations are by Jenny Speckels (JS) or Giovanni Maki (GM) and are credited by these initials in the figure captions.

Expansion of the male palp was accomplished by immersing it in a concentrated solution of KOH,

Figure 4. Mating of *Ambohima andrefana*. A, male (top), female (bottom). B, male (top), female (bottom); note female biting male leg I. C, male (bottom), female (top); note female biting male leg I and male leg II claspers grasping base of female palps (arrow). D, male (bottom), female (top); note male leg II claspers grasping base of female palps (arrow). A, CASENT9005931 (male), 9019919 (paratype female). B, C, CASENT9005931 (male), 9019918 (female). D, CASENT9005932 (holotype male), 9019920 (female).

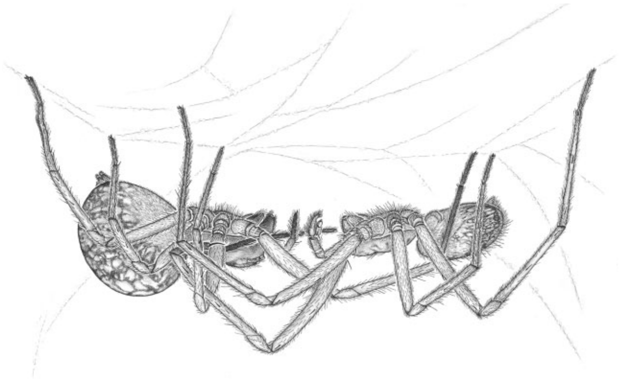

Figure 5. Mating of *Phyxelida tanganensis* from Amani, Tanzania. Female on left, male on right. Illustration by JS.

heating for 15 min beneath a desk lamp, and then transferring the palp to tap water where expansion of the haematodochae occurred.

Scanning electron micrographs were taken using a Hitachi S-520 or Leo 1450VP instrument at the California Academy of Sciences. Specimens were critical point dried, sputter coated with gold-palladium, and mounted on copper wire with white glue. A limited number of specimens were available for scanning electron microscopy analysis: therefore, descriptions of features based on electron microscopy (e.g. spinneret spigot morphology) may understate variation.

The sections on material examined report type and other specimens. Records are arranged by localities, specimens for each locality are summed for depository, and specimen database numbers are listed

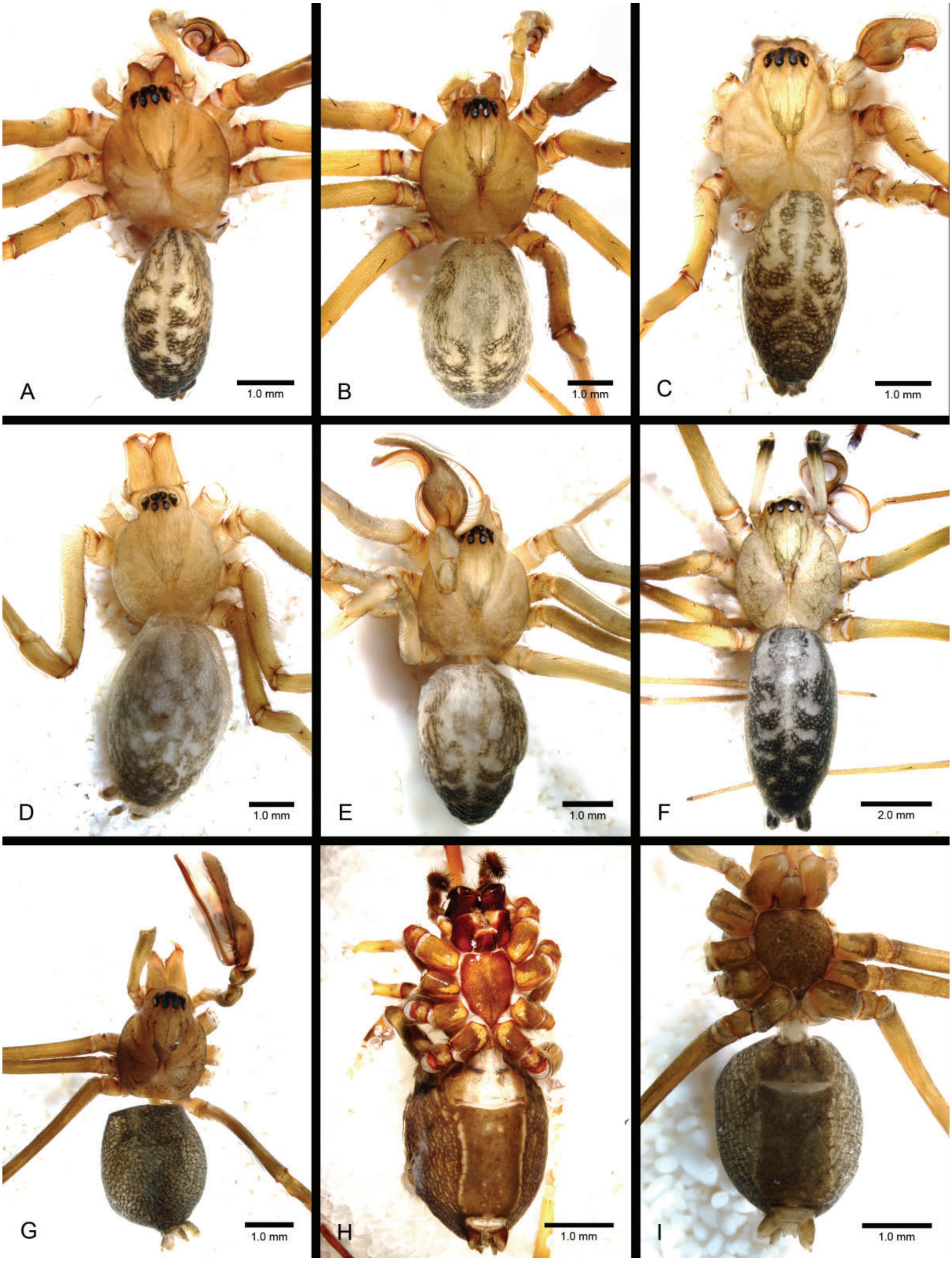

Figure 6. Habitus of *Ambohima*. A, *A. andrefana*, male, dorsal, Analavelona, CASENT9020321. B, *A. andrefana*, male, dorsal, Zombitse, CASENT9005931. C, *A. vato*, male, dorsal, Itremo, CASENT9016755. D, *A. zoky*, holotype male, dorsal, CASENT9017018. E, *A. sublima*, male, dorsal, Ambohimanga, CASENT9016200. F, *A. sublima*, male, dorsal, Talatakely, CASENT9024485. G, I, *A. maizina*, holotype male, CASENT9016206. G, dorsal. I, ventral. H, *A. ranohira*, female, ventral, Ranohira, CASENT9019986.

thereafter by depository. The specimen numbers assigned, e.g. CASENT . . . , represent identifiers for this *specimen-level database* and should not be taken to imply institutional ownership of specimens. Institutional ownership by the California Academy of Sciences is denoted ‘CASC’.

Many specimens were reared to adulthood in the laboratory. These were typically kept in glass vials (29 × 80 mm) with damp cotton at one end, or in 18 × 9 × 5-cm plastic boxes. Spiders were fed live flies (*Drosophila melanogaster* Meigen, or *Musca domestica* L.), mealworm larvae (*Tenebrio molitor* L.), and a variety of wild caught live insects. All observations on web construction, prey capture, courtship, and mating were made in the laboratory.

Abbreviations and conventions. *Male palp*: AN, anneli of subtegulum; C, conductor; CA, conductor apex; DTA, dorsal tibial apophysis; E, embolus; MA, median apophysis; P, petiole of subtegulum; PP, pars pendula of embolus; PTA, prolateral tegular apophysis; RL, retrolateral lobe of tibial apex; RTA, retrolateral tegular apophysis; ST, subtegulum; T, tegulum. *Vulva*: CD, copulatory duct; CO, copulatory opening; FD, fertilization duct; LL, lateral lobe of epigynum; LTR, lateral transverse ridge along anterior margin of median lobe of epigynum; ML, median lobe of epigynum; S, spermatheca; SA, spermathecal apex; SB, spermathecal base; SP, spermathecal poreplate. *Spinnerets*: AC, aciniform gland spigot; ALS, anterior lateral spinnerets; CR, cribellum; CY, cylindrical gland spigot; MAP, major ampullate gland spigot; mAP, minor ampullate gland spigot; MS, PLS modified spigot; n, nubbin; PC, paracribellar spigot; PI, piriform gland spigot; PLS, posterior lateral spinnerets; PMS, posterior median spinnerets; t, tartipore. *Somatic morphology*: AER, anterior eye row; AL, anterior lateral eyes; AM, anterior median eyes; ITC, inferior tarsal claw; OA, ocular area; OAL, ocular area length; OQA, ocular quadrangle, anterior; OQP, ocular quadrangle, posterior; PER, posterior eye row; PM, posterior median eyes; PL, posterior lateral eyes; STC, superior tarsal claws. *Institutions*: AMNH, American Museum of Natural History; CASC, California Academy of Sciences, San Francisco; MCZ, Museum of Comparative Zoology, Harvard; MNHN, Muséum National d’Historie Naturelle, Paris; MRAC, Royal Museum for Central Africa, Tervuren; USNM, Smithsonian Institution, Washington, DC; ZMUC, Zoological Museum, University of Copenhagen.

References to figures in this paper are listed with an initial capital (Fig.); references to figures published elsewhere are listed in lower-case type (fig.).

As suggested by Agnarsson & Kuntner (2007) we consider it important to cite original descriptions in the references: the convention of not citing such original works undervalues the primary literature of taxonomy.

PHYLOGENETIC ANALYSIS

Molecular phylogenetic analysis

We take a molecular approach to examining the phylogeny of the Malagasy phyxelidid fauna. Morphological characters at the level of Madagascar phyxelidid species are few and subtle, and for this reason we have not conducted a morphological analysis. Morphological synapomorphies are discussed at the familial, tribal, and generic level. When possible we used freshly caught tissues but for some species we were limited to specimens that were collected as much as 14 years previously and that had been preserved at room temperature in 75% ethanol. The poor suitability of this material somewhat limited our taxon sampling, but nevertheless we were able to obtain data for four markers from populations of all Malagasy described and new species with the exception of *Ambohima pauliani*, known from the unique type specimen collected prior to 1986.

Taxon sampling

We assembled a dataset comprising DNA sequences for a total of 48 specimens. Of these, 32 individuals represent Malagasy phyxelidids, including specimens of the previously described species *Ambohima sublima* Griswold 1990*, Phyxelida malagasyana* Griswold, 1990 and *P. fanivelona* Griswold 1990, and representatives of several new species. Other Phyxelididae represented include *Phyxelida tanganensis* (Simon & Fage, 1922) and *P. bifoveata* (Strand, 1913) from Tanzania, *Malaika longipes* (Purcell, 1904) and *Themacrys irrorata* Simon, 1906 from South Africa (all subfamily Phyxelidinae, tribe Phyxelidini), *Vidole capensis* (Pocock, 1900) and *Xevioso kulufa* Griswold, 1990 and *X. colobata* Griswold, 1990 from South Africa (subfamily Phyxelidinae, tribe Vidoleini) and an undescribed species of *Vytfutia* from Borneo (subfamily Vytfutiinae, tribe Vytfutiini). *Vytfutia* represents the only representative of Phyxelididae from Asia. The putative phyxelidid sister family Titanoecidae (Griswold *et al*., 2005) is represented by a species of *Goeldia* from Chile. More distant outgroup taxa include *Uroctea durandi* (Latreille, 1809) (Oecobiidae), *Stegodyphus mimosarum* Pavesi, 1883 (Eresidae), *Oncodamus dicipiens* Harvey, 1995 (Nicodamidae), and an unidentified *Ikuma* species from South Africa (Palpimanidae). The analyses were rooted with *Hickmania troglodytes* (Higgins & Petterd, 1883) (Austrochilidae). Choice of outgroups and rooting are in accordance with recent phylogenetic analyses of Entelegynae (Griswold *et al*., 2005; Miller *et al*., 2010). Most sequences were obtained by A.D.C. and H.M.W., and many of these sequences have been previously published by Miller *et al*. (2010).

The placement of Phyxelididae within the Araneomorphae remains unstable: previous morphological phylogenetic studies suggested Titanoecidae as their sister group under all (Griswold *et al.*, 1999) or some (Griswold *et al.*, 2005: fig. 219) parameters. Recent molecular phylogenetic studies of Entelegynae (Miller *et al.*, 2010; Spagna, Crews & Gillespie, 2010) did not include Titanoecidae, so this relationship remains untested with molecular data. Whereas the relationship of Phyxelididae to Titanoecidae may remain unsettled, that of tribe Phyxelidini (our taxon of interest) to tribe Vidoleini is sound (Griswold *et al.*, 2005), and therefore our taxon sampling is sufficient to test interrelationships within Phyxelidini, i.e. among those from Africa and Madagascar. The published phyxelidid phylogeny (Griswold, 1990) suggested that there were parallel sets of relationships between Madagascar and Africa, i.e. of *Ambohima* to the Malaika group and of the Madagascan to African *Phyxelida*, so our dataset included members of both potential outgroups. Our taxon sampling gives the Malagasy populations every opportunity to cluster with their previously suggested sister groups, or together. Our taxon sampling also provides two potential nodes basal to the Phyxelidini, i.e. Vidoleini – Phyxelidini, and Titanoecidae – Phyxelididae.

A list of taxa sampled, collection localities, and GenBank accession numbers is provided in Table 1. Voucher specimens for all sequenced individuals are deposited at the California Academy of Sciences, San Francisco, CA. Complete collection data for vouchers is listed in the Appendix.

Gene selection

DNA sequence collection and alignment

Prior to extraction, field collected specimens were either placed in 75% EtOH and kept in the museum collection at room temperature or were placed in 95% EtOH and stored in a freezer (–20 °C). Because of the age of some specimens (up to 14 years) and preservation of some in 75% ethanol at room temperature, it was not possible to get nuclear DNA sequences for all taxa: see Table 1. Studies have shown that taxa missing partial data are useful for interpreting homology among characters, that in most cases they do not create inaccuracies in the phylogeny, and that although they may reduce resolution they may also improve accuracy (Wiens, 2003, 2004; Burleigh *et al.*, 2004; Santini & Tyler, 2004).

Total genomic DNA was isolated by grinding one or two legs in lysis buffer and was purified using the DNeasy Blood & Tissue Kit (Qiagen Inc., Valencia, CA, USA) following the manufacturer's protocols. A suite of primers, listed in Table 2, was used to amplify a portion of the mitochondrial protein coding gene cytochrome c oxidase subunit 1 (COI), the nuclear protein coding gene histone-3 (H3), and the ribosomal nuclear genes 28S and 18S. The four fragments were amplified using standard protocols (see Wood, Griswold & Spicer, 2007).

Amplified PCR product was prepared for cycle sequencing using a mixture of Shrimp Alkaline Phospatase (SAP) and Exonuclease I (ExoI) enzymes (USB Corporation, Cleveland, OH, USA) following the manufacturer's protocol. Cleaned PCR product was cycle sequenced in both the forward and the reverse direction using a Big Dye Terminator v3.1 Kit (Applied Biosystems, Foster City, CA, USA) and was visualized on an ABI Prism 3130xl Genetic Analyzer (Applied Biosystems).

The quality of forward and reverse sequences was confirmed using Sequencher version 4.7 (Gene Codes Co., Ann Arbor, MI, USA) by assembling forward and reverse sequences into aligned contigs. Consensus sequences were exported from each high-quality contig. Each gene was aligned using the online interface (http://align.genome.jp/) for ClustalW (Thompson, Higgins & Gibson, 1994; Larkin *et al.*, 2007) using the default settings. Alignments were visually inspected using MacClade v4.08 (Maddison & Maddison, 2005) and no egregious errors were found. Protein coding genes were translated into amino acids and checked for stop codons using MacClade v4.08. The four alignments were then combined to form a concatenated data set. All DNA sequences were deposited in GenBank under the accession numbers listed in Table 1.

Phylogenetic analysis

Phylogenetic analyses were carried out using parsimony, likelihood, and Bayesian methods. Each marker was analysed separately using these methods (Fig. 61A–D). Parsimony, likelihood, and Bayesian methods were also used to analyse the concatenated four-marker data set. To test how the alignment may have affected the results, gapped characters were removed manually from the concatenated data set which was then analysed using parsimony, Bayesian, and likelihood.

Parsimony searches were performed in PAUP* version 4.0b10 (Swofford, 2003) using the random stepwise addition option of the heuristic search for 1000 replicates with the number of trees held set to increase automatically by 100, tree bisection-reconnection (TBR) branch swapping, collapse of zero-length branches, and equal weighting of all characters. To measure the robustness of branching patterns of the parsimony trees, bootstrap analyses (Felsenstein, 1985; Hillis & Bull, 1993) were executed by using the closest stepwise addition of the heuristic search for 1000 replicates: these are reported for all

Table 1. List of species used for phylogenetic analysis, voucher numbers, localities, genes sequenced and accession numbers

Taxon	Code	CASENT no.	Locality	DNA sequence	GenBank accession no.
Hickmania troglodytes	13_11	9023515	Australia	COI, 28S, 18S, H3	Miller *et al*., 2010
Ikuma sp.	11_6	9023778	South Africa	COI, 28S, 18S, H3	Miller *et al*., 2010
Oncodamus decipiens	10_10	9023688	Australia	COI, 28S, 18S, H3	Miller *et al*., 2010
Stegodyphus mimosarum	9_6	9024084	MA: Ranomafana	COI, 28S, 18S, H3	Miller *et al*., 2010
Uroctea durandi	13_7		Greece	COI, 28S, 18S, H3	Miller *et al*., 2010
Uroctea durandi	14_8		France	28S, 18S	Miller *et al*., 2010
Vytfutia sp.	P29	9023841	Borneo	COI, 28S, 18S, H3	JF411122, JF411226, JF411186, JF411151
Goeldia sp.	T15	9016517	Chile	COI, 28S, 18S, H3	JF411083, JF411188, JF411152, JF411123
Vidole capensis	10_14	9023622	South Africa	COI, 28S, 18S, H3	Miller *et al*., 2010
Vidole capensis	P08	9024915	South Africa	COI, 28S, 18S, H3	JF411121, JF411225, JF411185, JF411150
Xevioso kulufa	P31	9023795	South Africa	COI, 28S, 18S, H3	JF411084, JF411189, JF411153, JF411124
Xevioso colobata	P30	9024995	South Africa	COI, 28S, 18S	JF411085, JF411190, JF411154
Malaika longipes	P09	9026021	South Africa	COI, 28S, 18S, H3	JF411086, JF411191, JF411155, JF411125
Themacrys irrorata	P37	9023635	South Africa	COI, 28S, 18S, H3	JF411111, JF411215, JF411175, JF411144
Phyxelida tanganensis	P36	9019849	Tanzania	COI, 28S	JF411087, JF411192
Phyxelida bifoveata	P35	9019855	Tanzania	COI, 28S, 18S, H3	JF411088, JF411193, JF411156, JF411126
Ambohima zandry	P39	9003543	MA: Montagne d'Ambre	COI, 28S, 18S, H3	JF411089, JF411194, JF411157, JF411127
Ambohima zandry	P18	9006874	MA: Montagne d'Ambre	28S, 18S	JF411227, JF411187
Ambohima avaratra	P01	9003544	MA: Montagne d'Ambre	COI, 28S, 18S, H3	JF411110, JF411214, JF411174, JF411143
Ambohima andrefana	P17	9019919	MA: Zombitse	COI, 28S, H3	JF411092, JF411197, JF411130
Ambohima andrefana	P11	9018656	MA: Analavelona	COI, 28S, 18S, H3	JF411094, JF411199, JF411160, JF411131
Ambohima andrefana	P21	9019974	MA: Analavelona	COI, 28S, 18S, H3	JF411095, JF411200, JF411161, JF411132
Ambohima andrefana	P04	9005930	MA: Zombitse	COI, 28S	JF411093, JF411198
Ambohima ranohira	P03	9005937	MA: Isalo	COI, 18S	JF411096, JF411162
Ambohima ranohira	P19	9019987	MA: Isalo	COI, 28S, 18S, H3	JF411098, JF411202, JF411164, JF411134
Ambohima ranohira	P22	9016953	MA: Analalava	COI, 28S, 18S, H3	JF411097, JF411201, JF411163, JF411133
Ambohima antsinanana	P42	9029887	MA: Ambalavao	COI, 28S, 18S, H3	JF411101, JF411205, JF411166, JF411137
Ambohima vato	P02	9005936	MA: Itremo	COI, 28S, 18S, H3	JF411099, JF411203, JF411165, JF411135
Ambohima vato	P20	9005810	MA: Itremo	COI, 28S, H3	JF411100, JF411204, JF411136
Ambohima sublima	P23	9016226	MA: Ambohimanga	COI, 28S, 18S, H3	JF411102, JF411206, JF411167, JF411138
Ambohima sublima	P24	9016217	MA: Ambohimanga	COI, 28S	JF411103, JF411207
Ambohima sublima	P33	9015040	MA: Ambohitantely	COI, 28S, 18S, H3	JF411104, JF411208, JF411168, JF411139
Ambohima sublima	P28	9019991	MA: Andranomay	COI, 28S, 18S	JF411105, JF411209, JF411169
Ambohima sublima	P27	9019990	MA: Andranomay	COI, 28S, 18S, H3	JF411106, JF411210, JF411170, JF411140
Ambohima sublima	4052	9024052	MA: Ranomafana	COI, 28S, 18S, H3	JF411108, JF411212, JF411172, JF411141
Ambohima sublima	P07	9024485	MA: Ranomafana	COI, 28S, 18S	JF411107, JF411211, JF411171
Ambohima sublima	P34	9018170	MA: Ambohijanahary	COI, 28S, 18S, H3	JF411109, JF411213, JF411173, JF411142
Ambohima maizina	P26	9016206	MA: Marojejy	COI, 28S, 18S, H3	JF411090, JF411195, JF411158, JF411128
Ambohima zoky	P25	9017018	MA: Antsiranana	COI, 28S, 18S, H3	JF411091, JF411196, JF411159, JF411129
Rahavavy fanivelona	P13	9016960	MA: Ranomafana	COI, 28S, 18S	JF411112, JF411216, JF411176
Rahavavy fanivelona	P32	9016979	MA: Ranomafana	COI, 28S, 18S, H3	JF411113, JF411217, JF411177, JF411145
Rahavavy ida	P16	9019100	MA: Ranomafana	COI, 28S, 18S, H3	JF411114, JF411218, JF411178, JF411146
Rahavavy ida	P06	9003423	MA: Ranomafana	COI, 28S, 18S, H3	JF411115, JF411219, JF411179, JF411147
Rahavavy malagasyana	P05	9019981	MA: Andisibe	COI, 28S, 18S	JF411116, JF411220, JF411180
Rahavavy malagasyana	P10	9001352	MA: Angavokely	COI, 28S, 18S, H3	JF411117, JF411221, JF411181, JF411148
Rahavavy malagasyana	P12	9020000	MA: Manjakatompo	COI, 28S, 18S, H3	JF411118, JF411222, JF411182, JF411149
Manampoka atsimo	P40	9031165	MA: Andohahela	COI, 28S, 18S	JF411120, JF411224, JF411184
Manampoka atsimo	P41	9031166	MA: Andohahela	COI, 28S, 18S	JF411119, JF411223, JF411183

CASENT, California Academy of Sciences Entomology Department; MA, Madagascar.

Table 2. List of primers used for DNA sequencing

Locus	Primer	Sequence	Primer citation
COI	HCO-2198	TAAACTTCAGGGTGACCAAAAAATCA	Folmer *et al*., 1994
	LCO-1490	GGTCAACAAATCATAAAGATATTGG	Folmer *et al*., 1994
	C1-N-2191 (Nancy)	CCCGGTAAAATTAAAATATAAACTTC	Simon *et al*., 1994
	LCO1490-oono	CWACAAAYCATARRGATATTGG	Modified from Folmer *et al*., 1994
28S	28SO	GAAACTGCTCAAAGGTAAACGG	Hedin & Maddison, 2001
	28SC	GGTTCGATTAGTCTTTCGCC	Hedin & Maddison, 2001
	L0264cs	CGGGTTGCTTGGGAGTGC	Modified from Maddison *et al*., 2009
	28SOcs	CGTGAAACTGCTCAGAGG	Modified from Hedin & Maddison, 2001
	28SA	GACCCGTCTTGAAACACGGA	Whiting *et al*., 1997
	28SR	CCGTGTTTCAAGACGGGTCG – modified reverse of 28SA	Whiting *et al*., 1997
	28SmidF	CTGGCGGCGAGTAGGTCG	This study
	28SmidR	ACTCGCGCACATGTTAGAC	This study
H3	H3aF	ATGGCTCGTACCAAGCAGACVGC	Colgan *et al*., 1998
	H3aR	ATATCCTTRGGCATRATRGTGAC	Colgan *et al*., 1998
	H3nF	ATGGCTCGTACCAAGCAGAC	Colgan *et al*., 1998
18S	18S1F	TACCTGGTTGATCCTGCCAGTAG	Giribet *et al*., 1996
	18S5R	CTTGGCAAATGCTTTCGC	Giribet *et al*., 1996
	18S5F	GCGAAAGCATTTGCCAAGAA	Giribet *et al*., 1996
	18S9R	GATCCTTCCGCAGGTTCACCTAC	Giribet *et al*., 1996
	18S3Fl	GTTCGATTCCGGAGAGGGAGC	Modified from Giribet *et al*., 1996
	18S3Rs	GCTCCCTCTCCGGAATCGAAC	Modified from Giribet *et al*., 1996
	18S_5_9_intF	ATTCCGWTAACGADCGAG	Miller *et al*., 2010
	18S_5_9_intR	CTCGHTCGTTAWCGGAAT	Miller *et al*., 2010
	18S6_5F	GCTTAATTTGACTCAACACG	This study
	18S_7Rmod	GCATCWCWGACCTGTTATTGC	Modified from Giribet *et al*., 1996
	18S4F	CCAGCAGCCGCGCTAATTC	Giribet *et al*., 1996

Table 3. Uncorrected pairwise differences

	COI	H3	28S	18S
Within Madagascar species	0–0.0988	0–0.0366	0–0.0206	0
Between Madagascar species	0.0654–0.1611	0–0.0732	0.0103–0.1259	0.0006–0.0064
Between Madagascar and African phyxelidid species	0.1012–0.1903	0.0427–0.1221	0.1187–0.1811	0.0173–0.0334

nodes (bs). Due to extremely low divergences in 18S (see Table 3) the parsimony analysis of this marker was taking too long a time to complete in PAUP, so this marker was instead analysed under the default settings using TNT v.1.1, which is faster than PAUP because it incorporates New Technology algorithms (Goloboff, Farris & Nixon, 1993).

Bayesian analyses were implemented in MrBayes version 3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). Using the Akaike information criterion (AIC; Akaike, 1973), the best fit substitution model was estimated using MrModeltest version 2.2 (Nylander, 2004) for 28S, 18S and each of the three codon positions in the protein coding H3 and COI genes, resulting in eight partitions for the concatenated data set. Bayesian analyses were performed using four chains, the analysis was run twice simultaneously, and the starting trees were randomly generated. The analysis was run for 50 000 000 generations, with sampling every 1000th generation. All analyses were checked to ensure that the deviation of split frequencies was below 0.01. The two simultaneous analyses were evaluated for convergence using Tracer version 1.4 (Rambaut & Drummond, 2007). The burn-in value was visualized and determined using Tracer v1.4 by summarizing posterior distribu-

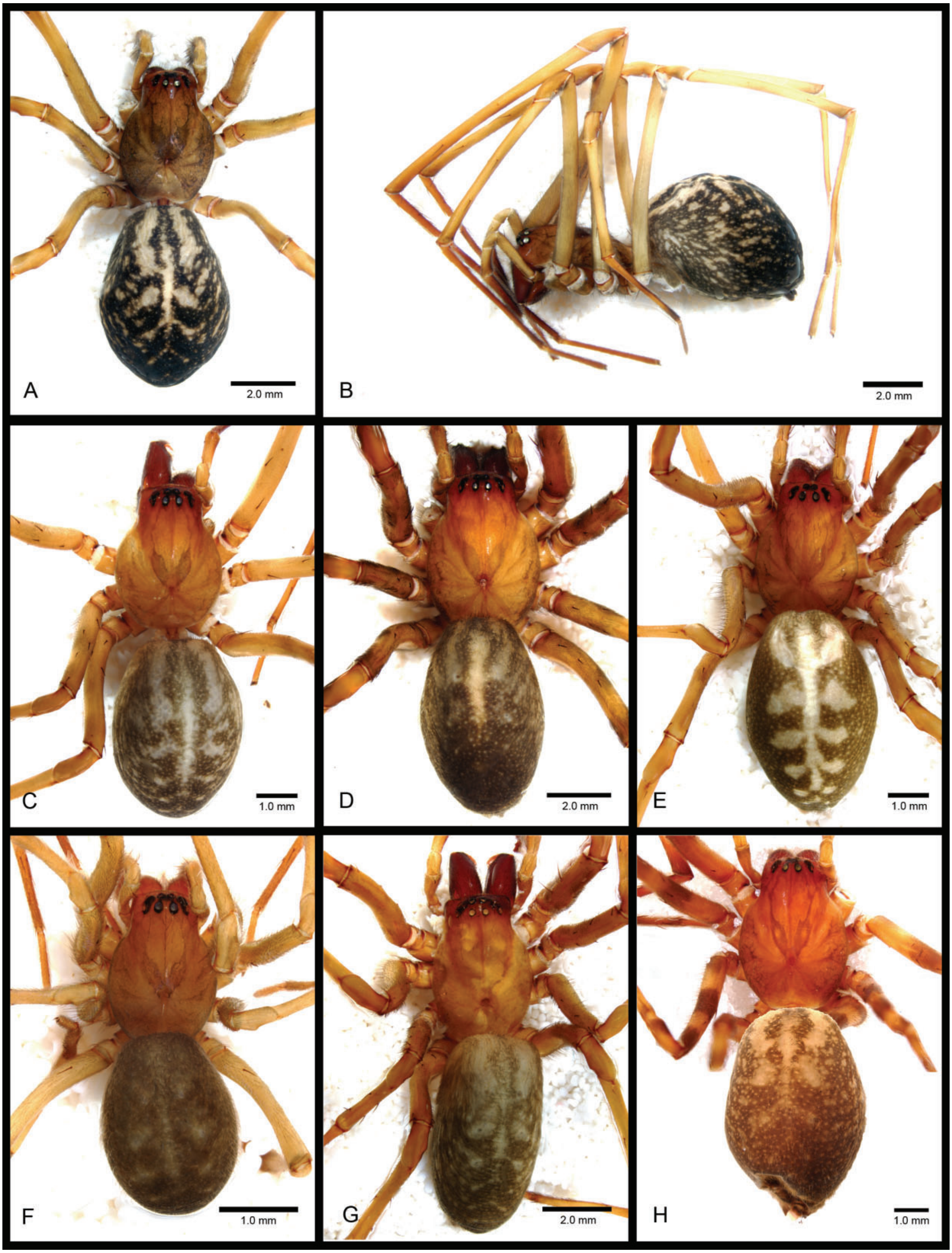

Figure 7. Habitus of *Ambohima* females. A, B, *A. antsinanana* from Andringitra, CASENT9029887. A, dorsal. B, lateral. C, *A. vato* from Itremo, CASENT9020002, dorsal. D, *A. ranohira* from Analalava, CASENT9019989, dorsal. E, *A. avaratra* from Montagne d'Ambre, CASENT9017012, dorsal. F, *A. zandry*, Montagne d'Ambre, CASENT9017021, dorsal. G, *A. zoky*, Montagne d'Ambre, CASENT9020320, dorsal. H, *A. pauliani*, holotype, dorsal.

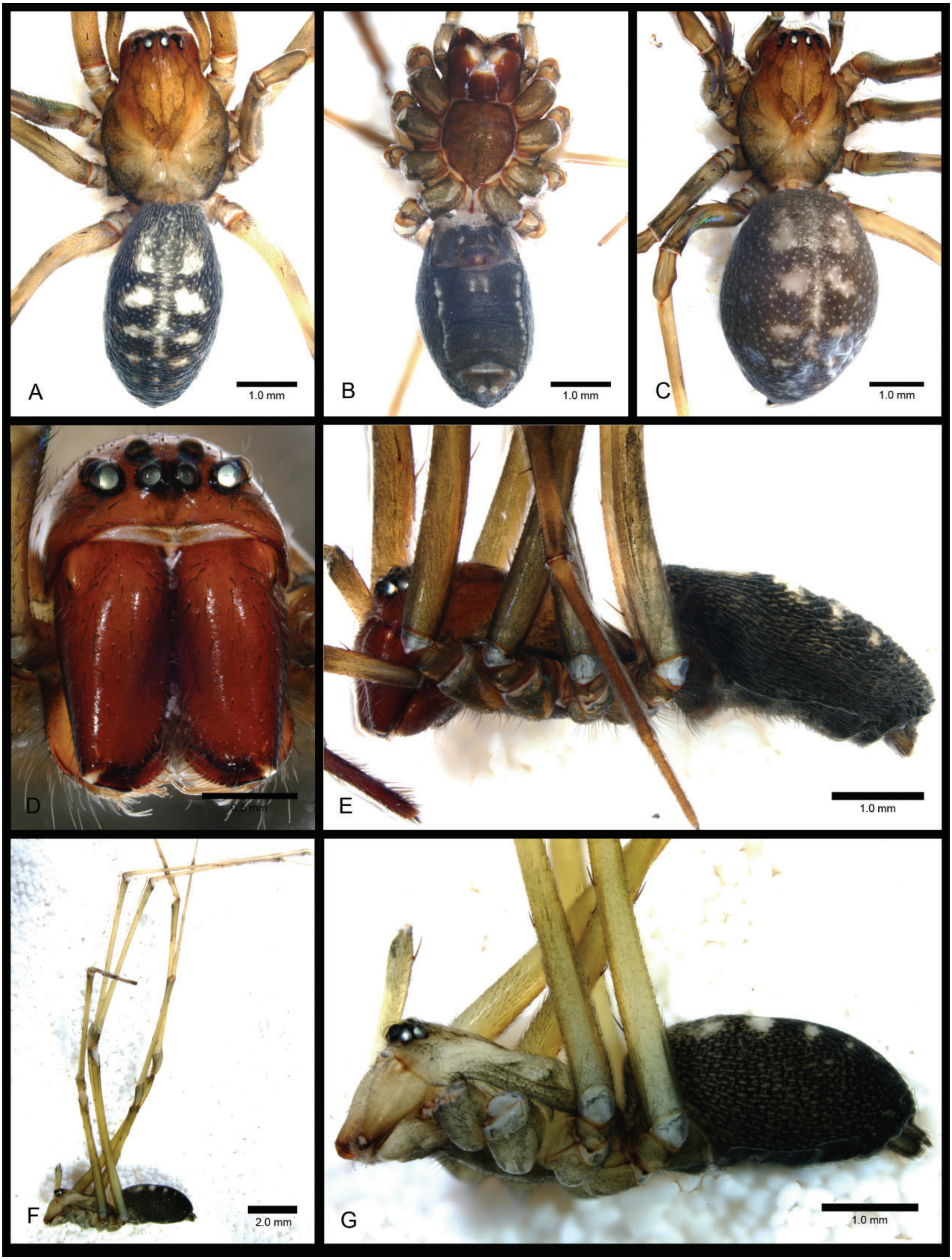

Figure 8. Habitus of *Manampoka atsimo*, holotype male and paratype females, Andohahela, CASENT9031164. A–E, female. F, G, male. A, C, dorsal. B, ventral. D, face, anterior. E–G, lateral.

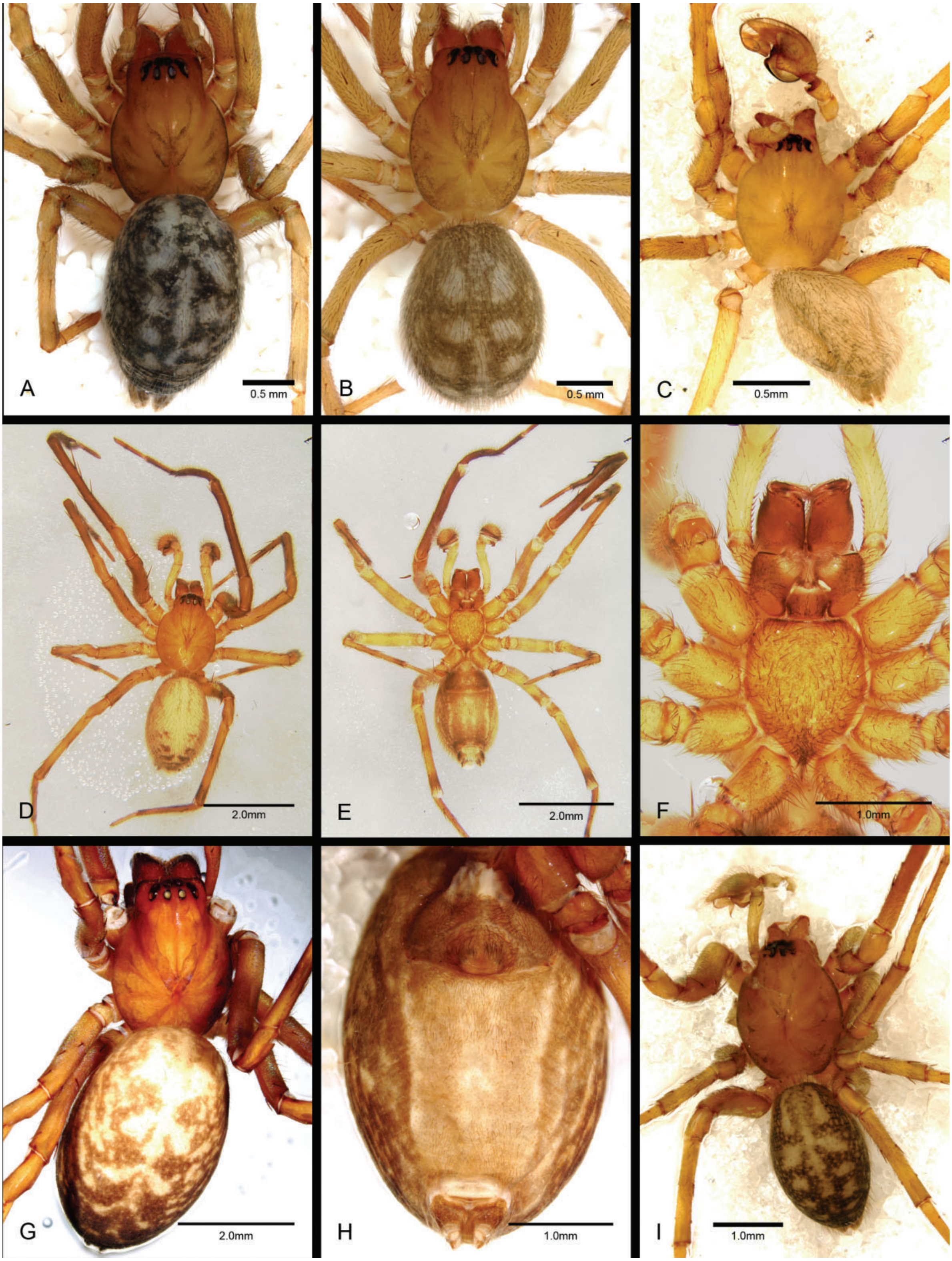

Figure 9. Habitus of *Rahavavy*. A, *R. malagasyana*, female from Andasibe, dorsal, CASENT9019982. B, C, *R. ida*, dorsal. B, female from Ranomafana, CASENT9016988. C, holotype male, CASENT9003423. D–F, *R. fanivelona*, male, Vohiparara, CASENT9016970. D, dorsal. E, ventral. F, cephalothorax, ventral. G–I, *R. malagasyana*. G, holotype female, dorsal. H, holotype female, venter of abdomen. I, male from Perinet, CASENT9016182, dorsal.

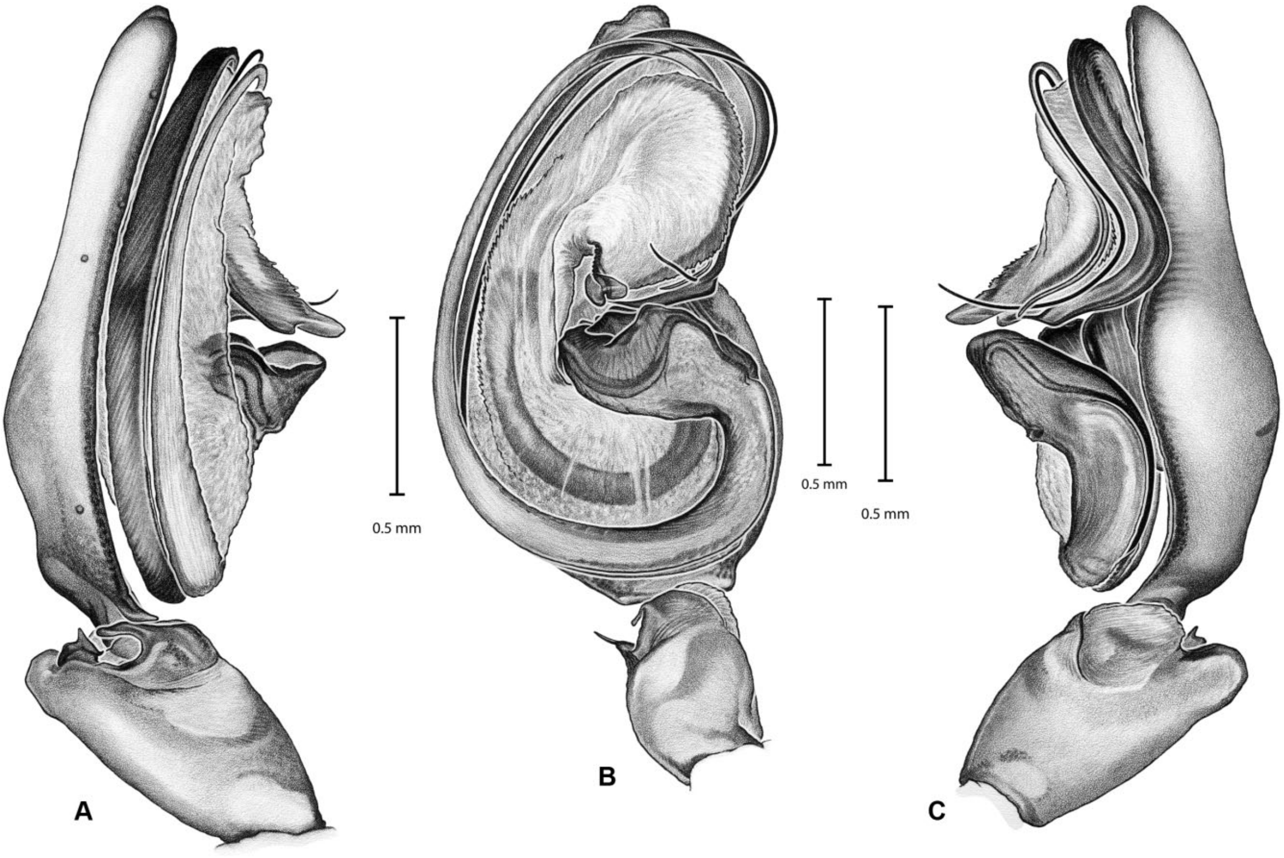

Figure 10. Left male palpus of *Ambohima andrefana* from Zombitse (CASENT9005930), tibia and tarsus. A, prolateral. B, ventral. C, retrolateral. Illustrations by GM.

tions of scalar values, which identified the first 25% of the initial trees to be discarded (burnin = 12 500), resulting in a final consensus tree with node support expressed as posterior probabilities (pp).

Maximum-likelihood (ML) analyses were performed using Randomized Axelerated Maximum Likehood or RAxML v7.0.4 (Stamatakis, 2006) via the Cipres Portal (Miller *et al*., 2009b) using the same eight partitions for the concatenated data as in the Bayesian analysis. All free model parameters were estimated by RAxML using the GAMMA model of rate heterogeneity. To assess robustness of the resulting phylogeny, 1000 bootstrap (bs) replicates were performed.

Species criteria

Within the Malagasy Phyxelididae we recognize as species those groups of terminals in our molecular analysis that are supported by a pp of 1.00 in the Bayesian analysis and that are diagnosable morphologically in our key to species.

RESULTS

Phylogenetic results

Our alignment resulted in a concatenated data set with a final length of 3587 bp, consisting of 658 bp for COI, 328 bp for H3, 1745 bp for 18S, and 856 bp for 28S. Uncorrected pairwise differences for each gene are reported in Table 3, which shows the amount of genetic difference within and between Malagasy phyxelidid species, and between the Malagasy and African phyxelidid species. The models selected by MrModeltest v2.2 for each eight partitions in the Bayesian analysis are: GTR+I+G for COI 1st and 2nd position, 18S and 28S; GTR+G for COI 3rd and H3 3rd position; GTR+I for H3 1st position; SYM for H3 2nd position.

The analyses of each gene individually using Bayesian, ML, and parsimony resulted in phylogenies that had few conflicts between genes or between results from the concatenated data set. The Bayesian single-gene phylogenies are shown in Figure 61A–D and the Bayesian concatenated analysis is shown in Figure 62. There were very few conflicts in the concatenated

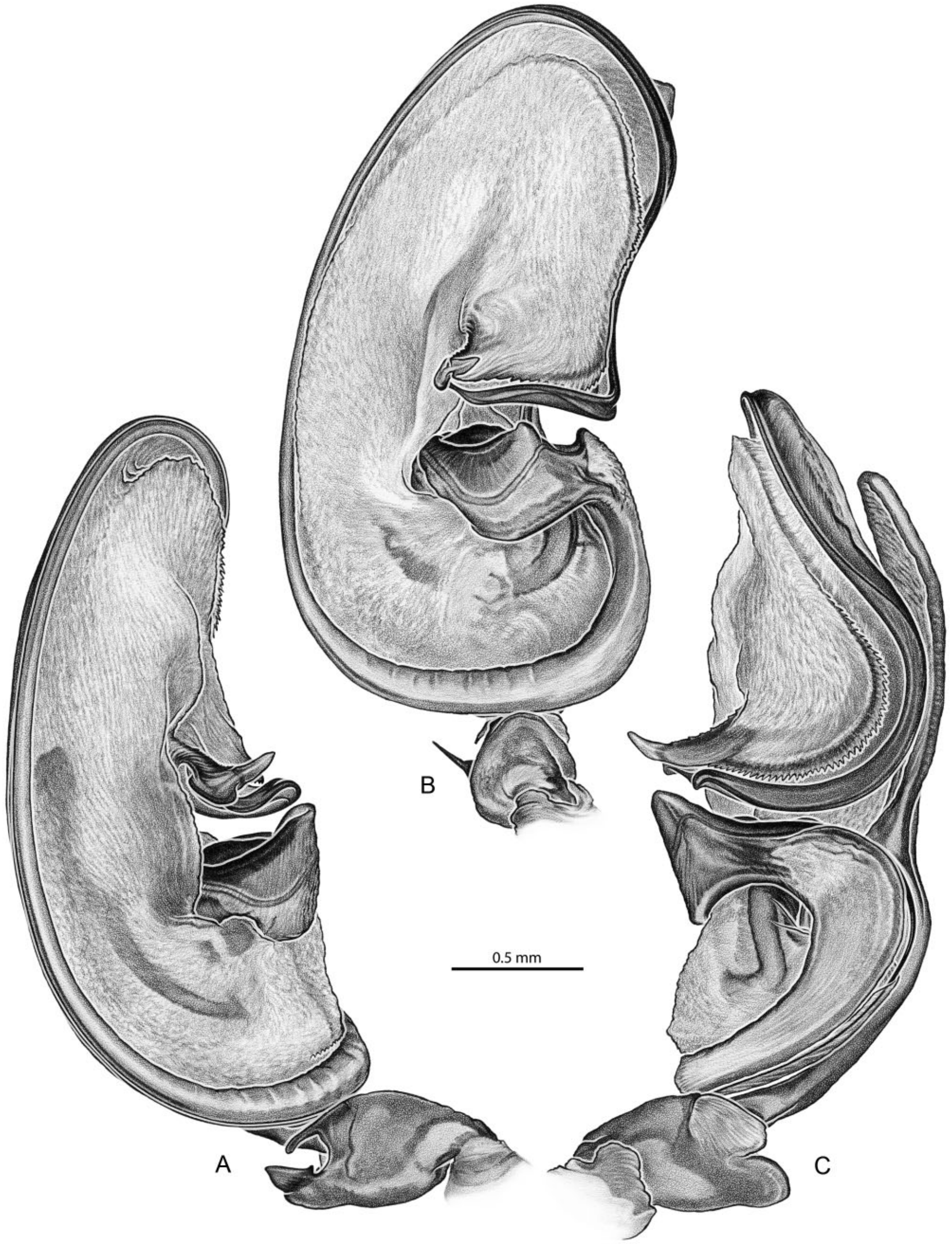

Figure 11. Left male palpus of *Ambohima maizina*, holotype from Marojejy (CASENT9016206), tibia and tarsus. A, prolateral. B, ventral. C, retrolateral. Illustrations by GM.

Bayesian, likelihood, and parsimony analyses and these results are summarized in Figure 60. The minor conflicts between genes and analyses are discussed below. Analyses run on the concatenated data set with gapped characters removed were also without major conflicts (also discussed below), suggesting that the alignment did not influence the results. The four-gene concatenated Bayesian, ML, and parsimony analyses are mostly identical except that the parsimony analysis has less resolution. The parsimony analysis resulted in 54 minimum-length trees of 4043 steps. We report boostrap support values and posterior probabilities. Only the boostrap support values of the strict consensus tree are reported for the parsimony analysis in the summary phylogeny (Fig. 60).

