

Madagascar: an unexpected hotspot of social *Anelosimus* spider diversity (Araneae: Theridiidae)

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Abstract. The spider genus *Anelosimus* Simon, 1891 (Theridiidae) currently contains over forty described species, found worldwide in tropical to warm temperate areas. American *Anelosimus* are all social, a rare trait among spiders, but social behaviour has