PHYLOGENY

All three analyses of the concatenated data set agreed on the essentials, with only two conflicts (Fig. 60).

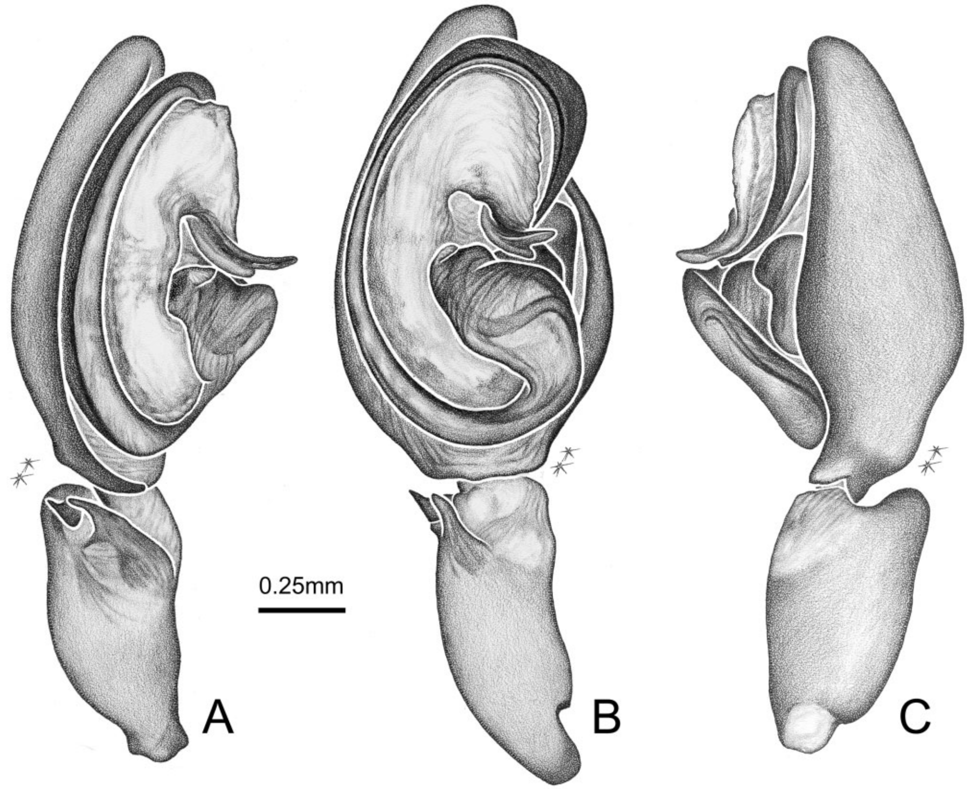

Figure 12. Left male palpus of *Ambohima ranohira* from Betroka (CASENT9016178), tibia and tarsus. A, prolateral. B, ventral. C, retrolateral. Illustrations by JS.

The first difference is regarding the placement of the new genus *Manampoka* (Fig. 60, node E) in the concatenated data set: in the Bayesian analysis *Manampoka* was sister to *Rahavavy* with pp = 0.93 and in the Parsimony analysis it was sister to the genera *Rahavavy* + *Ambohima* with bs = 63%. The placement of *Manampoka* + *Rahavavy* was also strongly supported by the following analyses with their support values listed as posterior probabilities (pp) or bootstrap (bs): likelihood concatenated data (bs = 55%); Bayesian, likelihood, and parsimony concatenated data with gaps removed (pp = 1.0, bs = 90%, bs = 70%); COI-only Bayesian (pp = 1.0) and likelihood (bs = 92%); and 18S-only likelihood (bs = 58%). Alternatively, the clade *Rahavavy* + *Ambohima*, with *Manampoka* as sister, was supported by the following analyses: 28S-only Bayesian (pp = 0.70) and parsimony (bs = 51%). Unfortunately we were unable to sequence H3 for individuals from *Manampoka*, which might have resolved these incongruencies. The other difference is regarding the placement of the *Ambohima sublima* individual (P33) from Ambohitantely in the concatenated data set analyses, which is sister to the individuals from Ambohimanga (P23, P24) with bs = 74% in the parsimony analysis, and is sister to the individuals from Andranomay (P27, P28) with bs = 67% in the ML analysis. The grouping P33 + (P23 + P24) is further supported by the following analyses: Bayesian concatenated data (pp = 0.63); Bayesian and parsimony concatenated data with gaps removed (pp = 0.97, bs = 83%); and COI-only Bayesian (pp = 0.96), likelihood (bs = 78%), and parsimony (bs = 95%). Alternatively the grouping P33 + (P27 + P28) is supported by these additional analyses: likelihood concatenated data with gaps removed (bs = 70%); and 28S-only Bayesian (pp = 0.72) and parsimony (bs = 54%). We discuss the remaining results based on the Bayesian four-marker analysis (Fig. 60). Basal groups with pp of 1.00 included the Entelegynae (Fig. 60, node A) and Phyxelididae plus Titanoecidae (Fig. 60, node B). Oecobiidae, represented by two *Uroctea* (13.7 and 14.8), clustered with Phyxelididae plus Titanoecidae with a pp of 1.00. Phyxelidid monophyly was not corroborated by our results: the titanoecid *Goeldia* (T15) clustered with Phyxelidini plus Vidoleini to the exclusion of *Vytfutia* (P29) with a pp of 0.83. Typical phyxelidids, i.e. Phyxelidini plus Vidoleini, clustered with a pp of 1.00 (Fig. 60, node C) and within this group the tribe Vidoleini (*Vidole capensis*, P08 and 10.14, and *Xevioso colobata*, P30, and *X. kulufa*, P31), clustered with a pp of 1.00. Monophyly of the tribe Phyxelidini was not

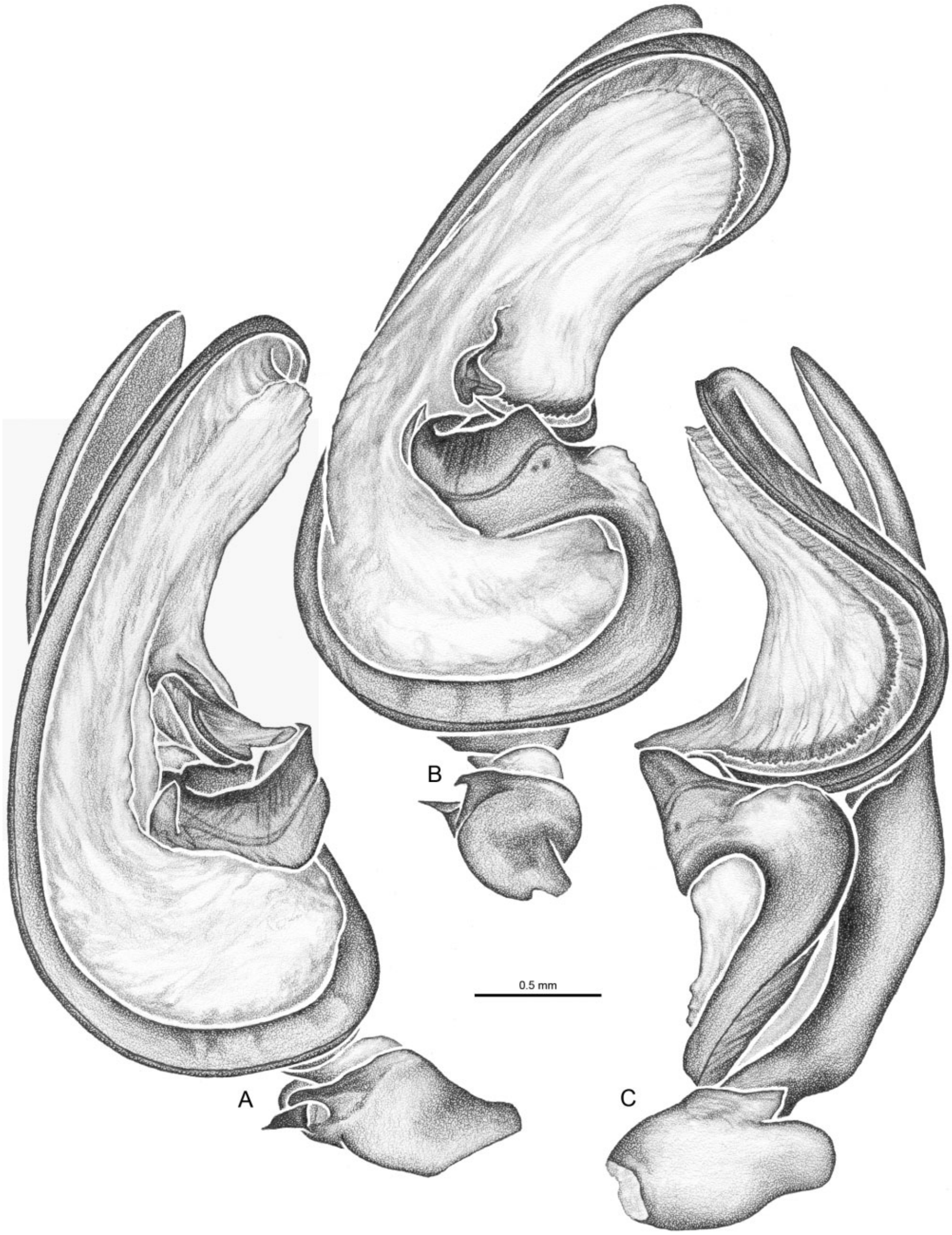

Figure 13. Left male palpus of *Ambohima sublima* from Ambohimanga (CASENT9016199), tibia and tarsus. A, prolateral. B, ventral. C, retrolateral. Illustrations by JS.

corroborated. *Malaika longipes* (P09) and *Themacrys irrorata* (P37) clustered with a pp of 0.98: these in turn clustered with the Vidoleini, but with a pp of 0.89. The two *Phyxelida* species, *P. tanganensis* (P36) and *P. bifoveata* (P35), clustered with a pp of 1.00: these in turn clustered with the Malagasy phyxelidids, but only with a pp of 0.67.

All of the Malagasy phyxelidids cluster together with a pp of 1.00 at node D (Fig. 60), corroborating the monophyly of this family in Madagascar. Within the Madagascar Phyxelididae, three groups are supported with a pp of 1.00. At node E (Fig. 60) the individuals P41 and P42 from Manangotry cluster, representing *Manampoka atsimo* gen. nov., sp. nov. At node F (Fig. 60) seven individuals cluster including P13 and P32 from Ranomafana (equivalent to *Phyxelida fanivelona*) and P12 from Manjakatompo (representing *Phyxelida malagasyana*). Because these taxa are not closely related to true *Phyxelida*, i.e. *P. tanganensis* (P36) and *P. bifoveata* (P35), we propose the new genus *Rahavavy* to include the three species represented in the analysis by these seven

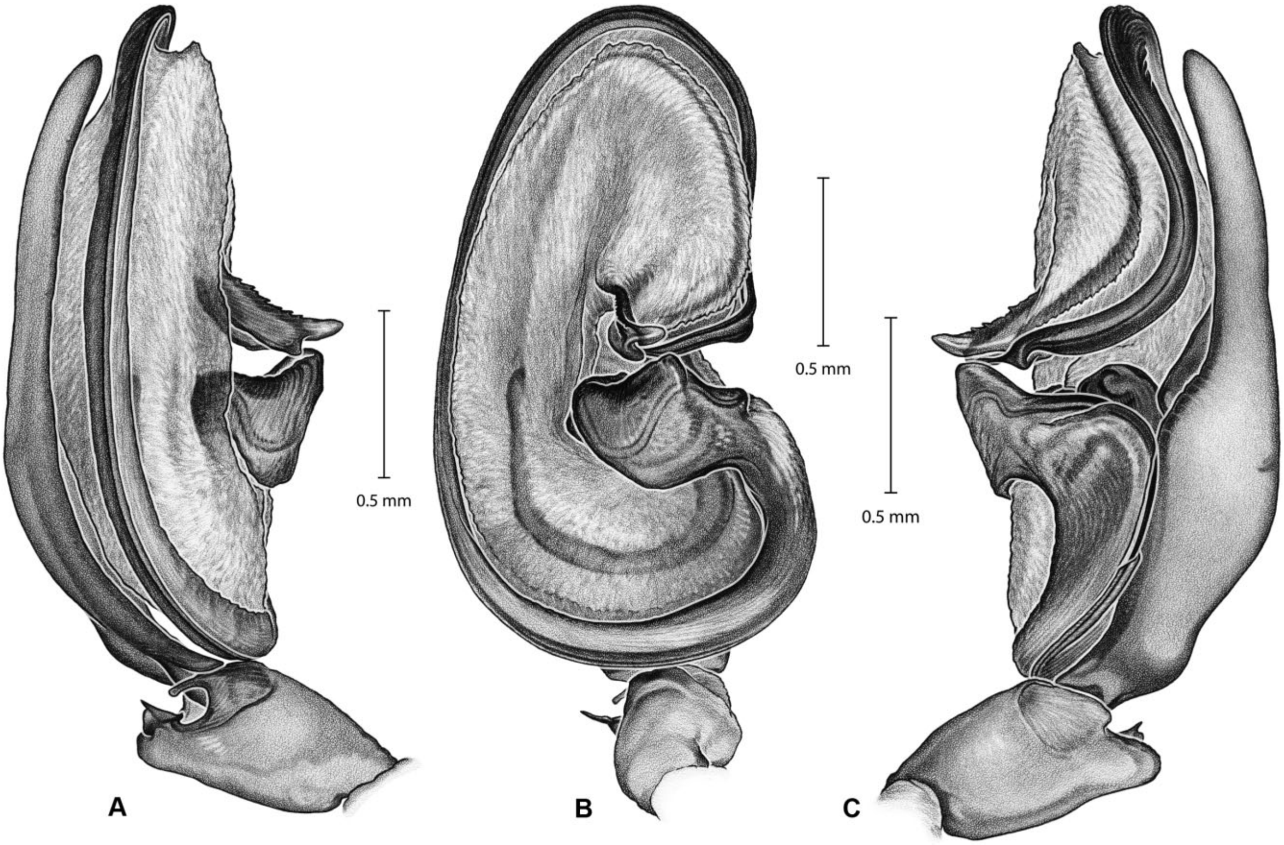

Figure 14. Left male palpus of *Ambohima vato* from Itremo (CASENT9005809), tibia and tarsus. A, prolateral. B, ventral. C, retrolateral. Illustrations by GM.

individuals. Finally, at node G (Fig. 60), 23 individuals cluster with a pp of 1.00. Included in this grouping are individuals P23 and P24 from Ambohimanga, representing the type locality of the type species of *Ambohima*, *A. sublima*. We therefore consider this entire group of 23 individuals as representing the genus *Ambohima*. Within the genera of Malagasy phyxelidids defined above we recognize species as those groups supported by a pp of 1.00 and that are diagnosable morphologically. *Manampoka atsimo* (P41 and P42 from Manangotry) clusters with the genus *Rahavavy* with a pp of only 0.93. Further, we note that *Manampoka* have an equal number of potential synapomorphies with each of *Ambohima* and *Rahavavy*. Female *Manampoka* share a spiral spermathecal chamber with some *Rahavavy*. Male *Manamopka* share a modification of the male second metatarsus with male *Ambohima*. This mosaic of potential morphological synapomorphies and ambiguity in the molecular results further complicate the phylogenetic placement of *Manampoka*, and we prefer to consider this a separate genus.

Within the new genus *Rahavavy* (Fig. 60, node F) the seven individuals from five populations cluster into three taxa with pp of 1.00. Individuals P13 and P32 from Ranomafana are equivalent to *Rahavavy fanivelona* (Griswold, 1990), individuals P06 and P16 from Ranomafana represent the new species *Rahavavy ida*, and the individuals P10 from Angavokely, P05 from Andasibe, and P12 from Manjakatompo represent *Rahavay malagasyana* (Griswold, 1990). *Rahavavy ida* and *R. fanivelona* cluster with a pp of 0.99: interestingly, these sister taxa occur in sympatry at Ranomafana, although some field data suggest that they may not be microsympatric, with *R. ida* occurring in the forest floor litter and *R. fanivelona* being principally arboreal.

The remaining 23 individuals from 14 populations comprise the genus *Ambohima* (Fig. 60, node G). Morphologically diagnosable and well-supported (pp of 1.00) groups that are endemic to a single locality are P39 plus P18 from Montagne d'Ambre (*Ambohima zandry* sp. nov.), and P02 and P20 from Itremo (*Ambohima vato* sp. nov.). More widespread species, known from a few to several localities, include *A. andrefana* sp. nov., known from Zombitse (P04 and P17) and Analavelona (P11 and P21), *A. ranohira* sp. nov., known from three localities in the vicinity of the

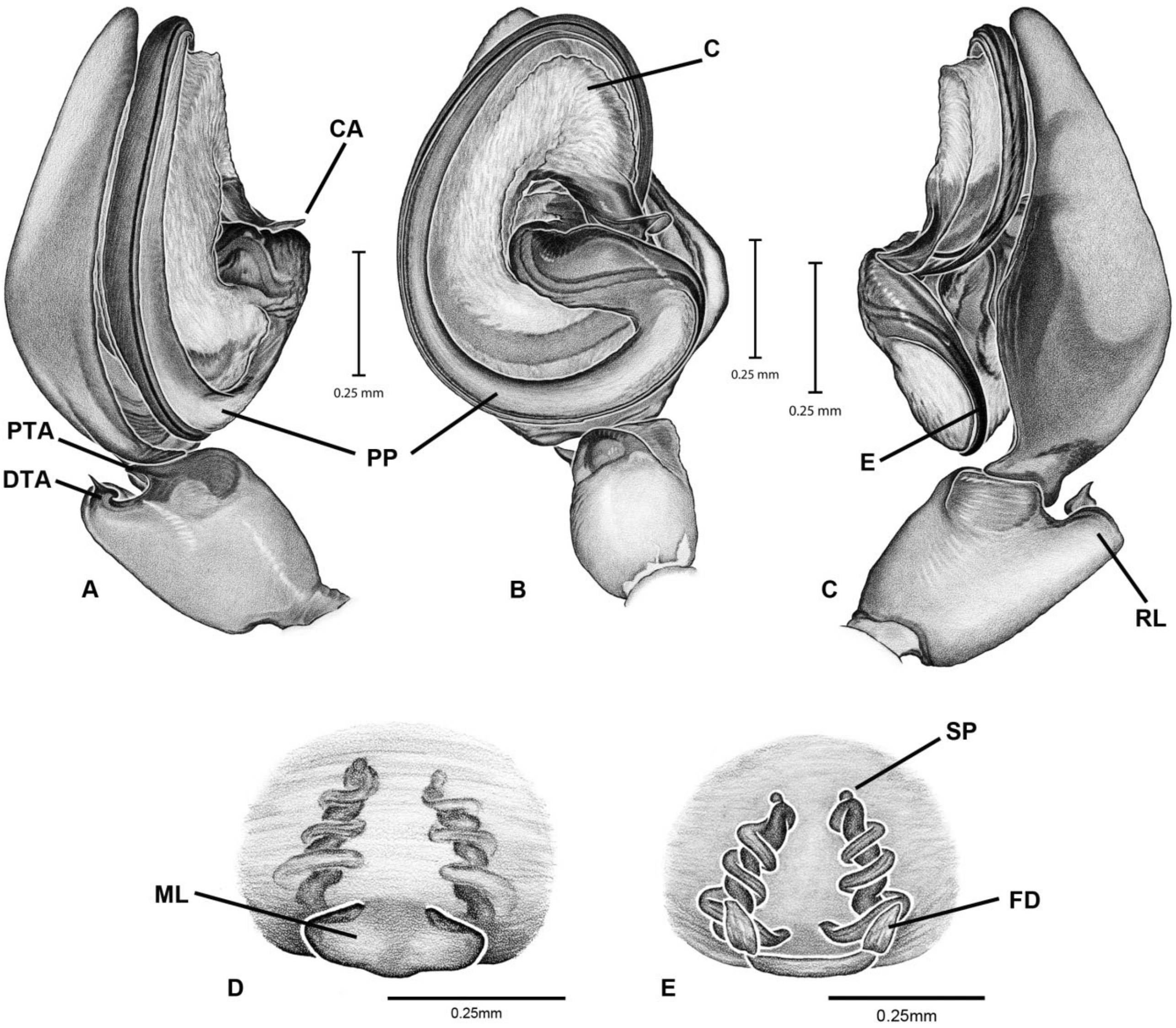

Figure 15. *Ambohima zandry* from Montagne d'Ambre. A–C, left male palpus of holotype CASENT9003543, tibia and tarsus. D, E, vulva of female CASENT9017020. A, prolateral. B, ventral. C, retrolateral. D, ventral. E, dorsal. Illustrations A–C by GM, D, E by JS. C: conductor, CA: conductor apex, DTA: dorsal tibial apophysis, E: embolus, FD: fertilization duct, ML: median lobe of epigynum, PP: pars pendula of embolus, PTA: prolateral tegular apophysis, RL: retrolateral lobe of tibial apex, SP: spermathecal poreplate.

Isalo massif (P03 from Isalo, P22 from Analalava, and P19 from Ranohira), and *A. sublima* Griswold 1990. *Ambohima sublima* is represented in our analysis by eight individuals from five populations, which cluster with a pp of 1.00 (Fig. 60, node H): P23 and P24 from Ambohimanga (the type locality for *A. sublima*), P27 and P28 from Andranomay, P07 and 4052 from Ranomafana, P33 from Ambohitantely, and P34 from Ambohijanahary. Whereas there are groupings within *A. sublima* that are also supported by pp of 1.00, we are not able to diagnose these and consider *A. sublima* as a widespread, variable species. Finally, there are four populations each represented by a single individual that are distinct enough to be considered as representing new species: P01 from Montagne d'Ambre (*A. avaratra*), P25 from near Antsiranana (*A. zoky*), P26 from the Marojejy massif (*A. maizina*), and P42 from the Andringitra massif (*A. antsinanana*).

Unfortunately, there is little phylogenetic structure within *Ambohima* that has high support. A clade of four species from south-central Madagascar supported by a pp of 1.00 includes *A. vato*, *A. antsinanana*, *A. ranohira*, and *A. andrefana* (Fig. 60, node I).

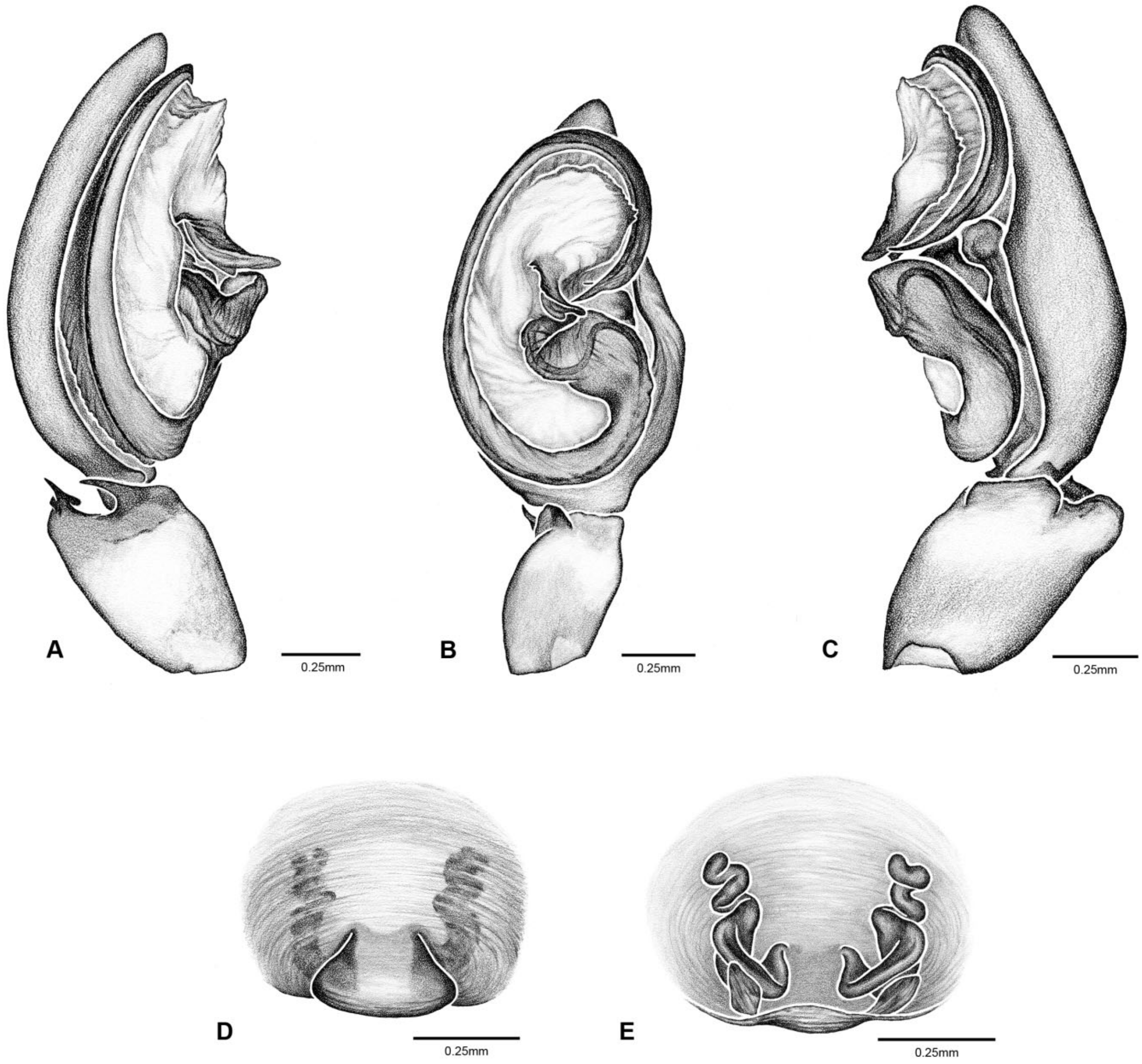

Figure 16. *Ambohima zoky*. A–C, left male palpus of holotype CASENT9017018 from 7 km SE Antsiranana. D, E, vulva of female from Montagne d'Ambre, CASENT9017015, A. prolateral. B, ventral. C, retrolateral. D, ventral. E, dorsal. Illustrations by JS.

Within this clade the southern species *A. antsinanana*, *A. ranohira*, and *A. andrefana* form a group with pp of 0.99 (Fig. 60, node J), and within this group the western species *A. ranohira* and *A. andrefana* are sister groups with a pp of 0.97 (Fig. 60, node K). *Ambohima zandry* and *A. avaratra*, two species from far northern Madagascar, cluster with a pp of only 0.92, but unique morphological features suggest that these are sister species. Both have female spermathecae that have spermathecal ducts spiralling around a central, longitudinal spiral chamber and with a poreplate at the apex of the spermathecae (Fig. 34C, D, H, I). Resolutions of the relationships among these groups to and among the remaining species, *A. sublima*, *A. zoky*, and *A. maizina*, are supported by pp of 0.92 or less.

DISCUSSION

Sequence divergence

Mitochondrial divergence is very high among and within the Malagasy phyxelidid species (Table 3).

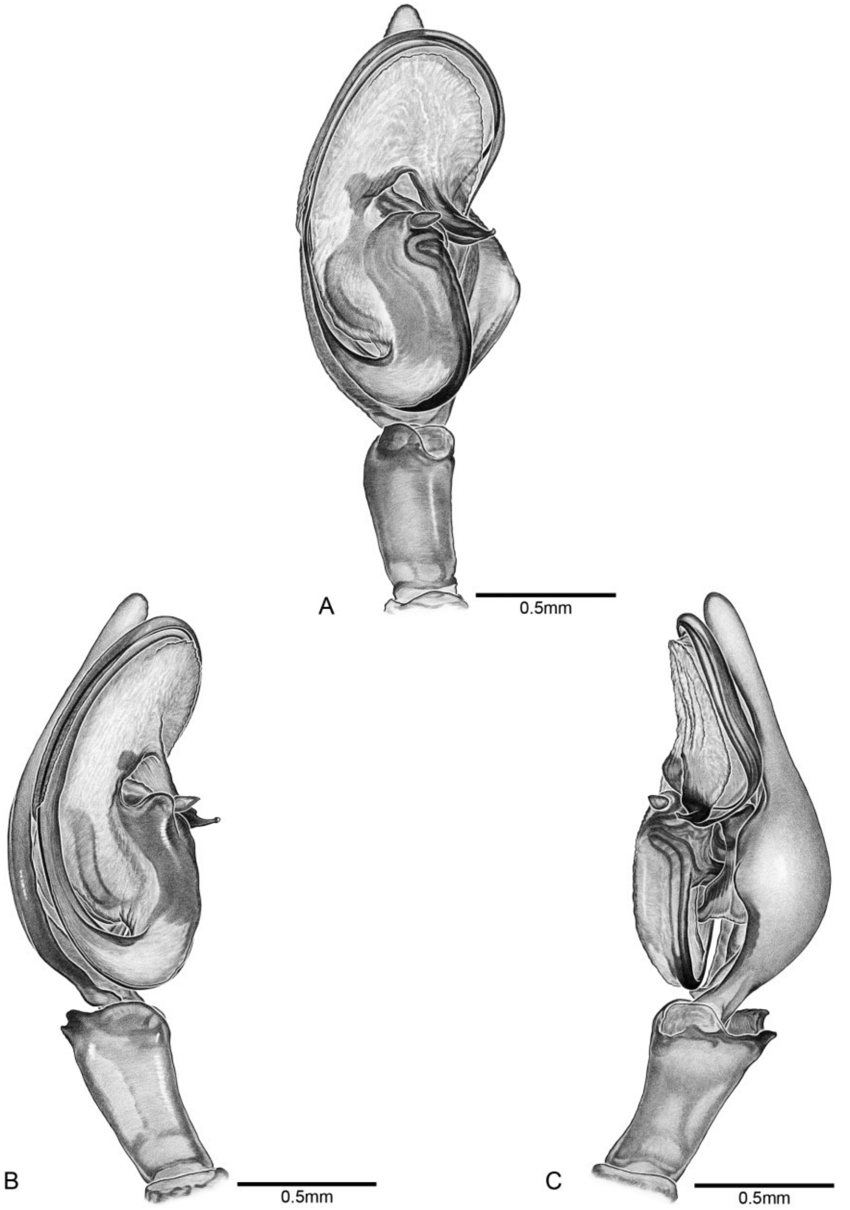

Figure 17. Left male palpus of *Manampoka atsimo*, holotype from Manangotry, CASENT9031164, tibia and tarsus. A, prolateral. B, ventral. C, retrolateral. Illustrations by GM.

Comparable mitochondrial divergences have been found in Malagasy archaeid spiders (Wood *et al*., 2007) and in California trap-door spiders (Bond *et al*., 2001). Archaeids, trap-door spiders, and phyxelidid spiders are not known to disperse by ballooning, unlike other groups of spiders. These low dispersal capabilities may allow for high genetic population divergence and speciation by vicariance, even in the absence of morphological change (Bond *et al*., 2001). The high rate of mitochondrial divergence within the Malagasy phyxelidids deserves further study, particularly if fossils become available to calibrate a molecular clock.

MADAGASCAR BIOGEOGRAPHY

Intercontinental relationships

There is a long tradition of interpreting Madagascar's biota as an ancient relict of Gondwanaland, implying isolation on the island through the mechanism of continental drift. There are two current models for Gondwana breakup. The model most widely accepted,

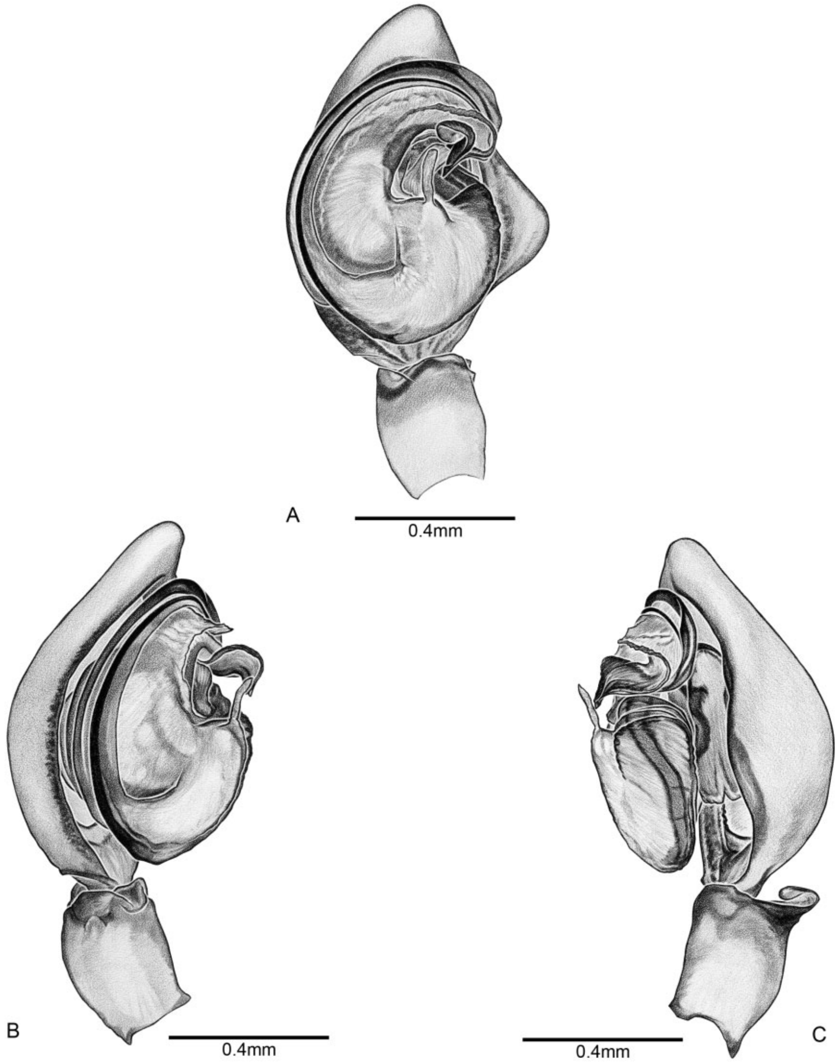

Figure 18. Left male palpus of *Rahavavy fanivelona* from Vohiparara, CASENT9016975, tibia and tarsus. A, prolateral. B, ventral. C, retrolateral. Illustrations by GM.

and which could even be called 'standard' (e.g. http://en.wikipedia.org/wiki/Continental_drift, accessed 10 April 2009) postulates a separation between Madagascar plus India from the other parts of Gondwana, i.e. ancestral Africa, Antarctica, Australia, New Zealand, New Caledonia, and South America, beginning about 165 Mya (Rabinowitz *et al.*, 1983; Smith, Smith & Funnell, 1994; Scotese, 2000) and complete isolation of Madagascar/India by 140 Mya (Seward, Grujic & Schreurs, 2004). This model implies that, if originating through vicariance, Malagasy taxa should be sister taxa of those occurring in other parts of Gondwanaland. A second model, labelled 'alternative' by its earliest proponents (Hay *et al.*, 1999), suggests that after separating from Africa the minicontinent formed by ancestral Madagascar plus India remained connected to South America via a land bridge to Antarctica until about 80 Mya (Krause *et al.*, 1997; Sampson *et al.*, 1998; Case, 2002). This land bridge between Antarctica and Madagascar–India is thought to include the Kerguelen Plateau (Krause *et al.*, 1997) or Gunnerus Ridge (Case, 2002). This model implies that Gondwanaland relicts in Madagascar should have close relatives in South America, to the exclusion of Africa. Whereas the 'alternative' model has been widely invoked, for example by Krause *et al.* (2006, 2007), Upchurch (2008), and Vitt & Caldwell (2009: 371), it has also been extensively criticized as untenable (Ali & Aitchison, 2008, 2009; Ali & Krause, 2011). To fit a Gondwanaland vicariance scenario the organisms in question should at least exhibit intercontinental distributions that fit one of these models for Gondwanaland breakup, and ideally show evidence of sufficient age through fossils and/or a divergence time

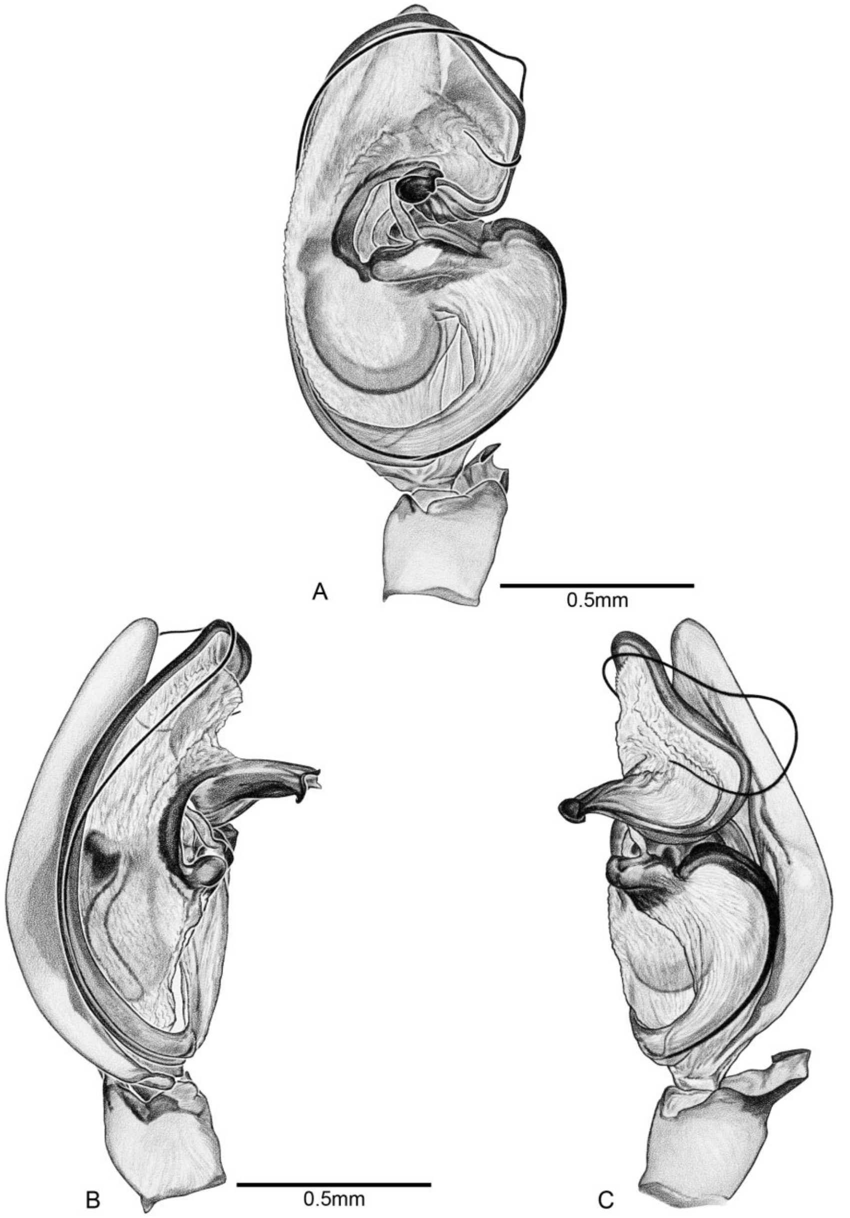

Figure 19. Left male palpus of *Rahavavy ida*, holotype from Talatakely, CASENT9003423, tibia and tarsus. A, prolateral. B, ventral. C, retrolateral. Illustrations by GM.

analysis using molecular data. In spite of continuing uncritical assumption of a Gondwanan history for Madagascar's biota (e.g. Paulian & Viette, 2003), the vast majority of Malagasy taxa meet none of the criteria for this Gondwanan vicariance explanation. In a recent review of a broad sample of phlyogenetic studies of Malagasy plants, invertebrates and vertebrates, Yoder & Nowak (2006) noted that for most endemic clades of Madagascar organisms the closest sister-group relationships are to Africa (thereby failing the geographical test for Gondwanan vicariance) and that for the majority of taxa for which divergence times have been estimated their origin in Madagascar is in the Cenozoic, far too young to have been derived through Gondwanan vicariance. Indeed, even for some vertebrate taxa that show a near perfect distributional match to patterns predicted by Gondwanan breakup, i.e. cichlid fish (Sparks & Stiassny, 2003; Sparks & Smith, 2004), divergence time estimation through molecular phylogenetics suggests that the pattern may be too young to be a product of vicariance (Vences *et al.*, 2001). Currently only three extant vertebrate taxa, boine snakes, iguanid lizards, and podocnemid turtles, are known to conclusively fit a vicariance scenario.

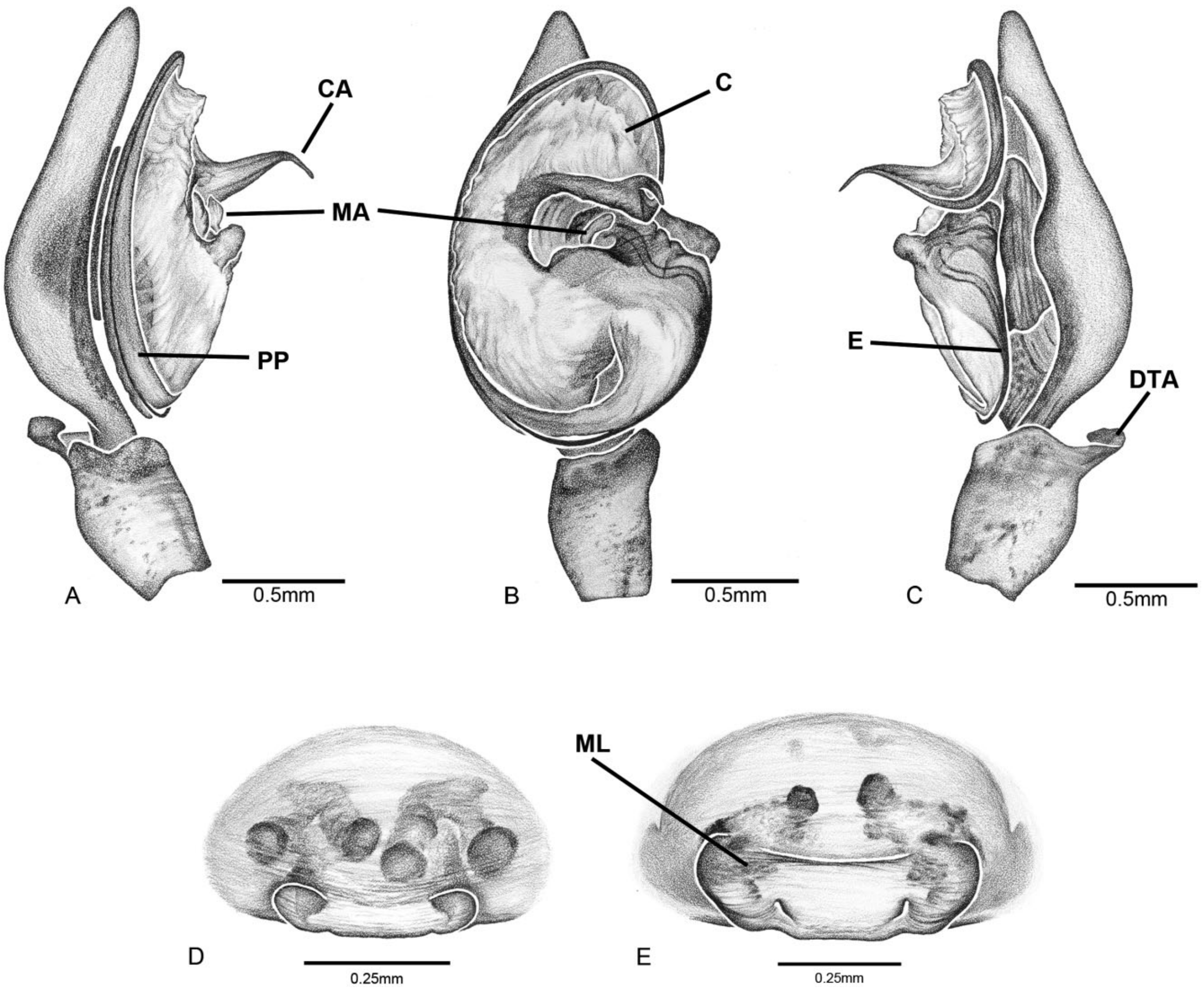

Figure 20. Genitalia of *Rahavavy malagasyana*. A–C, left male palpus from Perinet (CASENT9016182). A, prolateral. B, ventral. C, retrolateral. D, epigynum, ventral, Manjakatompo (CASENT9032843). E, epigynum, ventral, Manjakatompo (CASENT9017006). Illustrations by JS. C: conductor, CA: conductor apex, DTA: dorsal tibial apophysis, E: embolus, MA: median apophysis, ML: median lobe of epigynum, PP: pars pendula of embolus.

Using multiple gene loci coupled with a Bayesian divergence age analysis, Noonan & Chippendale (2006) found that these taxa, which have a disjunct relationship between Madagascar and South America, are old enough to have attained this distribution by vicariance through the 'alternative' model, i.e. a continuing connection between Madagascar and South America via Antarctica after Africa had become isolated (Hay *et al*., 1999).

MADAGASCAR SPIDERS: REVIEW OF STUDIES ON THE RELATIONSHIPS, AGE, AND MODE OF ORIGIN

Griswold (2003) presented a comprehensive review of the biogeography of Madagascar spiders. Like other Madagascan organisms, spiders exhibit remarkable richness and endemism. The vast majority of Madagascar spiders show phylogenetic and/or taxonomic affinities to Africa; far fewer show affinities to Asia, and only a handfull exhibit distributions that could result from continental drift, whether by the 'standard' or 'alternative' models.

In spite of their richness and endemism, Madagascar spiders have been subjected to few phylogenetic analyses that specified their sister groups, and to date only a few such analyses (Andriamalala, 2007; Agnarsson *et al*., 2009; Kuntner & Agnarsson, 2011a, b) have specifically performed a divergence time estimation through molecular phylogenetics. Each suggests Cenozoic dispersal to Madagascar. The following

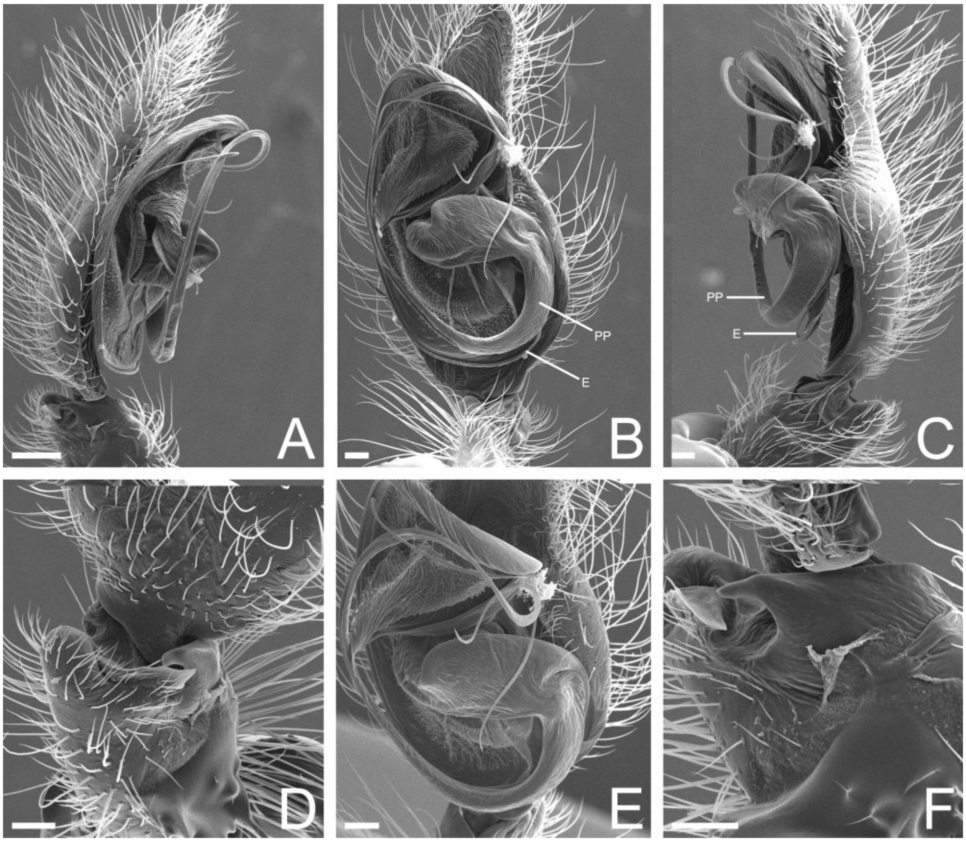

Figure 21. Right male palpus of *Ambohima andrefana* from Zombitse (SEM images flipped to appear left) CASENT9005933. A, prolateral. B, ventral. C, retrolateral. D, tibia, dorsal, showing DTA. E, bulb, apicoventral. F, tibia, prolateral, showing DTA and PTA. Scale bars: A = 200 µm, B–F = 100 µm. E: embolus, PP: pars pendula of embolus.

phylogenetic studies sample a broad range of the spider fauna and, with few exceptions, show a close phylogenetic relationship between Madagascar and Africa (Emerit, 1972, 1994; Wesolowska, 1986; Sierwald, 1987; Griswold, 1990, 1991, 2000, 2001; Bjørn, 1997; Wood *et al.*, 2007; Wood, 2008; Agnarsson *et al.*, 2009; Kuntner & Agnarsson, 2011a, b). Phylogenetic relationships to Asia emerge from fewer studies (Lehtinen, 1981; Raven, 1985; Griswold, 1993, 2000; Andriamalala, 2007).

The presence of austral biotic elements in Madagascar has long been explained by invoking an ancient Gondwana origin through continental drift (e.g. Legendre, 1977). Several groups of spiders have southern hemisphere disjunct distributions: the families Archaeidae (Africa, Australia, Madagascar), Cyatholipidae (Madagascar, Africa, Australia, New Zealand), Gallieniellidae (Madagascar, Africa, Australia, Argentina), Migidae (Madagascar, Africa, South America, Australia, New Zealand, New Caledonia), and Zorocratidae (Mesoamerica, Africa, Madagascar, south Asia), and such disjunctions are also found in the gnaphosid genus *Camillina* (Madagascar, Africa, Americas, and Pacific and Indian Ocean islands) and desid genus *Desis* (Madagascar, Africa, Australia, IndoMalaysia, New Caledonia, South America). Do any of these disjunct distributions fit a model for continental drift (Smith *et al.*, 1994; Hay *et al.*, 1999; Scotese, 2000; Case, 2002)? At this time such relationships have been suggested for only four groups of spiders, and only one of these has been subject to a comprehensive global phylogenetic analysis. Exemplar-based studies of higher classification suggest that the sister genera of the Malagasy Calocteninae (Ctenidae) occur in South America (Silva Dávila, 2003), that those of the Malagasy Idiopidae (Raven, 1985) and zorocratid genus *Uduba* (Griswold, 1993, 2000) occur in Sri Lanka, and the closest relatives of the Malagasy and Sri Lankan taxa together are in the Americas rather than Africa, a distribution consistent with the ‘alternative’ model of Gondwana breakup (Krause *et al.*, 1997; Sampson *et al.*, 1998; Hay *et al.*, 1999). Only the tree trap-door spider family Migidae has been subject to a compre-

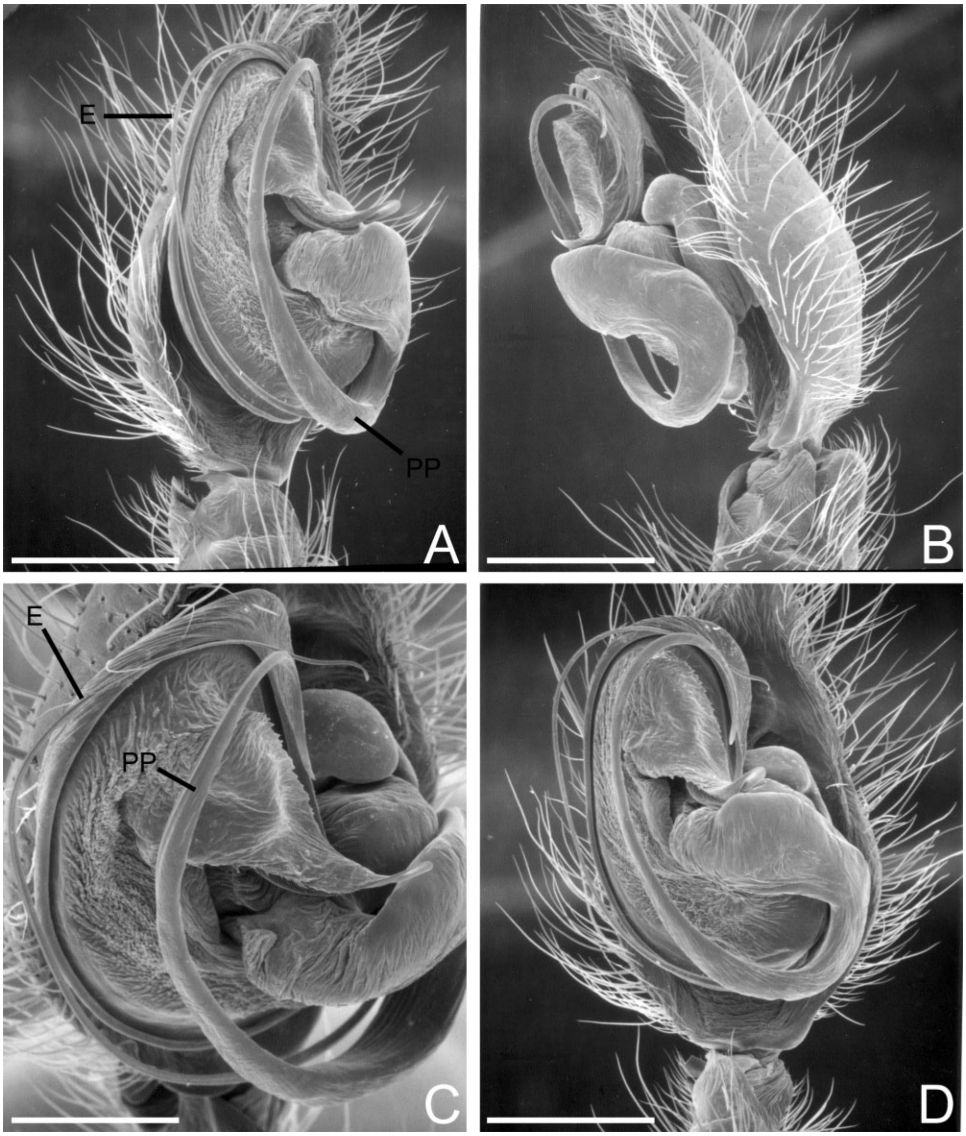

Figure 22. Right male palpus of of *Ambohima ranohira* from Betroka (SEM images flipped to appear left) CASENT9016178. A, prolateral. B, retrolateral. C, proapical. D, ventral. Scale bars: A, B, D = 430 μm, C = 250 μm. E: embolus, PP: pars pendula of embolus.

hensive global phylogenetic analysis treating all the Malagasy species and multiple clades from the other southern continents (Griswold & Ledford, 2001). The three Malagasy migid genera form a monophyletic group that is the sister group of taxa occurring in Australia, New Zealand, South America, and Africa, reflecting the pattern suggested by the 'standard' model for continental drift (Rabinowitz *et al*., 1983; Scotese, 2000; Seward *et al*., 2004). In sum, it appears that one Malagasy spider group (Migidae) may be considered Gondwanan in the sense of having attained its disjunct distribution through isolation through continental drift, that three others (calocteine Ctenidae, Idiopidae, and Zorocratidae) are good candidates (but exhibiting patterns conforming to different historical scenarios), and that the vast majority of Madagascar's spider fauna came there by dispersal. An appropriate question is 'how many dispersals', which is addressed for one taxon by our current study of Madagascar's Phyxelididae.

MADAGASCAR PHYXELIDIDAE

MADAGASCAR PHYXELIDIDAE: GLOBAL RELATIONSHIPS

Phyxelidids were formerly considered as an example of multiple (perhaps three) clades that show indepen-

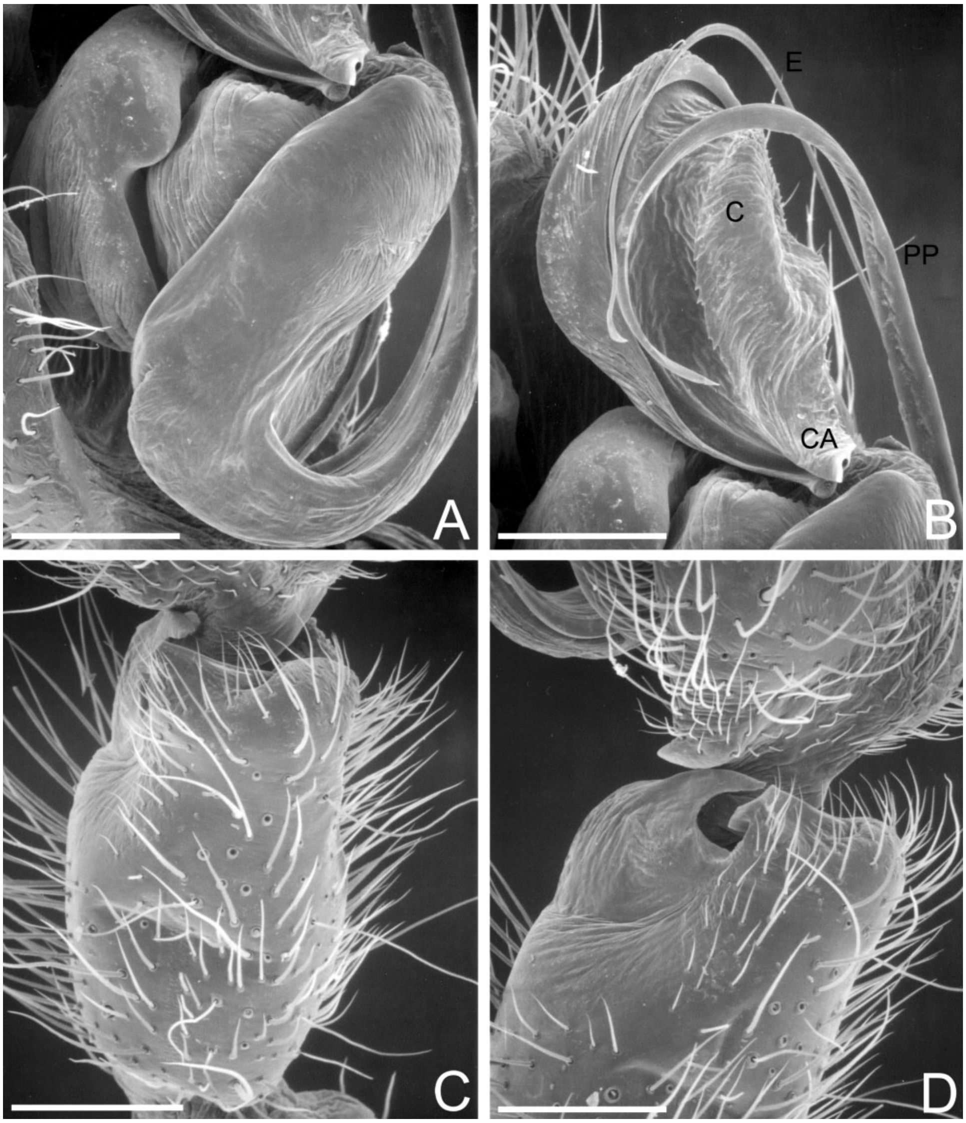

Figure 23. Right male palpus of of *Ambohima ranohira* from Betroka (CASENT9016178). A, bulb with embolic base, retroapical. B, apex of conductor, with pars pendula and truncus separated. C, tibia, dorsal. D, tibia, proapical. Scale bars: A–D = 200 µm. C: conductor, CA: conductor apex, E: embolus, PP: pars pendula of embolus.

dent relationships between Madagascar and tropical east Africa (Griswold, 2000). The results of our molecular phylogenetic analysis, corroborated by a morphological synapomorphy, i.e. the rotation of the clasping spine on male metatarsus I from retrolateral to prolateral (Figs 1, 9D), support the monophyly of the Malagasy phyxelidids, which are probably related to phyxelidids from eastern or southern Africa. This in turn implies a single invasion of Madagascar, not multiple invasions. Other spider examples of multiple Africa–Madagascar relationships, i.e. Cyatholipidae and Zorocratidae (Griswold, 2000), also deserve re-examination.

MADAGASCAR BIOGEOGRAPHY

Patterns within the island: the signal from the Phyxelididae

Unfortunately, the lack of well-supported structure on the phyxelidid cladogram allows us to say little about the relationships within Madagascar. The genus *Manampoka* is known only from one place at Andohahela

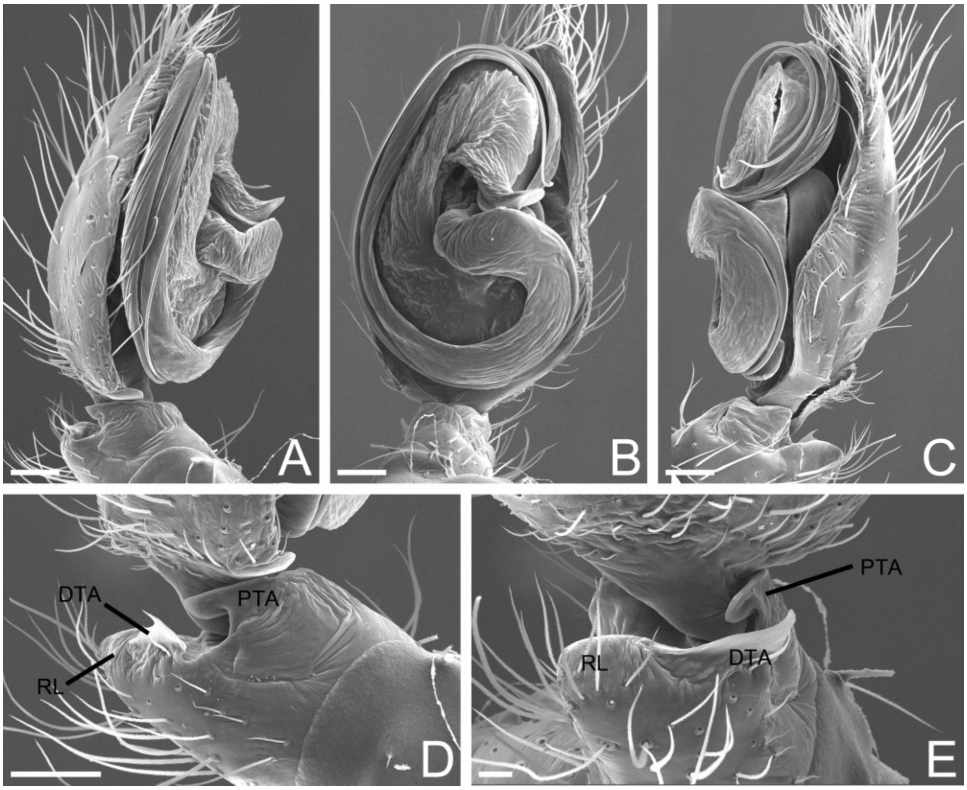

Figure 24. Right male palpus of *Ambohima zandry* from Montagne d'Ambre (SEM images flipped to appear left), CASENT9006874. A, prolateral. B, ventral. C, retrolateral. D, tibia, prolateral, showing RL, DTA, and PTA. E, tibia, dorsal. Scale bars: A–D = 100 μm, E = 30 μm. DTA: dorsal tibial apophysis, PTA: prolateral tibial apophysis, RL: retrolateral lobe of tibial apex.

in south-eastern Madagascar (Fig. 59). The three species of *Rahavavy* occur in rainforests along the eastern escarpment from south central to central Madagascar (Figs 58, 59). Remarkably, the sister species *R. fanivelona* and *R. ida* occur in sympatry at Ranomafana, whereas *R. malagasyana* occurs in east central Madagascar. *Ambohima* extends widely in eastern Madagascar from the far north to the far south (Figs 57–59). Only *A. andrefana* and *A. sublima* (marginally) extend into western Madagascar, the former species occurring at Zombitse and Analavelona (Fig. 57). It is unclear if this absence from western Madagascar is an artefact of collecting. The Fisher/Griswold arthropod survey team (2001–2005) collected extensively in western Madagascar, but this team collected few phyxelidids. C.E.G. and H.M.W. have collected in the west at Ankarafantsika, Kirindy, Zombitse, and Beza Mahafaly: in spite of careful searching at each site for phyxelidids, these were found only at Zombitse. Identifiable biogeographical patterns within *Ambohima* include the occurrence of several phylogenetically isolated, geographically restricted species in northern Madagascar, i.e. *Ambohima zandry* and *A. avaratra*, which morphological data suggest are sister groups, and *A. maizina*, *A. zoky*, and *A. pauliani* (the last-named not included in the phylogenetic analysis for lack of suitable material for DNA extraction); distribution of *A. sublima* along the eastern escarpment from Ranomafana to Andranomay, with some extension to a relict forest in the west at Ambohijanahary (Fig. 57); and a clade of four species distributed across the island from south-east to south-west. Representing this last-named clade, *Ambohima andrefana* from western forests (Fig. 57) is sister to *A. ranohira* from the central plateau and south-west (Fig. 59); sister to these two is *A. antsinanana* from the eastern escarpment at Andringitra (Fig. 58); and sister to these three is *A. vato* from the isolated Itremo massif in south central Madagascar (Fig. 58). There are several cases of sympatry in Madagascar phyxelidids, typically between a large and small species. The small *Ambohima zandry* occurs in sympatry with the larger *A. avaratra* (its probable sister species) and also with *A. zoky* at Montagne d'Ambre in far northern Madagascar, and *Ambohima sublima* occurs in sympatry with the

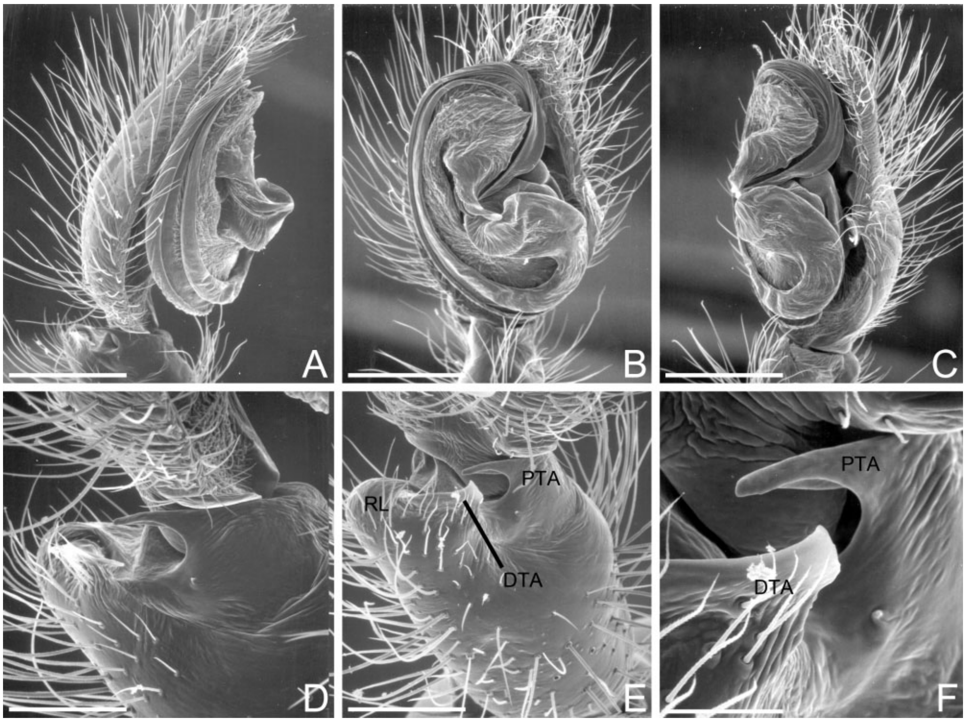

Figure 25. Right male palpus of *Ambohima zoky* holotype from Antsiranana (SEM images flipped to appear left) CASENT9017018. A, prolateral. B, ventral. C, retrolateral. D, tibia, prolateral, showing DTA and PTA. E, tibia, prodorsal, showing RL, DTA, and PTA. F. Tibia, dorsal, apices of DTA and PTA. Scale bars: A–C = 430 μm, D, F = 158 μm, E = 200 μm. DTA: dorsal tibial apophysis, PTA: prolateral tibial apophysis, RL: retrolateral lobe of tibial apex.

much smaller *Rahavavy malagasyana* in the escarpment region east of Antananarivo and with *Rahavavy ida* and *R. fanivelona* at Ranomafana. *Manampoka atsimo* and *Ambohima ranohira* may occur in sympatry at Andohahela, but it is likely that the former is restricted to moist and the latter to dry habitats (Fig. 59). Finally, the sister-species pair *Rahavavy ida* and *R. fanivelona* occur in sympatry at Ranomafana, although, as noted above, these may be restricted to different habitats.

In summary, most phyxelidid species in Madagascar, with the exceptions of *Ambohima ranohira*, *A. sublima*, and probably *Rahavavy malagasyana*, appear narrowly distributed. Within *Ambohima* there is a widespread eastern species (*A. sublima*), a northern clade (*A. zandry* and *A. avaratra*), and a southern and western clade (*A. andrefana*, *A. antsinanana*, *A. ranohira*, *A. vato*). Sympatric species typically include one large and one small, i.e. *A. sublima* and *R. fanivelona* at Ranomafana, *A. zoky* and *A. zandry* at Montagne d'Ambre. There are at least two cases of probable sister species in sympatry: *R. fanivelona* with *R. ida* and *A. avaratra* with *A. zandry*. Unfortunately, the weak support for many nodes on the cladogram (Fig. 60) precludes us from saying more about internal biogeographical patterns within Madagascar.

NATURAL HISTORY OF PHYXELIDIDAE

WEB BUILDING AND PREY CAPTURE

Ambohima make silken retreats within or under objects, e.g. beneath tree bark or under stones or fallen logs, and build prey capture webs that extend out from these retreats. The prey capture webs typically comprise one or more horizontal sheets of cribellate silk. Such webs have been observed in the field for *Ambohima andrefana*, *A. ranohira*, *A. sublima* (Fig. 2A), and *A. vato*. *Ambohima* hang beneath their webs (Fig. 2B). Captive individuals of *Ambohima andrefana* and *A. sublima* have been observed to construct webs and capture prey. Cribellate silk is carded with the carding leg IV braced against the opposite, mobile leg IV, which is 'type 2' cribellate silk carding behaviour (Eberhard, 1988). Prey are bitten and then slowly wrapped with alternate movements of legs IV. The fine structure of *Ambohima* cribellate silk has not been studied, but, given *Ambohima*'s complement of spigots, this silk

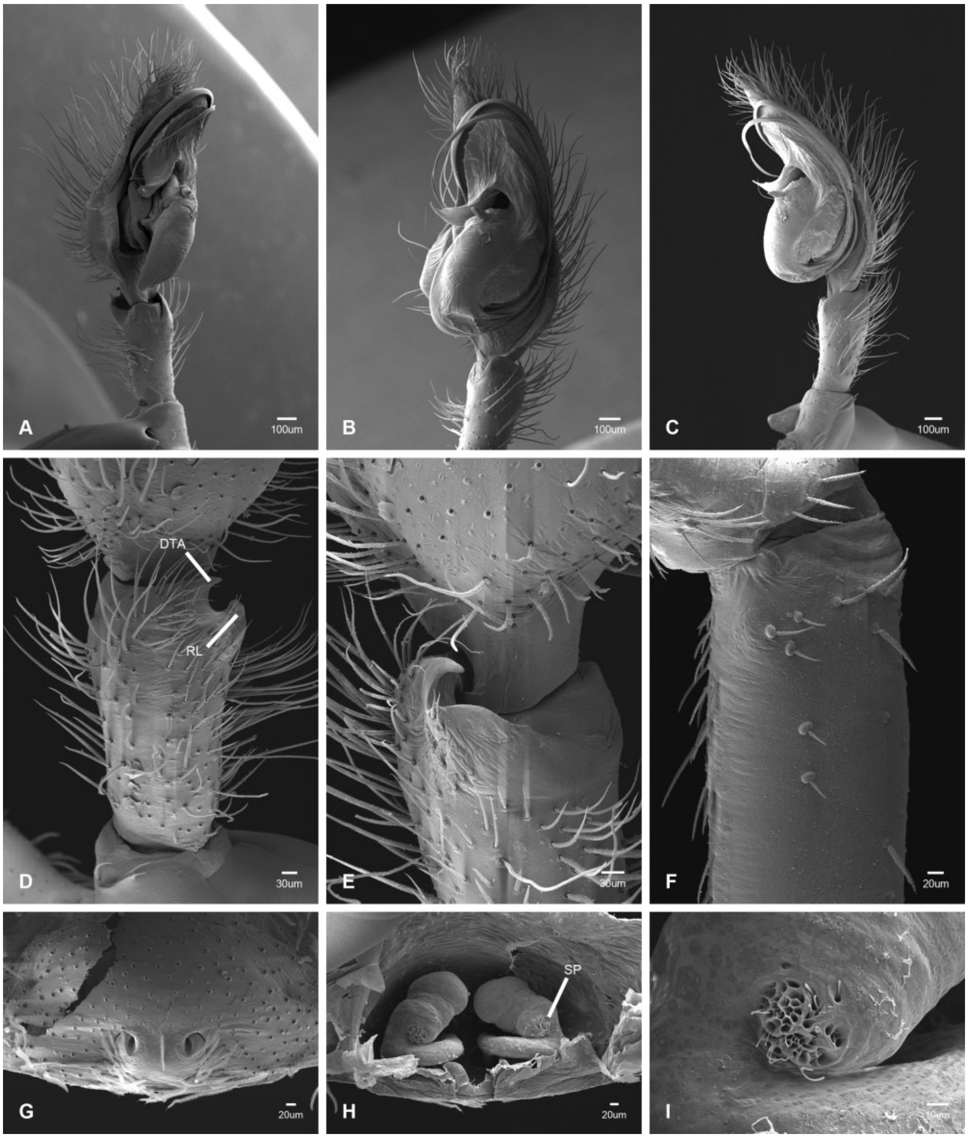

Figure 26. *Manampoka atsimo*, from Manangotry, CASENT9031164. A–F, right male palpus of holotype. G–I, vulva of female. A, retrolateral. B, ventral. C, prolateral. D, tibia, dorsal. E, apex of tibia, retrolateral. F, femur, prolateral. G, epigynum, ventral. H, spermathecae, dorsal. I, poreplate on left spermatheca, dorsal. DTA: dorsal tibial apophysis, RL: retrolateral lobe of tibial apex, SP: spermathecal poreplate.

is probably similar to that of *Phyxelida* (Griswold *et al.*, 2005: fig. 121A–C) with axial fibres and reserve warp present in the cribellate band. Webs of *Rahavavy fanivelona* have been observed at Vohiparara, Ranomafana, where they were built between leaf axils of *Pandanus* trees and within the scars of lost fronds on the trunks of tree ferns. These webs were concealed and appressed to the substrate. Building behaviour, prey capture and cribellate band fine structure have not been observed in *Rahavavy*. Webs of *Manampoka* and the other species of *Rahavavy* and *Ambohima* have not been recorded.

MATING BEHAVIOUR

The presence of modified setae and setal bases on the palpal femora of males and females suggests a stridulatory function that might play a role in courtship: such stridulation has not been definitively observed but precopulatory behaviours involving palpal jerking are suggestive. Modifications of male legs that may

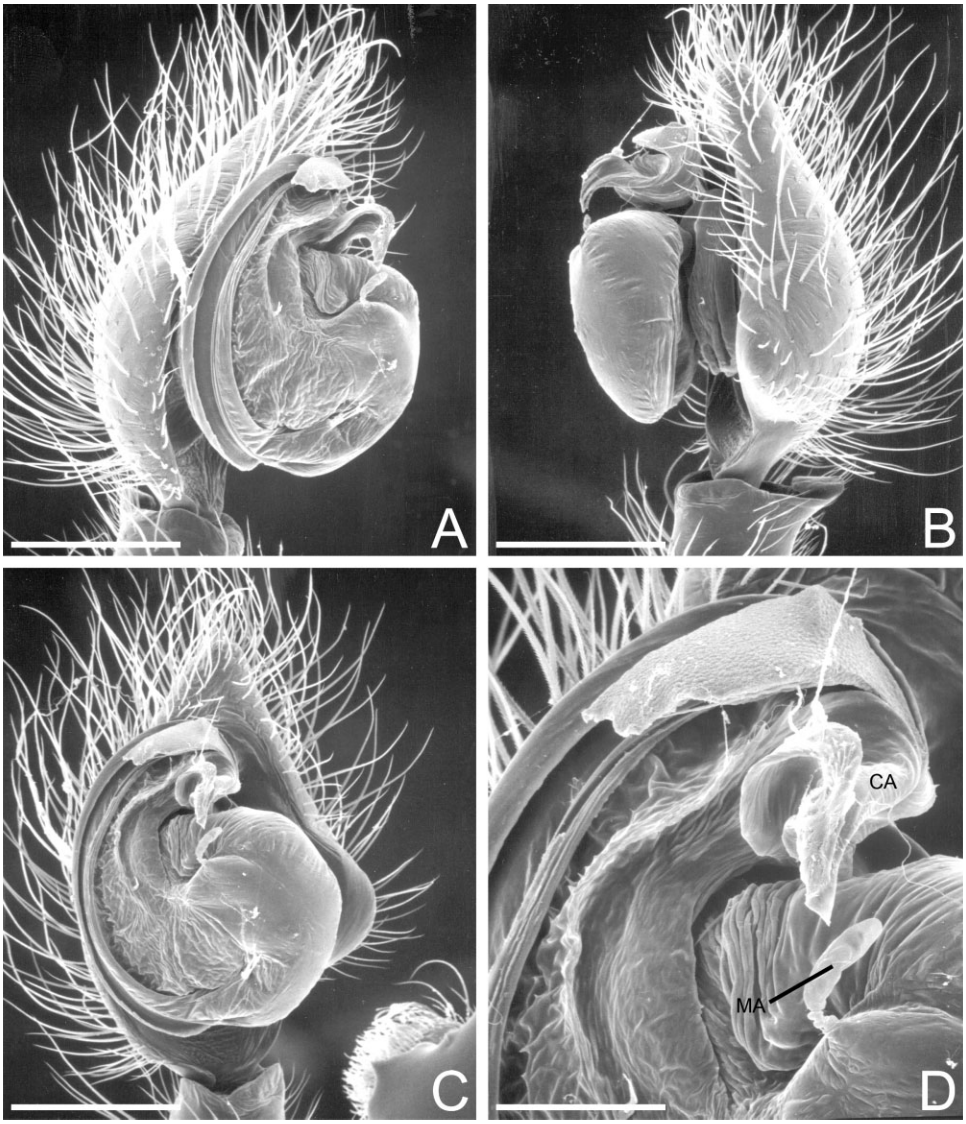

Figure 27. Right male palpus of *Rahavavy fanivelona* from Ranomafana (SEM images flipped to appear left), CASENT9016969. A, prolateral. B, retrolateral. C, ventral. D, bulb apex, ventral, close-up. Scale bars: A–C = 300 μm, D = 100 μm. CA: conductor apex, MA: median apophysis.

serve for clasping during courtship and mating are widespread in Mygalomorphae (e.g. Migidae, Griswold & Ledford, 2001; Microstigmatidae, Griswold, 1985) but are rare in Araneomorphae (e.g. some Orbiculariae, Miller *et al*., 2009a; some Haplogynae, e.g. Ramírez & Grismado, 1997), and indeed modification of the male metatarsus I is a synapomorphy for Phyxelididae (Griswold *et al*., 2005). Such modifications comprise concavities lined with shortened, spinule-like setae (all phyxelidid tribes), swollen projections (most Vidoleini), or enlarged, curved spines (Vytfutiini and Phyxelidini). We have observed courtship and mating in four phyxelidid species: *Xevioso* sp. nov. (Vidoleini), *Phyxelida tanganensis* (Simon & Fage, 1922) and *P. bifoveata* (Strand, 1913), and *Ambohima andrefana* sp. nov. (Phyxelidini) and we report our observations on these species. Complete collection data are presented in the Appendix under the designations ‘mating vouchers’.

Xevioso sp. nov. (CASENT9017131)

Juvenile specimens were collected at Mariepskop, South Africa, in December 1996 and moulted to maturity in captivity in separate glass tubes. A virgin male and female were placed together in a large container in February 1997; the female remained in her web in the rearing tube. She hung beneath webbing built in this tube. After about 1 h of exploration the male

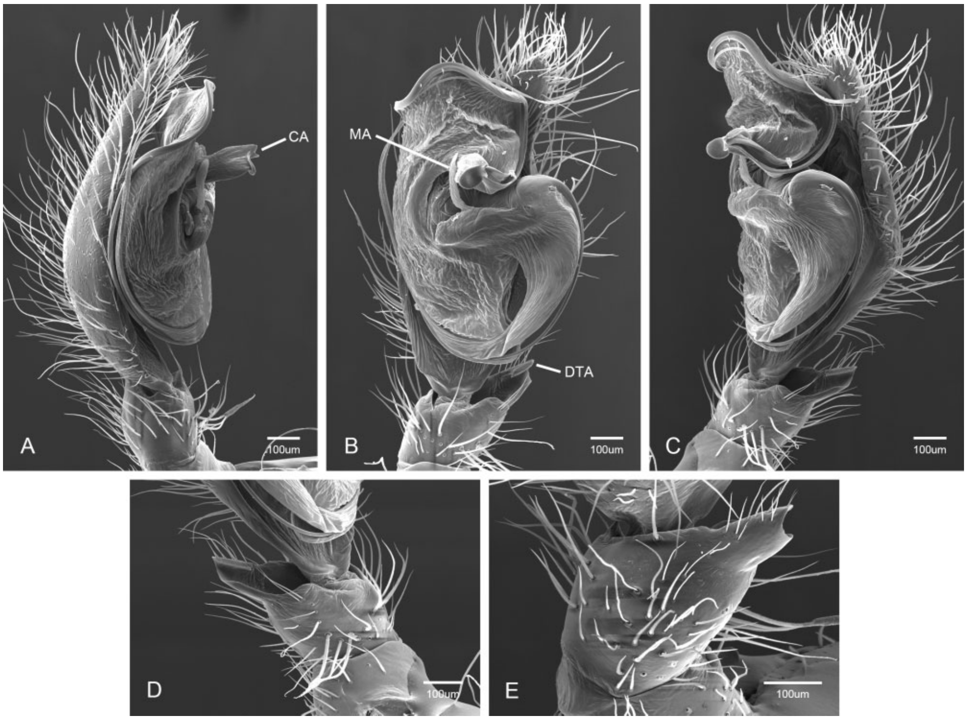

Figure 28. Right male palpus of *Rahavavy ida* from Talatakely (SEM images flipped to appear left), CASENT9003423. A, tibia and tarsus, prolateral. B, tibia and tarsus, ventral. C, tibia and tarsus, retrolateral. D, tibia, prolateral. E, tibia, dorsal. CA: conductor apex, DTA: dorsal tibial apophysis, MA: median apophysis.

entered the female's tube. The male probed the female's web and the female herself with his first legs; while probing his palps were held together and in front, and he simultaneously jerked these up and down. Copulation was observed once: the male braced the concavity and spur of his metatarsus I (similar to that depicted in Griswold, 1990: fig. 40a, b) against the retrolateral base of the coxa to femur of the female's palp or leg I (the male's legs I braced against different female limbs on different sides). The male inserted his palps alternately. The duration of the courtship and copulation was not recorded.

Phyxelida tanganensis (CASENT9017052)

Juvenile specimens were collected at Amani, Tanzania, in April 1995 and moulted to maturity in captivity. A virgin male and female were placed together in January 1996. Pre-contact behaviour was not recorded. After contact and prior to copulation the male and female hung beneath her sheet web and faced each other (Fig. 5). Legs II of the female were pushed to the side by legs II of the male and the male metatarsus I claspers grasped the female around the base of each femur II, near the trochanter–femur joint. During contact the female legs I were held together and extended across, i.e. under, the dorsum of the carapace and abdomen of the male. After the male and female legs were positioned, the male drummed on the female palps with his palps, both male palps drumming simultaneously. The male inserted his palps into the female epigynum alternatively; insertions lasted about 10 s each. The number of insertions and duration of copulation were not recorded.

Phyxelida bifoveata (CASENT9017047)

Juvenile specimens were collected at Mazumbai, Tanzania, in April 1995 and moulted to maturity in captivity. A virgin male and female were placed together in January 1996. Courtship and copulatory behavior was much as that recorded for *P. tanganensis*. After contact and prior to copulation the male and female hung beneath her sheet web and faced each other. Legs II of the female were pushed to the side by legs II of the male and the male metatarsus I claspers grasped the female around the base of each femur II, near the trochanter–femur joint. Female legs I were held dorsad of (under) the female's carapace by the male's crossed legs II. Like *P. tanganensis*, after the male and female legs were positioned, the male drummed on the female palps with his palps, both palps drumming simultaneously. The male inserted his palps into the female epigynum alternatively. The number of insertions and duration of copulation were not recorded.

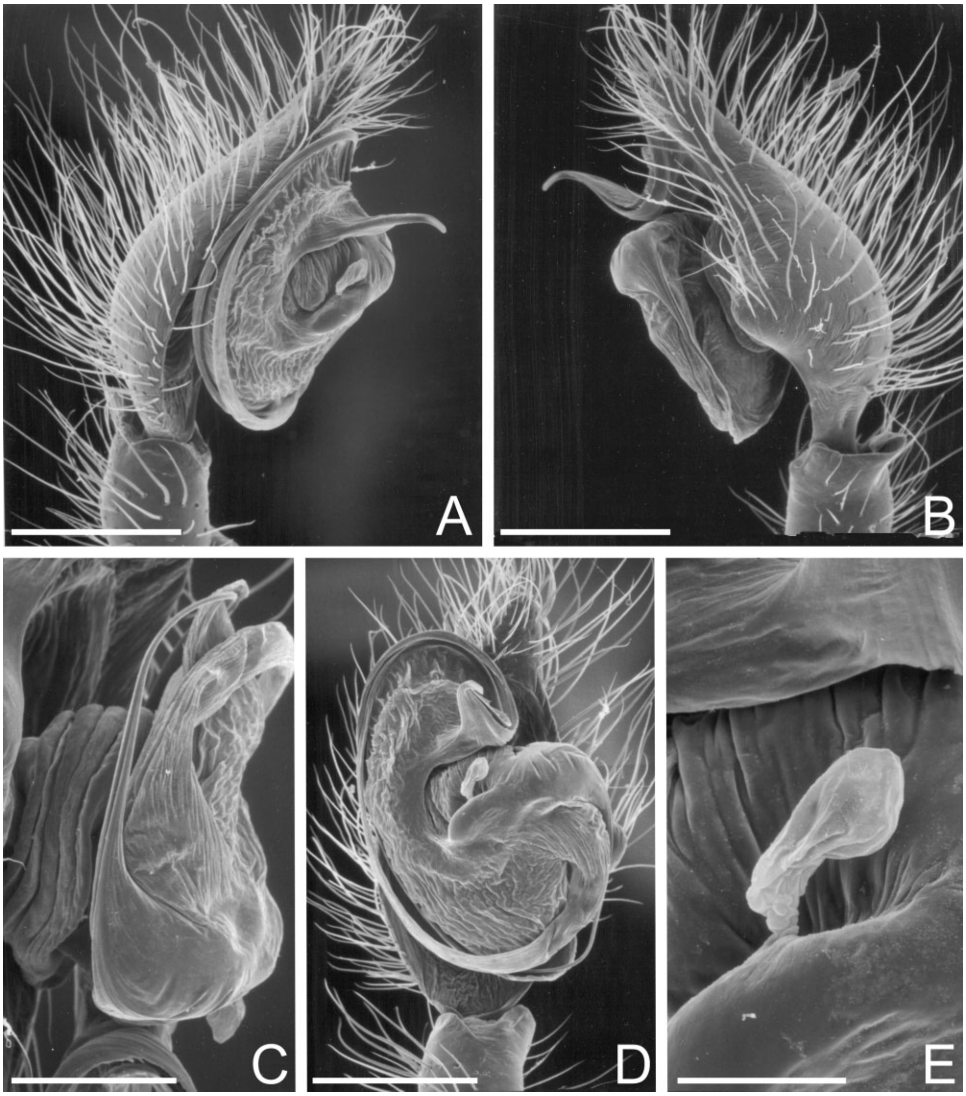

Figure 29. Right male palpus of *Rahavavy malagasyana* from Perinet (SEM images flipped to appear left), CASENT9016182. A, prolateral. B, retrolateral. C, prolateral, showing embolus and subtegulum. D, ventral. E, close up of MA, ventral. Scale bars: A, B, D = 300 μm, C = 120 μm, E = 60 μm.

Ambohima andrefana

Juvenile specimens were collected at Zombitse, Madagascar, in February 2003 and moulted to maturity in captivity. Four males (1, CASENT9005933; 2, CASEN T9005932; 3, CASENT9005931; 4, CASENT9005930) and five females (A, CASENT9019917; B, CASENT90 19920; C, CASENT9019919; D, CASENT9019918; E, CASENT9019994) were observed in five successful mating trials between May and August 2003. Virgin females were kept individually in plastic boxes (18 × 9 × 5 cm) and built webs beneath the lid of the container. Spiders hung beneath these webs, but for photography the lid, with web and spiders, was removed and inverted (Fig. 4A). In each mating trial a virgin male was introduced into a virgin female's container and web. All five successful matings were essentially the same. Precise counts or durations of activities were not recorded. The spiders hung beneath the female's web. Each male entered the female web, pulled at the silk with his palps, and, when facing the female, rapidly drummed or strummed the web with alternate movements of his palps. When face to face the female drummed the web with her palps in the same manner. Male–female contact involved a sudden spreading of the male's legs I and II (Fig. 4A). The male metatarsus II claspers grasped the female palps near the base of the palpal femur (Fig. 4C, D); simultaneously the female grasped one of the male's metatarsi I in her chelicerae (Fig. 4B, C). This bite was seen in all matings but no apparent damage to the male was

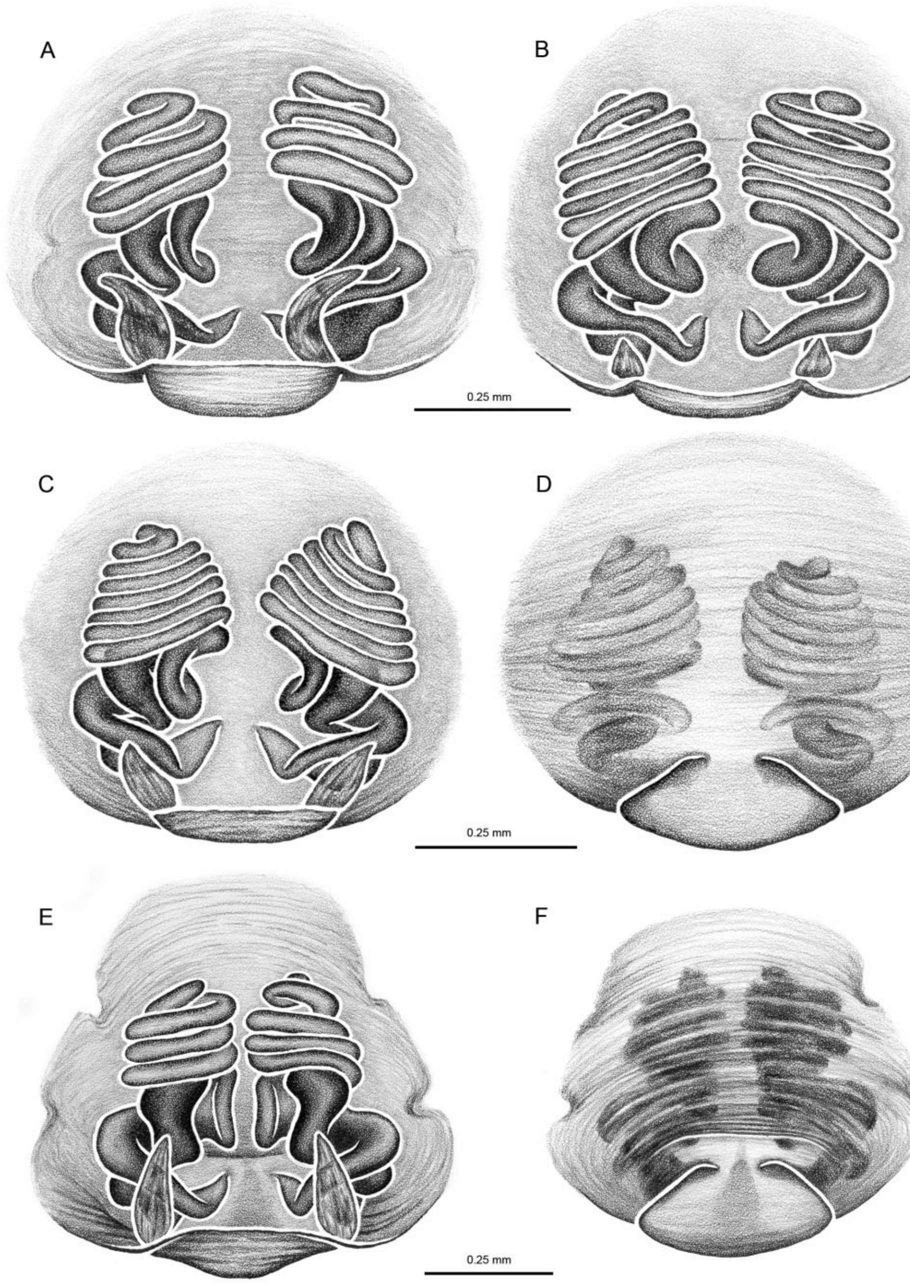

Figure 30. Female genitalia of *Ambohima sublima*. A–C, E, vulvae, dorsal. D, F, epigyna, ventral. A, Perinet, CASENT9016184. B, Ambohitantely, CASENT9016213. C, D, Ambohimanga, CASENT9016204. E, F, Ranomafana, CASENT9016193. Illustrations by JS.

observed. Male palps were inserted into the female epigynum alternately.

SUMMARY OF COURTSHIP AND MATING BEHAVIOUR

Common features of all phyxelidid matings observed are a grasping of the female's forelimbs (palps, leg II) near the base with male metatarsal claspers (Figs 4C, D, 5). The unique metatarsus I claspers functioned in this way in *Xevioso* and *Phyxelida*; remarkably, the metatarsus I claspers of male *Ambohima* did not grasp the female, only those of metatarsus II. Male metatarsi I of *Ambohima andrefana* were grasped by the female chelicerae (Fig. 4B, C): it will be interesting to learn if this biting behaviour is universal in *Ambohima*, all of which have claspers on male meta-

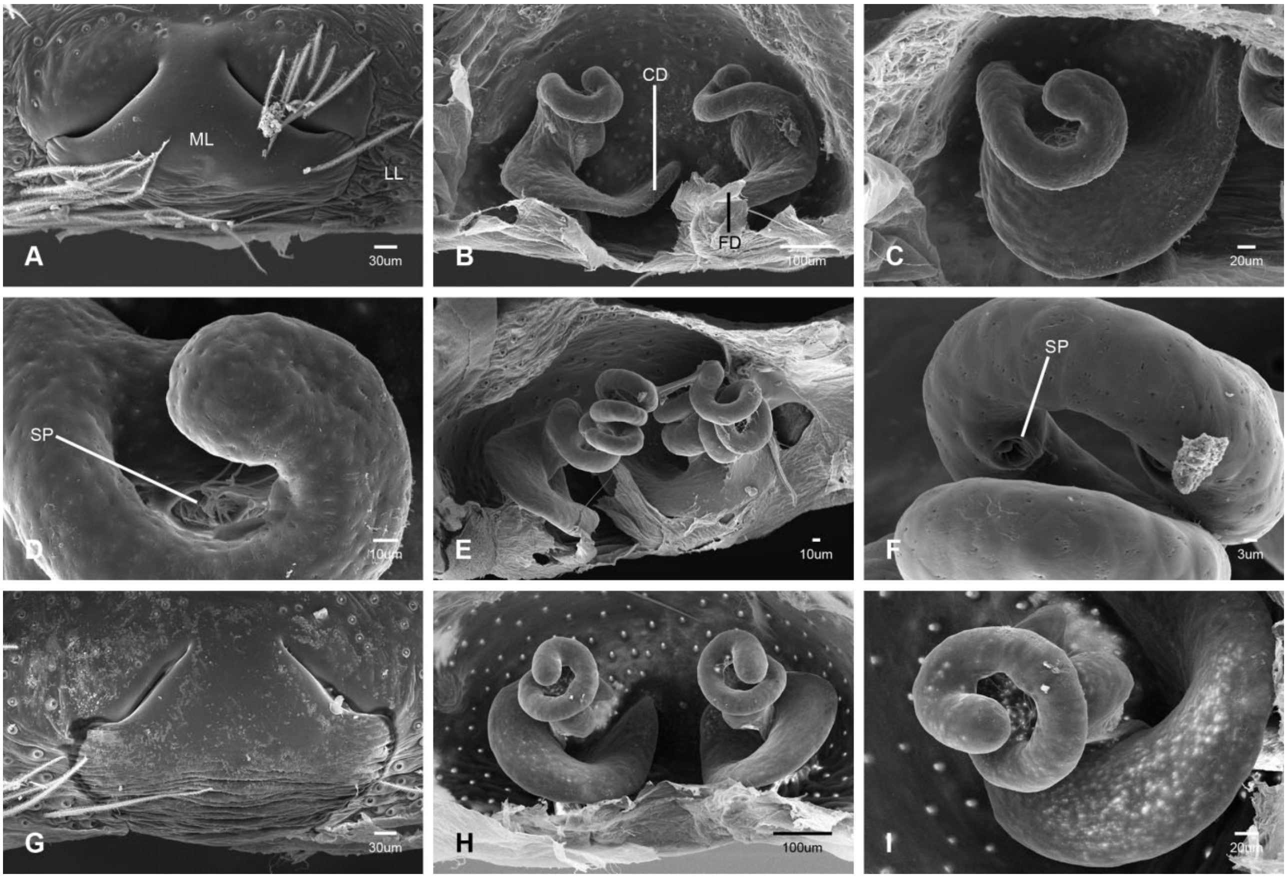

Figure 31. *Ambohima* female genitalia. A, G, epigyna, ventral. B–F, H, I, vulvae, dorsal. A–D, *A. ranohira*. E–I, *A. andrefana*. A–D, Ranohira, CASENT9019985. E, F, Analalava, CASENT9019978. G–I, Zombitse, CASENT9019919. CD: copulatory duct, FD: fertilization duct, LL: lateral lobe of epigynum, ML: median lobe of epigynum, SP: spermathecal poreplate.

tarsi I and II, and if this occurs in *Manampoka*, which also has claspers on male metatarsus II (and presumably metatarsus I). Rapid palpal drumming, vibration, or strumming was observed in all species, and in both *Ambohima* sexes simultaneously: this is suggestive of stridulation that may involve the thorn-like setae near the palpal femoral base (Fig. 46C). Vibratory courtship has not been recorded. Given the ease with which phyxelidids may be reared and maintained in captivity, investigation of vibratory courtship with laser vibrometry (e.g. Elias *et al*., 2003) would be very interesting.

TAXONOMY

PHYXELIDIDAE LEHTINEN 1967

Amaurobiidae Phyxelidinae Lehtinen 1967: 328. Griswold 1990.

Phyxelididae Lehtinen 1967. Elevated from subfamily of Amaurobiidae to family and placed as sister group of Titanoecidae by Griswold *et al*. 1999: 59. Discussion in Griswold *et al*. 2005: 35.

Diagnosis: Entelegyne, cribellate spiders with thorn-like setae located probasally on both female and male palpal femora (Figs 9F, 51D), a calamistrum that originates medially on the female metatarsus IV (Figs 46F, 51A), PMS paracribellar spigots that encircle the spinneret margin anteriorly and that are crowded together such that the bases are laterally flattened (Figs 52C, 54B) and male metatarsus I modified with clasping structures (Figs 1, 42–44).

Synapomorphies: Synapomorphies for the family implied by the phylogenetic analysis of Griswold *et al*. (2005) were thorn-like setae located probasally on both the female and male palpal femora, a calamistrum that originates medially on the female metatarsus IV, PMS paracribellar spigots that encircle the spinneret margin anteriorly and that are crowded

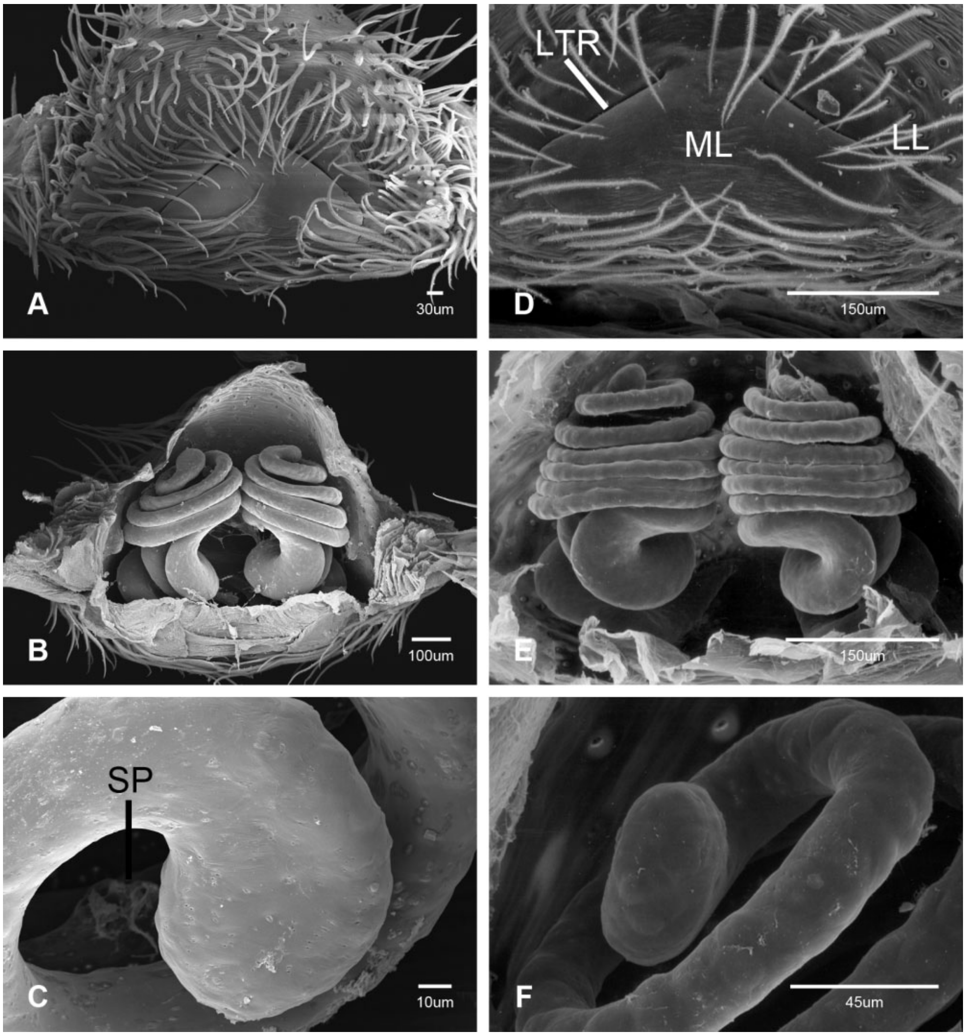

Figure 32. *Ambohima sublima* female genitalia. A–C, Talatakely, CASENT9024053. D–F, Ambohimanga, CASENT9020323. A, D, epigyna, ventral. B, E, vulvae, dorsal. C, F, close-up of spermathecae. LL: lateral lobe of epigynum, LTR: lateral transverse ridge along anterior margin of median lobe of epigynum, ML: median lobe of epigynum, SP: spermathecal poreplate.

together such that the bases are laterally flattened, and male metatarsus I modified with clasping structures. In this analysis (Griswold *et al*., 2005) further synapomorphies united the tribes Phyxelidini and Vidoleini: a bilaterally divided chilum (Figs 8D, 47B) and branched median tracheae. Other potential synapomorphies uniting Phyxelidini and Vidoleini include epiandrous spigots separated into two bunches (Figs 48D, E, 50A, D) and a conspicouous, enlarged, dark seta (Figs 47D, 55B, F) arising laterally from the tip of the PLS. This seta could not be scored for the *Vytfutia* specimens available for the 2005 paper; subsequent examination of new *Vytfutia* specimens revealed that it is lacking in Vytfutiini. These synapomorphies remain valid after the present study.

Description: Eight eyes in two nearly straight rows (Figs 1, 47A), canoe-shaped tapeta (Fig. 47B), chelicerae with a large boss (Fig. 50B), and with teeth and thickened setae along the fang furrow (Figs 49A, B, 50C), may be scaly or ridged cuticle laterally as possible stridulatory surface (Fig. 50B, E); cheliceral gland opens on flat cuticle (Figs 49F, 50F); chilum entire (Vytfutiini) or divided (Phyxelidini, Vidoleini) (Figs 8D, 47B); endite with apical serrula (Fig. 49C, E); labrum with flattened, anteriad pointing labral tongue, tongue apex free, deeply concave, with plumose setae dorsally and laterally on labrum, minute, bristle-like setae occur distad of tongue apex (Fig. 49D); sternum shield-shaped, posteriorly blunt to pointed, labium free (Fig. 47C); tarsal trichobothria

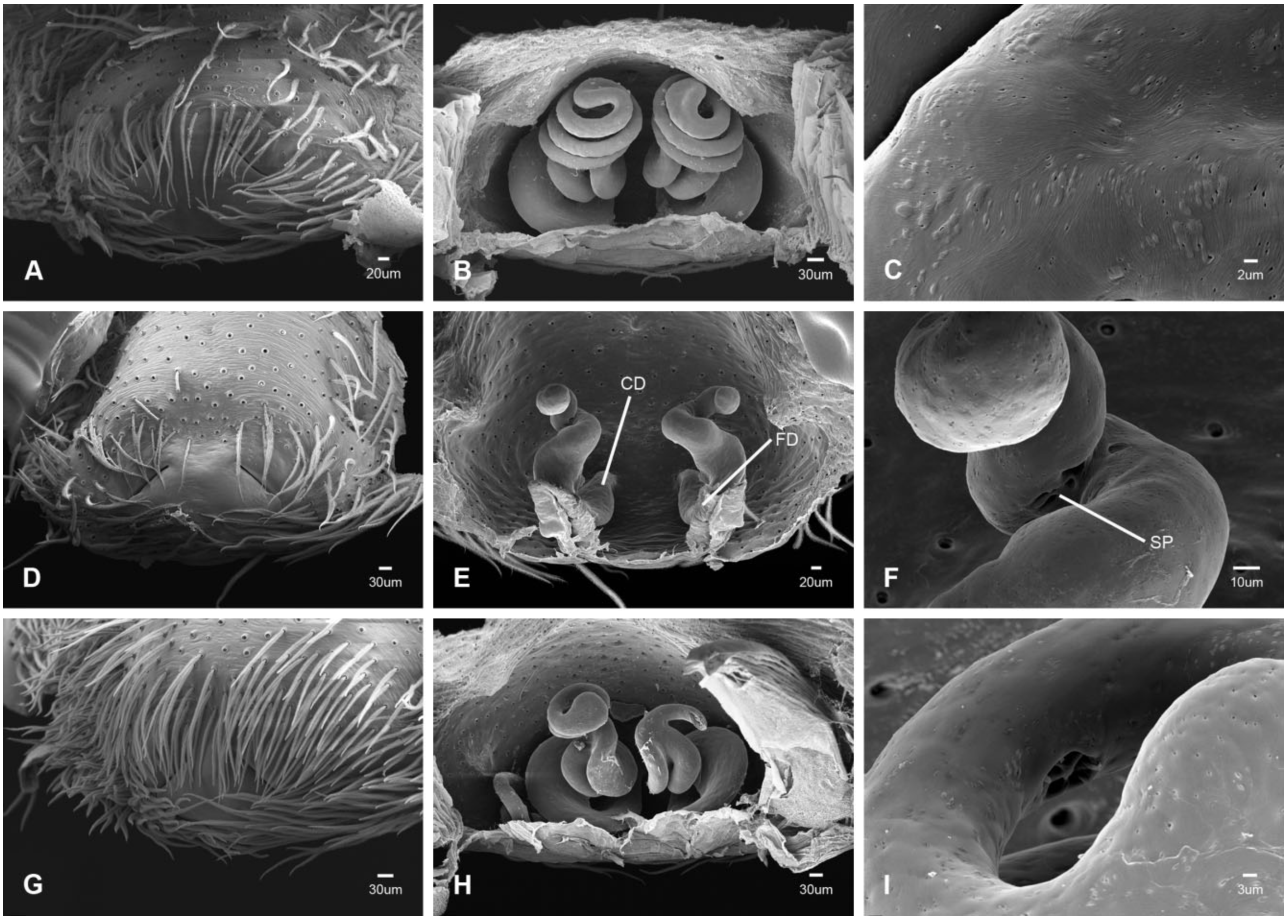

Figure 33. *Ambohima* female genitalia. A, D, G, epigyna, ventral. B, C, E, F, H, I, vulvae, dorsal. A–C, *A. vato*, Itremo, CASENT9005552. D–F, *A. zoky*, Montagne d'Ambre, CASENT9017016. G–I, *A. antsinanana*, Andringitra, CASENT9029887. CD: copulatory duct, FD: fertilization duct, SP: spermathecal poreplate.

absent, with only a single, subapical trichobothrium on metatarsi, multiple dorsal trichobothria on tibiae, trichobothria with transverse ridges (Fig. 51E); tarsal organ capsulate with round orifice (Figs 48F, 51G); setae plumose (Fig. 50F), rarely (*Malaika*) also with feathery scales; palpal femora of both sexes with probasal thorns comprising enlarged setal bases and/or thickened setae (Figs 46C, 48A, 51D); femora to metatarsi of legs with spines; trochanters shorter than coxae (Fig. 46A), trochanters unnotched (Fig. 46B, E), autospasy at coxa–trochanter joint; males of most species with metatarsus I modified (Figs 1, 42–44), median concavity typically retrolateral, prolateral in Malagasy taxa, only leg I modified in most genera, legs I and II modified in *Ambohima* (Fig. 1) and *Manampoka*; leg tarsi with three claws, STC with single row of teeth, ITC smooth or with a single tooth, serrate accessory setae, claw tufts and scopulae absent (Figs 48B, 51F); female palp with toothed claw (Figs 48C, 51C); metatarsi III and IV apical preening combs present (Vidoleini) or absent (Phyxelidini, Vytfutiini); calamistrum linear, originating near middle of metatarsus IV (Figs 46F, 51A), with multiple rows of teeth on calamistral setae (Fig. 51B); lateral tracheae simple, medians simple (Vytfutiini, some Phyxelidini) or with few to many branches (Phyxelidini, Vidoleini); pedicel with lorum transversely divided (Fig. 46D), epiandrous spigots grouped into two lateral bunches (Phyxelidini, Vidoleini) (Figs 48D, E, 50A, D) or absent (Vytfutiini); cribellum divided (Fig. 54D) with two fields of uniformly distributed strobilate cribellate spigots (Fig. 54C); female ALS with one (Vytfutiini) or two (Phxelidini and Vidoliini) MAP spigots and one large tartipore at the inner edge and field of more than 30 PI spigots with round base margins, these interspersed with tartipores (Figs 52B, 55A, D); male ALS similar except posterior MAP spigot replaced by nubbin (Figs 53B, 56B); female PMS with numerous (12–30) PC spigots encircling anterior margin (Figs 52C, 54E), PC spigot bases elongate, pressed together and flattened (Fig. 54B), each PC spigot surmounted by a single strobilate shaft, spigot cuticle ridged; one large mAP spigot with nubbin and tartipore posteriad to this, posteriorly several AC and 1–4 CY spigots (Figs 52C, 55C); male PMS with PC spigots replaced by encircling row of nubbins, with large median tartipore and nubbin that replaces mAP spigot (Figs 53C, 56F); female PLS with domed apical segment, with stout, curved seta apicolaterally (Fig. 55B, F) (Phxelidini and Vidoleini), absent from Vytfutiini; with apical MS spigot, MS flanking PC spigots present or absent, field of several AC and two or more mesal CY spigots (Figs 52D, 55E); males lack CY spigots, MS spigot replaced by large nubbin (Figs 53D, 56E); anal tubercle small, simple, with slender setae (Fig. 54F); male palpal tibia with dorsoapical process (DTA) (Figs 25E, 26D, 28B, E), sclerotized (Phyxelidini, Vytfutiini) or partly sclerotized and partly hyaline (Vidoleini), additional RTA present in *Vytfutia*, some taxa may have enlarged retrolateral lobes (RL) (Figs 24D, E, 25E, 26D) and/or prolateral processes (PTA) (Figs 24D, 25E, F); cymbium without processes, trichobothria or chemosensory scopulae (Figs 22B, 27B); male palpal bulbs diverse (Figs 21A–C, 26A–C, 27A–D), Vytfutiini and Phyxelidini with conductor (C) and median apophysis (MA), the latter lacking in *Ambohima*, Vidoleini with three to five conical tegular processes of dubious homology; female epigyna simple with median (ML) and lateral (LL) lobes, without teeth (Figs 26G, 31A, 32D), vulvae entelegyne, various, fertilization ducts (FD) posterior (Figs 31B, 33E, 35E, H); webs cribellate, may be substrate limited and radiate from retreat (Griswold *et al*., 2005: fig. 202A, B, E, F), or have aerial sheets (Fig. 2A), spiders walk on or hang beneath webs (Figs 2B, 5), cribellate silk carding type II form (carding leg braced with mobile leg IV), at least Phyxelidini wrap prey after bite with slow alternating movements of legs IV; cribellate band (studied in *Phyxelida*) entire, cribellar fibrils cylindrical with nodules, axial fibres and reserve warp present (Griswold *et al*., 2005: fig. 121A–C).

KEY TO PHYXELIDIDAE OF MADAGASCAR

1.	Males	2
	Females	13
2(1).	Leg 2 modified with metatarsal clasping structure	3
	Leg 2 unmodified (***Rahavavy* gen. nov.**)	11
3(2).	Palpal bulb lacking median apophysis (Fig. 10A–C); palpal tibia with prolateral hook (PTA) (Fig. 25E, F) (*Ambohima*)	4
	Palpal bulb with median apophysis (Fig. 17A–C); palpal tibia without prolateral processes (Fig. 26D, E)	***Manampoka atsimo* gen. nov., sp. nov.**
4(3).	Embolic base with a raised, distal cone (Figs 11B, 13B, 14B)	5
	Embolic base flat or convex (Figs 12B, 15B)	8
5(4).	Cymbium large, cymbium length/ carapace length > 0.90 (Figs 3B, 6E, G)	6
	Cymbium smaller, cymbium length/ carapace length < 0.80 (Fig. 6C)	7
6(5).	Abdomen dorsally uniform grey (Fig. 6G, I); femora lacking spines	***Ambohima maizina* sp. nov.**
	Abdomen with dorsal pattern, may be chevrons or herringbone (Figs 1, 3B, 6E); femora with spines	*Ambohima sublima* Griswold 1990. (part, Antananarivo and Toamasina Provinces)
7(5).	Legs elongate, length femur I greater than 3.0 times carapace length (Fig. 2B)	*Ambohima sublima* Griswold 1990. (part, Fianarantsoa Province)
	Legs shorter, length femur I less than 2.5 times carapace length (Fig. 6C)	***Ambohima vato* sp. nov.**
8(4).	Reservoir course across embolic base sinuate (Figs 10B, 16B)	9
	Reservoir course across embolic base nearly straight (Fig. 15B)	***Ambohima zandry* sp. nov.**
9(8).	Embolus base narrow, narrower than width of exposed conductor between embolic base and proximal turn of embolus (Fig. 10B); metatarsus I slender at base of clasping concavity (Fig. 42A–C)	10
	Embolus base broad, much broader than width of exposed conductor between embolic base and proximal turn of embolus (Fig. 12B); metatarsus I swollen and projecting dorsally at base of clasping concavity (Fig. 42J–L)	***Ambohima ranohira* sp. nov.**
10(9).	Embolus base narrower than embolic loop (Fig. 10B)	***Ambohima andrefana* sp. nov.**
	Embolus base width about equal to embolic loop (Fig. 16B)	***Ambohima zoky* sp. nov.**
11(2).	Conductor apex elongate, extending ventrad of bulb in lateral view (Figs 19B, C, 20A, C)	12
	Conductor apex short, not extending ventrad of bulb (Fig. 18B, C)	*Rahavavy fanivelona* (Griswold, 1990)

12(11). Conductor apex slender, tapering to a point (Fig. 20A, C)............*Rahavavy malagasyana* (Griswold, 1990)
Conductor apex truncate (Fig. 19B, C)............***Rahavavy ida* sp. nov.**
13(1). Lateral margins of epigynal median lobe nearly parallel (Figs 26G, 35D, G); spermathecal poreplate located near entrance of copulatory duct to spermatheca (Figs 26H, 35B, E, H)............14
Lateral margins of epigynal median lobe converging anteriorly (Figs 31A, G, 32A, D); spermathecal poreplate located near spermathecal apex (Figs 31D, 33F, 34H)............17
14(13). Epigynum as long as wide, copulatory openings conspicuous (Figs 26G, 35A)............15
Epigynum wider than long, copulatory openings inconspicuous (Fig. 35D, G)............16
15(14). Spermathecae with two anterior lobes (Fig. 35B, C), epigynum as in Figures 35A and 41C............*Rahavavy fanivelona* (Griswold, 1990)
Spermathecae with anterodorsal coil (Fig. 26H), epigynum as in Figure 26G............***Manampoka atsimo* gen. nov., sp. nov.**
16(15). Copulatory ducts with anterodorsal spiral with fewer than five poorly defined turns, copulatory openings widely spaced, epigynum median lobe wider than three times length, convex or with narrow transverse concavity (Figs 20D, E, 35G–I, 41E)............*Rahavavy malagasyana* (Griswold, 1990)
Copulatory ducts with anterodorsal spiral with more than six turns, epigynum median lobe width less than 2.5 times length, with deep transverse concavity, copulatory openings close together, inconspicuous ventrally, large openings hidden in deep, anteromedian depression, visible dorsally in cleared preparations (Figs 35D–F, 41A)............***Rahavavy ida* sp. nov.**
17(13). Spermathecal ducts spiralling around a central, longitudinal spiral chamber (Fig. 34B, G); poreplate at spermathecal apex (Fig. 34D, I)............18
Spermathecal ducts lacking such a central, longitudinal chamber, with or without a spiral (Fig. 31B, H); poreplate proximad of spermathecal apex (Figs 31F, 33F)............19
18(17). Spermathecal ducts make four or more spiral turns (Figs 34B, 38C, D); spider large, total length greater than 7.00; abdomen with dorsal herringbone pattern (Fig. 7E)............***Ambohima avaratra* sp. nov.**
Spermathecal ducts make three or fewer spiral turns (Figs 34G, 38E, F); spider small, total length less than 5.00; abdomen with markings obscure (Fig. 7F)............***Ambohima zandry* sp. nov.**
19(17). Apex of spermathecae with one or more spirals (Figs 32B, E, 39J–L)............20
Apex of spermathecae with a simple, median bend, lacking spirals (Figs 31B, 39D–F)............***Ambohima ranohira* sp. nov.**
20(19). Spermathecae anteriorly with three or more tight, transverse coils (Fig. 37D, F)............21
Spermathecae anteriorly with coils well separated, transverse or oblique (Fig. 37A, C, E)............22
21(20). Spermathecae anteriorly with three coils (Fig. 37D, F)............***Ambohima vato* sp. nov.**
Spermathecae anteriorly with four or more coils (Fig. 40C–I)............*Ambohima sublima* Griswold 1990
22(20). Spermathecal base with longitudinal, bilobed chamber (Fig. 37B, C)............23
Spermathecal base simple (Figs 37A, E, 39J–L)............24
23(22). Spermathecal coils close together, two or fewer (Fig. 37B)............***Ambohima antsinanana* sp. nov.**
Spermathecal coils separated, three or more (Fig. 37C)............*Ambohima pauliani* Griswold 1990
24(22). Spermathecal apex a tight corkscrew coil (Fig. 37A, E)............***Ambohima zoky* sp. nov.**
Spermathecal apex with 2–4 open coils (Fig. 39J–L)............***Ambohima andrefana* sp. nov.**

AMBOHIMA GRISWOLD 1990

Ambohima Griswold 1990: 126; Platnick 2011.

Type species: Ambohima sublima Griswold 1990, by original designation.

Diagnosis: Male palpal bulb (Figs 10A–B, 22A–D) lacking median apophysis, with conductor greatly hypertrophied, apex directed mesad, origin of embolus retrolateral, embolus concealed in conductor groove completely encircling bulb; male palpal tibia with unique, backwards-pointing prolateral hook (PTA) (Figs 24D, E, 25E, F); male metatarsi I (Fig. 42A–O) and II (Fig. 1) having prolateral, spinule-lined concavity at midsegment, at base of concavity a short, prolateral process surmounted by stout clasping spine. Epigynum with broad, oval posterior median lobe (ML), copulatory openings slit-like and converging anteromedially (Fig. 30D, F).

Synapomorphies: Synapomorphies for *Ambohima* include the loss of the male palpal median apophysis (Figs 10A–B, 22A–D) and the backwards-pointing prolateral hook (PTA) on male palpal tibia (Figs 24D, E, 25E, F), both unique in Phyxelididae; and epigynal copulatory openings that are slit-like and converging anteromedially (Fig. 30D, F) and spermathecae with an anterior straight or spiral blind-ending duct (Figs 31B, 33E).

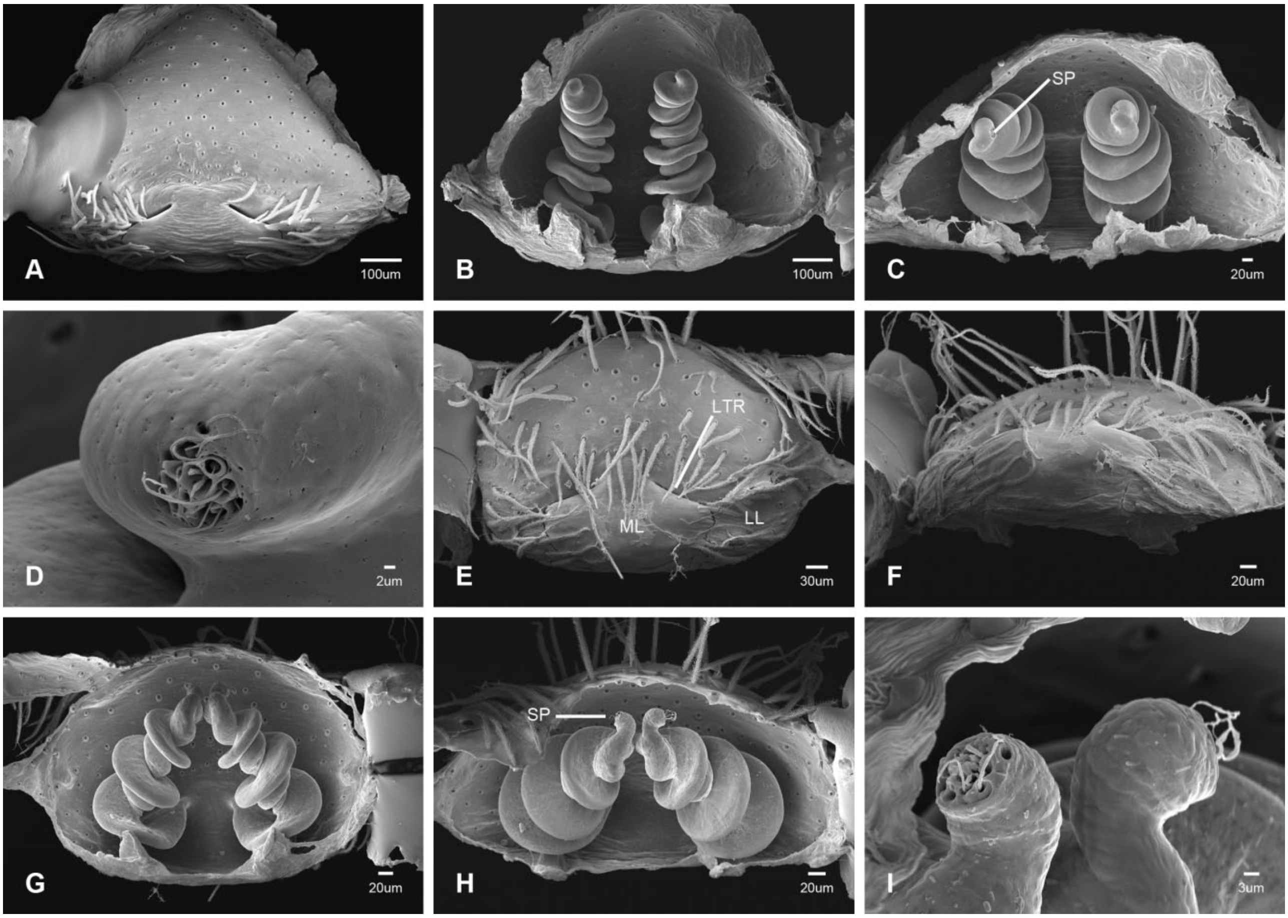

Figure 34. *Ambohima* female genitalia. A, E, epigyna, ventral. F, epigynum, posterior. B–D, G–I, vulvae, dorsal. A–D, *A. avaratra*, Montagne d'Ambre, CASENT9017012. E–I, *A. zandry*, Montagne d'Ambre, CASENT9017019. LL: lateral lobe of epigynum, LTR: lateral transverse ridge along anterior margin of median lobe of epigynum, ML: median lobe of epigynum, SP: spermathecal poreplate.

Description: Total length 3.70–10.90. Typical markings with carapace orange-brown, margin of pars thoracica dusky, with broad, dusky, V-shaped mark anteriad of thoracic fovea and dusky longitudinal band on each side extending anteriorly along pars cephalica, with dusky reticulations laterad of eyes; black pigment surrounding each eye and extending between AM and between lateral eyes (Fig. 6A–F); chelicerae, sternum, labium, coxae, legs, and palpi yellow-brown to orange-brown, sternum dusky, labium and palpal coxa lighter near tips (Fig. 47C), legs unmarked or with annulations (Figs 3A, B, 7B); abdomen grey-brown, dorsum with anterior light longitudinal markings that may comprise a herringbone pattern, chevrons, or a median band that is narrowed posteriorly with lateral extensions (Fig. 7A–H), dorsum unmarked in *A. maizina* sp. nov. (Fig. 6G), venter with pair of bold, entire, longitudinal light bands (Fig. 6H); differences from these markings are noted in species descriptions. Carapace length 1.15–1.48 times width, height 0.21–0.45 times width, thoracic fovea narrow oval, length 0.14–0.28 carapace length; PER straight to slightly recurved, AER straight, PER width 2.00–3.22 times OA length; clypeal height 1.23–5.51 times AM diameter; chelicerae smooth or with very weak wrinkles, length 4.06–8.00 times clypeal height, pro- and retromargins of fang furrow with 5–8 heterogeneous teeth (Fig. 49A, B); sternum length 1.10–2.53 times width, base narrowed, apex may be prolonged, pointed, a right angle, or blunt; labium broad, notched at base, length slightly greater than width (Fig. 47C). Legs long to elongate, femur I of females 1.18–2.72, of males 1.57–3.62 times carapace length, metatarsus I of males 1.38–3.77 times carapace length; leg formula 1423; male metatarsi I and II with prolateral, spinule-lined concavity at midsegment, at base of concavity a short, prolateral process surmounted by stout clasping spine (Fig. 1), legs otherwise unmodified; metatarsi lacking apical combs; calamistrum

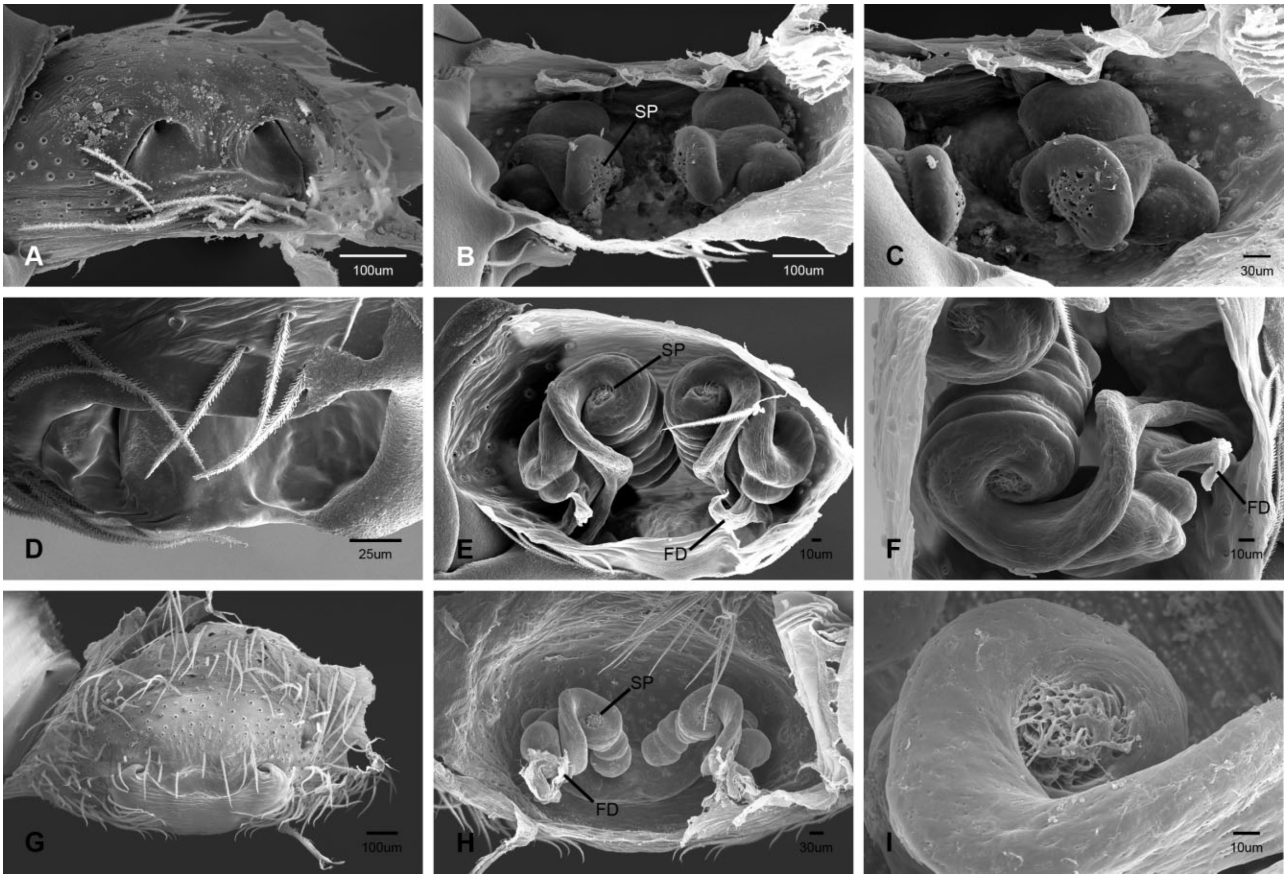

Figure 35. *Rahavavy* female genitalia. A, D, G, epigyna, ventral. B, C, E, F, H, I, vulvae, dorsal. A–C, *R. fanivelona*, Vohiparara, CASENT9016964. D–F, *R. ida*, Talatakely, CASENT9016990. G–I, *R. malagasyana*, Manjakatompo, CASENT9017011. FD: fertilization duct, SP: spermathecal poreplate.

subapical, origin at 0.40–0.50 distance from metatarsus base, length about one-third metatarsus length (Fig. 46F). Spination (based on *Ambohima sublima*: different species and even individuals within species exhibit small variations in the presence/absence and position of spines). Male: palp: femur d0-0-0-1; leg I: femur p0-1-1–1, r0-1-0-1, tibia p0-1-1-0, v1-0-1-0, r0-1-1-0, metatarsus p0-1(clasper)-0-1, v1-1-1-1, r0-1-0-1; leg II: femur d1-0-1-0, p0-1-1-1, r0-1-0-1, tibia p0-1-1-0, v0-0-0-1, r0-1-1-0, metatarsus p0-1(clasper)-0-1, v2-2-0-1, r0-1-0-1; leg III: femur p0-0-0-1, tibia d1-0-0-0, p0-1-1-0, v0-0-0-2, r0-1-1-0, metatarsus p0-1-0-2, v2-2-0-1, r0-1-0-2; leg IV: femur d1-0-0-0, p0-0-0-1, r0-0-0-1, tibia d1-0-0-0, p0-1-1-0, v0-0-0-2, r0-1-1-0, metatarsus v2-1-1-2. Female: palp: femur d0-0-0-1, patella d0-0-1, tibia d0-0-0-1, p0-1-1-0, tarsus p1-0-1-0, v0-0-1-2-1-2-3-2, r1-0-0-0-0; leg I: femur d1-0-0-0, p0-1-1-1, r0-0-1-1, tibia p0-1-1-0, v0-1-1-1, r0-1-1-0, metatarsus p0-1-0-1, v2-0-2-1, r0-1-0-1; leg II: femur d0-1-1-0, p0-1-1-1, r0-1-1-1-1, tibia p0-1-1-0, v0-1-0-2, r0-1-1-0, metatarsus p0-2-0-1, v2-2-0-1, r0-1-0-1; leg III: femur d1-0-1-0, p0-1-1-1, r0-1-0-1, tibia p0-1-1-0, v0-1-0-2, r0-1-1-0, metatarsus p0-1-0-2, v2-0-2-1, r0-1-0-2; leg IV: femur d1-1-0-0, p0-0-0-1, r0-0-0-1, tibia p0-1-1-0, v0-1-0-2, r0-1-1-0, metatarsus p0-1-0-1, v2-0-2-1, r0-0-0-1. Abdomen dorsal markings as in Figures 6A–G, 7C–H, typically with posterior chevrons dorsally although markings obscure to uniform in some species, venter with longitudinal bands narrow and entire. Tracheae (observed in penultimate male *Ambohima sublima*, CASENT9016997) with medians and laterals simple. Spinnerets (based on SEM examination of *Ambohima ranohira* and *A. sublima*): Female ALS (Fig. 52B) with two MAP spigots, the anterior largest, with large tartipore adjacent to these; PI spigot field of 30 to more than 80 spigots with rounded bases, interspersed with numerous small tartipores; male ALS (Fig. 53B) with posterior MAP spigot reduced to nubbin, but with comparable number of PI spigots as female; female PMS (Fig. 52C) with anteriorly encircling row of 15–25 PC spigots, these crowded together so that the bases are laterally flattened, centrally a large mAP spigot with a broad, squat base and conical

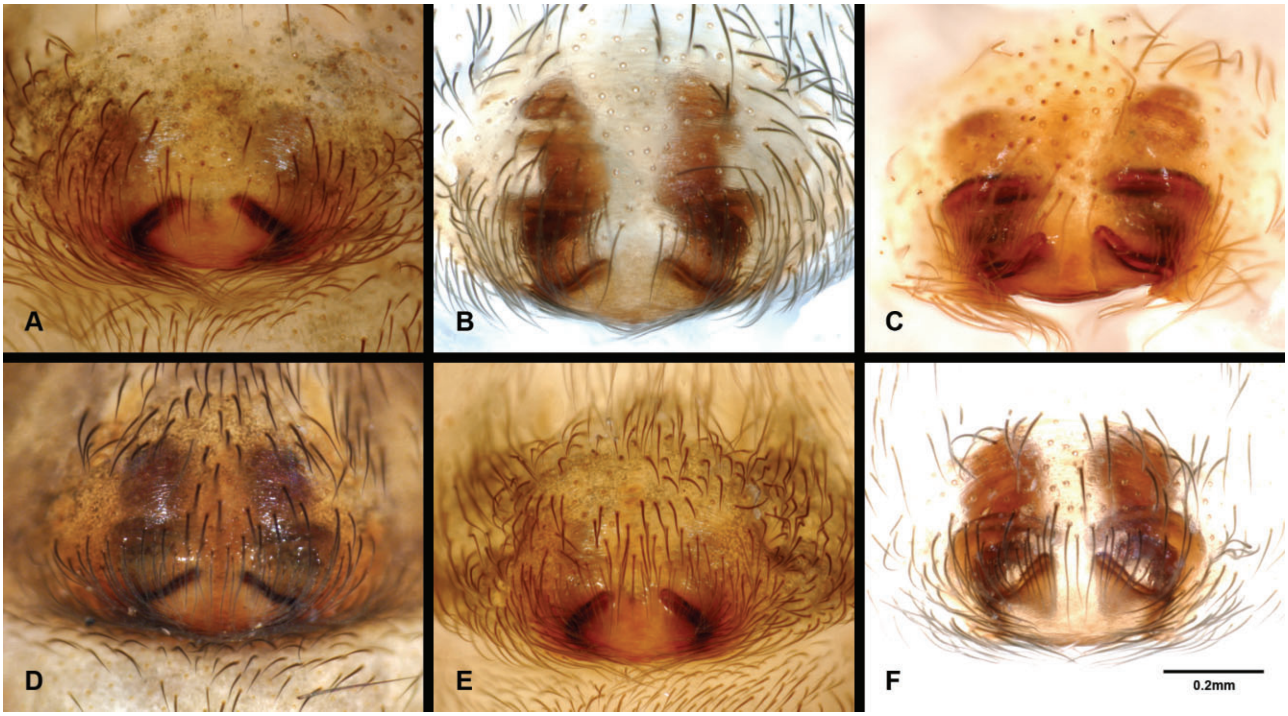

Figure 36. Epigyna of *Ambohima*, ventral view. A, *A. zoky*, Montagne d'Ambre, CASENT9020320. B, *A. antsinanana*, Andringitra, CASENT9029888. C, *A. pauliani*, holotype. D, *A. vato*, Itremo, CASENT9020002. E, *A. zoky*, Montagne d'Ambre, CASENT9017014. F, *A. vato*, Itremo, CASENT9005552. Scale bar applies to all images.

shaft, mesad and posteriad of this are 5–7 AC spigots, and posteriorly one CY spigot with a long, conical base and conical shaft; males (Fig. 53C) retain the AC spigots but lack the CY spigot, PC spigots are replaced by nubbins, and the central mAP spigot is replaced by a large nubbin; female PLS (Fig. 52D) with retroapical stout, curved seta (black in life), one subapical MS spigot with 1–2 flanking nubbins, a field of 12–20 AC spigots, and one basal and 1 anteromedian CY spigot; males (Fig. 53D) lack the CY spigots, have fewer AC spigots, and the MS spigot region is replaced by a huge nubbin. Palpal femur with anterobasal group of 3–8 setae set in enlarged bases, at least some distal setae shortened and enlarged as thorns, these setae forming a row or triangular group (Fig. 46C); male palpal tibia (Figs 24D, E, 25E, F) with a sclerotized dorsal blade-shaped process (DTA), a dorsally prolonged prolateral hook (PTA) and a prominent retrodorsal lobe (RL); cymbium narrowed for apical half; palpal bulb (Fig. 45C, D) with small, sclerotized petiole at base of subtegulum, this with 4–5 anneli, tegulum central, small relative to hypertrophied conductor, reservoir course a simple curve within tegulum, without switchbacks, median apophysis absent; embolus slender, a narrow tapering blade to a thread-like spine, lamellar pars pendula (PP) large (Figs 21B, C, 22A, C), readily detached from truncus of embolus (E), conductor (C) greatly hypertrophied, with embolic groove completely encircling bulb, apex (CA) directed mesad (Fig. 23B). Epigynum (Figs 31A, 32D, 34E) with broad, oval to trapezoidal ML, copulatory openings slit-like or hidden beneath recurved lateral transverse ridges (LTR); spermathecae with an anterior straight or spiral blind-ending duct, fertilization duct posterior (Figs 31B, 33E).

Composition: Ten species.

Distribution: Madagascar (Figs 57–59)

AMBOHIMA ANDREFANA SP. NOV. (FIGS 4A–D, 6A, B, 10A–C, 21A–E, 31E–I, 39G–L, 42A–C, 46C, 57)

Types: Holotype male (CASENT9005932) and paratype female (CASENT9019919) collected in dry forest on sandy soil at an elevation of 770 m at Parc National Zombitse, 19.8 km 84° E Sakaraha, 22°50′36″S, 44°42′36″E, Toliara Province, Madagascar, 5–9 February 2003, by C. Griswold, D. Silva, and J. J. Rafonomezantsoa, deposited in CASC.

Etymology: The specific name is from the Malagasy word for west; a noun in apposition.

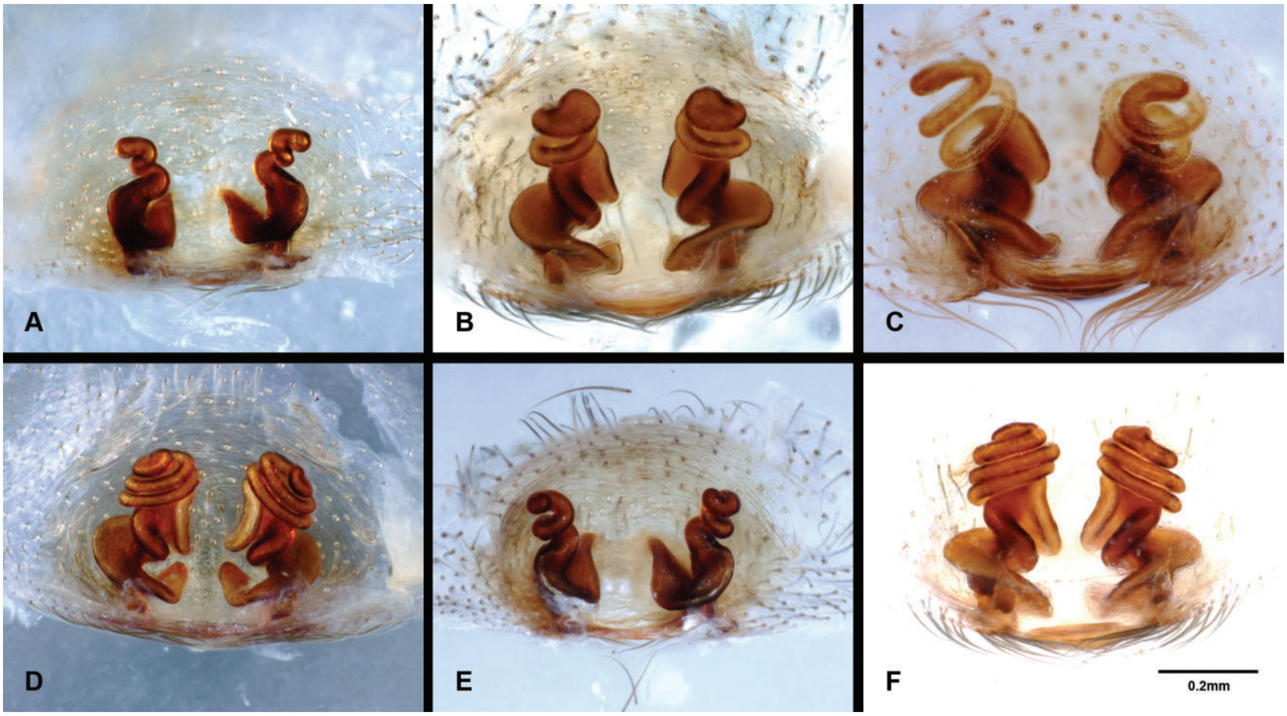

Figure 37. Vulvae of *Ambohima*, dorsal view. A, *A. zoky*, Montagne d'Ambre, CASENT9020320. B, *A. antsinanana*, Andringitra, CASENT9029888. C, *A. pauliani*, holotype. D, *A. vato*, Itremo, CASENT9020002. E, *A. zoky*, Montagne d'Ambre, CASENT9017015. F, *A. vato*, Itremo, CASENT9005552. Scale bar applies to all images.

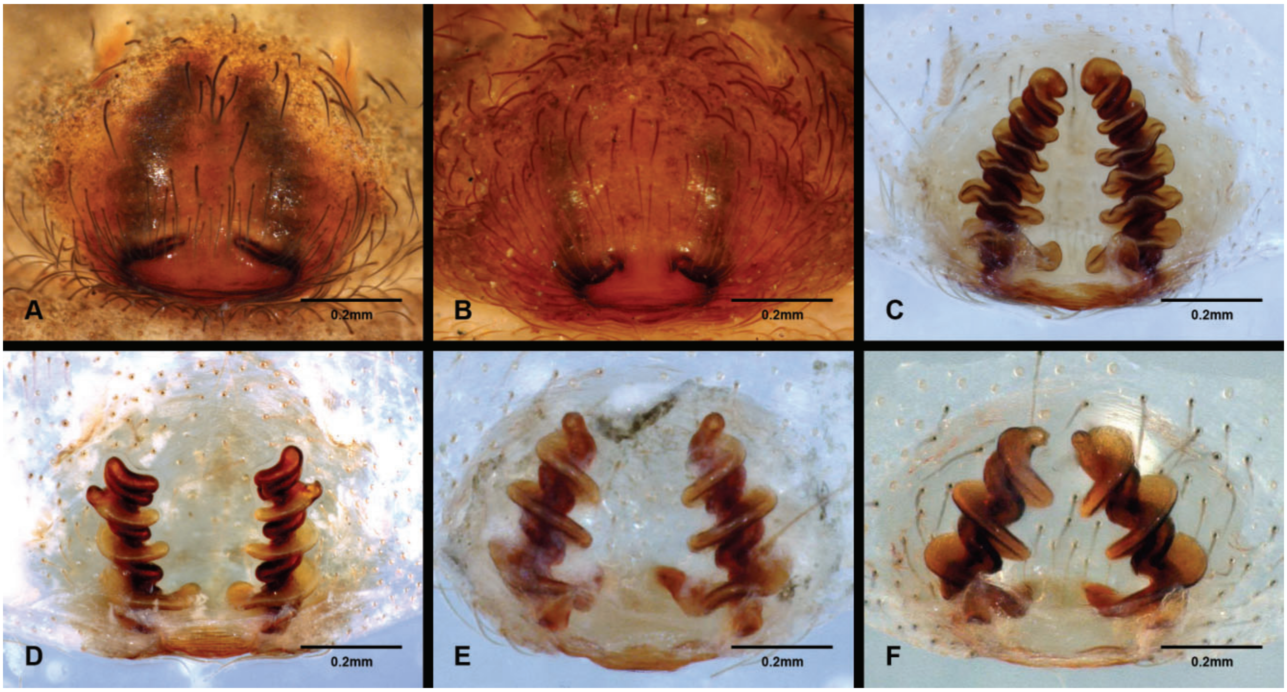

Figure 38. *Ambohima* female genitalia. A, B, epigyna, ventral. C–F, vulvae, dorsal. A–D, *A. avaratra*. A, C, Montagne d'Ambre, CASENT9003544. B, D, Rousettes, CASENT9017013. E, F, *A. zandry*, Montagne d'Ambre. E, CASENT9017021. F, CASENT9003543.

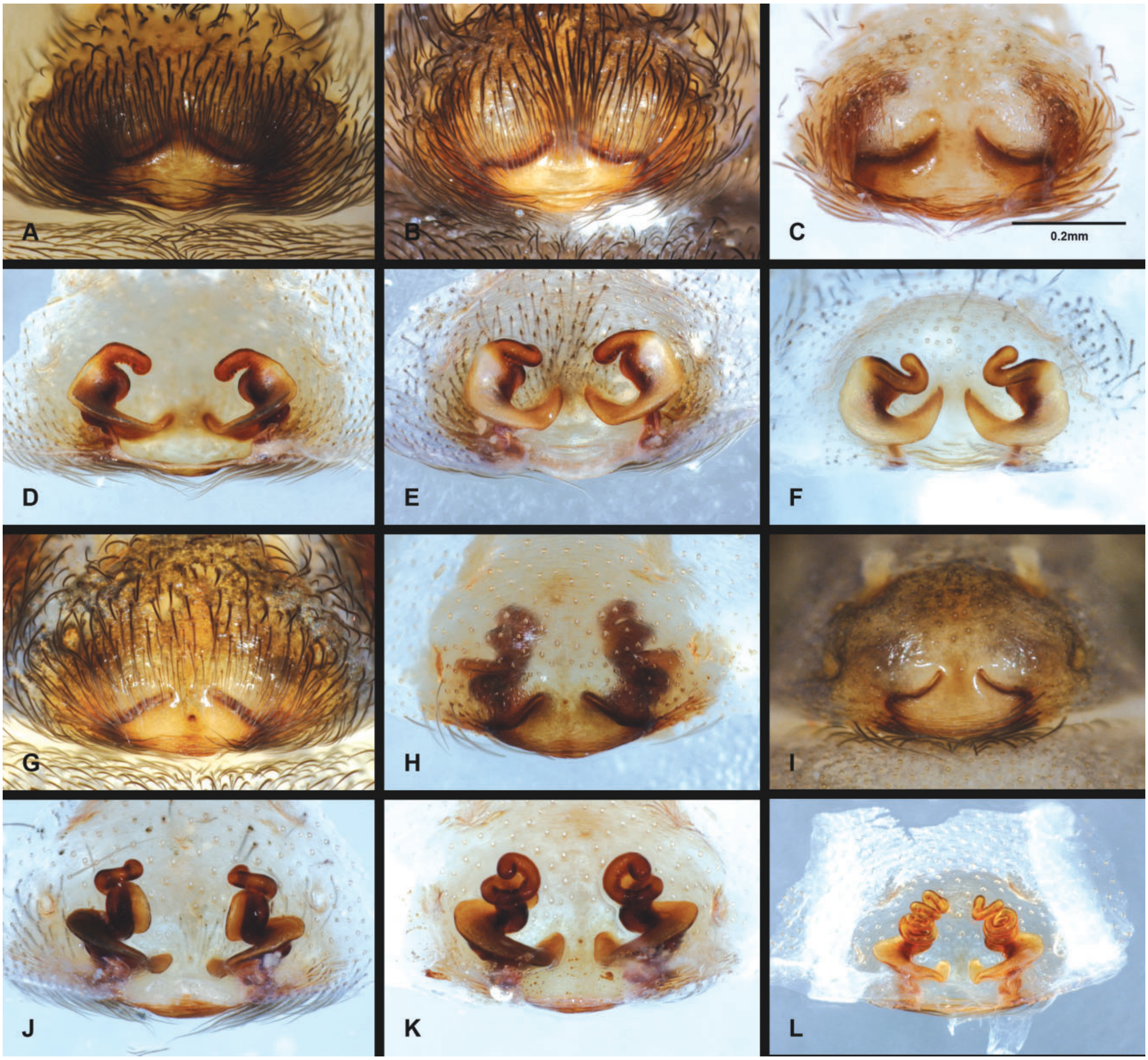

Figure 39. *Ambohima* female genitalia. A–F, *A. ranohira*. G–L, *A. andrefana*. A–C, G–I, epigyna, ventral. D–F, J–L, vulvae, dorsal. A, D, Ranohira, CASENT9005788. B, E, Analalava, CASENT9019989. C, Ambalavao, CASENT9025741. F, Analalava, CASENT9019985. G, J, Zombitse, CASENT9019920. H, K, Zombitse, CASENT9019919. I, L, Analavelona, CASENT9019978.

Diagnosis: Male with palp as in Figures 10A–C and 21A–F, embolic base convex to nearly flat, narrow, narrower than width of exposed conductor between embolic base and proximal turn of embolus and narrower than embolic loop, reservoir course across embolic base sinuate. Female vulva as in Figures 31E–I and 39G–L, spermathecal base simple, apex with 2–4 open coils.

Male (Holotype): Total length 8.00. Markings similar to Figure 6A, B. Carapace 3.90 long, 3.15 wide; thoracic fovea 1.05 long, length 0.27 times carapace length; clypeus 0.26 high; ocular area 0.45 long, 0.96 wide; ratio of eyes AM/AL/PM/PL, 1.13:2.67:1.0:1.13, diameter of PM 0.15. Chelicerae 1.30 long, slender, smooth, promargin of fang furrow with seven teeth, retromargin with six teeth. Sternum 2.08 long, 1.68 wide; labium 0.68 long, 0.60 wide; palpal coxa 1.16 long, 0.56 wide. Legs elongate, femur I length 1.89 times carapace length; metatarsi I and II prolateral concavity and clasping spines as in Figure 42A–F, segment slightly swollen basad of concavity. Leg

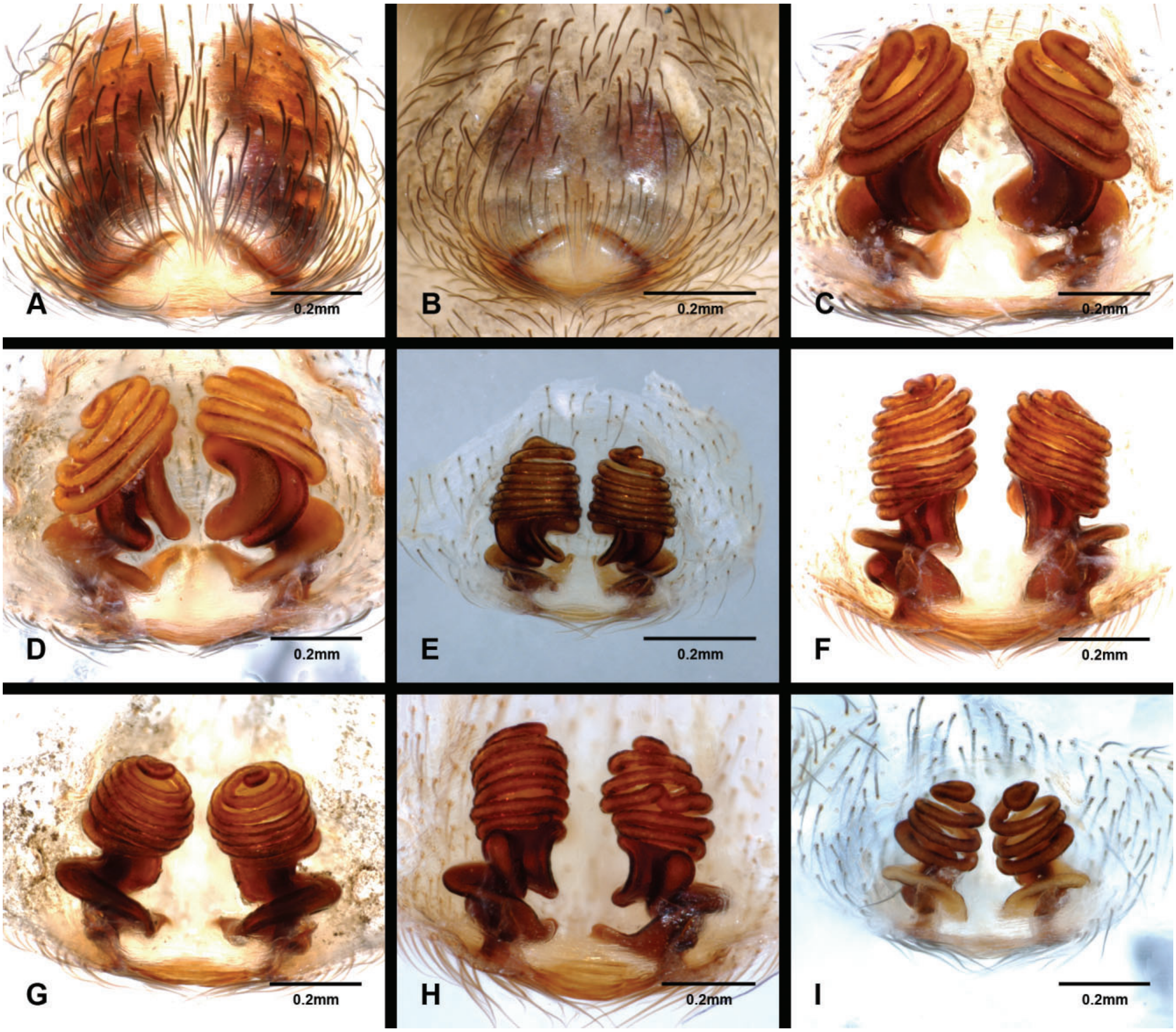

Figure 40. *Ambohima sublima* female genitalia. A, B, epigyna, ventral. C–I, vulvae, dorsal. A, C, Talatakely, CASENT9024053. B, Anjozorobe, CASENT9019990. D, Talatakely, CASENT9024052. E, Anjozorobe, CASENT9019991. F, Ambohitantely, CASENT9015040. G, Ambohijanihary, CASENT9018170. H, Angavokely, CASENT9016209. I, Mitsinjo, CASENT9036009.

measurements (femur + patella + tibia + metatarsus + tarsus = [total]: I: 7.40 + 2.00 + 7.70 + 7.60 + 2.60 = [27.30]; II: 6.50 + 1.65 + 6.30 + 6.00 + 2.10 = [22.55]; III: 5.50 + 1.40 + 4.65 + 4.95 + 2.00 = [18.50]; IV: 7.00 + 1.50 + 6.55 + 7.15 + 2.35 = [24.55]; palp: 2.05 + 0.80 + 0.85 + (absent) + 1.75 = [5.45]. Palpal femur with probasal row of three thorn-like setae; tibia with dorsal blade (DTA) short, hatchet-shaped, prolateral hook (PTA) short, stout (Fig. 21D, F); cymbium length 0.45 times carapace length; palpal bulb as in Figures 10A–C and 21A–F, length 1.45 times width, embolic base convex, narrow, narrower than width of exposed conductor between embolic base and proximal turn of embolus and narrower than embolic loop, reservoir course across embolic base sinuate.

Variation (N = 6): Total length 5.25–8.00, specimens from Analavelona are smaller, less than 6 mm total length, whereas those from Zombitse are greater than 7 mm; carapace length 1.21–1.27 times width, height 0.25–0.31 times width; PER width 2.13–2.60 times OAL; OQP 1.13–1.30 times OQA; clypeal height 1.71–3.80 times AM diameter; cheliceral length 4.06–6.00 times clypeal height; sternum length 1.20–1.27 times width; femur I length 1.85–2.11 times carapace length; metatarsus I length 1.86–2.20 times carapace

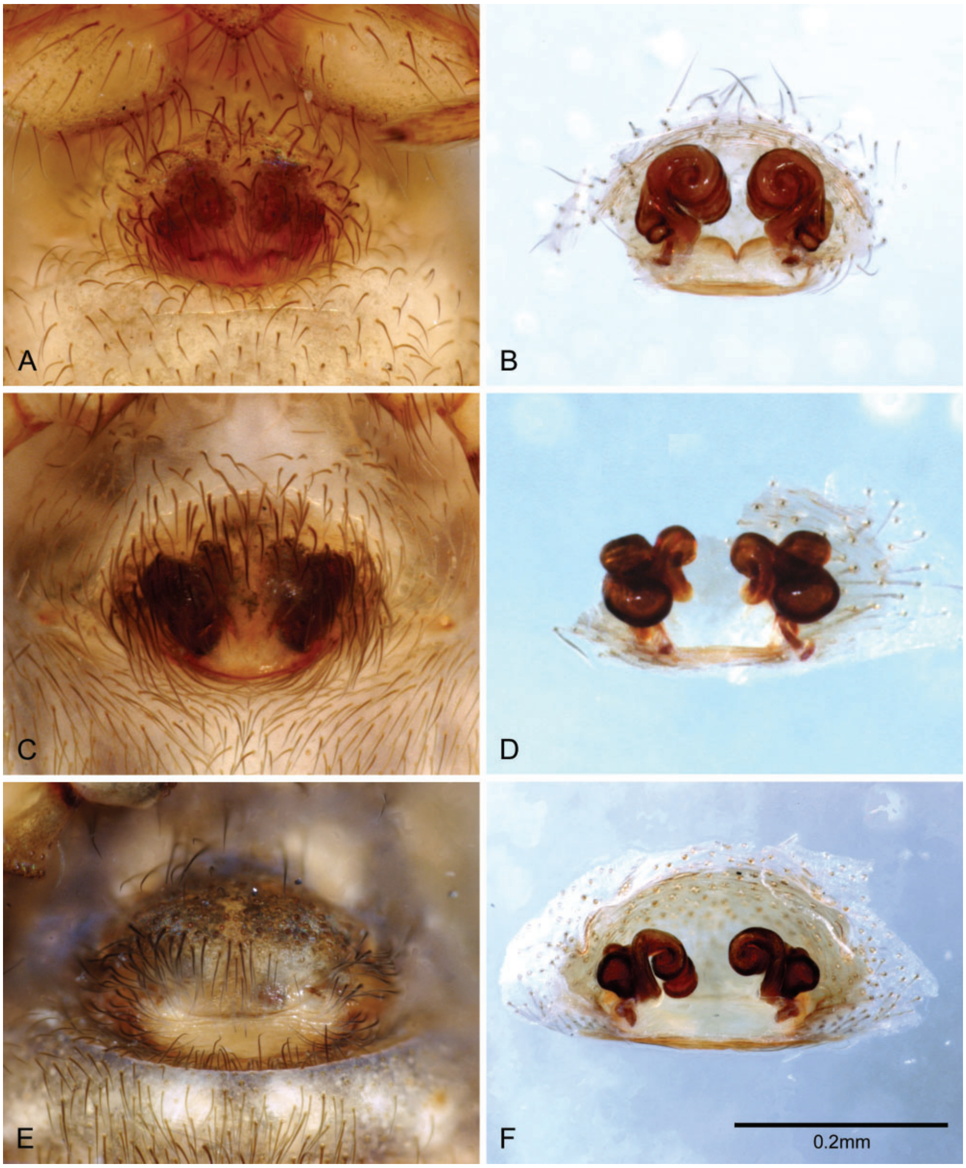

Figure 41. Female genitalia of *Rahavavy* species. A, B, *R. ida* from Talatakely, CASENT9016195. C, D, *R. fanivelona* from Vohiparara. C, epigynum, ventral, CASENT9016237. D, vulva, dorsal, CASENT9016238. E, F, *R. malagasyana* from Manjakatompo, CASENT9005753. A, C, E, epigynum, ventral. B, D, F, vulva, dorsal.

length; cymbium length 0.45–0.50 times carapace length; the metatarsus shape basad of the clasper concavity may be nearly cylindrical (Analavelona and some Zombitse, Fig. 42A–C) to slightly swollen (some Zombitse, Fig. 42D–F).

Female (Paratype): Total length 9.80. Markings similar to Figure 4A. Carapace 3.95 long, 3.00 wide; thoracic fovea length 0.18 times carapace length; clypeus 0.34 high; ocular area 0.43 long, 1.20 wide; ratio of eyes AM/AL/PM/PL, 1.13:2.93:1.06:1.00, diameter of PM 0.15. Chelicerae 1.50 long, robust, smooth, promargin of fang furrow with six teeth, retromargin with seven teeth. Sternum 2.20 long, 1.60 wide; labium 0.74 long, 1.60 wide; palpal coxa 1.22 long, 0.56 wide. Femur I length 1.40 times carapace length. Palpal femur with three anterobasal thorns. Calamistrum origin at 0.40 from metatarsus base, length 0.35 that of segment. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [total]) I: 5.55 + 1.35 + 5.25 + 5.00 + 2.15 = [19.30]; II: 4.59 + 1.55 + 3.80 + 3.65 + 1.80 = [15.30]; III: 3.90 + 1.30 + 3.00 + 3.00 + 1.50 = [12.70]; IV: 4.80 + 1.45 + 4.25 + 4.30 + 1.75 = [16.55]; palp: 1.65 + 0.60 + 0.80 +

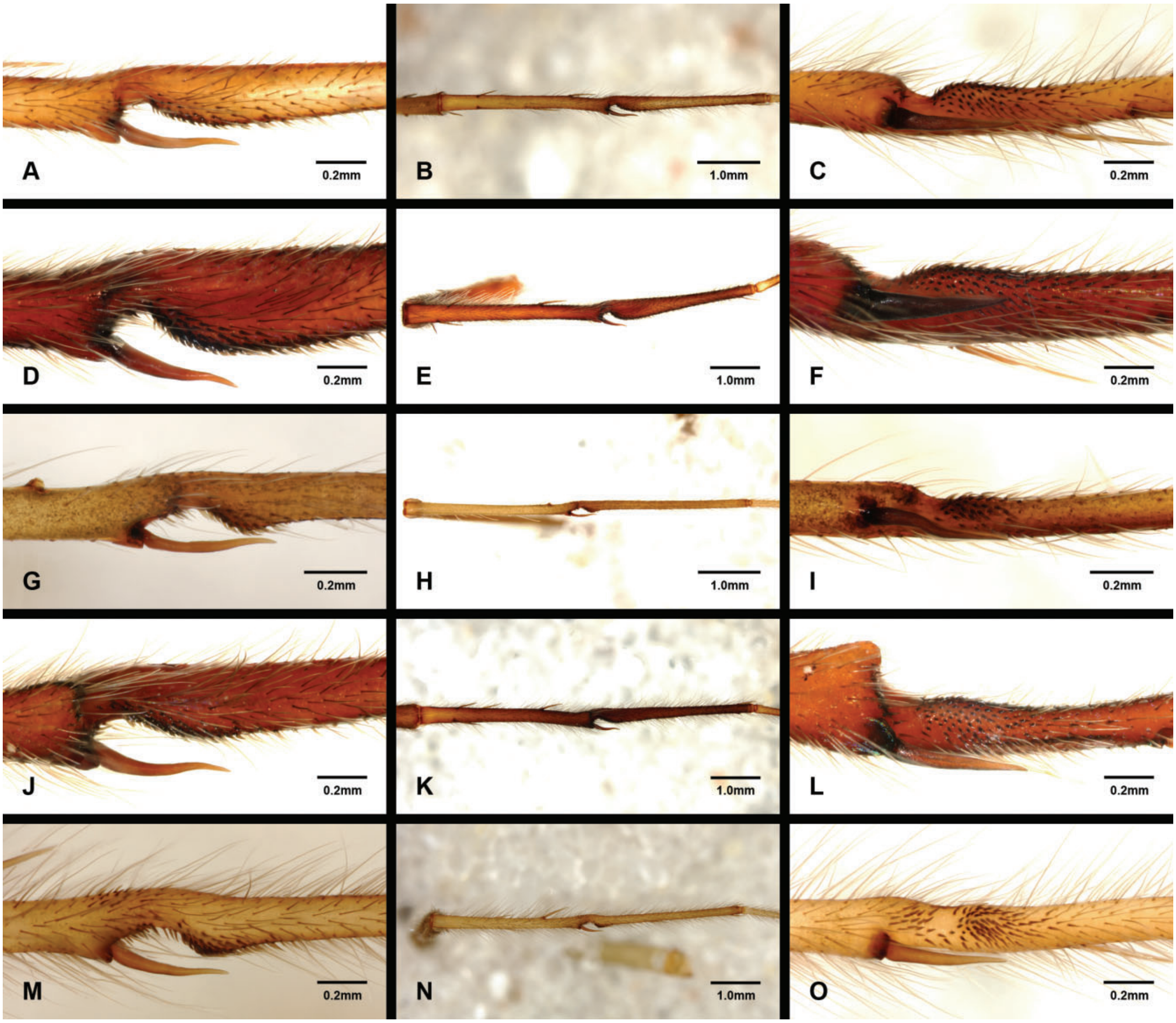

Figure 42. *Ambohima* male leg I metatarsal claspers, left. A, D, G, J, M, clasper close up, dorsal. B, E, H, K, N, metatarsus, dorsal. C, F, I, L, O, clasper close up, prolateral. A–C, *A. andrefana*, Analavelona, CASENT9018656. D–F, *A. andrefana*, Zombitse, CASENT9005930. G–I, *A. maizina*, holotype, CASENT9016206. J–L, *A. ranohira*, Ranohira, CASENT9005788. M–O, *A. sublima*, Ambohimanga, CASENT9016227.

(absent) + 1.90 = [4.95]. Epigynum as in Figure 39H; vulva as in Figure 39K, spermathecal apex with two open coils.

Variation (N = 9): Total length 4.00–10.50, specimens from Analavelona are smaller, less than 8 mm total length, whereas those from Zombitse are greater than 8 mm; carapace length 1.28–1.40 times width, height 0.24–0.41 times width; PER width 2.25–2.95 times OAL; OQP 1.14–1.30 times OQA; clypeal height 1.88–5.51 times AM diameter; cheliceral length 4.10–6.33 times clypeal height; retromargin of fang furrow with 6–7 teeth; sternum length 1.11–1.38 times width; femur I length 1.28–1.41 times carapace length; metatarsus I 1.03–1.27 times carapace length. The vulvae of Zombitse specimens are simple with two open coils (Figs 31H, I, 39J, K), whereas those from Analavelona may have as many as four apical open coils (Fig. 39L).

Natural history: Spiders were collected in tropical dry forest (Zombitse), where they made sheet webs beneath fallen logs, and in montane forest (Analavelona). At Zombitse females were mature in the field during early February, but males were still juveniles and were reared to maturity in captivity. Mating

Figure 43. *Ambohima* male leg I metatarsal claspers, left. A, D, G, J, M, clasper close up, dorsal. B, E, H, K, N, metatarsus, dorsal. C, F, I, L, O, clasper close up, prolateral. A–C, *A. sublima*, Andranomay, CASENT9004080. D–F, *A. sublima*, Talatakely, CASENT9016994. G–I, *A. vato*, Itremo, CASENT9005809. J–L, *A. zandry*, Montagne d'Ambre, CASENT9003543. M–O, *A. zoky*, Antsiranana, CASENT9017018.

behaviour was observed several times (Fig. 4A–D). See section on Mating behaviour.

Distribution: Known from south-western Madagascar (Fig. 57).

Material examined: MADAGASCAR: **Toliara Prov.** Parc National Zombitse, 19.8 km 84° E Sakaraha, 22°50′36″S, 44°42′36″E, elev. 770 m, general collecting in dry forest on sandy soil, 5–9 February 2003, C. Griswold, D. Silva, and J. J. Rafonomezantsoa, holotype, 1 ♂, CASC (CASENT9005932), paratype, 1 ♀ (CASENT9019919), 1 ♂, 4 ♀, CASC (CASENT9019917, 9019918, 9019920, 9019994, 9005930); Forêt Classée d'Analavelona, 29.2 km 343° NNW Mahaboboka, 22°40′30″S, 44°11′24″E, elev. 1100 m, montane rainforest, 18–22 February 2003, Fisher-Griswold Arthropod Team, general collecting, 1 ♂, 1 ♀, CASC (CASENT9018656), yellow pan trap, 1 ♂, CASC (CASENT9020321), pitfall trap, 2 ♀, CASC (CASENT9019978, 9018640), sifted litter of leaf mould and rotten wood, 4 ♀, CASC (CASENT9019974, 9019975, 9019976, 9019977); Forêt Classée d'Analavelona, 29.2 km 343° NNW Mahaboboka, 22°40′30″S, 44°11′12″E, elev. 1050 m, montane rainforest, 21 February 2003, Fisher-

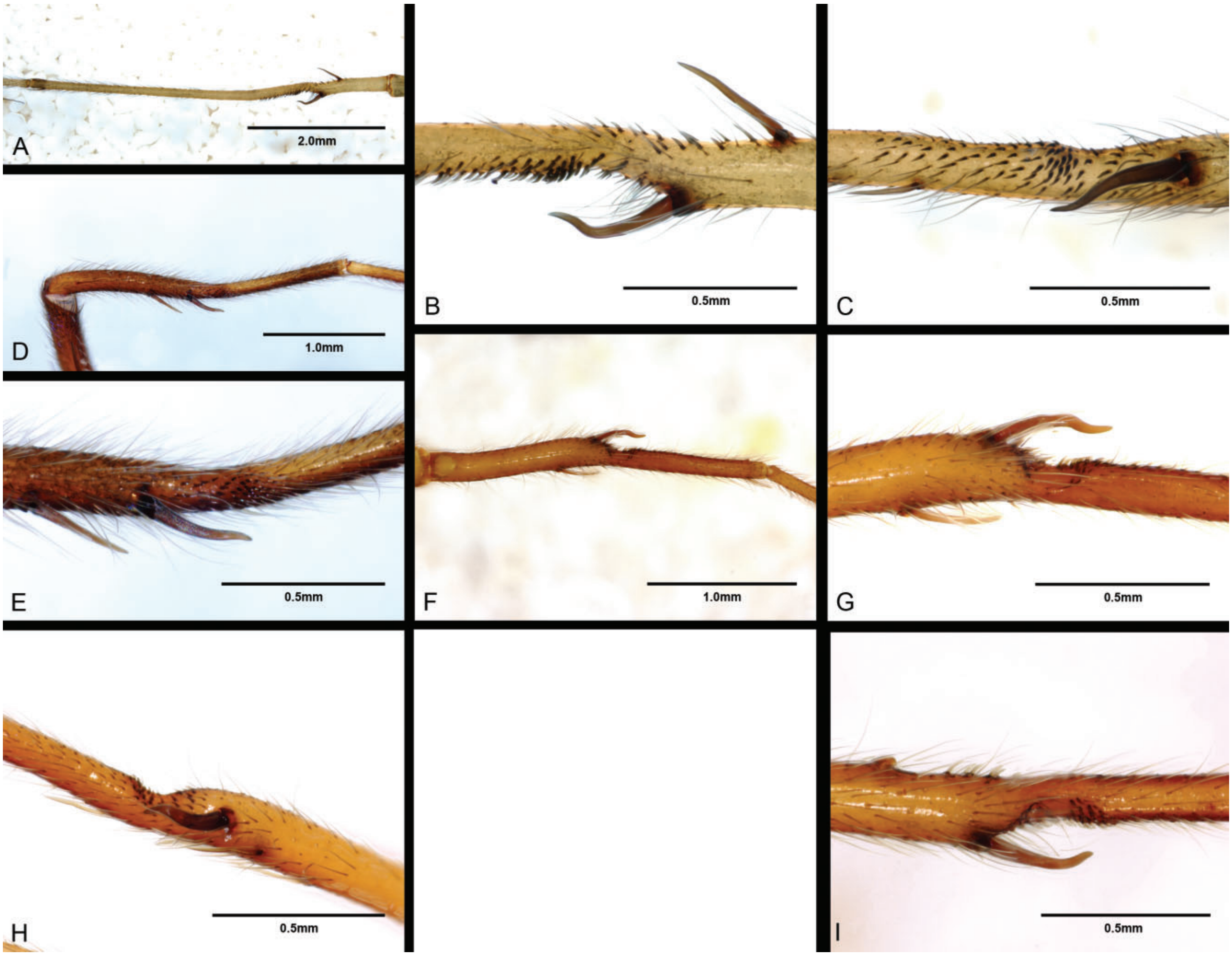

Figure 44. Photographs of male claspers of *Manampoka* and *Rahavavy*. A–C, *Manampoka atsimo*, holotype, CASENT9031164, right metatarsus II. A, dorsal. B, dorsal, close up. C, prolateral. D, E, *Rahavavy fanivelona* from Vohiparara, CASENT9016975, left metatarsus I. D, prolateral. E, prolateral, close up. F, G. *Rahavavy malagasyana* from Andasibe, CASENT9016182, right metatarsus I. F, dorsal. E, dorsal, close up. H, I, *Rahavavy ida* from Talatakely, CASENT9003423, right metatarsus I. H, prolateral, right, close up. I, dorsal, left, close up.

Griswold Arthropod Team, sifted litter of leaf mould and rotten wood, 1 ♀, CASC (CASENT9018399); Forêt Classée d'Analavelona, 33.2 km 344° NNW Mahaboboka, 22°40′30″S, 44°11′14″E, elev. 1300 m, montane rainforest, 22–26 February 2003, Fisher-Griswold Arthropod Team, 3 ♀, CASC (CASENT9018641, 9019979, 9019980).

AMBOHIMA ANTSINANANA SP. NOV.

(FIGS 7A, B, 33G–I, 36B, 37B, 58)

Types: Holotype female (CASENT9029888) collected by sifting leaf litter at 1580 m elevation at Parc National Andringitra, Fianarantsoa Province, Madagascar, on 7 January 2009 by H. Wood, deposited in CASC.

Etymology: The specific name is from the Malagasy word for east; a noun in apposition.

Diagnosis: Female vulva as in Figures 33H and 37B, spermathecal base with longitudinal, bilobed chamber, spermathecal coils close together, two or fewer.

Male: Unknown.

Female (Holotype): Total length 8.10. Markings similar to Figure 7A, B. Carapace 3.30 long, 2.50 wide; thoracic fovea length 0.18 that of carapace; clypeus 0.24 high; ocular area 0.45 long, 1.08 wide; ratio of eyes AM/AL/PM/PL, 1.43: 3.00:1.14:1.00, diameter of PM 0.16. Chelicerae 1.40 long, robust,

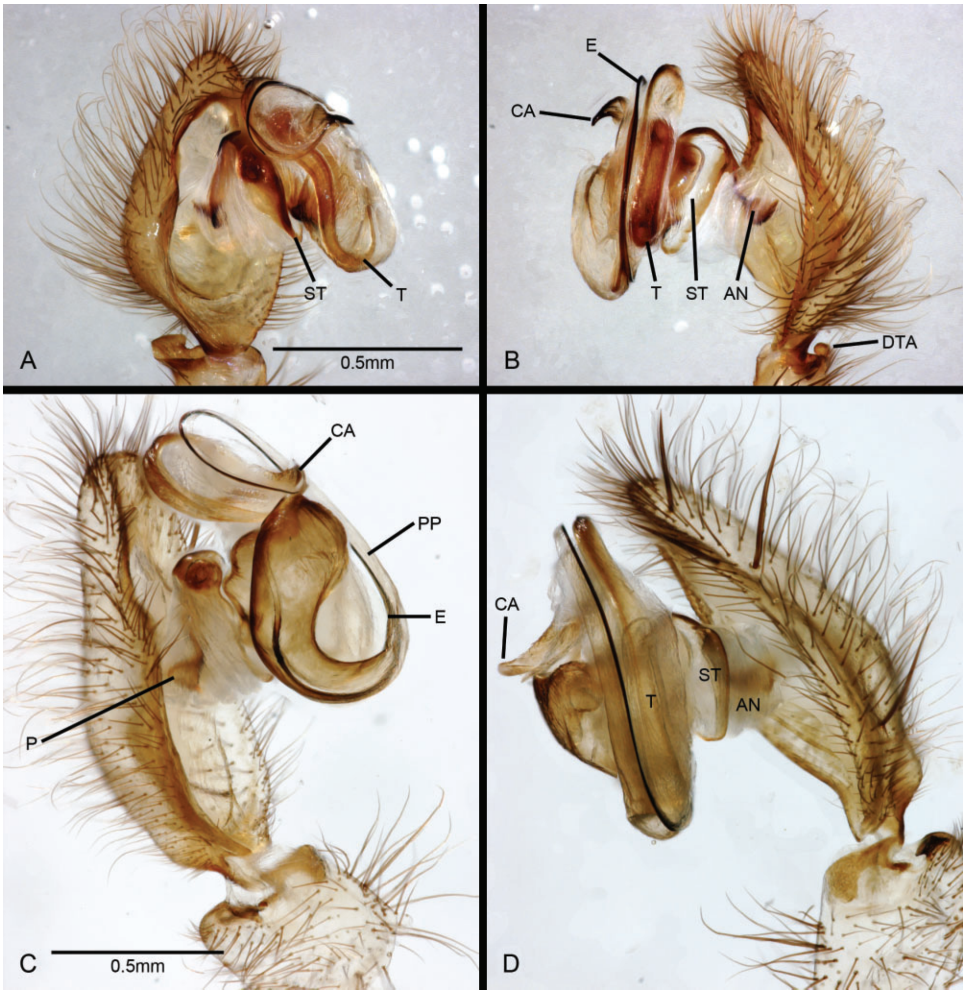

Figure 45. Expanded male palps of *Rahavavy fanivelona*, A, B (CASENT9016967) and *Ambohima ranohira*, C, D (CASENT9005790). A, C, retrolateral. B, D, prolateral. AN: anneli of subtegulum, CA: conductor apex, DTA: dorsal tibial apophysis, E: embolus, P: petiole of subtegulum, PP: pars pendula of embolus, ST: subtegulum, T: tegulum.

smooth, promargin of fang furrow with six teeth, retromargin with seven teeth. Sternum 1.74 long, 1.40 wide; labium 0.62 long, 0.56 wide; palpal coxa 1.10 long, 0.46 wide. Femur I length 2.00 times carapace length. Palpal femur with three anterobasal thorns. Calamistrum origin at 0.50 from metatarsus base, length 0.35 that of segment. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [total]) I: 6.60 + 1.35 + 6.20 + 6.00 + 2.70 = [22.85]; II: 5.15 + 1.20 + 4.35 + 4.20 + 2.05 = [16.95]; III: 4.15 + 1.05 + 3.30 + 3.40 + 1.80 = [13.70]; IV: 5.90 + 1.15 + 4.65 + 4.65 + 4.50 = [20.85]; palp: 1.55 + 0.55 + 0.80 + (absent) + 1.70 = [4.60]. Epigynum as in Figure 36B; vulva as in Figure 37B, spermathecal base with longitudinal, bilobed chamber, two spermathecal coils close together.

Variation (N = 2): Total length 8.10–9.20; carapace length 1.32–1.38 times width, height 0.36–0.40 times width; PER width 2.40–2.98 times OAL; OQP 1.20–1.21 times OQA; clypeal height 1.50–1.60 times AM diameter; cheliceral length 5.53–5.83 times clypeal height; promargin of fang furrow with 5–6 teeth, retromargin of fang furrow with 6–7 teeth; sternum length 1.24–1.31 times width; femur I length 2.00–2.13 times carapace length; metatarsus I 1.82–1.95 times carapace length; epigynum as in Figures 33G and 36B, vulva as in Figures 33H, I and 37B.

Natural history: Occurs in primary rainforest, on or near the ground.

Distribution: Known only from the type locality in southern Madagascar (Fig. 58).

Material examined: MADAGASCAR: **Fianarantsoa Prov**. Parc National Andringitra, 34 km S Ambalavao, 22°08′48.9″S, 46°57′03.4″E, elev. 1580 m, sifting

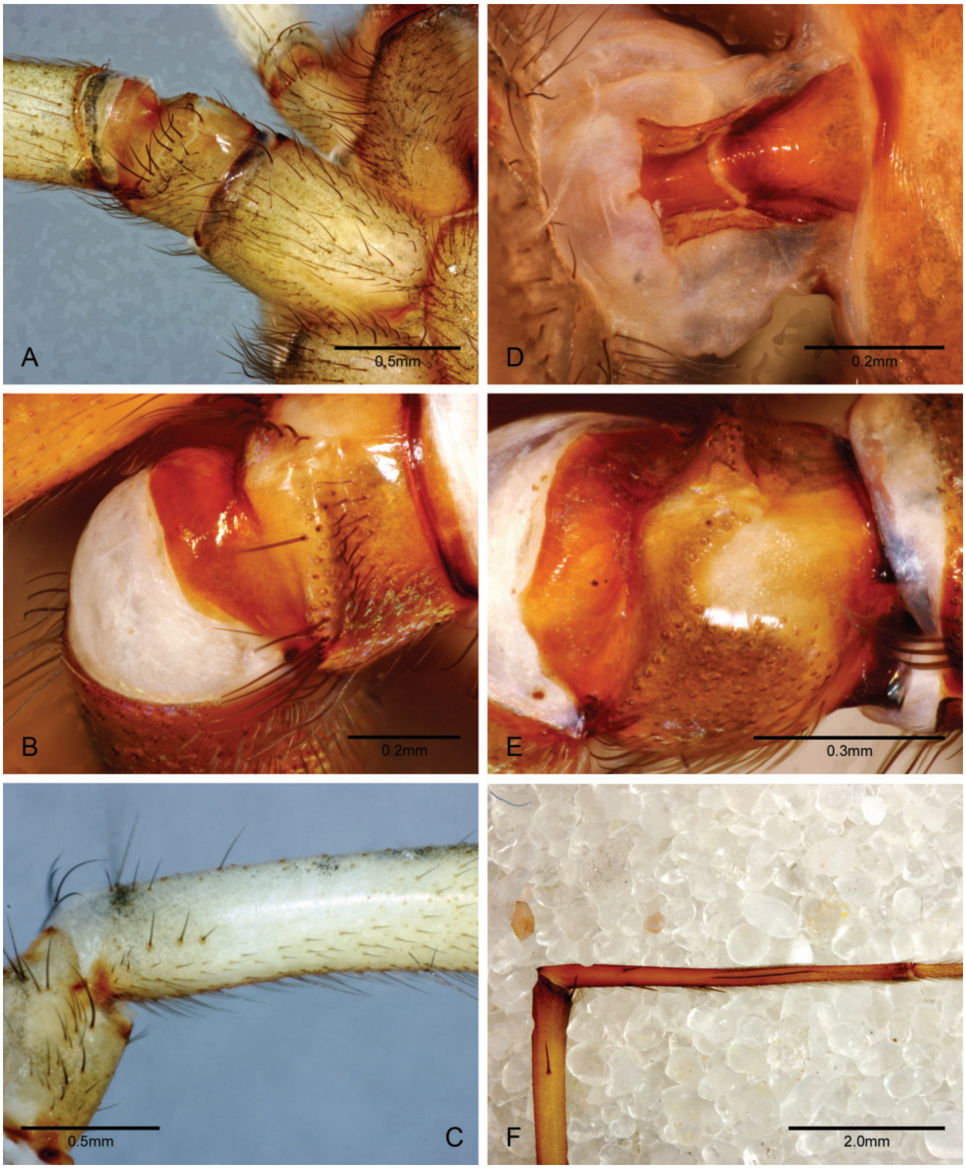

Figure 46. Morphology of *Ambohima*. A, *A. sublima* male from Ambohimanga, CASENT9016225, right coxa-trochanter I, ventral. C, *A. andrefana*, male from Zombitse, CASENT9005930, palpal femur prolateral showing thorns. B, D–F, *A. ranohira* female from Ranohira, CASENT9019986. B, trochanter I, right. D, pedicle, dorsal. E, trochanter IV, left. F, metatarsus IV, retrolateral, showing calamistrum.

litter in day in primary rainforest, 7 January 2009, H. Wood, holotype ♀, CASC (CASENT9029888), 1 ♀, CASC (CASENT9029887).

AMBOHIMA AVARATRA SP. NOV.
(FIGS 7E, 34A–D, 38A–D, 58)

Types: Holotype female collected by beating low vegetation in montane rainforest at 1300 m elevation in Parc National Montagne d'Ambre, Antsiranana Province, Madagascar, 2–7 February 2001, by J. J. Rafanomezantsoa, CASENT9003544, deposited in CASC.

Etymology: The specific name is from the Malagasy word for north; a noun in apposition.

Diagnosis: Female vulva as in Figures 34B–D and 38C, D, spermathecal ducts spiralling around a central, longitudinal spiral chamber, ducts make four or more spiral turns.

Male: Unknown.

Female (Holotype): Total length 8.50. Markings similar to Figure 7E. Carapace 2.65 long, 2.25 wide; thoracic fovea 0.50 long, length 0.19 that of carapace;

Figure 47. Morphology of *Ambohima ranohira*, female from Ranohira, CASENT9019986. A, face. B, clypeus and bipartite chilum. C, cephalothorax, ventral. D, spinnerets.

clypeus 0.18 high; ocular area 0.40 long, 0.99 wide; ratio of eyes AM/AL/PM/PL, 1.15:2.54:1.00:1.31, diameter of PM 0.13. Chelicerae 1.34 long, robust, smooth, promargin of fang furrow with seven teeth, retromargin with five teeth. Sternum 1.66 long, 1.32 wide; labium 0.58 long, 0.54 wide; palpal coxa 1.00 long, 0.44 wide. Femur I length 2.25 times carapace length. Palpal femur with three anterobasal thorns. Calamistrum origin at 0.45 from metatarsus base, length 0.30 that of segment. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [total]: I: 6.00 + 1.30 + 5.85 + 5.55 + 2.25 = [20.95]; II: 4.70 + 1.20 + 3.95 + 3.85 + 1.85 = [15.55]; III: 3.80 + 1.05 + 3.15 + 3.25 + 1.60 = [12.85]; IV: 5.10 + 1.10 + 4.30 + 4.40 + 1.75 = [16.65]; palp: 1.50 + 0.60 + 0.85 + (absent) + 1.95 = [4.90]. Epigynum as in Figure 38A, spermathecal ducts spiralling around a central, longitudinal spiral chamber, outside ducts make six spiral turns (Fig. 38C), poreplate at apex of spermathecae (Fig. 34C, D).

Variation (N = 3): Total length 8.00–9.00; carapace length 1.18–1.38 times width, height 0.33–0.41 times width; PER width 2.48–2.97 times OAL; OQP 1.33–1.39 times OQA; clypeal height 1.38–2.00 times AM diameter; cheliceral length 5.83–7.44 times clypeal height; pro- and retromargins of fang furrow with 5–7 teeth; sternum length 1.26–1.28 times width; femur I length 1.89–2.26 times carapace length; metatarsus I 1.50–2.09 times carapace length; epigynum as in Figures 34A and 38A, B, vulva with 4–6 outer spirals (Figs 34B, C, 38C, D).

Natural history: Unknown except that a specimen was collected by beating low vegetation in montane rainforest.

Distribution: Known only from Montagne d'Ambre in far northern Madagascar (Fig. 58).

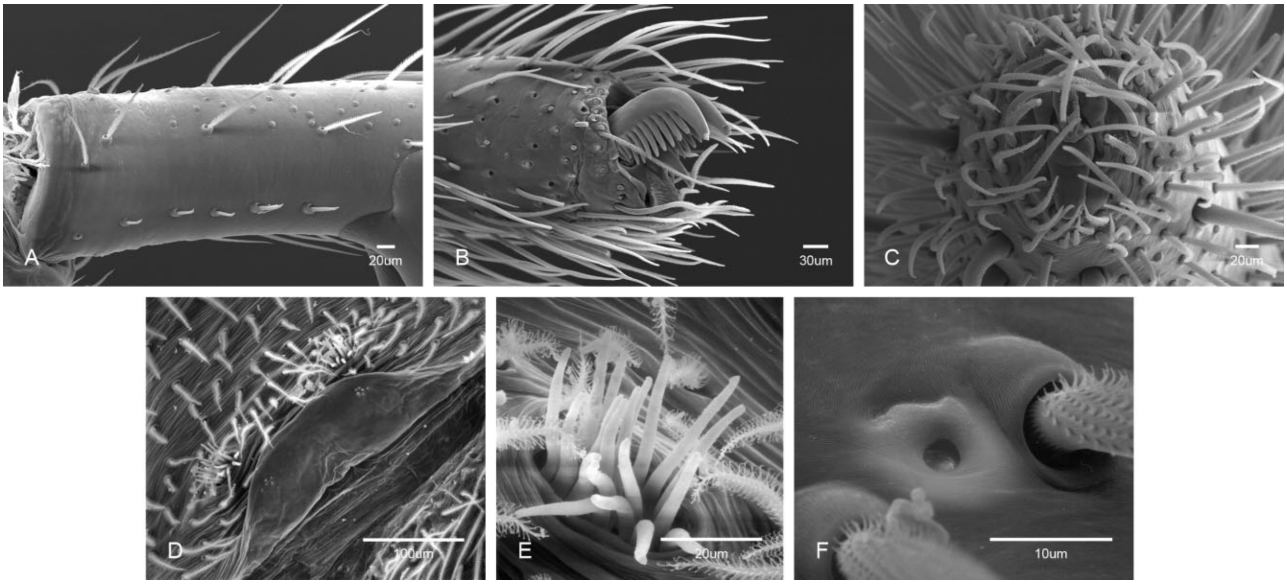

Figure 48. Morphology of Phyxelididae. A, *Rahavavy ida* male, right palpal femur, prolateral showing thorns, CASENT9003423. B, C, *Ambohima ranohira*, female, CASENT9019986. B, right tarsus I, claws, retrolateral. C, right palpus, apical. D–F, *Ambohima sublima* male from Ambohimanga, CASENT9020323. D, epiandrous region showing epiandrous spigots. E, right bunch of epiandrous spigots. F, tarsal organ I.

Material examined: MADAGASCAR: **Antsiranana Prov**. Parc National Montagne d'Ambre, 12.2 km 211° SSW Joffreville, 12°35′47″S, 49°9′34″E, elev. 1300 m, beating low vegetation in montane rainforest, 2–7 February 2001, J. J. Rafanomezantsoa, holotype ♀, CASC (CASENT9003544); P. N. Montagne d'Ambre, 2.79 air km NE of park entrance, 12°32′S, 49°10′E, elev. *c.* 1000 m, forest, 21–30 November 1993, C. Griswold, S. Larcher, R. Andriamasamanana, N. Scharff and J. Coddington, 1 ♀, CASC (CASENT9017012); Montagne d'Ambre, Forêt des Rousettes, December 1946, J. Millot, 1 ♀, MNHN (CASENT9017013).

AMBOHIMA MAIZINA SP. NOV.

(FIGS 6G, I, 11A–C, 42G–I, 57)

Types: Holotype male (CASENT9016206) collected by beating vegetation at 1875 m elevation at source Andranomifototra, R. N. I. Marojejy, Antsiranana Province, Madagascar, 13–19 November 1996, E. Quinter, deposited in AMNH.

Etymology: The specific name is from a Malagasy word for the dark; a noun in apposition.

Diagnosis: Male with palp as in Figure 11A–C, embolic base with a raised, distal cone, cymbium large, length greater than carapace length, palpal prolateral tibial hook long, narrow, distinguished from *A. sublima* by having the abdominal dorsum uniform grey (Fig. 6G) and by having fewer leg spines, e.g. lacking spines on the femora.

Male (Holotype): Total length 5.00. Markings of dorsum as in Figure 6G, abdomen grey-brown, dorsum unmarked, venter with dark area between longitudinal light bands (Fig. 6I). Carapace 2.25 long, 1.80 wide; thoracic fovea 0.38 long, length 0.15 carapace length; clypeus 0.18 high; ocular area 0.31 long, 0.74 wide; ratio of eyes AM/AL/PM/PL, 1.54:2.54:1.00:1.36, diameter of PM 0.11. Chelicerae 0.90 long, slender, smooth, promargin of fang furrow with six teeth, retromargin with seven heterogeneous teeth. Sternum 1.34 long, 1.12 wide; labium 0.46 long, 0.42 wide; palpal coxa 0.78 long, 0.40 wide. Legs elongate, femur I length 2.51 times carapace length; metatarsi I and II prolateral concavity and clasping spines as in Figure 42G–I, segment not swollen basad of concavity; apart from claspers legs with very few spines, only mt I r0-1-0-0, v0-0-0-1, T II p0-1-1-0, mt II r0-0-1-0, v2-0-0-1, T III r0-0-1-0, mt III p0-1-0-0, r0-1-0-0, v0-0-0-1. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [total]): I: 5.70 + 1.00 + 6.10 + 5.50 + 2.40 = [20.70]; II: 4.50 + 0.90 + 4.35 + 3.85 + 1.85 = [15.45]; III: 3.70 + 0.70 + 3.10 + 3.15 + 1.60 = [12.25]; IV: 5.00 + 0.85 + 4.60 + 4.55 + 1.85 = [16.85]; palp: 1.75 + 0.50 + 0.50 + (absent) + 2.50 = [5.25]. Palpus as in Figure 11A–C, femur with triangular group of five thorn-like setae; tibia with dorsal blade (DTA) broad, prolateral hook (PTA) long, slender; cymbium length 1.11 times cara-

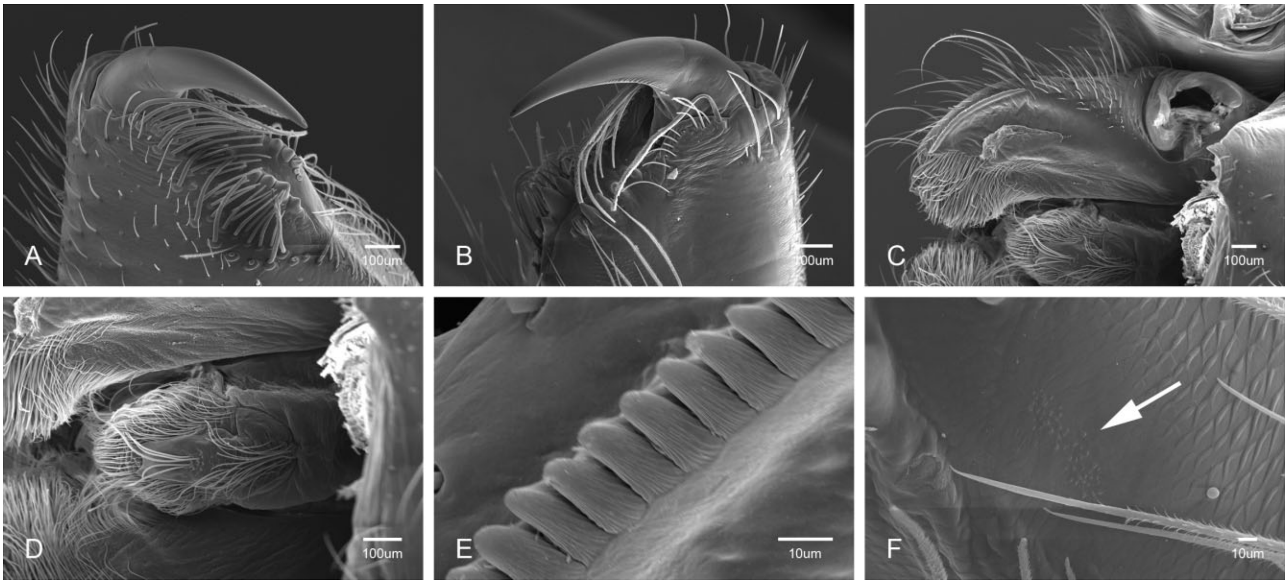

Figure 49. Morphology of *Ambohima ranohira* female from Ranohira, CASENT9019986. A, left chelicera, promargin. B, left chelicera, retromargin. C, right endite, dorsal. D, labrum, dorsal. E, serrula on right endite, close up. F, cheliceral gland pores (arrow).

pace length, palpal bulb length 1.8 times width, embolus base with dorsal conical projection, reservoir course in embolus base gently curved.

Female: Unknown.

Natural history: Unknown; the unique male specimen was taken by beating vegetation.

Distribution: Known only from the type locality on the Marojejy Massif in north-eastern Madagascar (Fig. 57).

Material examined: MADAGASCAR: **Antsiranana Prov**. source Andranomifototra, R. N. I. Marojejy, 11.0 km NW Manantenina, elev. 1875 m, 14°26.8′S, 49°44.1′E, 13–19 November 1996, E. Quinter, holotype ♂, AMNH (CASENT9016206).

AMBOHIMA PAULIANI GRISWOLD 1990
(FIGS 7H, 36C, 37C, 57)

Ambohima pauliani Griswold 1990: 130; Platnick 2011.

Type: Holotype female from Maroantsetra, Tamatave District, Madagascar, collected in September by R. Paulian, deposited in AMNH, examined.

Diagnosis: Female vulva as in Figure 37C, spermathecal base with transverse, bilobed chamber, anteriorly with three widely separated spermathecal coils.

Female (Holotype): Total length 9.69. Markings of dorsum as in Figure 7H. Carapace 4.18 long, 3.16 wide; thoracic fovea broad, deep, length 0.11 carapace; clypeus 0.32 high; ocular area 0.43 long, 1.28 wide; ratio of eyes AM/AL/PM/PL, 1.00:1.20:1.00:1.20, diameter of PM 0.16. Chelicerae 1.84 long, with weak ventrolateral wrinkles, promargin of fang furrow with six, retromargin with five large teeth and one minute tooth. Sternum 2.19 long, 1.63 wide, labium 0.84 long, 0.72 wide; palpal coxa 1.39 long, 0.66 wide. Legs elongate, femur I length 0.85 times carapace length. Palpal femur with row of four anterobasal thorns becoming shorter distally, distal two stoutest. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [total]): I: 3.59 + 0.84 + 3.38 + 3.19 + 1.31 = [12.31]; II: 2.81 + 0.75 + 2.34 + 2.28 + 1.03 = [9.21]; III: 2.38 + 0.66 + 1.78 + 1.88 + 0.88 = [7.58]; IV: 3.09 + 0.72 + 2.47 + 2.56 + 1.00 = [9.84]; palp: 0.97 + 0.38 + 0.50 + (absent) + 1.09 = [3.24]. Epigynum as in Figure 36C, vulva as in Figure 37C, spermathecal base with transverse, bilobed chamber, three anterior spermathecal coils widely separated.

Male: Unknown.

Distribution: Known only from the type locality at the northern end of Antongil Bay on the north-east coast of Madagascar (Fig. 57).

Material examined: MADAGASCAR: **Antsiranana Prov.** Maroantsetra, September, R. Paulian, holotype ♀, AMNH.

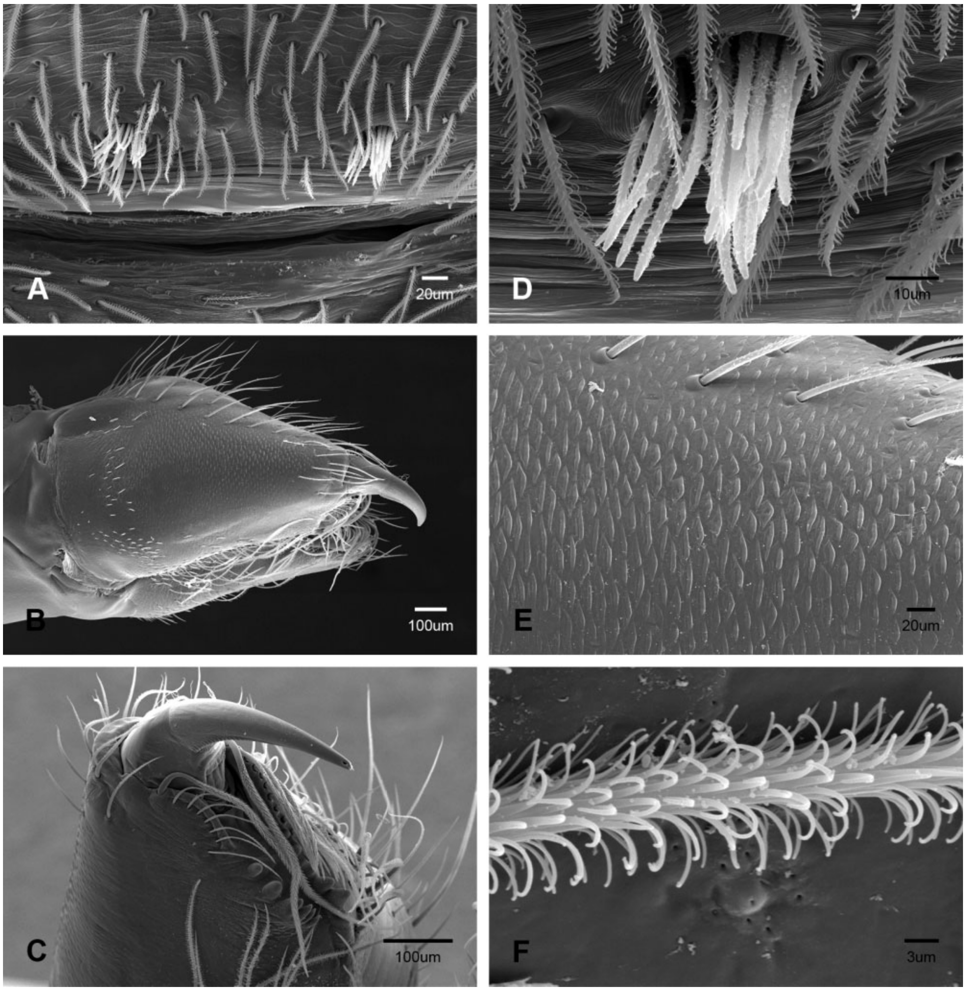

Figure 50. Morphology of *Rahavavy fanivelona* from Vohiparara. A, D, male, CASENT9016969. B, C, E, F, female, CASENT9016966. A, epiandrous spigots, ventral. B, right chelicera, lateral. C, right chelicera, retrolateral. D, epiandrous spigots, left bunch, ventral. E, right chelicera, lateral showing cuticle texture. F, right chelicera, fang furrow showing plumose seta and cheliceral gland pores.

AMBOHIMA RANOHIRA SP. NOV.

(FIGS 3A, 6H, 7D, 12A–C, 22A–D, 23A–D, 31A–D, 39A–F, 42J–L, 45C, D, 46B, D–F, 47A–D, 48B, C, 49A–F, 59)

Types: Holotype male and paratype female (CASENT9005788) taken from a web under a large stone in gallery forest at 725 m elevation at Parc National d'Isalo, 9.1 km 354° N Ranohira, 22°28′54″S, 45°27′42″E, Fianarantsoa Province, Madagascar, 27–31 January 2003, by C. Griswold, deposited in CASC.

Etymology: The specific name is a noun in apposition from the type locality.

Diagnosis: Male with palp as in Figure 12A–C, embolic base convex, broad, much broader than width of exposed conductor between embolic base and proximal turn of embolus, reservoir course across embolic base sinuate; clasper concavity on metatarsi I and II swollen and protruding at base (Fig. 42J–L). Female vulva as in Figures 31B and 39D–F, apex of spermathecae with a simple, median bend, lacking spirals.

Male (Holotype): Total length 6.80. Markings similar to Figure 3A. Carapace 3.35 long, 2.65 wide; thoracic fovea 0.85 long, length 0.25 times carapace length; clypeus 0.18 high; ocular area 0.39 long, 0.87 wide; ratio of eyes AM/AL/PM/PL, 1.25:2.66:1.00:1.17, diameter of PM 0.12. Chelicerae 1.00 long, slender, smooth, pro- and retromargins of fang furrow with six teeth. Sternum 1.84 long, 1.40 wide; labium 0.60 long, 0.56 wide; palpal coxa 1.00 long, 0.46 wide. Legs elongate, femur I length 2.00 times carapace length; metatarsi I and II prolateral concavity and clasping

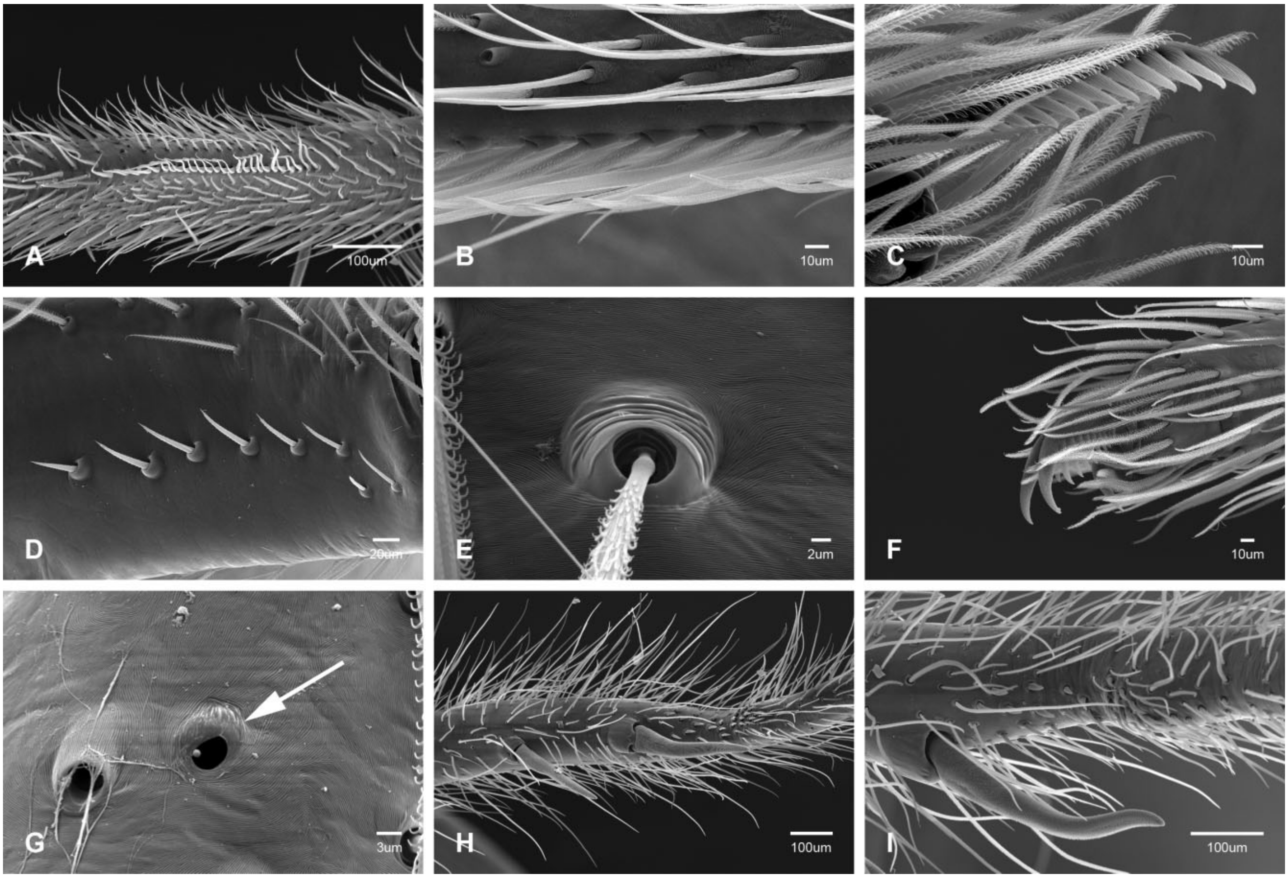

Figure 51. Morphology of *Rahavay fanivelona* from Vohiparara. A–G, female, CASENT9016966. A, calamistrum, left leg IV. B, calamistrum, close-up. C, palp claw, left, prolateral. D, left palpal femur, prolateral. E, metatarsus IV trichobothrial base. F, left tarsus IV, claws, retrolateral. G, left tarsus IV, tarsal organ. H, I, male left leg I, CASENT9016969. H, prolateral. I, clasping spine, dorsal.

spines as in Figure 42J–L, segment swollen and projecting dorsally basad of cavity. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [total]): I: 6.70 + 1.60 + 6.90 + 6.60 + 2.55 = [24.35]; II: 5.85 + 1.45 + 5.50 + 5.00 + 2.10 = [19.90]; III: 4.85 + 1.25 + 4.05 + 4.40 + 1.75 = [16.30]; IV: 6.20 + 1.35 + 6.00 + 6.40 + 2.25 = [22.20]; palp: 1.95 + 0.70 + 0.65 + (absent) + 1.30 = [4.60]. Palpus as in Figures 12A–C, 22A–D and 23A–D, femur with probasal row of four thorn-like setae; tibia with dorsal blade (DTA) trapezoidal, prolateral hook (PTA) short, stout; cymbium length 0.39 that of carapace; palpal bulb length 1.82 times width, embolic base convex, broad, much broader than width of exposed conductor between embolic base and proximal turn of embolus, reservoir course across embolic base sinuate.

Variation (N = 6): Total length 6.60–8.10; carapace length 1.25–1.38 times width, height 0.25–0.37 times width; PER width 2.23–2.58 times OAL; OQP 1.05–1.25 times OQA; clypeal height 1.25–1.83 times AM diameter; cheliceral length 4.48–5.82 times clypeal height; promargin of fang furrow with 6–7 teeth, retromargin of fang furrow with 5–7 teeth; sternum length 1.27–1.58 times width; femur I length 1.86–2.15 times carapace length; metatarsus I 1.86–2.03 times carapace length.

Female (Paratype): Total length 10.00. Markings of dorsum similar to Figure 7D, venter as in Figures 6H and 47C. Carapace 4.80 long, 3.50 wide; thoracic fovea 0.80 long, length 0.17 carapace length; clypeus 0.42 high; ocular area 0.50 long, 1.36 wide; ratio of eyes AM/AL/PM/PL, 1.20:2.80:1.13:1.00, diameter of PM 0.17. Chelicerae 1.74 long, robust, smooth, pro- and retromargins of fang furrow with seven teeth. Sternum 2.56 long, 1.90 wide; labium 0.86 long, 0.80 wide; palpal coxa 1.44 long, 0.64 wide. Femur I length 1.42 times carapace length. Palpal femur with anterobasal group of two small and a separate row of three thorns. Calamistrum origin at 0.45 from metatarsus base, length 0.35 that of segment. Leg measurements

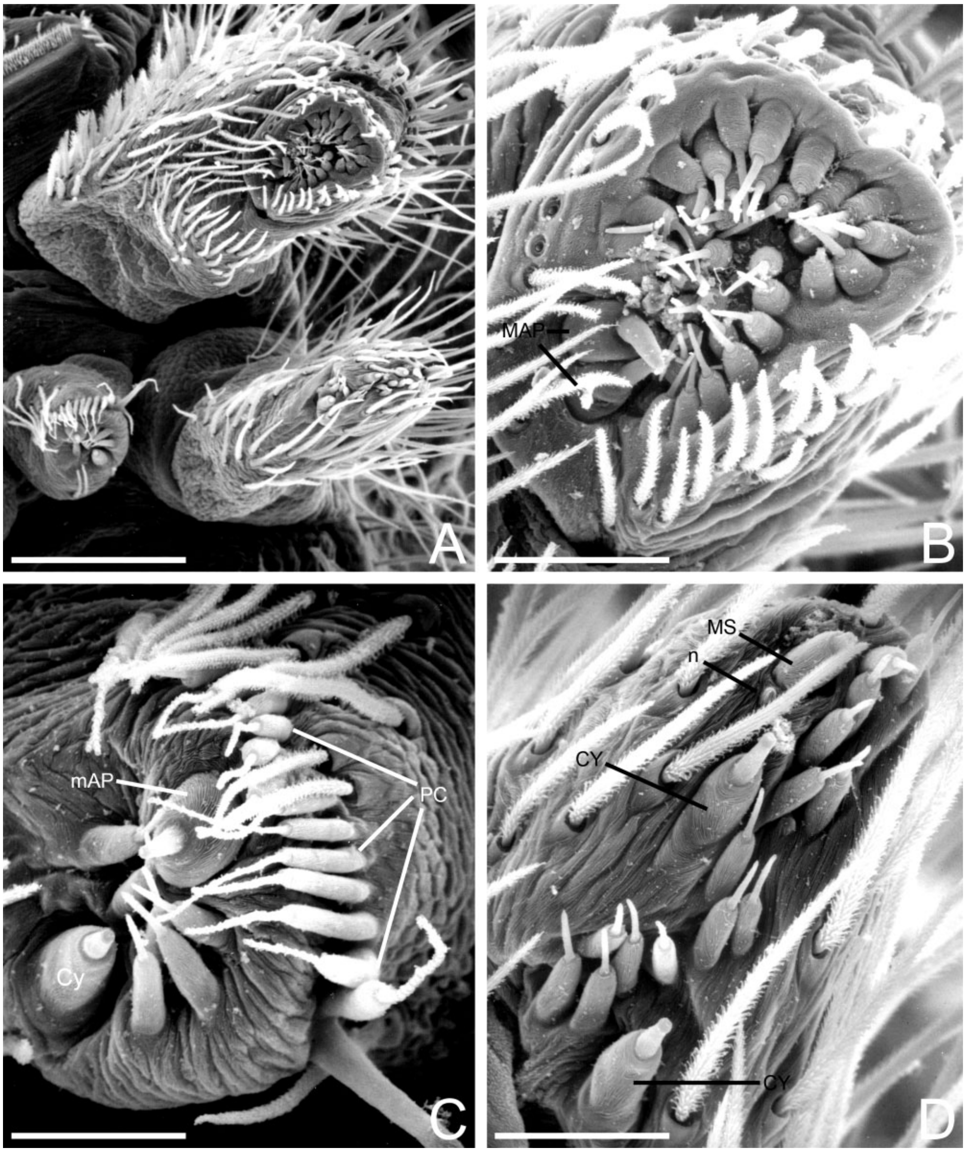

Figure 52. Left spinnerets of female *Ambohima sublima* from Ambohimanga, CASENT9020323. A, overview. B, ALS. C, PMS. D, PLS. Scale bars: A = 150 μm, B = 43 μm, C, D = 30 μm. CY: cylindrical gland spigots, MAP: major ampullate gland spigot, mAP: minor ampullate gland spigot, MS: PLS modified spigot, n: nubbin, PC: paracribellar spigot.

(femur + patella + tibia + metatarsus + tarsus = [total]): I: 6.80 + 1.90 + 6.70 + 6.35 + 2.75 = [24.50]; II: 5.60 + 1.80 + 4.65 + 4.65 + 2.15 = [18.85]; III: 4.80 + 1.50 + 3.65 + 3.90 + 1.85 = [15.70]; IV: 5.85 + 1.65 + 5.40 + 5.10 + 2.15 = [20.15]; palp: 2.00 + 0.75 + 1.10 + (absent) + 2.10 = [5.95]. Epigynum as in Figure 39A; vulva with apex of spermathecae with a simple, median bend (Fig. 39D).

Variation (N = 5): Total length 5.70–10.40; carapace length 1.37–1.45 times width, height 0.29–0.43 times width; PER width 2.63–2.86 times OAL; OQP 2.63–2.86 times OQA; clypeal height 1.43–2.47 times AM diameter; cheliceral length 4.14–5.60 times clypeal height; pro- and retromargins of fang furrow with 5–7 teeth; sternum length 1.22–1.42 times width; femur I length 1.42–1.65 times carapace length; metatarsus I length 1.22–1.43 times carapace length; epigynum as in Figures 31A and 39A–C, vulva as in Figures 31B–D and 39D–F.

Natural history: This species occurs in tropical dry forest and gallery forest in dry areas, and tolerates drier conditions than known for other Madagascar phyxelidids. This species may also be found in disturbed areas, including the interior of buildings.

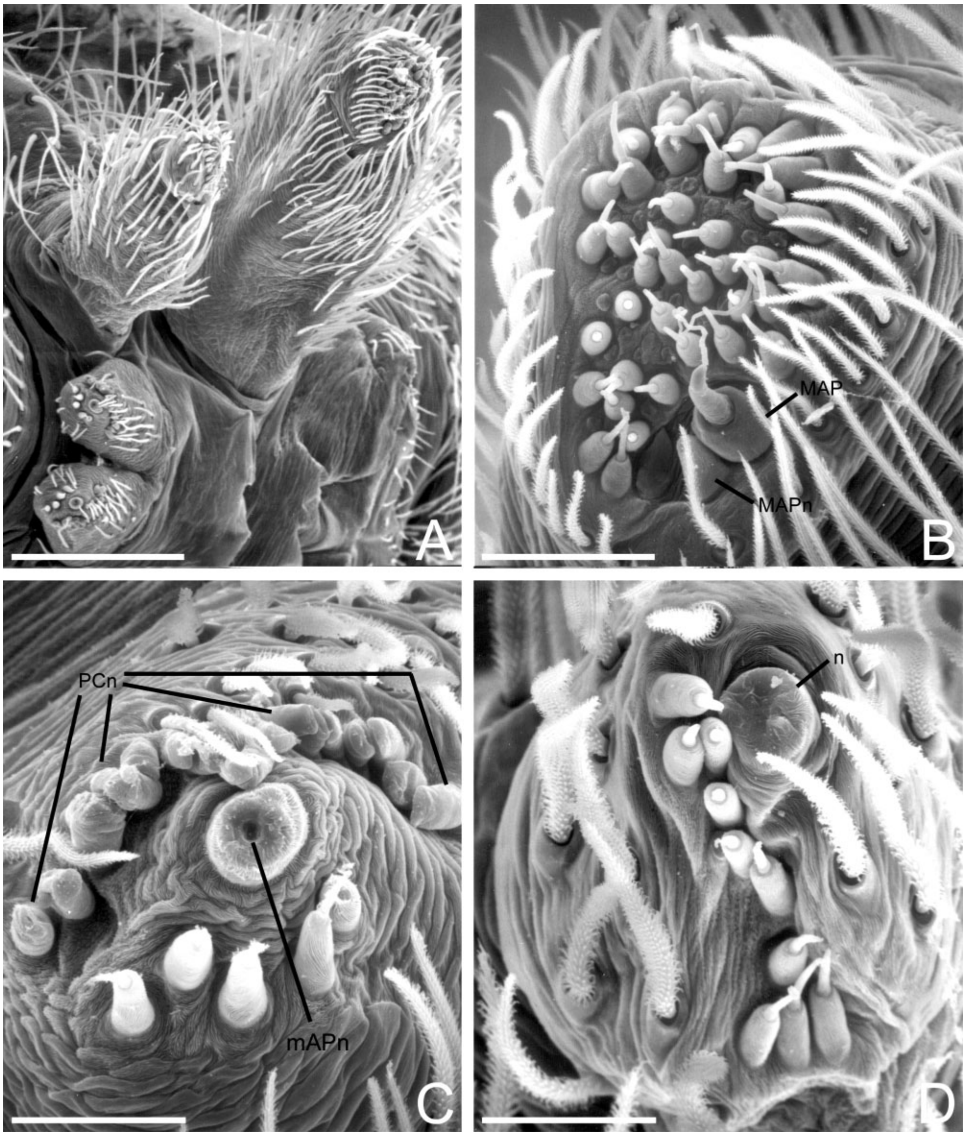

Figure 53. Right spinnerets of male *Ambohima sublima* from Ambohimanga, CASENT9020323. A, overview. B, ALS. C, PMS. D, PLS. Scale bars: A = 200 µm, B = 43 µm, C, D = 25 µm. MAP: major ampullate gland spigot, MAPn: major ampullate gland spigot nubbin, mAPn: minor ampullate gland spigot nubbin, n: nubbin of PLS modified spigot, PCn: paracribellar spigot nubbins.

Distribution: Known from the plateau region of southern Madagascar (Fig. 59).

Material examined: MADAGASCAR: **Fianarantsoa Prov.** Forêt d'Analalava, 29.6 km 280° W Ranohira, 22°35′30″S, 045°07′42″E, elev. 700 m, dry forest on sandy soil, 1–5 February 2003, C. Griswold, D. Silva and J. J. Rafonomezantsoa, 5 ♀, CASC (CASENT9016953, 9019988, 9020322, 9019989, 9005873); Parc National d'Isalo, 9.1 km 354° N Ranohira, 22°28′54″S, 045°27′42″E, elev. 725 m, in gallery forest, 27–31 January 2003, C. Griswold, D. Silva and J. J. Rafonomezantsoa, 1 ♂ holotype, 1 ♀ paratype, CASC (CASENT9005788), 2 ♂, 6 ♀, CASC (CASENT9019987, 9005937, 9021371, 9005938, 9019985, 9019986, 90218642, 9017228); Parc National d'Isalo, gallery forest along Sahanafa River, 29.2 km 351° N Ranohira, 22°18′48″S, 045°17′30″E, elev. 500 m, 10–13 February 2003, Fisher-Griswold Arthropod Team, 1 ♀, CASC (CASENT9016724); Isalo N. P., north end, 25 May 1992, V. Roth, 1 ♀, CASC (CASENT9017024); Ambalavao, Hotely, in *Tegenaria*-like web in corner of dark outhouse, 25 May 1992, V. Roth, 1 ♀, CASC (CASENT9025741). **Toliara Prov**. 18 km NNW Betroka, 23°09′59″S, 045°58′07″E, elev. 825 m, 4–9 December 1994, M. Ivie and A. Pollock, 1

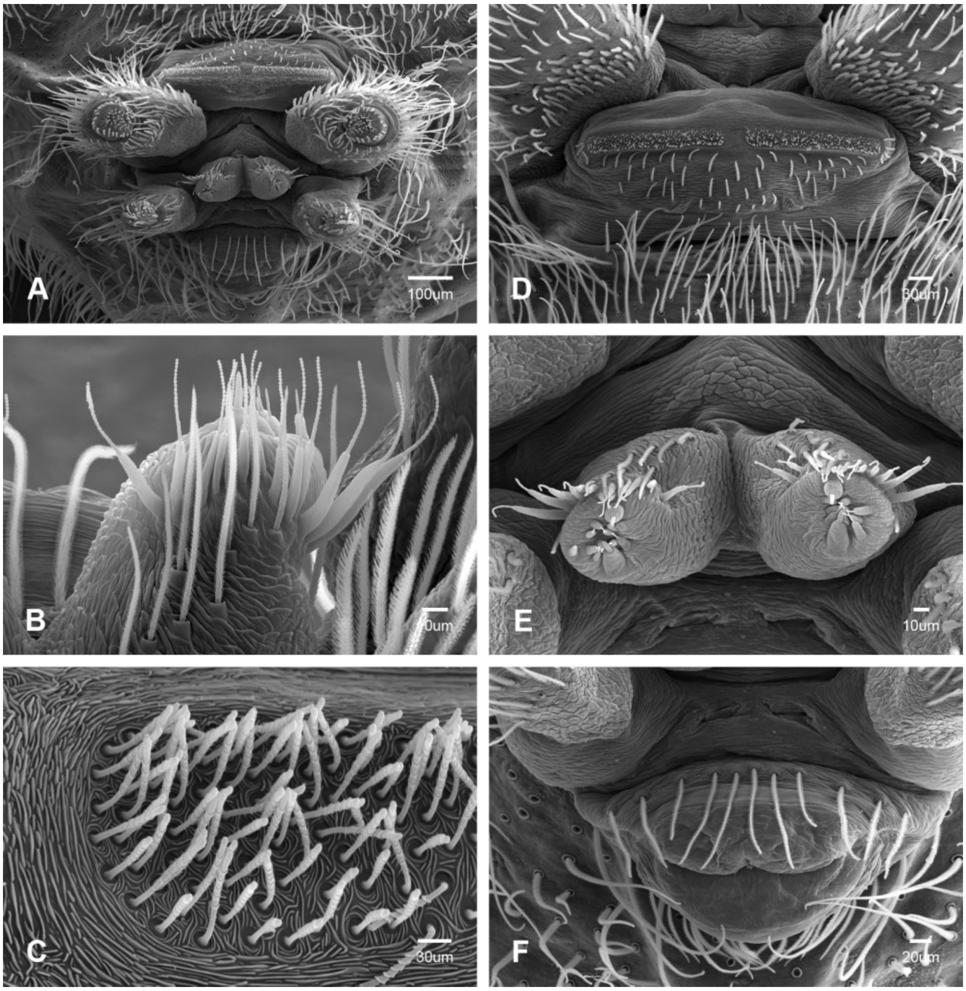

Figure 54. Spinnerets of female *Rahavavy fanivelona* from Vohiparara, CASENT9016966. A, overview. B, right PMS, anterior. C, cribellum, right edge. D, cribellum, whole. E, PMS. F, anal tubercle.

♂, CASC (CASENT9016178); Andohahela N. P., Parcelle II, Tsimela, 24°56.21'S, 46°37.60′E, elev. 180 m, 21–25 October 2002, R. Harin'Hala, 1 ♂, CASC (CASENT2026292).

AMBOHIMA SUBLIMA GRISWOLD 1990
(FIGS 1,2A, B, 3B, 6E, F, 13A–C, 30A–F, 32A–F, 40A–I, 42M–O, 43A–F, 46A, 48D–F, 52A–D, 53A–D, 57)

Ambohima sublima Griswold 1990: 128; Platnick 2011.

Types: Holotype male and paratype female from Ambohimanga Village (18°44′S, 47°34′E), Tananarive District, Madagascar (Dec. 1959; R. Legendre), deposited in MNHN, examined.

Diagnosis: Male with palp as in Figure 13A–C, embolic base with a raised, distal cone, cymbium large, length typically greater than 0.75 times carapace length (Figs 3B, 6E, F), palpal tibial prolateral hook long, narrow; distinguished from *A. maizina* by having the abdomen dorsally with chevron or herringbone pattern (Figs 1, 3B, 6E, F) and legs more spinose, with spines on all leg femora. Some *A. sublima* males from Ranomafana have short cymbia, i.e. length 0.71 of carapace length: these may be distinguished from males of *A. vato* sp. nov. by the much longer legs, femur I length greater than 3.0 times carapace length (Fig. 2B). Female epigynum as in Figures 32A, D and 40B, vulva as in Figures 32B, E and 40C–I, spermathecal base with longitudinal, bilobed chamber, anteriorly with four or more coils.

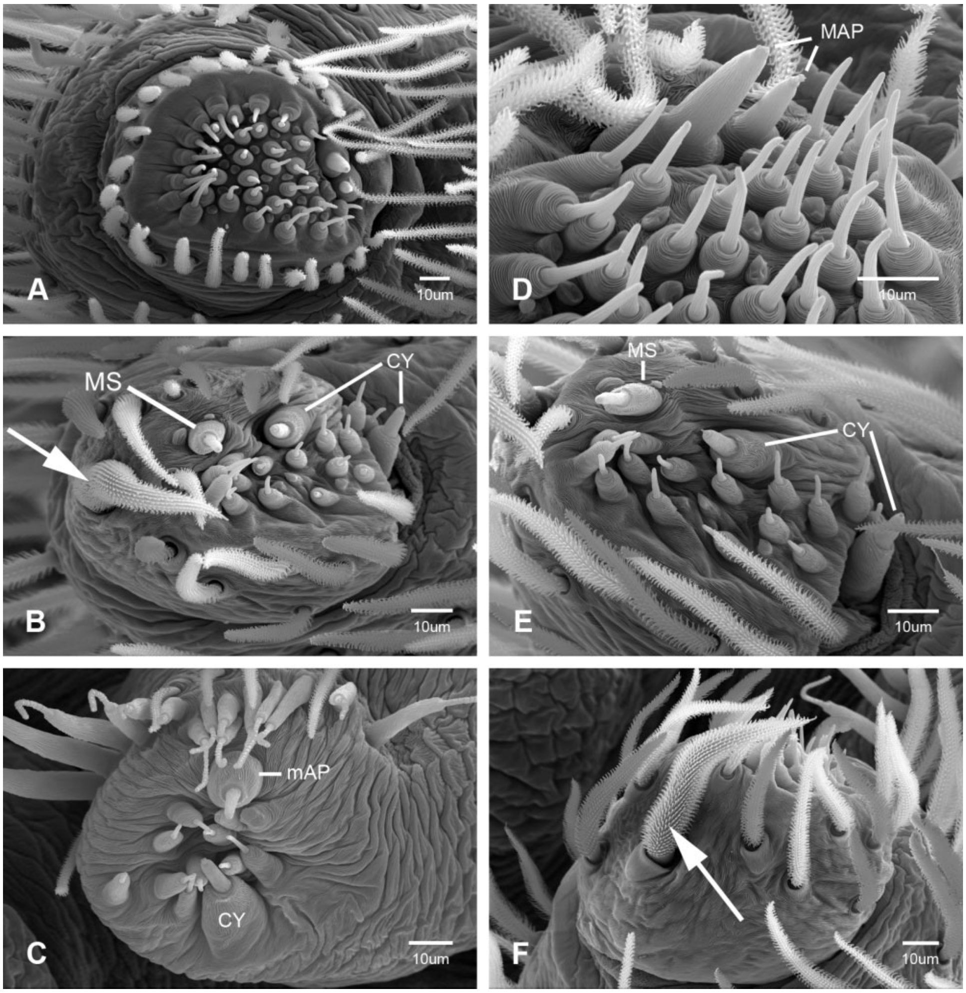

Figure 55. Right spinnerets of female *Rahavavy fanivelona* from Vohiparara, CASENT9016966. A, ALS. B, PLS, apical view. C, PMS. D, close up of ALS. E, PLS. F, PLS, posterior view. CY: cylindrical gland spigots, MAP: major ampullate gland spigots, mAP: minor ampullate gland spigot, MS: PLS modified spigot. Arrows to stout, black seta at PLS apex.

Male (Ambohimanga, CASENT9016200): Total length 6.00. Markings as in Figure 6E. Carapace 2.70 long, 2.25 wide, margin entire; thoracic fovea broad, deep, narrowed posteriorly, length 0.22 times that of carapace; clypeus 0.18 high; ocular area 0.36 long, 0.82 wide; ratio of eyes AM/AL/PM/PL, 1.42:2.91:1.00:1.08, diameter of PM 0.12. Chelicerae 1.00 long, slender, smooth, promargin of fang furrow with two small and five large teeth, retromargin with six large teeth. Sternum 1.52 long, 1.24 wide, apex pointed; labium 0.52 long, 0.48 wide; palpal coxa 0.88 long, 0.40 wide. Legs elongate, femur I length 2.32 times carapace length; metatarsi I and II with segment cylindrical basad of prolateral, spinule-lined concavity. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [total]): I: 6.25 + 1.30 + 7.80 + 6.15 + 2.50 = [24.00]; II: 5.30 + 1.15 + 4.85 + 4.60 + 2.05 = [17.95]; III: 4.35 + 0.95 + 3.75 + 3.90 + 1.65 = [14.60]; IV: 5.75 + 1.10 + 5.50 + 5.75 + 2.10 = [20.20]; palp: 1.90 + 0.65 + 0.65 + (absent) + 2.60 = [5.80]. Palpus as in Figure 13A–C, femur with row of five slender, anterobasal setae set in enlarged bases, distal two short, stout, thorn-like; tibia with dorsal process (DTA) broad, blade-like, apically pointed, prolateral hook (PTA) at base of cymbium long, narrow, curved, pointed, dorsad-directed (Fig. 6E); cymbium narrowed for apical half, large, length 0.95 times carapace length; palpal bulb length 1.88 times width, embolic base with a raised, distal cone.

Variation (N = 10): Total length 6.00–9.00; carapace length 1.20–1.30 times width, height 0.29–0.43 times width; PER width 2.09–3.22 times OAL; OQP 1.00–1.19 times OQA; clypeal height 1.23–2.15 times AM diameter; cheliceral length 4.71–6.00 times clypeal

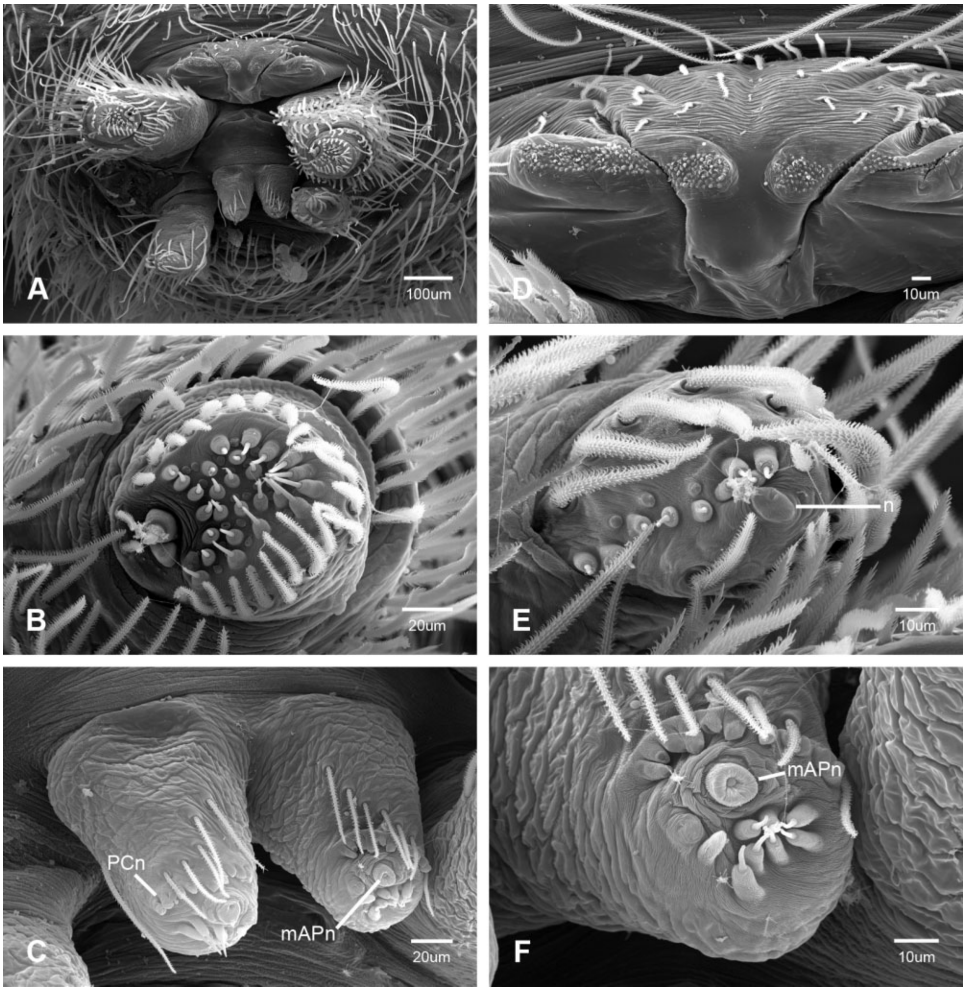

Figure 56. Spinnerets of male *Rahavavy fanivelona* from Vohiparara, CASENT9016969. A, overview. B, ALS, left. C, PMS, anterior. D, cribellum. E, PLS, left. F, PMS, left. mAPn: minor ampullate gland spigot nubbin, n: PLS modified spigot nubbin, PCn: paracribellar spigot nubbins.

height; promargin of fang furrow with 5–6 teeth, retromargin of fang furrow with 6–7 teeth; sternum length 1.17–1.26 times width; femur I length 2.18–3.62 times carapace length; metatarsus I length 2.11–3.77 times carapace length; cymbium length 0.71–1.14 times carapace length. Specimens from the southern end of the species range (Fianarantsoa Province) are larger (greater than 7 mm body length vs. less than 7 mm body length), have longer legs (femur I greater than 3 times carapace length vs. less than 2.5 times carapace length) and most individuals have relatively smaller cymbia (Fig. 6F) (less than 0.75 times carapace length vs. about as long as carapace length, although one Ranomafana male has a cymbium 0.92 times carapace length) compared with specimens from the northern part (Antananarivo and Toamasina Provinces) that have huge cymbia (Figs 1,3B, 6E).

Female (Ambohimanga, CASENT9016200): Total length 6.50. Markings as in male. Carapace 3.30 long, 2.40 wide; thoracic fovea deep, narrowed posteriorly, length 0.12 carapace; clypeus 0.22 high; ocular area 0.35 long, 1.02 wide, PER weakly procurved; ratio of eyes AM/AL/PM/PL, 1.41:3.58:1.00:1.00, diameter of PM 0.14. Chelicerae 1.34 long, robust, smooth, promargin of fang furrow with six teeth, retromargin with four large and two minute teeth. Sternum 1.74 long, 1.42 wide, apex prolonged, blunt; labium 0.60 long, 0.56 wide; palpal coxa 0.96 long, 0.56 wide. Femur I length 1.54 times carapace length. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [total]): I: 5.10 + 1.30 + 4.90 + 4.40 + 2.05 = [17.75]; II: 3.95 + 1.05 + 3.25 + 3.10 + 1.60 = [12.95]; III: 3.30 + 1.05 + 2.55 + 2.65 + 1.40 = [10.95]; IV: 4.40 + 1.10 + 3.70 + 3.55 + 1.60 = [14.35]; palp: 1.50 + 0.55 + 0.75 + (absent) + 1.70 = [4.50]. Calamistrum

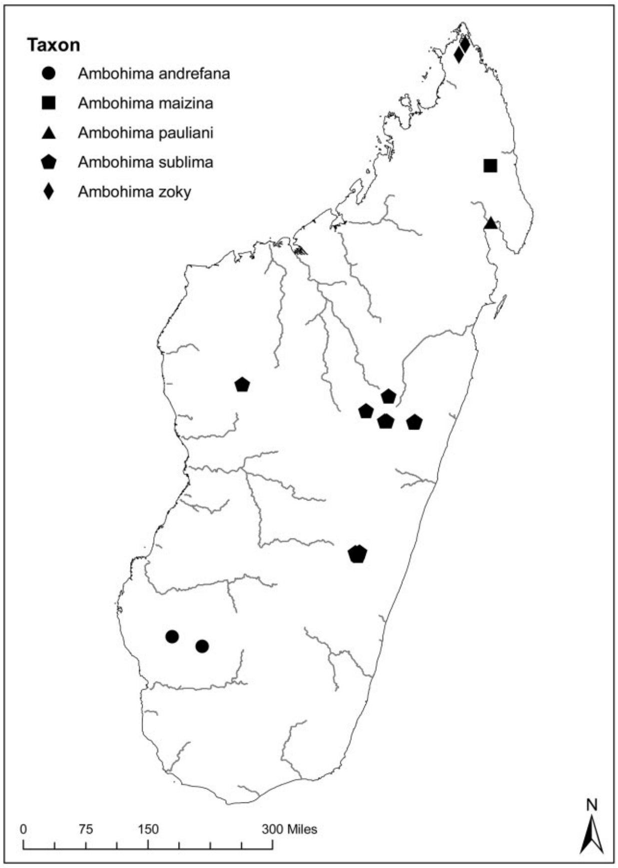

Figure 57. Distribution of Madagascar Phyxelididae.

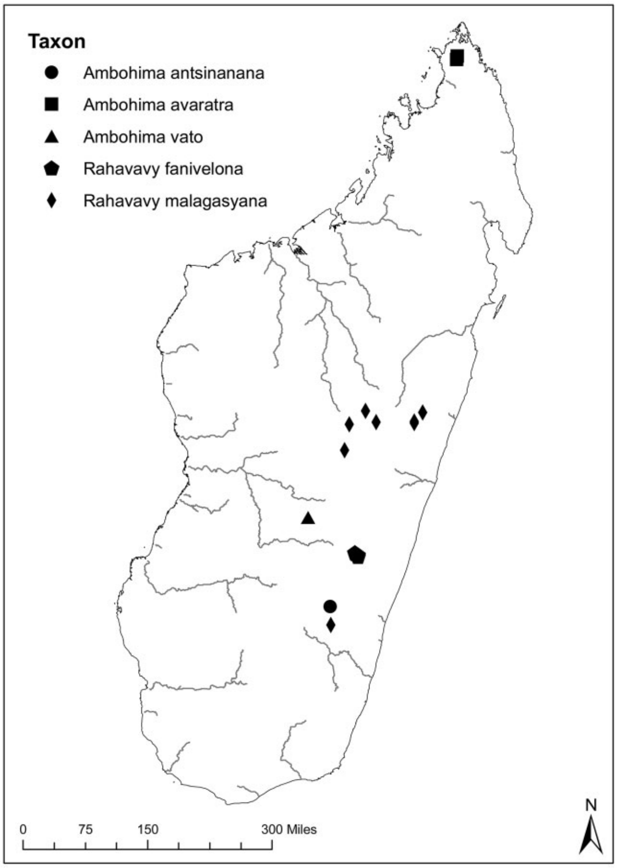

Figure 58. Distribution of Madagascar Phyxelididae.

origin at 0.40 from metatarsus base, length 0.35 that of segment. Epigynum as in Figure 30D, copulatory openings oblique, slit-like, ML trapezoidal, sides angled, posterior margin procurved; spermathecae as in Figure 30C, each with posterior copulatory duct leading to broad, twisted, longitudinal bilobed chamber which leads to anterior spiralled duct making seven turns to apical blind-ending bulb, internal duct arising at base of spiral and extending posteriad within curve of outer chamber.

Variation (N = 16): Total length 5.80–10.90; carapace length 1.15–1.40 times width, height 0.26–0.43 times width; PER width 2.29–2.24 times OAL; OQP 1.09–1.28 times OQA; clypeal height 1.57–2.13 times AM diameter; cheliceral length 4.64–6.11 times clypeal height; promargin of fang furrow with 6–7 teeth, retromargin of fang furrow with 5–6 teeth; sternum length 1.11–1.25 times width; femur I length 1.50–2.72 times carapace length; metatarsus I 1.18–2.46 times carapace length. Epigyna as in Figures 30D, F, 32A and 40B. Vulvae as in Figures 30A–C, E, 32B, E, and 40C–I: the number of spiral turns of the vulva duct varies from as few as four (specimens from Fianarantosa Province) (Figs 30E, 40D) to as many as ten (specimens from Antananarivo and Toamasina Provinces) (Figs 30C, 40E).

Natural history: This species makes retreats beneath stones, logs, and bark of standing or fallen trees. Webs comprise a sheet that extends out from this retreat (Fig. 2A).

Distribution: Known from rainforests and scattered forest patches along the eastern escarpment and highlands in central to south-central Madagascar, with extension to the isolated Forêt d'Ankazotsihitafototra in the west (Fig. 57).

Material examined: MADAGASCAR: **Antananarivo Prov.** 3 km 41° NE Andranomay, 11.5 km 147° SSE Anjozorobe, 18°28′24″S, 47°57′36″E, elev. 1300 m, montane rainforest, 5–13 December 2000, Fisher-Griswold Arthropod Team, 6 ♀, CASC (CASENT9019990, 9019993, 9019992, 9019991, 9004077, 9004111), 'beneath leaves of fallen Ravenala', 1 ♂, 1 ♀, CASC (CASENT9004080); Ambohimanga Village, 18°44′S; 47°34′E, December 1959, R.

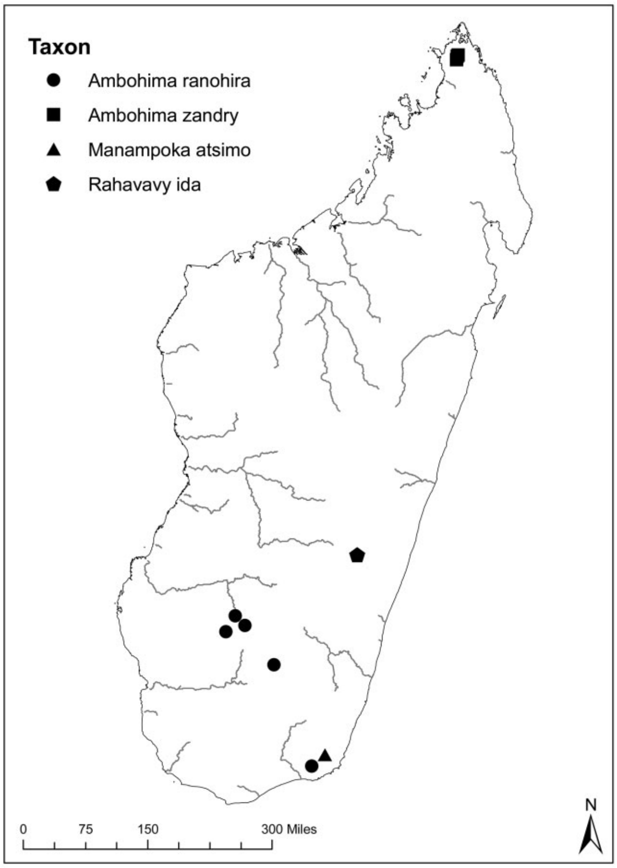

Figure 59. Distribution of Madagascar Phyxelididae.

Legendre, holotype ♂, paratype ♀, MNHN; Ambohimanga, 18°44′S, 34°47′E, elev. 1400 m, 1 November 1993, R. Andriamasamanana, J. Coddington, C. Griswold, S. Larcher & N. Scharff, 4 ♂ 15 ♀, CASC (CASENT9016224, 9016200, 9016220, 9016225, 9016218, 9016204, 9016217, 9016202, 9016299, 9016198, 9016203, 9016205), 1 ♂ 2 ♀, ZMUC (CASENT9016221), 1 ♂ 1 ♀, USNM (CASENT9016201, 9016219), from beneath stone, with eggs, 1 ♀, CASC (CASENT9016222); Ambohimanga, 18°44′S, 34°47′E, elev. 1400 m, 2 December 1993, C. Griswold, 1 ♂, 2 ♀, CASC (CASENT9020323); Ambohimanga, 18°44′S, 34°47′E, elev. 1400 m, 2 December 1993 (moulted in captivity), C. Griswold, 3 ♂, CASC (CASENT9016226, 9016227, 9016227); Ambohimanga, June, J. Millot, 1 ♀, MNHN; Forêt Mangidy, July 1941, J. Millot, 1 ♀, MNHN (CASENT9025740); R. S. d'Ambohitantely, primary forest, *c.* 20.9 km 72° NE d'Ankazobe, 18°13′30.3″S, 47°16′44″E, elev. 1574 m, montane rainforest, 19 March 2003, D. Andriamalala & D. Silva, 1 ♀, CASC (CASENT9015040); Forêt d'Ambohitantely, July 1941, J. Millot, 1 ♀, MNHN (CASENT9016212); Angavokely, November 1946, J. Millot, 1 ♀, MNHN (CASENT9032844); Gr. Angavokely, 1946, J. Millot, 7 ♀, MNHN (CASENT9016208, 9016209, 9016211, 9016210); Angavokely, grotte de la reine, 1946, J. Millot, 1 ♀, MNHN (CASENT9016207). **Fianarantsoa Prov.** Parc National Ranomafana, Talatakely forest, 42.3 km 58° NE Fianarantsoa, 21°15′28.0″S, 47°25′21.8″E, elev. 1050 m, general collecting in montane rainforest, 24 December 2005–14 January 2006, H. Wood, J. Miller, J.J. Rafonomezantsoa, E. Rajeriarison, and V. Andriamananony, 3 ♀, CASC (CASENT9024053, 9024052, 9024485); Talatakely forest, 42.3 km 58° NE Fianarantsoa, 21°15′28.0″S, 47°25′21.8″E, elev. 1050 m, montane rainforest, general collecting day and night, 24 December 2005–14 January 2006, H. Wood, J. Miller, J.J. Rafonomezantsoa, E. Rajeriarison, V. Andriamananony, 1 ♂, CASC (CASENT9022484); Talatakely, 21°14.9′S, 47°25.6′E, 9–30 April 1998, C. Griswold, D. Kavanaugh, N. Penny, D. Ubick, M. Raherilalao, J. Schweikert & S. Ranorainarisoa, 3 ♀, CASC (CASENT9016997, 9016994); Talatakely, 21°14.9′S, 47°25.6′E, 9–30 April 1998, C. Griswold, D. Kavanaugh, N. Penny, D. Ubick, M. Raherilalao, J. Schweikert & S. Ranorainarisoa, 1 ♂, 6 ♀, CASC (CASENT9016997, 9016994, 9016992, 9016994, 9016993, 9017000); Talatakely, 21.25041°S, 47.41945°E, elev. 900 m, 2–22 January 2001, D. & K. Kavanaugh, R. Brett, E. Elsom & F. Vargas, 1 ♀, CASC (CASENT9003502); 7 km W Ranomafana, elev. 900 m, *c.* 21°12′S, 47°27′E, 20–31 January 1990, W. E. Steiner, 1 ♂, USNM, 7 km W Ranomafana, elev. 1100 m, 1–7 November 1988, W. E. Steiner, 1 ♂, USNM; Parc National Ranomafana, Talatakely, 21°15′S, 47°25′E, elev. 900 m, 5–7 December 1993, R. Andriamasamanana, C. Griswold, S. Larcher & N. Scharff, 2 ♀, CASC (CASENT9016189, 9016192), 1 ♀, USNM (CASENT9016190), 1 ♀, ZMUC (CASENT901688); Parc National Ranomafana, Vohiparara, 21°14′S, 47°24′E, elev. 900 m, 5–7 December 1993, R. Andriamasamanana, C. Griswold, S. Larcher & N. Scharff, 1 ♀, CASC (CASENT9016191); Parc National Ranomafana, Vohiparara, Sahamalaotra forest, 41.1 km 54° NE Fianarantsoa, 21°14′19.9″S, 47°23′39.2″E, elev. 1200 m, montane rainforest, general day collecting, 26 December 2005–14 January 2006, H. Wood, J. Miller, J.J. Rafonomezantsoa, E. Rajeriarison, & V. Andriamananony, 1 ♀, CASC (CASENT9024826); Parc National Ranomafana, c. 2 km N Vohiparara village, 21°14.8′S, 47°25.7′E, at road cut, 11–12 April 1998, C. Griswold, D. Kavanaugh, N. Penny, D. Ubick, M. Raherilalao, J. Schweikert & S. Ranorainarisoa, 3 ♀, CASC (CASENT9016999, 9016998, 9017001); Parc National Ranomafana, 2.3 km N Vohiparara village, 21°12.8′S, 47°23.0′E, elev. *c.* 1100 m, 24–25 April 1998, C. Griswold, D. Kavanaugh, N. Penny, D.

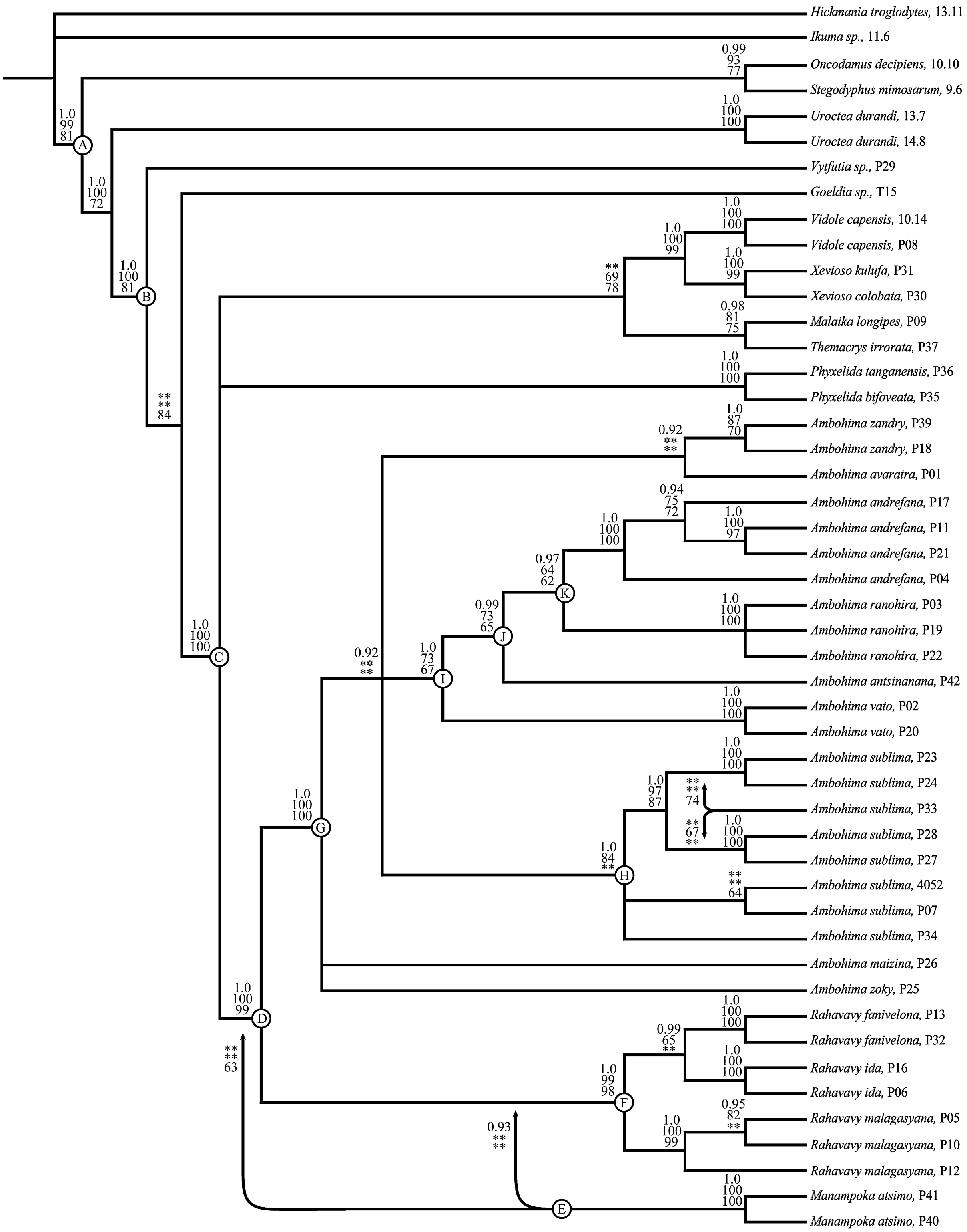

Figure 60. Summary phylogeny of Bayesian, maximum-likelihood (ML) and Parsimony analyses. Top, middle, and bottom numbers at nodes represent Bayesian posterior probabilities, ML bootstrap values, and parsimony bootstrap values, respectively. Circled numbers are nodes discussed in the text. We only reported branches with posterior probabilities above 0.90 and bootstrap values above 60; nodes with support below these values are labelled ** if partially supported or collapsed.

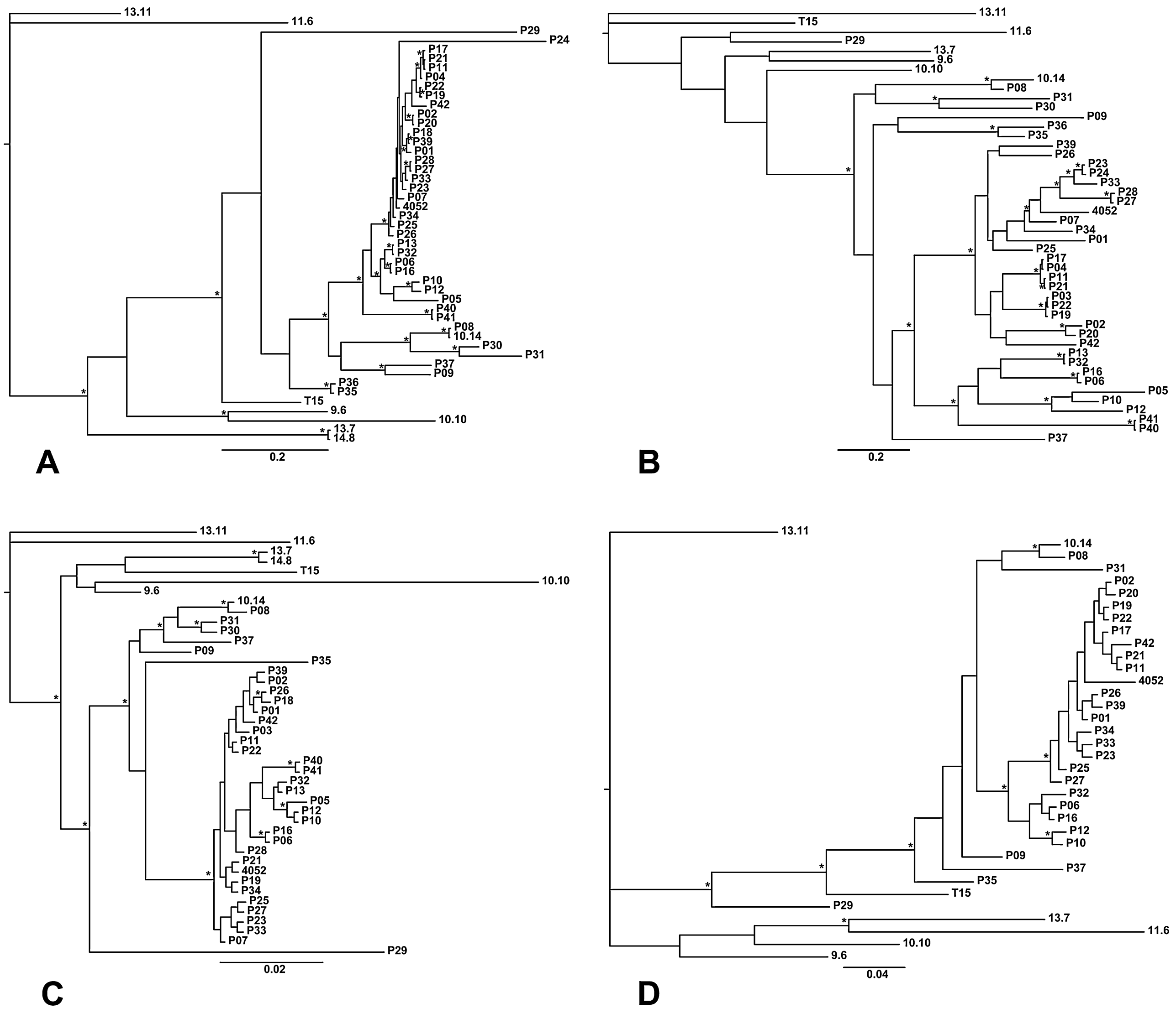

Figure 61. Single marker phylograms from Bayesian analyses. See Figure 60 for taxon names associated with specimen numbers. Posterior probabilities greater than or equal to 0.90 are labelled *. A, 28S. B, COI. C, 18S. D, H3.

Ubick, M. Raherilalao, J. Schweikert & S. Ranorainarisoa, 1 ♀, CASC (CASENT9017002); Parc National Ranomafana, Trail F, 29 April 1992, B. Roth, 1 ♀, MCZ (CASENT9016193). **Toamasina Prov.** Station Forestier Analamazaotra, administered by Mitsinjo, 0.75 km N Andasibe, 18°55.783′S, 48°24.696′E, elev. 964 m, general collecting day and night in primary montane rainforest, 31 January–3 February 2009, D. Andriamalala, C. Griswold, G. Hormiga, A. Saucedo, N. Scharff, and H. Wood, 4 ♀, CASC (CASENT9036009, 9029884, 9029884); Perinet, 18°56′S, 48°24′E, elev. 1000 m, 4–5 November 1993, R. Andriamasamanana, J. Coddington, C. Griswold, S. Larcher & N. Scharff, 2 ♀, CASC (CASENT 9016186, 9016187), 1 ♀, USNM (CASENT9016185), 1 ♀, ZMUC (CASENT9016184); Analamazaotra (Perinet) August 1945, J. Millot, 1 ♀, MNHN (CASENT9032845); Perinet, 18°55′S, 48°25′E, 1–3 August 1992, V. & B. Roth, 1 ♀, CASC (CASENT9016183); 60 mi. E Tana, 18°54′35″S, 47°55′28″E, elev. 1045 m, 1 August 1992, V. & B. Roth, 2 ♀, CASC (CASENT9016235), under edge of shaded road cut, 1 ♂, 2 ♀, CASC (CASENT9016232, 90162324, 9016233); 60 mi. W Moramanga, 18°54′44″S, 47°53′37″E, elev. 1300 m, 5 August 1992, V. & B. Roth, 2 ♀, CASC (CASENT9016179); 50 km W Moramanga, 18°54′35″S, 47°53′37″E, elev. 1300 m, 1 August 1992, V. & B. Roth, 2 ♀, CASC (CASENT9016181, 9016180). **Toliara Prov.** Rés. Spéciale d'Ambohijanahary, Forêt d'Ankazotsihitafototra, 35.2 km 312° NW Ambaravaranala, 18°16′00″S, 045°24′24″E, elev. 1050 m, general

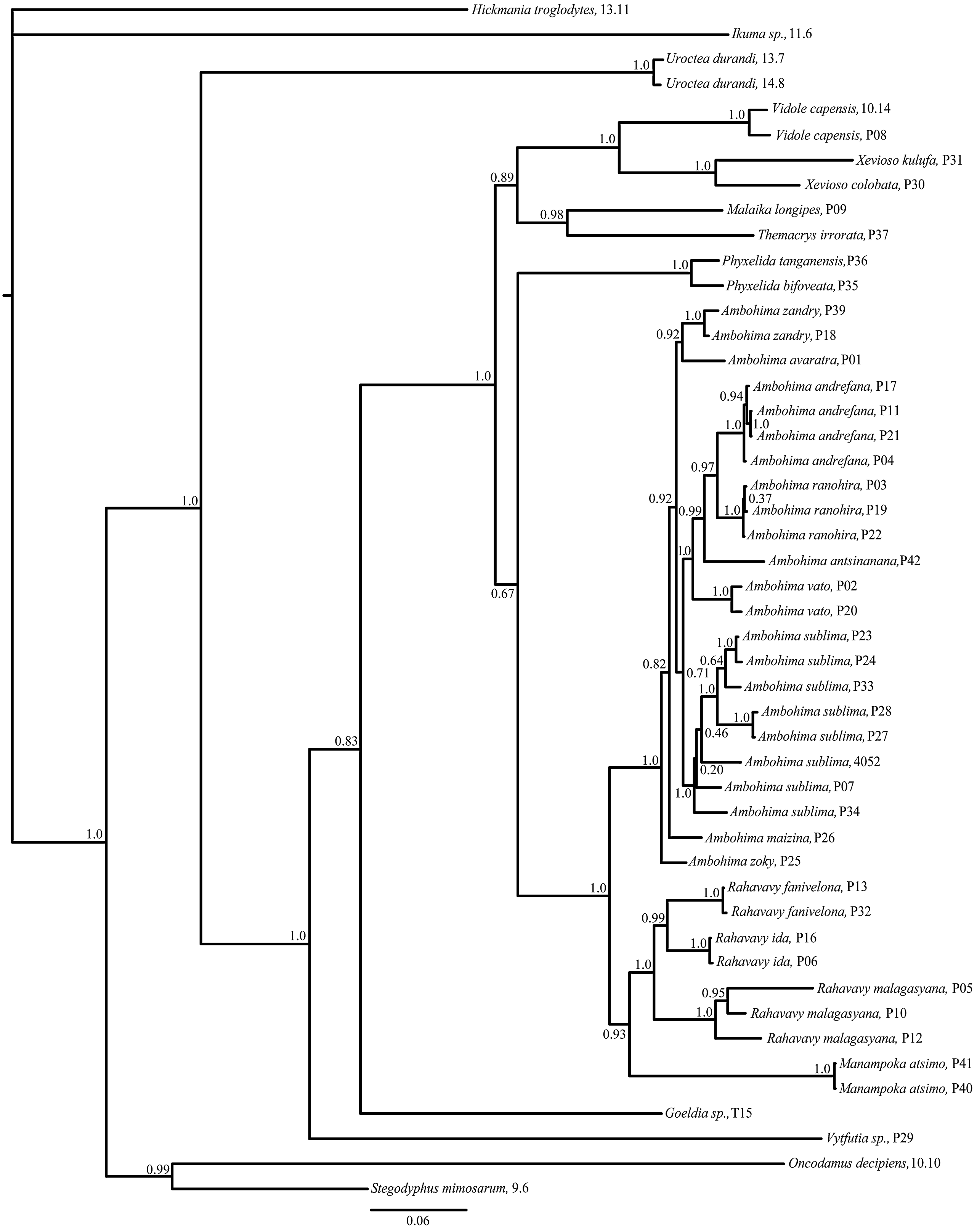

Figure 62. Concatenated four-gene phylogram from Bayesian analysis. Branch support values are shown as posterior probabilities.

collecting in montane rainforest, 13–17 January 2003, Fisher-Griswold Arthropod Team, 1 ♀, CASC (CASENT9018170).

AMBOHIMA VATO SP. NOV.
(FIGS 6C, 7C, 14A–C, 33A–C, 36D, F, 37D, F, 43G–I, 58)

Types: Holotype male and paratype female (CASENT9020002) collected in montane rainforest at 1550 m elevation in Forêt d'Atsirakambiaty, 7.6 km 285° WNW Itremo, 20°35′36″ S, 046°33′48″ E, Fianarantsoa Province, Madagascar, 22–26 January 2003, C. Griswold, D. Silva, and J. J. Rafonomezantsoa, deposited in CASC.

Etymology: The specific name is from the Malagasy word for rock; a noun in apposition.

Diagnosis: Male with palp as in Figure 14A–C, embolic base with a raised, distal cone, cymbium small, cymbium length less than 0.75 times carapace length; palpal tibial prolateral hook short and broad. The cymbial length of *A. vato* overlaps with that of some *A. sublima* specimens from Fianarantsoa Province, but males of *A. vato* may be distinguished by their smaller size and shorter legs, femur I length less than 2.5 times carapace length (compare Fig. 6C with 6F). Female vulva as in Figures 33B and 37D, F, base bilobed, anteriorly with three or fewer tight, transverse coils.

Note: Individuals from the Itremo massif resemble *A. sublima* in male and female genitalia such that diagnosis is difficult. The molecular phylogeny places these in a species group distant from *A. sublima* so that we describe the new species *A. vato* to accommodate the Itremo population.

Male (Holotype): Total length 6.70. Markings similar to Figure 6C. Carapace 3.10 long, 2.40 wide; thoracic fovea 0.60 long, length 0.19 carapace; clypeus 0.28 high; ocular area 0.37 long, 0.89 wide; ratio of eyes AM/AL/PM/PL, 1.06:2.40:1.26:1.00, diameter of PM 0.19. Chelicerae 1.32 long, slender, smooth, promargin of fang furrow with six teeth, retromargin with four large and one minute teeth. Sternum 1.94 long, 1.64 wide; labium 0.74 long, 0.64 wide; palpal coxa 1.26 long, 0.50 wide. Legs elongate, femur I length 2.29 times carapace length; metatarsi I and II prolateral concavity and clasping spines as in Figure 43G–I, segment slightly swollen basad of cavity. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [total]): I: 7.10 + 1.45 + 7.50 + 7.40 + 2.75 = [26.20]; II: 5.90 + 1.25 + 5.65 + 5.50 + 2.75 = [21.05]; III: 5.00 + 1.15 + 4.15 + 4.65 + 1.95 = [16.90]; IV: 6.40 + 1.25 + 6.05 + 6.70 + 2.45 = [22.85]; palp: 1.65 + 0.55 + 0.55 + (absent) + 1.95 = [4.70]. Palpal femur with probasal row of four thorn-like setae; tibia with dorsal blade (DTA) hatchet-shaped, prolateral hook (PTA) slender, blunt-tipped; cymbium length 1.80 times width, 0.63 length of carapace; palpal bulb as in Figure 14A–C, length 1.75 times width, embolus base with raised cone, reservoir course in embolus base strongly sinuate, space between embolus base and proximal embolic curve 1.15 times embolus base width.

Variation (N = 3): Total length 5.30–6.70; carapace length 1.26–1.29 times width, height 0.28–0.33 times width; PER width 2.22–2.54 times OAL; OQP 0.91–1.12 times OQA; cheliceral length 4.71–5.00 times clypeal height; retromargin of fang furrow with 5–6 teeth; sternum length 1.18–1.27 times width; femur I length 1.98–2.29 times carapace length; metatarsus I 1.76–2.39 times carapace length; cymbium length 0.63–0.73 times carapace length.

Female (Paratype): Total length 8.20. Markings as in Figure 7C. Carapace 3.50 long, 2.65 wide; thoracic fovea length 0.17 times that of carapace; clypeus 0.28 high; ocular area 0.42 long, 1.13 wide; ratio of eyes AM/AL/PM/PL, 1.33:2.73:1.13:1.00, diameter of PM 0.17. Chelicerae 1.42 long, robust, smooth, promargin of fang furrow with six teeth, retromargin with five teeth. Sternum 1.84 long, 1.48 wide; labium 0.72 long, 0.64 wide; palpal coxa 1.20 long, 0.54 wide. Femur I length 1.75 times carapace length. Palpal femur with four anterobasal thorns. Calamistrum origin at 0.50 from metatarsus base, length 0.30 that of segment. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [total]): I: 6.10 + 1.60 + 5.95 + 5.00 + 2.40 = [21.05]; II: 4.95 + 1.40 + 4.05 + 4.00 + 1.95 = [16.35]; III: 4.05 + 1.20 + 3.10 + 3.30 + 1.70 = [13.35]; IV: 5.15 + 1.30 + 4.40 + 4.50 + 1.90 = [17.25]; palp: 1.55 + 0.60 + 0.85 + (absent) + 1.85 = [4.85]. Epigynum as in Figure 36D; vulva as in Figure 37D, spermatheca with bilobed basal chamber and three tight distal spirals.

Variation (N = 4): Total length 6.30–8.20; carapace length 1.32–1.44 times width, height 0.34–0.42 times width; PER width 2.53–3.05 times OAL; OQP 1.10–1.34 times OQA; cheliceral length 4.56–5.25 times clypeal height; pro- and retromargins of fang furrow with 5–7 teeth; sternum length 1.13–1.24 times width; femur I length 1.59–1.74 times carapace length; metatarsus I 1.43–1.54 times carapace length; epigyna as in Figures 33A and 36D, F, vulvae as in Figures 33B and 37D, F.

Natural history: Spiders were collected in montane rainforest, where they make typical *Ambohima* webs, similar to Figure 2A, beneath bark or fallen objects on the ground.

Distribution: Known only from the type locality in a mountainous region of south-central Madagascar (Fig. 58).

Material Examined: MADAGASCAR: **Fianarantsoa Prov.,** Forêt d'Atsirakambiaty, 7.6 km 285° WNW Itremo, elev. 1550 m, 20°35′36″S, 046°33′48″E, montane rain forest, 22–26 January 2003, C. Griswold, D. Silva and J. J. Rafonomezantsoa, 1 ♂ holotype, 1 ♀ paratype (CASENT9020002), web in base of fallen palm frond, 1 ♀, CASC (CASENT9005810), together in web in fallen palm frond, 1 ♂, 1 ♀, CASC (CASENT9005809), 3 ♂ 4 ♀, CASC (CASENT9005936, 9017395, 9020003, 9017304, 9005975, 9016756, 9005552).

AMBOHIMA ZANDRY SP. NOV.
(FIGS 7F, 15A–E, 24A–E, 34E–I,
38E, F, 43J–L, 59)

Types: Holotype male and paratype female (CASENT9003543) collected by beating low vegetation in montane rainforest in Parc National Montagne d'Ambre, Antsiranana Province, Madagascar, 2–7 February 2001 by J. J. Rafonomezantsoa, deposited in CASC.

Etymology: The specific name is from the Malagasy word for a little one; a noun in apposition.

Diagnosis: Male with palp as in Figures 15A–C and 24A–E, embolic base convex, reservoir course across embolic base nearly straight. Female vulva as in Figures 15E, 34G, H, and 38E, F, spermathecal ducts spiralling around a central, longitudinal spiral chamber, ducts make three or fewer spiral turns.

Male (Holotype): Total length 3.80. Markings similar to Figure 7F, carapace pale yellow-brown, markings faint, legs unmarked; abdomen grey-brown, dorsum with obscure paired light markings. Carapace 1.85 long, 1.50 wide; thoracic fovea 0.22 long, length 0.12 times that of carapace; clypeus 0.10 high; ocular area 0.26 long, 0.56 wide; ratio of eyes AM/AL/PM/PL, 1.30:2.40:1.00:1.10, diameter of PM 0.10. Chelicerae 0.74 long, slender, smooth, pro- and retromargins of fang furrow with six teeth. Sternum 1.06 long, 0.90 wide; labium 0.30 long, 0.34 wide; palpal coxa 0.56 long, 0.30 wide. Legs long, femur I length 1.56 times carapace length; metatarsi I and II prolateral concavity and clasping spines as in Figure 43J–L, segment cylindrical at base of concavity. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [total]: I: 2.90 + 0.70 + 2.85 + 2.55 + 1.30 = [10.30]; II: 2.30 + 0.75 + 2.20 + 1.90 + 1.05 = [8.20]; III: 1.90 + 0.65 + 1.55 + 1.70 + 0.90 = [6.70]; IV: 2.60 + 0.70 + 2.35 + 2.50 + 1.05 = [9.20]; palp: 0.75 + 0.35 + 0.25 + (absent) + 0.75 = [2.10]. Palpus as in Figures 15A–C and 24A–E; femur with basal triangular group of eight thorn-like setae; tibia with dorsal blade (DTA) broadened distally, prolateral hook (PTA) short; cymbium length 1.60 times width, 0.40 times carapace length; palpal bulb length 1.50 width, embolic base convex, reservoir course across embolic base nearly straight.

Variation (N = 2): Carapace length 1.23–1.27 times width, height 0.30–0.40 times width; PER width 2.15–2.48 times OAL; OQP 1.21–1.30 times OQA; cheliceral length 5.50–7.40 times clypeal height; sternum length 1.13–1.18 times width.

Female (Paratype): Total length 3.70. Markings similar to Figure 7F. Carapace 1.70 long, 1.25 wide; thoracic fovea short, broad, length 0.08 that of carapace; clypeus 0.10 high; ocular area 0.20 long, 0.56 wide; ratio of eyes AM/AL/PM/PL, 1.37:2.62:1.00:1.12, diameter of PM 0.08. Chelicerae 0.72 long, robust, smooth, pro- and retromargins of fang furrow with five teeth. Sternum 0.90 long, 0.82 wide; labium 0.30 long and wide; palpal coxa 0.52 long, 0.24 wide. Femur I length 1.17 times carapace length. Palpal femur with row of five anterobasal thorns. Calamistrum origin at about 0.35 from metatarsus base, length 0.40 that of segment. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [total]): I: 2.00 + 0.65 + 1.80 + 1.55 + 0.95 = [6.95]; II: 1.55 + 0.55 + 1.20 + 1.20 + 0.80 = [5.30]; III: 1.30 + 0.40 + 1.00 + 1.00 + 0.70 = [4.40]; IV: 1.80 + 0.55 + 1.40 + 1.40 + 0.80 = [5.95]; palp: 0.70 + 0.30 + 0.40 + (absent) + 0.70 = [2.10]. Epigynum similar to Figure 15D; spermathecal ducts spiralling around a central, longitudinal spiral chamber, outer ducts make two spiral turns (Fig. 38F).

Variation (N = 5): Total length 3.70–4.10; carapace length 1.33–1.38 times width, height 0.37–0.44 times width; PER width 2.41–2.90 times OAL; OQP 1.23–1.36 times OQA; cheliceral length 5.50–7.20 times clypeal height; promargin of fang furrow with 5–7 teeth, retromargin of fang furrow with 5–6 teeth; sternum length 1.10–1.16 times width; femur I length 1.18–1.34 times carapace length; metatarsus I 1.08–1.11 times carapace length; median lobe of epigynum triangular to nearly trapezoidal, outer vulval ducts make 2–3 spiral turns (Figs 15E, 34G, H, 38E, F).

Natural history: Found on or near the ground in montane rainforest.

Distribution: Known only from Montagne d'Ambre in far northern Madagascar (Fig. 59).

Material examined: MADAGASCAR: **Antsiranana Prov.** P. N. Montagne d'Ambre, 2.79 air km NE of park entrance, 12°32′S, 49°10′E, elev. *c.* 1000 m, forest, 21–30 November 1993, C. Griswold, S. Larcher, R. Andriamasamanana, N. Scharff and J. Coddington, 2 ♀, CASC (CASENT9017021, 9017022), 1 ♀, ZMUC (CASENT9017019), 1 ♀, USNM (CASENT9017020); Parc Nationale Montagne d'Ambre, 12.2 km 211° SSW Joffreville, 12°35′47″S, 49°9′34″E, elev. 1300 m, pitfall trap in montane rainforest, 2–7 February 2001, Fisher-Griswold Arthropod Team, 1 ♂, CASC (CASENT9006874); Montagne d'Ambre, 12°30′57″S, 49°11′04″E, 12 August 1992, V and B. Roth, 1 ♀, CASC (CASENT9017023), beating low vegetation in montane rainforest, 2–7 February 2001, J. J. Rafanomezantsoa, holotype ♂, paratype ♀, CASC (CASENT9003543).

AMBOHIMA ZOKY SP. NOV.

(FIGS 6D, 7G, 16A–E, 25A–F, 33D–F, 36A, E, 37A, E, 43M–O, 57)

Types: Holotype male (CASENT9017018) from 7 km SE Antsiranana, Antsiranana Province, Madagascar, collected 17 August 1992 by Vince and Barbara Roth, deposited in CASC.

Etymology: The specific name is from the Malagasy word for big one; a noun in apposition.

Diagnosis: Male with palp as in Figures 16A–C and 25A–F, embolic base convex, reservoir course across embolic base sinuate, embolus base narrow, width about equal to embolic loop, narrower than width of exposed conductor between embolic base and proximal turn of embolus. Female vulva as in Figures 16E, 33E and 37A, E, spermathecal base simple, apex a tight corkscrew coil.

Male (Holotype): Total length 8.13. Markings as in Figure 6D. Cephalothorax and legs pale yellow-brown, abdomen grey-brown, dorsum with anterior light longitudinal mark. Carapace 3.36 long, 2.54 wide; thoracic fovea 0.53 long, length 0.15 times that of carapace; clypeus 0.17 high; ocular area 0.50 long, 1.03 wide; ratio of eyes AM/AL/PM/PL, 1.10:1.40:1.00:1.10, diameter of PM 0.20. Chelicerae 1.33 long, slender, smooth, pro- and retromargins of fang furrow with five teeth. Sternum 1.84 long, 1.53 wide; labium 0.74 long, 0.58 wide; palpal coxa 1.19 long, 0.47 wide. Legs elongate, femur I length 2.42 times carapace length; metatarsi I and II prolateral concavity and clasping spines as in Figure 43M–O, segments cylindrical basad of concavity. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [total]): I: 8.11 + 1.69 + 8.44 + 7.88 + 3.19 = [29.31]; II: 6.50 + 1.56 + 6.25 + 5.94 + 2.50 = [22.75]; III: 5.50 + 1.25 + 4.56 + 5.00 + 2.13 = [18.44]; IV: 7.19 + 1.56 + 6.50 + 7.06 + 2.50 = [24.81]; palp: 1.69 + 0.56 + 0.81 + (absent) + 1.44 = [4.50]. Palp as in Figures 16A–C and 25A–F; femur with probasal row of five thorn-like setae; tibia with dorsal blade (DTA) broad apically, prolateral hook (PTA) long, tapering to acute point; cymbium length 1.40 times width; palpal bulb length 1.45 times width, embolic base convex, reservoir course across embolic base sinuate, embolus base narrow, width about equal to embolic loop, narrower than width of exposed conductor between embolic base and proximal turn of embolus.

Female (Montagne d'Ambre, CASENT9020320): Total length 9.70. Markings as in Figure 7G. Carapace 4.30 long, 2.90 wide; thoracic fovea length 0.14 times that of carapace; clypeus 0.32 high; ocular area 0.53 long, 1.36 wide; ratio of eyes AM/AL/PM/PL, 1.40:3.40:1.06:1.00, diameter of PM 0.16. Chelicerae 1.82 long, robust, smooth, pro- and retromargins of fang furrow with seven teeth. Sternum 2.16 long, 1.76 wide; labium 0.86 long, 0.76 wide; palpal coxa 1.40 long, 0.68 wide. Femur I length 1.40 times carapace length. Palpal femur with row of three anterobasal thorns. Calamistrum origin at 0.45 from metatarsus base, length 0.45 that of segment. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [total]): I: 6.00 + 1.65 + 5.45 + 5.10 + 2.50 = [20.70]; II: 4.90 + 1.50 + 3.90 + 3.75 + 1.95 = [16.00]; III: 4.00 + 1.25 + 2.90 + 3.20 + 1.60 = [12.95]; IV: 5.15 + 1.45 + 4.40 + 4.30 + 1.85 = [17.15]; palp: 1.70 + 0.70 + 1.00 + (absent) + 1.90 = [5.30]. Epigynum as in Figure 36A; vulva as in Figure 37A, spermathecal base simple, apical coil of spermatheca makes two open spirals.

Variation (N = 5): Total length 8.00–10.80; carapace length 1.38–1.48 times width, height 0.30–0.45 times width; PER width 2.41–2.62 times OAL; OQP 1.08–1.15 times OQA; clypeal height 1.53–2.13 times AM diameter; cheliceral length 5.41–6.77 times clypeal height; promargin of fang furrow with 6–7 teeth, retromargin of fang furrow with 5–7 teeth; sternum length 1.21–1.26 times width; femur I length 1.40–1.51 times carapace length; metatarsus I length 1.19–1.33 times carapace length; epigyna as in Figures 16D, 33D and 36A, E, vulvae is in Figures 16E, 33E, F and 37A, E.

Natural history: Unknown.

Distribution: Known only from far northern Madagascar (Fig. 57).

Material examined: MADAGASCAR: **Antsiranana Prov.** Montagne d'Ambre, 12°30′57.6″S, 49°11′04.8″E, 12 August 1992, V. & B. Roth, 7 ♀, CASC (CASENT9020320, 9017017, 9017014, 9017016, 9017015); 7 km SE Antsiranana, 12°19′58″S, 49°17′39″E, 17 August 1992, V. & B. Roth, holotype ♂, CASC (CASENT9017018).

MANAMPOKA GEN. NOV.

Type species: Manampoka atsimo sp. nov., here designated.

Etymology: The generic name is from the Malagasy verb meaning to surprise, and is feminine in gender.

Note: These large phyxelidids resemble *Ambohima* but possess a mosaic of derived characters. Like other Malagasy phyxelidids the male metatarsal claspers are prolateral (Fig. 44A–C), not retrolateral, as in African and Asian phyxelidids. The presence of a clasper on male metatarsus II is a potential synapomorphy shared with *Ambohima* and the female vulva (Fig. 26H) with an anterodorsally projecting capsule containing an internal spiral chamber is a potential synapomorphy with *Rahavavy*. In some molecular phylogenetic analyses this species grouped with *Rahavavy*, but never with high support values, and it never grouped with *Ambohima*. As morphological data are equivocal, we propose a separate, new genus for this surprising species.

Diagnosis: Males have a unique combination of characters: the palpal bulb (Figs 17A–C, 26A–F) has a small median apophysis (like *Rahavavy* but unlike *Ambohima*) and male metatarsi II (Fig. 44A–C) and probably I (legs I are missing from the unique male) have a prolateral, spinule-lined concavity at midsegment, with a short, prolateral process surmounted by a stout clasping spine at the base of this concavity (like *Ambohima* but unlike *Rahavavy*). The female vulva (Fig. 26H) is like that of most *Rahavavy* in having an anterodorsally projecting capsule containing an internal spiralled chamber. The epigynum (Fig. 26G) differs from *Ambohima* in that the anterior margins of the median lobe are transverse rather than oblique, and from *Rahavavy* in that the external copulatory openings are large and the median lobe is prolonged posteriorly.

Synapomorphies: The cuspule-like median apophysis on the male palpal bulb (Figs 17A, C, 26B) and male palpal tibia with a retrolateral lobe of the apex (RL) that is longer than the dorsal tibial apophysis (DTA) (Fig. 26D) are synapomorphies for *Manampoka*.

Description: Total length 5.40–7.00. Carapace length 1.30–1.38 times width, height 0.30–0.49 width, thoracic fovea length twice width, length 0.06–0.20 carapace length; PER straight to slightly recurved, AER straight, ocular area width 2.50–3.10 times length; clypeal height 1.40–2.20 times AM diameter; chelicerae smooth, length 4.60–5.50 times clypeal height, with small basal boss, pro- and retromargins of fang furrow with 5–7 heterogeneous teeth; sternum length 1.02–1.36 times width, posterior apex a blunt point; labium rectangular. Legs elongate, female femur I length 1.70–2.00 times carapace length, male femur II 2.40 times carapace length; leg formula 1423; male metatarsi II (Fig. 44A–C) (and probably I) having prolateral, spinule-lined concavity at midsegment, at base of concavity a short, prolateral process surmounted by stout clasping spine, legs otherwise unmodified; metatarsi lacking apical combs; calamistrum subapical, origin at 0.45 from metatarsus base, length 0.55 that of segment. Male spination: palp: femur d0-0-0-1; leg I: (unknown); leg II: femur d1-1-0-0, p0-1-1-1, r0-1-1–1, tibia p0-1-1-0, r0-1-1-1, metatarsus d1-0-0-0, p0-1(clasper)-0–1, v2-0-0-1, r0-0-0-1; leg III: femur d1-1-0-0, p0-0-1–1, r0-1-1–1, patella d0-1, tibia d1-0-0-0, p0-1-1-0, r0-0-0-1, metatarsus d1-0-0-0, p0-1-0-1, v1-2-0-2; leg IV: femur d1-1-0-0, r0-0-0-1, tibia d1-1-1-0, p0-0-1-0, v0-0-0-1, metatarsus d1-1-0-0, p0-0-0-1, r0-0-0-1, v1-0-1–1. Female spination: palp: femur d0-0-1–1, patella d0-0-1, tibia d0-0-0-1, p0-1-1-0, tarsus p1-0-2–2-3, v0-0-0-1-1-1-1-1-1, r1-0-0-1-0; leg I: femur d1-0-0-0, p0-1-1-1, r0-0-1–1, tibia p0-1-1-0, v0-0-2-0, r0-1-1-0, metatarsus p1-0-0-1, v1-0-2-2, r1-0-0-0; leg II: femur d1-1-1-0, p0-1-1–1, r0-1-1–1-1, tibia d1-0-0-0, p0-1-1-0, v0-1-0-2, r0-1-1-0, metatarsus p1-0-0-1, v0-0-2–2, r0-1-0-0; leg III: femur d1-1-0-0, p0-0-0-1, r0-0-0-1, tibia d1-0-0-0, p0-1-1-0, v0-1-0-2, r0-1-1-0, metatarsus p0-1-1–1, v2-0-2–2, r0-1-1-0; leg IV: femur d1-1-1-0, r0-0-0-1, tibia p0-1-1-0, v0-0-0-2, r0-1-1-0, metatarsus p0-1-0-0, v1-2-1–2. Tracheae not examined. Spinnerets not examined with SEM but light microscopic examination suggests that these are typical of Phyxelidini, e.g. divided cribellum, an encircling row of paracribellar spigots on the PMS, and a black, stout seta retroapically on the PLS. Palpal femur with anterobasal group of slender setae set in enlarged bases (Fig. 26F); male palpal tibia (Fig. 26D, E) with dorsoapical blade (DTA) and retroapical lobe (RL); palpal bulb (Figs 17A–C, 26A–C) length twice width, embolus base retromedian, reservoir course in embolus base straight except initial loop, embolus a slender thread-like spine, lamellar pars pendula slender, conductor greatly hypertrophied, with embolic groove completely encircling bulb, apex pointing retrolaterally; median apophysis a small, pointed cuspule, arising retromedially near embolus base. Epigynum (Fig. 26G) with broad, semicircular median lobe (ML), anterior margins transverse, copulatory openings large; vulva (Fig. 26H, I) with copulatory ducts arising mesally, extending laterally to enter vulval capsule posteriorly, large poreplate posteriorly on vulval capsule, anterodorsally projecting capsule containing internal spiral chamber, fertilization duct posterior.

Composition: One species.

Distribution: Known only from the type locality in Parc National Andohahela, southern Madagascar (Fig. 59).

MANAMPOKA ATSIMO SP. NOV.

(FIGS 8A–G, 17A–C, 26A–I, 44A–C, 59)

Types: Holotype male and two paratype females (CASENT9031164) from primary montane rainforest at 670 m elevation in Parc National Andohahela, Parcelle I, Manangotry, Toliara Province, Madagascar, collected between 23 December 2008 and 3 January 2009 by Fernando Álvarez-Padilla and Hannah Wood, deposited in CASC.

Etymology: The specific name is from the Malagasy word for south; a noun in apposition.

Diagnosis: By the characters of the genus.

Male (Holotype): Total length 5.60. Markings as in Figure 8F, G. Carapace light orange-brown, margin of pars thoracica dusky, with broad, dusky, V-shaped mark anteriad of thoracic fovea and dusky longitudinal band on each side extending anteriorly along pars cephalica, with dusky reticulations laterad of eyes; black pigment surrounding each eye and extending between AM and between lateral eyes; chelicerae, sternum, labium, coxae, legs, and palpi pale yellow-brown; abdomen dark grey, dorsum with median light band and four pairs of light spots. Carapace 2.60 long, 2.00 wide; thoracic fovea 0.50 long, length 0.19 times that of carapace; clypeus 0.20 high; ocular area 0.35 long, 0.80 wide; ratio of eyes AM/AL/PM/PL, 1.46:2.61:1.07:1.00, diameter of PM 0.14. Chelicerae 1.00 long, slender, smooth, promargin of fang furrow with four small and three large teeth, retromargin with seven small teeth. Sternum 1.50 long, 1.10 wide; labium 0.50 long, 0.44 wide; palpal coxa 0.84 long, 0.40 wide. Legs elongate, leg I absent from specimen, femur II length 2.49 times carapace length; metatarsi II with prolateral concavity and clasping spine (Fig. 44A–C). Note: As all other Malagasy phyxelidids have at least leg I with a prolateral clasping concavity and spine, we assume that such a clasper occurs on metatarsus I of this species as well. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [total]): I: [missing]; II: 6.25 + 1.10 + 6.00 + 5.70 + 2.40 = [21.45]; III: 5.10 + 1.00 + 4.35 + 4.70 + 1.90 = [17.05]; IV: 6.50 + 1.05 + 6.20 + 6.50 + 2.35 = [22.60]; palp: 1.65 + 0.55 + 0.70 + (absent) + 1.55 = [4.45]. Palpus as in Figures 17A–C and 26A–F; femur with five probasal thorn-like setae; tibia with dorsoapical blade (DTA) and retroapical lobe (RL); palpal bulb length 2 times width, embolus base retromedian, reservoir course in embolus base straight except initial loop, space between embolus base and proximal embolic curve 0.58 embolus base width; conductor one half bulb length, apex pointing retrolaterally; median apophysis a small, pointed cuspule, arising retromedially near embolus base.

Female (paratype): Total length 6.00. Markings as in Figure 8A–E, carapace orange-brown, shading to dusky laterally, pars cephalica shading anteriorly to red-brown; black pigment surrounding each eye and extending between lateral eyes; sternum, labium, and palpal coxa dusky red-brown; legs and palpi orange-brown; abdomen dark grey, dorsum with median longitudinal light band and four pair of light spots, venter with pair of faint longitudinal light bands. Carapace 2.85 long, 2.15 wide; thoracic fovea length 0.06 times that of carapace; clypeus 0.26 high; ocular area 0.34 long, 0.93 wide; ratio of eyes AM/AL/PM/PL, 1.25:3.16:1.00:1.00, diameter of PM 0.12. Chelicerae 1.20 long, robust, smooth, promargin of fang furrow with four small and two large teeth, retromargin with seven small teeth. Sternum 1.20 long, 1.18 wide; labium 0.56 long, 0.50 wide; palpal coxa 0.94 long, 0.40 wide. Palpal femur with three anterobasal thorns. Calamistrum origin at 0.45 from metatarsus base, length 0.55 times that of segment. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [total]): I: 4.75 + 1.15 + 4.65 + 4.10 + 1.95 = [16.60]; II: 3.70 + 1.00 + 3.20 + 3.00 + 1.50 = [12.40]; III: 3.00 + 0.95 + 2.50 + 2.45 + 1.30 = [10.20]; IV: 4.10 + 1.00 + 3.65 + 3.50 + 1.15 = [13.40]; palp: 1.40 + 0.50 + 0.50 + (absent) + 1.40 = [4.05]. Epigynum as in Figure 26G, anterior margins of median lobe transverse, external copulatory openings large; vulva as in Figure 26H, I, with anterodorsally projecting capsule containing internal spiral chamber.

Variation (N = 6): Total length 5.40–7.00; carapace length 1.32–1.38 times width, height 0.38–0.49 times width; PER width 2.53–3.10 times OAL; OQP 1.11–1.27 times OQA; clypeal height 1.67–2.17 times AM diameter; cheliceral length 4.58–5.40 times clypeal height, promargin of fang furrow with 6–7 teeth, retromargin of fang furrow with 5–7 teeth; sternum length 1.02–1.25 times width; femur I length 1.67–1.91 times carapace length; metatarsus I length 1.44–1.70 times carapace length.

Natural history: Recorded from primary montane rainforest.

Distribution: Known only from the type locality at Manangotry in Parc National Andohahela, far southern Madagascar (Fig. 59).

Material examined: MADAGASCAR: **Toliara Prov.,** Parc National Andohahela, Parcelle I, Manangotry, off route 118, 34 km N Tolagnaro, 24°44′35.0″S, 46°51′23.3″E, elev. 670 m, 23 December 2008–3 January 2009, primary montane rainforest, general collecting day and night, F. Álvarez-Padilla and H. Wood, holotype ♂ and 2 ♀ paratypes, CASC (CASENT9031164), 10 ♀, CASC (CASENT9031168, 9031167, 9031165, 9031166, 9031167, 9031168).

RAHAVAVY GEN. NOV.

Type species: ***Phyxelida fanivelona*** Griswold 1990, here designated.

Etymology: The generic name is from the Malagasy for sister, and is feminine in gender.

Note: Two Malagasy species were described in 1990 from females only and placed in the genus *Phyxelida*, i.e. *Phyxelida malagasyana* Griswold, 1990 and *Phyxelida fanivelona* Griswold, 1990. Results from the molecular analysis for an array of phyxelidid taxa (Fig. 60), and morphological data from the newly discovered males of these species, i.e. the prolateral position of the metatarsal clasping structure (Fig. 44D–I), reveal that they are not congeneric with *Phyxelida* but instead belong in a clade with other Malagasy phyxelidids. These species are herein transferred to the new genus *Rahavavy*.

Diagnosis: Male metatarsi I (Figs 44D–I, 51H, I) with prolateral, spinule-lined concavity at midsegment with short, prolateral process surmounted by stout clasping spine at base of concavity, male metatarsi II unmodified (unlike *Ambohima* and *Manampoka*); male palpal bulb (Figs 18C, 19A, 27D) with median apophysis (like *Manampoka* but unlike *Ambohima*); epigynum differs from *Ambohima* in that anterior margins of the median lobe are transverse rather than oblique, and from *Manampoka* in that the median lobe is short, extending slightly posteriorly (Fig. 35A, D, G); female vulva differs from *Ambohima* in being capsulate with internal chambers (Fig. 35C, E, H).

Synapomorphies: The male palpal tibia with a DTA that is inrolled and extending retroapically (Figs 20A, C, 28D, E) and stout, thorn-like setae on the palpal femora of both sexes (Figs 9F, 48A, 51D) are synapomorphies for *Rahavavy*.

Description: Total length 3.10–8.60. Markings differ significantly among species and are described under each species description. Carapace length 1.21–1.60 times width, height 0.30–0.56 width; thoracic fovea narrow oval, length 3–5 times width, strongly limited at least anteriorly and laterally, length 0.10–0.20 carapace length; PER straight to slightly recurved, AER straight, ocular area width 1.94–3.71 times length; clypeal height 1.06–2.29 times AM diameter; chelicerae smooth with fine scales laterally (Fig. 50E), with small boss (Fig. 50B), length 4.09–7.69 times clypeal height, pro- and retromargins of fang furrow with 5–7 heterogeneous teeth (Fig. 50C), cheliceral gland on flat cuticle, with numerous pores (Fig. 50F); sternum length 0.97–1.33 times width, apex a blunt point (Fig. 9F). Legs long to elongate, femur I 0.96–1.60 times carapace length; leg formula 1423; male metatarsi I (Figs 44D–I, 51H, I) with prolateral, spinule-lined concavity at midsegment, at base of concavity a short, prolateral process surmounted by stout clasping spine, legs otherwise unmodified; metatarsi lacking apical combs; calamistrum subapical, origin at 0.40–0.45 distance from metatarsus base, length about 0.5 times metatarsus length. Spination (based on males and females of *Rahavavy fanivelona*: differences observed in *R. ida* and *R. malagasyana* are noted in [brackets]). Male: palp: femur d0-0-0-0; leg I: femur d0-0-1-0, p0-0-1-1, r0-0-0-1, tibia p0-1-1-0[1], v1-0-0-2, r0-1-1-0, metatarsus p0-1-1(clasper)-1, v0-0-0-2, r0-1-0-0; leg II: femur d0-0-1-0, p0-0-1-1, r0-0-0-1, tibia p0-1-1-0, v2-1-2, r0-1-1-0, metatarsus p0-1-1-1, v0-2-1-2, r1-1-0-0; leg III: femur p1-1-0-0, tibia d1-0-0-0, p0-1-1-0, v1-0-0-2, r0-1-1-0, metatarsus p0-1-0-2, v2-2-0-1, r1-1-0-2; leg IV: femur d1-1-0-0, p0-0-0-1, r0-0-0-1, tibia p0-1-1-0, v1-0-0-2, r0-1-1-0, metatarsus d1-0-0-0, p0-0-1-2, v2-1-1-1, r0-0-0-2. Female: palp: femur d0-0-0-1, tibia p0-1-1-0, tarsus p1-0[1]-1-0, v0-0[1]-1-3-1[3]-2-2, r0[1]-0-2-0; leg I: femur d0-1-0-0, p0-1[0]-1-1, r0-1[0]-0-1[0], tibia p0-1-1-0[1], v1[0]-1[0]-2, r0-1-1-0, metatarsus p0-1-0-1, v2-1[2]-0-1, r0-1[0]-0-1[0]; leg II: femur d1[0]-1-0-0, p0-1-1-1, r0-1[0]-0-1[0], tibia d1[0]-0-0-0, p0-1-1-0, v2[0]-2[0]-2, r0-1-1-0, metatarsus p1-1-0-2, v0-2-2[1]-1, r1-1-0-2; leg III: femur d0-1[0]-0-0, p0-0-1-1, r0-0-0-1, patella d0-0-1[0], tibia d1[0]-0-0-0, p0-1-1-0, v1[0]-1-2, r0-1-1-0, metatarsus p1-1-0-2, v2-0-2-1, r1-1-0-2; leg IV: femur d1-0[1]-1[0]-0, p0-0-0-1[0], r0-0-0-1, tibia d1-0-0-0, p0-1-1-0, v1[0]-1[0]-2, r0-1-1-0, metatarsus p1-0-0-2, v1[0]-0[2]-0-1, r1-0-0-2. Abdomen dorsal markings as in Figure 9A–D, G, I, with median longitudinal line or marks and lateral spots or posterior chevrons dorsally, venter with longitudinal bands narrow and entire. Male epiandrum with two bunches of spigots, about 20 on each side (Fig. 50A, D). Tracheae (examined in penultimate males of *Rahavavy malagasyana*, CASENT9005755) with simple lateral and median branches. Spinnerets (based on *R. fanivelona*, whose organs are typical of the genus): female (Figs 54A–F, 55A–F), male (Fig. 56A–F): with cribellum divided (Fig. 54D), more than two-thirds as wide as the base of the ALS, but very short (width greater than 10 times cribellum length), with uniformly distributed strobilate cribellar spigots (Fig. 54C); cribellar spigots replaced by nubbins in male (Fig. 56D); female ALS with two large MAP spigots with squat bases and long, tapering shafts on mesal margin (Fig. 55D), these separated from remainder of spinning field by shallow fold, with large tartipore situated on opposite side of fold; field of at least 36 PI spigots with rounded bases with concentric ridges (Fig. 55A), with a rounded margin between the base and shaft, and long, tapering shafts with longitudinal ridges; at least 20 small tartipores are scattered throughout PI spigot field; male ALS (Fig. 56B) similar except posterior MAP spigot reduced to nubbin and with fewer PI spigots (about 27) and small tartipores (fewer than 16); female PMS (Fig. 54B, E) with at least 15 PC spigots with strobilate shafts crowded together to encircle the anterior margin of the spinneret (Fig. 54B), replaced by nubbins in the male (Fig. 56F), one anteromedian mAP spigot with large, squat base and slender shaft (Fig. 55C), replaced by a nubbin in male (Fig. 56C, F), at least nine AC spigots, and a posterior CY spigot with a large, conical base and nearly cylindrical shaft; male lacks any vestige of CY spigot, and has fewer AC spigots (Fig. 56C, F); female mAP spigot is accompanied by two mesal nubbins; the male mAP nubbin has another small nubbin mesad of it; PLS of both sexes with large, stout, curved seta (black when viewed with light microscopy) at ectal margin; female PLS (Fig. 55B, E, F) with large anterior MS spigot with cylindrical base and shaft, accompanied by two flanking nubbins, MS replaced by single large nubbin in male (Fig. 56E); female has two CY spigots, anterior and basal, which have large, conical bases and tapering shafts, at least 14 AC spigots, and at least five small tartipores; male (Fig. 56E) lacks CY spigots, and has fewer AC spigots (nine) and tartipores (three or fewer). Palpal femur with anterobasal row of 5–8 stout setae set in enlarged bases, these setae shortened and enlarged as thorns (Figs 48A, 51D); male palpal tibia (Figs 20A, C, 28D, E) with inrolled DTA extending retroapically, RL weakly developed; palpal bulb (Fig. 45A, B) with petiole not apparent, anneli of subtegulum weakly developed, tegulum central, convex, oval, course of reservoir a simple curve within bulb, without switchbacks, median apophysis present, fleshy, arising at mid-bulb near embolic base; embolus slender, ranging from a narrow tapering blade to a thread-like spine, lamellar pars pendula accompanying embolus, conductor hypertrophied, with embolic groove completely encircling bulb, apex (CA) directed mesad or laterad, blunt to pointed (Figs 27A–D, 29A–E). Epigynum (Fig. 35A, D, G) with broad, oval to trapezoidal median lobe (ML), copulatory openings large, slit-like or hidden beneath recurved lateral transverse ridges (LTR); vulva complex, with capsulate structures(s) with internal chambers (Fig. 35B, C, E, F, H, I).

Composition: Three species.

Distribution: Madagascar (Figs 58, 59).

RAHAVAVY FANIVELONA (GRISWOLD, 1990) **COMB. NOV.** (FIGS 9D–F, 18A–C, 27A–D, 35A–C, 41C, D, 44D, E, 45A, B, 50A–F, 51A–I, 54A–F, 55A–F, 56A–F, 58)

Phyxelida fanivelona Griswold 1990: 182; Platnick 2011.

Types: Holotype and two paratype females from Fanivelona (Ambinanysakaleona), 20°32′S, 48°33′E, Fianarantsoa District, Madagascar (September; no collector data), deposited in AMNH, examined.

Diagnosis: Male with palp as in Figures 18A–C and 27A–D, bulb short, length less than 1.5 times width, cymbium projects retrolaterally beyond bulb, conductor apex pointed, reflexed back toward centre of bulb, median apophysis slender, cylindrical, length greater than five times width. Epigynum as in Figures 35A and 41C, ML oval, width about twice length, copulatory openings exposed, large, round, LTR recurved; spermathecae as in Figures 35B, C and 41D, each trilobed, copulatory ducts median.

Male (Vohiparara, CASENT9016960): Note: the male is described here for the first time. Total length 4.90. Markings similar to Figure 9D–F, carapace orange-brown, margin of pars thoracica dusky, with broad, dusky, V-shaped mark anteriad of thoracic fovea and dusky longitudinal band on each side extending anteriorly along pars cephalica; black pigment surrounding each eye and extending between AM and between lateral eyes; chelicerae, sternum, labium, coxae, legs, and palpi yellow-brown, legs unmarked; abdomen grey-brown, dorsum with paired dark markings posteriorly, venter with pair of bold, entire, longitudinal light bands. Carapace 2.20 long, 1.60 wide; thoracic fovea 0.22 long, length 0.14 times that of carapace; clypeus 0.14 high; ocular area 0.32 long, 0.62 wide; ratio of eyes AM/AL/PM/PL, 1.09:2.54:1.00:1.27, diameter of PM 0.11. Chelicerae 0.76 long, slender, smooth, promargin of fang furrow with two small and three large, retromargin with seven small teeth. Sternum 1.14 long, 1.00 wide; labium 0.34 long and wide; palpal coxa 0.60 long, 0.34 wide. Legs elongate, femur I length 1.30 times carapace length; metatarsus I prolateral concavity and clasping spine as in Figures 44D, E and 51H, I. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [total]): I: 2.85 + 0.95 + 3.00 + 2.75 + 1.15 = [10.70]; II: 2.35 + 0.85 + 1.95 + 2.00 + 0.95 = [8.10]; III: 1.90 + 0.70 + 1.55 + 1.70 + 0.85 = [6.70]; IV: 2.50 + 0.80 + 2.25 + 2.35 + 1.00 = [8.90]; palp: 1.05 + 0.40 + 0.45 + (absent) + 0.80 = [2.70]. Palpal femur with six probasal thorn-like setae (Fig. 9F); palp as in Figures 18A–C and 27A–D, tibial DTA inrolled, projecting retrodorsally (Figs 18C, 27B); bulb short, length less than 1.5 times width, cymbium projects retrolaterally beyond bulb, conductor apex pointed, reflexed back toward centre of bulb, median apophysis slender, cylindrical, length greater than five times width.

Variation (N = 5): Total length 4.00–5.60; carapace length 1.21–1.38 times width, height 0.30–0.41 times width; thoracic fovea length 0.22–0.24 times that of carapace; PER width 1.94–2.88 times OAL; OQP 1.21–1.30 times OQA; clypeal height 1.27–1.56 times AM diameter; cheliceral length 5.14–5.56 times clypeal height, promargin of fang furrow with 5–6 teeth, retromargin of fang furrow with 6–7 teeth; sternum length 1.14–1.23 times width; femur I length 1.29–1.49 times carapace length; metatarsus I length 1.23–1.37 times carapace length.

Female (paratype): Total length 5.94. Markings similar to male. Carapace 2.34 long, 1.66 wide, margin entire; thoracic fovea deep, narrowed posteriorly, length 0.12 times that of carapace; clypeus 0.18 high; ocular area 0.29 long, 0.82 wide; ratio of eyes AM/AL/PM/PL, 1.00:1.50:1.17:1.50, diameter of PM 0.11. Chelicerae 1.06 long, robust, smooth, promargin of fang furrow with six teeth, retromargin with four large and two minute teeth. Sternum 1.25 long, 1.00 wide, apex a right angle; labium 0.47 long, 0.44 wide; palpal coxa 0.78 long, 0.41 wide. Femur I length 1.20 times carapace length. Palpal femur with row of eight stout anterobasal setae set in enlarged bases (Fig. 51D). Calamistrum origin at 0.42 from metatarsus base, length 0.31 that of segment. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [total]): I: 2.81 + 0.93 + 2.43 + 2.31 + 1.06 = [9.54]; II: 2.19 + 0.81 + 1.69 + 1.69 + 1.00 = [7.38]; III: 1.81 + 0.69 + 1.31 + 1.38 + 0.88 = [6.07]; IV: 2.43 + 0.81 + 1.94 + 1.94 + 1.06 = [8.18]; palp: 0.88 + 0.44 + 0.50 + (absent) + 1.06 = [2.88]. Epigynum as in Figures 35A and 41C, ML oval, narrow, width 2.07 times length, posterior margin procurved, rebordered posteriorly, copulatory opening exposed; spermathecae as in Figures 35B, C and 41D, anterior margin of each with two lobes, with median copulatory duct leading to slender, median chamber with large poreplate at base, laterally a bilobed chamber.

Variation (N = 5): Total length 4.60–5.94; carapace length 1.32–1.46 times width, height 0.34–0.48 times width; PER width 2.57–3.71 times OAL; OQP 1.23–1.35 times OQA; clypeal height 1.50–2.20 times AM diameter; cheliceral length 4.09–5.67 times clypeal height, pro- and retromargins of fang furrow with 6–7 teeth; sternum length 1.10–1.33 times width; femur I length 1.03–1.42 times carapace length; metatarsus I length 0.88–1.21 times carapace length.

Natural history: Specimens have been collected in the leaf axils of large *Pandanus* trees in swamp forest, where they made small, irregular cribellate sheet webs between appressed leaf bases.

Distribution: Known only from Fianarantsoa Province in the eastern rainforests of south central Madagascar (Fig. 58).

Material examined: MADAGASCAR: **Fianarantsoa Prov.**, Fanivelona (Ambinanysakaleona), 20°32′S; 48°33′E (September; no collector data), 1 ♂, holotype, 2 ♀, paratypes (AMNH); Ranomafana National Park, Vohiparara, Piste Touristique, 21°13.6′S, 47°24.0′E, elev. *c.* 1000 m, on *Pandanus*, 19 April 1998, C. Griswold, D. Kavanaugh, N. Penny, D. Ubick, M. Raherilalao, J. Schweikert & S. Ranorainarisoa, 8 ♂, 7 ♀, CASC (CASENT9016975, 9016960, 9016974, 9016971, 9016239, 9016967, 9016968, 9016973, 9016980, 9016966, 9016970, 9016969, 9016961, 9016972), on tree fern, 26–27 April 1998, C. Griswold, D. Kavanaugh, N. Penny, D. Ubick, M. Raherilalao, J. Schweikert & S. Ranorainarisoa, 1 ♂, CASC (CASENT9032835); Vohiparara village, 21°12.8′S, 47°23.0′E, elev. *c.* 1100 m, 24–25 April 1998, C. Griswold, D. Kavanaugh, N. Penny, D. Ubick, M. Raherilalao, J. Schweikert & S. Ranorainarisoa, 1 ♀, CASC (CASENT9016976); c. 2 km N Vohiparara village, at road cut, 21°14.8′S, 47°235.7′E, elev. *c.* 1100 m, 24–25 April 1998, C. Griswold, D. Kavanaugh, N. Penny, D. Ubick, M. Raherilalao, J. Schweikert & S. Ranorainarisoa, 9 ♀, CASC (CASENT9016962, 9016963, 9016236, 9016979, 9016965, 9016978, 9016964); Ranomafana National Park, Talatakely, 21°15′S, 47°26′E, elev. 915–1000 m, 30 October–20 November 1998, V. Lee & K. Ribardo, 1 ♀, CASC (CASENT9016237), Talatakely, 21°14.9′S, 47°25.6′E, 19–30 April 1998, C. Griswold, D. Kavanaugh, N. Penny, D. Ubick, M. Raherilalao, J. Schweikert & S. Ranorainarisoa, 1 ♀, CASC (CASENT9016977); Ranomafana National Park, Vatoharanana, 21°16.7′S, 47°26.1′E, elev. *c.* 1200 m, primary forest, 15 April 1998, C. Griswold, D. Kavanaugh, N. Penny, D. Ubick, M. Raherilalao, J. Schweikert & S. Ranorainarisoa, 1 ♀, CASC (CASENT9016238).

RAHAVAVY IDA SP. NOV.

(FIGS 9B, C, 19A–C, 28A–E, 35D–F, 41A, B, 44H, I, 48A, 59)

Types: Holotype male and paratype female (CASENT9003423) from Talatakely, Parc National Ranomafana, Madagascar, collected in January 2001 from pitfall traps in disturbed rainforest by D. Kavanaugh, R. Brett, and E. Elsom, deposited in CASC. Paratype female (CASENT9016988), same locality, collected in leaf litter in April 1998 by C. Griswold and D. Ubick, also in CASC.

Etymology: The specific name honours Ida George Meikle, mother in law of Charles Griswold, who always offered encouragement in Arachnology; a noun in apposition.

Diagnosis: Male with palp as in Figures 19A–C and 28A–E, bulb elongate, length greater than 1.7 times width, embolic base projects retrolaterally beyond cymbium, conductor apex blunt, reflexed back toward centre of bulb. Epigynum as in Figure 35D, ML width less than 2.5 times length, copulatory openings inconspicuous ventrally, large openings hidden in deep, anteromedian depression, visible dorsally in cleared preparations (Fig. 41A, B); vulva as in Figures 35E, F and 41B, anterodorsal spiral of copulatory ducts with more than six well-defined turns.

Male (Holotype): Total length 3.40. Markings as in Figure 9C, like female except paler. Carapace 1.80 long, 1.40 wide; thoracic fovea 0.20 long, length 0.12 times that of carapace; clypeus 0.12 high; ocular area 0.24 long, 0.53 wide; ratio of eyes AM/AL/PM/PL, 1.25:2.62:1.00:1.25, diameter of PM 0.08. Chelicerae 0.70 long, slender, smooth, promargin of fang furrow with five teeth, retromargin with six teeth. Sternum 1.02 long, 0.90 wide; labium 0.30 long, 0.32 wide; palpal coxa 0.54 long, 0.24 wide. Legs elongate, femur I length 1.39 times carapace length; metatarsi I prolateral concavity and clasping spine as in Figure 44H, I. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [total]): I: 2.50 + 0.75 + 2.40 + 2.15 + 1.10 = [8.90]; II: 2.05 + 0.65 + 1.70 + 1.55 + 0.90 = [6.85]; III: 1.75 + 0.55 + 1.40 + 1.40 + 0.80 = [5.90]; IV: 2.40 + 0.65 + 2.10 + 2.10 + 0.95 = [8.20]; palp: 0.95 + 0.35 + 0.35 + (absent) + 1.15 = [2.80]. Palpal femur with six stout, thorn-like probasal setae (Fig. 48A); tibial DTA as in Figures 19C and 28D, E, bulb elongate, length greater than 1.7 times width, embolic base projects retrolaterally beyond cymbium, conductor apex blunt, reflexed back toward centre of bulb, median apophysis slender, length greater than 4.5 times width (Figs 19A–C, 28A–C).

Variation ($N = 2$): Total length 3.40–3.80; carapace length 1.25–1.29 times width, height 0.31–0.36 times width; PER width 2.21–2.26 times OAL; OQP 1.24–1.30 times OQA; clypeal height 1.40–1.50 times AM diameter; cheliceral length 5.00–5.83 times clypeal height, sternum length 1.13–1.14 times width; femur I length 1.33–1.39 times carapace length; metatarsus I length 1.19–1.25 times carapace length.

Female (Paratype): Total length 3.10. Markings similar to Figure 9B, carapace yellow-brown, shading to dusky laterally, pars cephalica shading anteriorly to orange-brown with posterior, darker V-shaped mark; black pigment surrounding each eye and extending between lateral eyes; carapace dark red-brown, boss yellow-brown; sternum, labium, and palpal coxa yellow-brown; legs and palpi yellow-brown; abdomen grey-brown, dorsum with median longitudinal broken light band and four pairs of lateral light spots. Carapace 1.50 long, 1.05 wide; thoracic fovea length 0.10 times that of carapace; clypeus 0.12 high; ocular area 0.19 long, 0.47 wide; ratio of eyes AM/AL/PM/PL, 1.33:2.00:1.00:1.33, diameter of PM 0.06. Chelicerae 0.58 long, robust, smooth, promargin of fang furrow with five teeth, retromargin with six teeth. Sternum 0.84 long, 0.72 wide; labium 0.28 long and wide; palpal coxa 0.46 long, 0.24 wide. Femur I length 1.07 times carapace length. Palpal femur with five anterobasal thorns. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [total]): I: 1.60 + 0.55 + 1.50 + 1.25 + 0.85 = [5.75]; II: 1.30 + 0.45 + 1.00 + 0.95 + 0.70 = [4.40]; III: 1.15 + 0.45 + 0.85 + 0.85 + 0.70 = [4.00]; IV: 1.55 + 0.50 + 1.30 + 1.20 + 0.75 = [5.30]; palp: 0.55 + 0.20 + 0.33 + (absent) + 0.70 = [1.78]. Calamistrum origin at 0.45 from metatarsus base, length 0.45 that of segment. Epigynum as in Figures 35D and 41 A, copulatory openings hidden in deep, anteromedian depression, visible dorsally in cleared preparations; vulva as in Figures 35E, F and 41B, anterodorsal spiral of copulatory ducts with more than six well-defined turns.

Variation (N-5): Total length 3.10–4.00; carapace length 1.39–1.43 times width, height 0.36–0.52 times width; PER width 2.33–2.95 times OAL; OQP 1.28–1.39 times OQA; clypeal height 1.43–2.14 times AM diameter; cheliceral length 4.83–6.00 times clypeal height; sternum length 1.14–1.22 times width; femur I length 1.03–1.07 times carapace length; metatarsus I length 0.73–0.97 times carapace length.

Natural history: Most records of this species are from leaf litter or pitfall traps, suggesting that *R. ida* is terrestrial.

Distribution: Known only from Ranomafana in south-eastern Madagascar (Fig. 59).

Material examined: MADAGASCAR: **Fianarantsoa Prov.** Ranomafana National Park, Talatakely, 21.25041°S, 47.41945°E, elev. 900 m, 'mixed tropical forest, pitfall traps', 4–16 January 2001, D. & K. Kavanaugh, R. Brett, E. Elsom & F. Vargas, holotype ♂ and paratype ♀, CASC (CASENT9003423), 21°14.9′S, 47°25.6′E, pitfall traps, 13–27 April 1998, C. Griswold, D. Kavanaugh, N. Penny, D. Ubick, M. Raherilalao, J. Schweikert & S. Ranorainarisoa, 1♀, CASC (CASENT9016990), 1 ♂, CASC (CASENT9003422), 21°15′S, 47°26′E, elev. 915–1000 m, 30 October–20 November 1998, V. Lee and K. Ribardo, 1 ♀, CASC (CASENT9016991), 21°14.9′S, 47°25.6′E, ex leaf litter, 19–30 April 1998, C. Griswold & D. Ubick, paratype ♀, CASC (CASENT9016988), 1 ♀, CASC (CASENT9016989), 21°12′S, 47°27′E, from foliage, April 1992, V. & B. Roth, S. Kariko, 1 ♀, CASC (CASENT9016197), 1 ♀, CASC (CASENT9017005), 1 ♀, CASC (CASENT9016196), 2 ♀, MCZ (CASENT9016195); Talatakely forest, 42.3 km 58° NE Fianarantsoa, 21°15′28.0″S, 47°25′21.8″E, elev. 1050 m, general collecting in montane rainforest, 24 December 2005–14 January 2006, H. Wood, J. Miller, J. J. Rafonomezantsoa, E. Rajeriarison, and V. Andriamananony, 1 ♀, CASC (CASENT9019100).

RAHAVAVY MALAGASYANA (GRISWOLD, 1990) **COMB. NOV.** (FIGS 9G–I, 20A–E, 29A–E, 35G–I, 41E, F, 44F, G, 58)

Phyxelida malagasyana Griswold 1990: 167; Platnick 2011.

Types: Holotype and paratype females collected at 2100 m at Majakatompo in the Ankaratra Mountains, 19°25′S, 47°12′E, Tananarive District, Madagascar, 25 November 1959, by E. S. Ross, deposited in CASC, type #16385, examined.

Diagnosis: Male with palp as in Figures 20A–C and 29A–E, bulb short, length less than 1.5 times width, embolic base projects retrolaterally beyond cymbium, conductor apex elongate, pointed, extending ventrad from bulb, median apophysis short, base narrow. Epigynum as in Figures 20D, E, 35G and 41E, ML broad, width greater than three times length, ML convex or with narrow, transverse concavity, copulatory openings inconspicuous, at upper lateral corners of ML; spermathecae as in Figures 35H, I and 41F, each with long, anteromedian lobate capsule with interior spiral chamber, with five or fewer poorly defined spirals, and with posterior dorsolateral lobe.

Male (Andasibe, CASENT9016182): (Note: the male is here described for the first time.) Total length 8.60. Markings as in Figure 9I. Carapace 2.08 long, 1.60 wide; thoracic fovea 0.36 long, length 0.18 times that of carapace; clypeus 0.13 high; ocular area 0.26 long, 0.53 wide; ratio of eyes AM/AL/PM/PL, 1.00:1.11:1.11:1.11, diameter of PM 0.10. Chelicerae 0.70 long, slender, smooth, pro- and retromargins of fang furrow with seven teeth. Sternum 1.12 long, 1.00 wide; labium 0.30 long, 0.34 wide; palpal coxa 0.61 long, 0.29 wide. Legs elongate, femur I length 1.29 times carapace length; metatarsus I concavity and clasping spines as in Figure 44F, G. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [total]): I: 2.68 + 0.96 + 2.72 + 2.32 + 1.00 = [9.68]; II: 2.22 + 0.76 + 2.04 + 1.76 + 0.88 = [7.66]; III: 1.88 + 0.48 + 1.60 + 1.56 + 0.80 = [6.32]; IV: 2.56 + 0.76 + 2.40 + 2.32 + 0.96 = [9.00]; palp: 1.00 + 0.34 + 0.34 + (absent) + 0.89 = [2.57]. Palpal femur with five probasal thorn-like setae; tibial DTA as in Figures 20A, C and 29B, bulb short, length less than 1.5 times width (Figs 20A–C, 29A–D), embolic base projects retrolaterally beyond cymbium, conductor apex elongate, pointed, extending ventrad from bulb, median apophysis short, length less than 2.5 times width, base narrower than apex (Fig. 29E).

Female (Holotype): Total length 7.00. Markings of dorsum as in Figure 9G, venter as in Figure 9H, carapace orange-brown, pars thoracica with margin dusky and with dusky anteromedian and median reticulate markings widening toward margin and posteriorly; with broad, dusky, V-shaped mark anteriad of thoracic fovea extending anteriorly as median line and with line on each side of pars cephalica with extensions to AL and AM; black pigment surrounding each eye and extending between AM and between lateral eyes; chelicerae red-brown; labium and palpal coxa red-brown, tips lighter; sternum, coxae, trochanters, legs, and palpi yellow-brown; sternum and coxae dusky; palpal tarsus, tibia I, and metatarsi – tarsi I and II red-brown; legs with faint dusky annuli:

basal, median and apical on femora II–IV, apical on patellae II–IV, and median and apical on tibiae and metatarsi II–IV; abdomen grey-brown, dorsum with anteromedian light paired marks and series of chevrons posteriorly, sides mottled with oblique longitudinal light and dark marks, venter (Fig. 9H) with longitudinal pair of narrow light bands. Carapace 3.09 long, 2.25 wide; thoracic fovea broad, short, deep, length 0.08 times carapace length; clypeus 0.26 high; ocular area 0.34 long, 0.99 wide; ratio of eyes AM/AL/PM/PL, 1.00:1.29:1.14:1.29, diameter of PM 0.13. Chelicerae 1.38 long, robust, smooth, promargin of fang furrow with six teeth, retromargin with four large teeth and one minute tooth. Sternum 1.66 long, 1.34 wide, margin entire, apex pointed; labium 0.58 long, 0.52 wide; palpal coxa 0.97 long, 0.53 wide. Femur I length 1.40 times carapace length. Palpal femur with row of eight short, slender anterobasal thorns. Calamistrum origin at 0.48 from metatarsus base, length 0.33 times that of segment. Leg measurements (femur + patella + tibia + metatarsus + tarsus = [total]): I: 4.25 + 1.31 + 3.88 + 3.81 + 1.75 = [15.00]; II: 3.56 + 1.13 + 2.81 + 2.81 + 1.38 = [11.69]; III: 3.00 + 0.94 + 2.25 + 2.25 + 1.25 = [9.69]; IV: 3.81 + 1.06 + 3.06 + 3.25 + 1.38 = [12.56]; palp: 1.31 + 0.56 + 0.69 + (absent) + 1.31 = [3.87]. Epigynum similar to Figures 20E and 41E, copulatory openings hidden beneath recurved LTR, ML broad, width 3.34 times length, oval, with transverse concavity, posterior margin gently procurved; spermathecae similar to Figures 35H, I and 41F, each with posteromedian copulatory duct leading to afferent duct within long, anteromedian lobe with five ill-defined spirals ending in apical bulb, and with posterior dorsolateral lobe containing spherical efferent chamber.

Variation (N = 15): This species varies in size and in epigynal morphology. The phylogenetic clustering of specimens from Manjakatompo, Andasibe, and Ambohimanga with a pp of 1.0 compels us to group disparate individuals together in a single species. Total length 5.25–8.40; carapace length 1.28–1.60 times width, height 0.32–0.56 times width; PER width 2.47–3.25 times OAL; OQP 1.21–1.50 times OQA; clypeal height 1.64–2.25 times AM diameter; cheliceral length 4.63–7.00 times clypeal height, promargin of fang furrow with 5–7 teeth, retromargin with 6–7 teeth; sternum length 1.10–1.26 times width; femur I length 0.96–1.50 times carapace length; metatarsus I length 0.76–1.45 times carapace length; palpal tarsus length 0.36–0.61 times carapace length. Epigynum with ML broad, width greater than 3.0 times length, lobe may be entire, e.g. specimens from Andasibe, some small specimens from Manjakatompo (Fig. 20D) or with a transverse concavity, as in the *malagasyana* type series from Majakatompo and some other specimens from Manjakatompo, Ambohimanga, and Angovokely (Figs 20E, 35G, 41E). A specimen from Ivohibe is tentatively assigned to this species in spite of occurring far south of other *R. malagasyana*: like other members of this species this specimen has a broad ML (length 3.7 times width) with a narrow transverse concavity.

Natural history: These spiders make small cribellate webs in leaf litter or under objects on or near the ground in rainforest.

Distribution: Known from highland and escarpment rainforests and forest fragments in central and south central Madagascar (Fig. 58).

Material examined: MADAGASCAR: **Antananarivo Prov**. Station Forrestiere Angavokely, 22 km E Antananarivo, 18°55.6′S, 47°45′E, elev. 1300 m, low canopy remnant forest, general collecting, 8 September 2001, D. Andriamalala, J. J. Rafanomenzantsoa & D. Ubick, 2♀, CASC (CASENT9001352); Sacred Forest, 10 km NE Tana, 18°45′32.6″S, 48°33′45.1″E, elev. 1300 m, 5 August 1992, V. & B. Roth, 2♀, CASC (CASENT9016230, 9016231); Ambohimanga, 18°44′S, 47°34′E, elev. 1400 m, berlese of fine leaf litter, 1 October 1993, R. Andriamasamanana, J. Coddington, C. Griswold, S. Larcher & N. Scharff, 1♀, ZMUC (CASENT9017004), 1♀, CASC (CASENT9017003); F. Manjakatompo (*sic*), November 1946, J. Millot, 7♀, MNHN (CASENT9017009, 9017007, 9032853), Manjakatompo, 2000 m, vieux troncs pourris, 1946, J. Millot, 5♀, MNHN (CASENT9017008, 9017010, 9017006), Majakatompo, Ankaratra Mountains, 19°25′S, 47°12′E, elev. 2100 m, November 25, 1959, E. S. Ross, 1♀ paratype CASC (CASENT9014037), 1♀ holotype CAS type #16385; Manjakatomopo, 17 km W Ambatolampy, 18°58′S, 47°17′E, elev. 1500 m, disturbed montane rainforest, general collecting night, 11 February 2003, D. Andriamalala & D. Silva, 10♀, CASC (CASENT9019995, 9019998, 9005754, 9020000, 9019999, 9020001, 9019996, 9005753, 9019997, 9019996). **Fianarantsoa Prov.** Res. Special Ivohibe, 7.5 km ENE Ivohibe, 22°28.2′S, 46°57.6′E, elev. 900 m, leaf litter, forest, 7–12 October 1997, B. L. Fisher, 1♀, CASC (CASENT9016981); Ambatofitorahana, 33 km S Ambositra, 13 March 1994, forêt naturelle, A. Pauly, 3♀ MRAC (MT201.625). **Toamasina Prov.** Res. Analamazaotra, Parc National Andasibe, 23 road km E Moramanga, 18°56′38″S, 48°25′3″E, elev. 960 m, rainforest, general collecting by day, 16–18 January 2003, D. Andriamalala, C. Griswold & D. Silva, 7♀, CASC (CASENT9019984, 9018280, 9005253, 9019981, 9018307, 9019983, 9019982); Perinet, 18°55′S, 48°25′E, 1–3 August 1992, V. & B. Roth, 1 ♂, CASC (CASENT9016182).

CONCLUSIONS

The phyxelidid spiders of Madagascar comprise a monophyletic group with nearest relatives in southern or eastern Africa, a phylogenetic pattern fitting no model of continental drift and suggesting a single dispersal from the African mainland, probably during the mid Tertiary, as hypothesized for numerous other invertebrate and vertebrate animal groups. These spiders have diversified into at least 14 species in Madagascar, many of which appear to be locally endemic.

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APPENDIX

Specimens used to generate data for this study. The list is organized by outgroup taxa, other Phyxelididae, and Madagascar Phyxelididae: for outgroups the species name is given with the family (according to Platnick, 2011 except as newly proposed in this work). Voucher designation (molecular specimen code or mating voucher) is designated in **bold**. Collection data follow this designation. For specimens that have been used in previous studies, this is indicated; specimens first sequenced for this study have been deposited at the California Academy of Sciences unless otherwise indicated.

OUTGROUP TAXA

Goeldia undetermined sp. (Titanoecidae)

T15 (CASENT9016517) – Chile, Region IX, Parque Nacional Villarica, 11–12 January 2003, S. Lew.

Hickmania troglodytes (Higgins & Petterd, 1883) (Austrochilidae)

13.11 (CASENT9023515) – Australia, Tasmania, Weldborough Pass Rainforest Walk, 28.6km 280° WNW St Helens, 41.21661°S, 147.93852°E, elev. 470 m, Nothofagus forest, general collecting 6–7 March 2006, C. Griswold, D. Silva.

Ikuma undetermined sp. (Palpimanidae)

11.06 (CASENT 9023778) – South Africa: Eastern Cape, Colchester, Pearson Park Nature and Pleasure Resort, E of Sundays River, 35 km NE Port Elizabeth, 33.698°S, 25.8385°E, 5 m, 16–17 February 2006, dune vegetation, J. Miller & H. Wood.

Oncodamus decipiens Harvey, 1995 (Nicodamidae)

10.10 (CASENT9023688) – Australia: Queensland, Binna Burra, Lamington N.P., 28.19398°S, 153.18692°E, elev. 790 m, 21–23 March 2006, C. Griswold, D. Silva, R. Raven. B. Baehr & M. Ramírez.

Stegodyphus mimosarum Pavesi, 1883 (Eresidae)

09-06 (CASENT 9024084) – Madagascar, Fianarantsoa, Parc National Ranomafana, Valbio Research Station, 42.4 km 58° NE Fianarantsoa, 21.2543°S, 47.4217°E, 900 m, 24 December 2005 to 15 January 2006, social web along road, H. Wood, J. Miller, J.J. Rafonomezantsoa, E. Rajeriarison, V. Andriamananony.

Uroctea durandi (Latreille, 1809) (Oecobiidae)

13.07, Greece: Peloponnesus, Didyma, 23 August 2007, Jiri Kral.

14.08, France: St. Tropez, Axel Schönhoffer. No voucher specimen.

OTHER PHYXELIDIDAE

Malaika longipes (Purcell, 1904)

P09 (CASENT9026021) – South Africa, Western Cape Prov., Table Mountain National Park, Newlands Forest, 33°58.440′S, 18°26.648′E, elev. 145 m, afromontane forest, 25 February 2006, H. Wood & J. Miller.

Phyxelida tanganensis (Simon & Fage, 1922)

P36 (CASENT9019849), **mating voucher** (CASENT9017052) – Tanzania, Tanga, E. Usambara Mtns, Amani, 5°5.7′S, 38°38′E, in forest, elev. 950 m, 22 October to 9 November 1995, moulted in captivity, C. E. Griswold.

Phyxelida bifoveata (Strand, 1913)

P35 (*CASENT*9019855), **mating voucher** (CASENT9017047) – Tanzania, Tanga, W. Usambara Mtns, Mazumbai, 4°49′S, 38°30′E, in forest, elev. 1400–1600 m, 11–19 November 1995, moulted in captivity, C. E. Griswold.

Themacrys irrorata Simon 1906

P37 (CASENT9023635) – South Africa, Mpumalanga, Blyde River Canyon Nature Reserve, 24°2′55″S, 30°46′40″E, elev. 1250 m, 8 March 2006, J. Miller, H. Wood.

Vidole capensis (Pocock, 1900)

10.14 (CASENT 9023622) – South Africa: Eastern Cape, Grahamstown, Dassiekrans, 33.3279°S, 26.5001°E, elev. 715 m, 20 February 2006, J. Miller, H. Wood.

P08 (CASENT9024915) – South Africa, Eastern Cape, Kai Mouth, 58 km NE East London, 32°41.207′S, 28°22.627′E, elev. 15 m, dune forest, 1–13 February 2006, J. Miller, H. Wood.

Vytfutia undescribed sp.

P29 (CASENT9023841) – Malaysia, Borneo, Sabah, Kinabalu National Park, on buildings at headquarters, 2–8 April 1996, C. Deeleman.

Xevioso undescribed sp.

mating voucher (CASENT9017131) – South Africa: Mpumalanga, Mariepskop, *c.* 15 km W Klaserie, indigenous forest, 24°33′S, 30°53′E, elev. 1365 m, 5 December 1996 (moulted in captivity), C. Griswold.

Xevioso colobata Griswold 1990

P30 (CASENT9024995) – South Africa, Mpumalanga, Blyde River Canyon Nature Reserve, 24°32′55″S, 30°46′40″E, elev. 1250 m, 8 March 2006, J. Miller, H. Wood.

Xevioso kulufa Griswold 1990

P31 (CASENT9023795) – South Africa, Limpopo, Entabeni Nature Reserve, 22°59′45.7″S, 30°15′52.1″E, elev. 1375 m, 11 March 2006, J. Miller, H. Wood.

MADAGASCAR PHYXELIDIDAE

Ambohima andrefana Griswold, Wood and Carmichael

P04 (CASENT 9005930), **P17** (CASENT9019919), **mating vouchers: Male 1** mated once, 6.v.2003 (CASENT9005933), **Male 2** mated once, 28.v.2003 (CASENT 9005932), **Male 3** mated twice, 30.vi and 3.vii.2003 (CASENT9005931), **Male 4** mated once, 14.viii.2003 (CASENT 9005930), **Female A** mated once, 3.vii.2003 (CASENT9019917), **Female B** mated once, 3.vii.2003 (CASENT9019920), **Female C** mated once, 30.vi.2003 (CASENT9019919), **Female D** mated once, 3.vii.2003 (CASENT9019918), **Female E** mated once, 14.viii.2003 (CASENT9019994) – MADAGASCAR, Toliara Prov. Parc National Zombitse, 19.8 km 84° E Sakaraha, 22°50′36″S, 44°42′36″E, elev. 770 m, general collecting in dry forest on sandy soil, 5–9 February 2003, C. Griswold, D. Silva, and J. J. Rafonomezantsoa.

P11 (CASENT9018656), **P21**, 1 ♀ (CASENT9019974) – Madagascar, Toliara Prov. Forêt Classée d'Analavelona, 29.2 km 343° NNW Mahaboboka, 22°40′30″S, 44°11′24″E, elev. 1100 m, montane rainforest, general collecting, 18–22 February 2003, Fisher-Griswold Arthropod Team.

Ambohima antsinanana Griswold, Wood and Carmichael

P42 (CASENT9029887) – Madagascar, Fianarantsoa Prov. Parc National Andringitra, 34 km S Ambalavao, 22°08′48.9″S, 46°57′03.4″E, elev. 1580 m, sifting litter in day in primary rain forest, 7 January 2009, H. Wood.

Ambohima avaratra Griswold, Wood and Carmichael.

P01 (CASENT9003544) – Madagascar, Antsiranana Prov. Parc National Montagne d'Ambre, 12.2km 211° SSW Joffreville, 12°35′47″S, 49°9′34″E, elev. 1300 m, beating low vegetation in montane rainforest, 2–7 February 2001, J. J. Rafanomezantsoa.

Ambohima maizina Griswold, Wood and Carmichael

P26 (CASENT9016206) – Madagascar, Antsiranana Prov. source Andranomifototra, R. N. I. Marojejy, 11.0 km NW Manantenina, elev. 1875 m, 14°26.8′S, 49°44.1′E, 13–19 November 1996, E. Quinter, deposited in AMNH.

Ambohima ranohira Griswold, Wood and Carmichael

P03 (CASENT 9005937) – Madagascar, Fianarantsoa Prov. Parc National d'Isalo, 9.1 km 354° N Ranohira, 22°28′54″S, 045°27′42″E, elev. 725 m, in gallery forest, 27–31 January 2003, C. Griswold, D. Silva, and J. J. Rafonomezantsoa.

P19 (CASENT9019987) – Madagascar, Fianarantsoa Prov. Parc National d'Isalo, 9.1 km 354° N Ranohira, 22°28′54″S, 045°27′42″E, elev. 725 m, in gallery forest, 27–31 January 2003, C. Griswold, D. Silva, and J. J. Rafonomezantsoa.

P22 (CASENT9016953) – Madagascar, Fianarantsoa Prov. Forêt d'Analalava, 29.6 km 280° W Ranohira, 22°35′30″S, 045°07′42″E, elev. 700 m, dry forest on sandy soil, 1–5 February 2003, C. Griswold, D. Silva, and J. J. Rafonomezantsoa.

Ambohima sublima Griswold 1990

P23 (CASENT9016226) – Madagascar, Antananarivo Prov. Ambohimanga, 18°44′S, 34°47′E, elev. 1400 m, 2 December 1993 (moulted in captivity), C. Griswold.

P24 (CASENT 9016217) – Madagascar, Antananarivo Prov. Ambohimanga, 18°44′S, 34°47′E, elev. 1400 m, 1 November 1993, R. Andriamasamanana, J. Coddington, C. Griswold, S. Larcher, and N. Scharff.

P33 (CASENT9015040) – Madagascar, Antananarivo Prov. R. S. d'Ambohitantely, primary forest, *c.* 20.9 km 72° NE d'Ankazobe, 18°13′30.3″S, 47°16′44″E, elev. 1574 m, montane rainforest, 19 March 2003, D. Andriamalala and D. Silva.

P34 (CASENT9018170) – Madagascar, Toliara Prov. Rés. Spéciale d'Ambohijanahary, Forêt d'Ankazotsihitafototra, 35.2 km 312° NW Ambaravaranala, 18°16′00″S, 045°24′24″E, elev. 1050 m, general collecting in montane rainforest, 13–17 January 2003, Fisher-Griswold Arthropod Team.

P27 (CASENT9019990), **P28** (CASENT9019991) – Madagascar, Antananarivo Prov. 3 km 41° NE Andranomay, 11.5 km 147° SSE Anjozorobe, 18°28′24″S, 47°57′36″E, elev. 1300 m, montane rainforest, 5–13 December 2000, Fisher-Griswold Arthropod Team.

4052 (CASENT9024052), **P07** (CASENT 9024485) – Madagascar, Fianarantsoa Prov. Parc National Ranomafana, Talatakely forest, 42.3 km 58° NE Fianarantsoa, 21°15′28.0″S, 47°25′21.8″E, elev. 1050 m, general collecting in montane rainforest, 24 December 2005–14 January 2006, H. Wood, J. Miller, J. J. Rafonomezantsoa, E. Rajeriarison, and V. Andriamananony.

Ambohima vato Griswold, Wood and Carmichael

P02 (CASENT9005936), **P20** (CASENT9005810) – Madagascar, Fianarantsoa Prov., Forêt d'Atsirakambiaty, 7.6 km 285° WNW Itremo, elev. 1550 m, 20°35′36″S, 046°33′48″E, montane rain forest, 22–26 January 2003, C. Griswold, D. Silva, and J. J. Rafonomezantsoa.

Ambohima zandry Griswold, Wood and Carmichael

P18 (CASENT9006874) – Madagascar, Antsiranana Prov. Parc Nationale Montagne d'Ambre, 12.2 km 211° SSW Joffreville, 12°35′47″S, 49°9′34″E, elev. 1300 m, pitfall trap in montane rainforest, 2–7 February 2001, Fisher-Griswold Arthropod Team.

P39 (CASENT9003543) – Madagascar, Antsiranana Prov. Montagne d'Ambre, 12°30′57″S, 49°11′04″E, beating low vegetation in montane rainforest, 2–7 February 2001, J. J. Rafanomezantsoa.

Ambohima zoky Griswold, Wood and Carmichael

P25 (CASENT9017018) – Madagascar, Antsiranana Prov. 7 km SE Antsiranana, 12°19′58″S, 49°17′39″E, 17 August 1992, V. & B. Roth.

Manampoka atsimo Griswold, Wood and Carmichael

P40 (CASENT9031165), **P41** (CASENT9031166) – Madagascar, Toliara Prov., Parc National Andohahela, Parcelle I, Manangotry, off route 118, 34 km N Taolagnaro, 24°44′35.0″S, 46°51′23.3″E, elev. 670 m, 23 December 2008–3 January 2009, primary montane rainforest, general collecting day and night, F. Álvarez-Padilla and H. Wood.

Rahavavy fanivelona (Griswold, 1990)

P13 (CASENT9016960) – Madagascar, Fianarantsoa Prov., Ranomafana National Park, Vohiparara, Piste Touristique, 21°13.6′S, 47°24.0′E, elev. *c.* 1000 m, on *Pandanus*, 19 April 1998, C. Griswold, D. Kavanaugh, N. Penny, D. Ubick, M. Raherilalao, J. Schweikert, and S. Ranorainarisoa.

P32 (CASENT 9016979) – Madagascar, Fianarantsoa Prov., *c.* 2 km N Vohiparara village, at road cut, 21°14.8′S, 47°25.7′E, elev. *c.* 1100 m, 24–25 April 1998, C. Griswold, D. Kavanaugh, N. Penny, D. Ubick, M. Raherilalao, J., Schweikert, and S. Ranorainarisoa.

Rahavavy ida Griswold, Wood and Carmichael

P06 (CASENT9003423) – Madagascar, Fianarantsoa Prov., Ranomafana National Park, Talatakely, 21.25041°S, 47.41945°E, elev. 900 m, 'mixed tropical forest, pitfall traps', 4–16 January 2001, D. & K. Kavanaugh, R. Brett, E. Elsom, and F. Vargas.

P16 (CASENT9019100) – Madagascar, Fianarantsoa Prov., Parc National Ranomafana, Talatakely forest, 42.3 km 58° NE Fianarantsoa, 21°15′28.0″S, 47°25′21.8″E, elev. 1050 m, general collecting in montane rainforest, 24 December 2005–14 January 2006, H. Wood, J. Miller, J.J. Rafonomezantsoa, E. Rajeriarison, and V. Andriamananony.

Rahavavy malagasyana (Griswold, 1990)

P05 (CASENT 9019981) – Madagascar, Toamasina Prov., Res. Analamazaotra, Parc National Andasibe, 23 road km E Moramanga, 18°56′38″S, 48°25′3″E, elev. 960 m, rainforest, general collecting by day, 16–18 January 2003, D. Andriamalala, C. Griswold, and D. Silva.

P10 (CASENT9001352) – Madagascar, Antananarivo Prov. Station Forestiere Angavokely, 22 km E Antananarivo, 18°55.6′S, 47°45′E, elev. 1300 m, low-canopy remnant forest, general collecting, 8 September 2001, D. Andriamalala, J. J. Rafonomenzantsoa, and D. Ubick.

P12 (CASENT9020000) – Madagascar, Antananarivo Prov. Manjakatomopo, 17 km W Ambatolampy, 18°58′S, 47°17′E, elev. 1500 m, disturbed montane rainforest, general collecting night, 11 February 2003, D. Andriamala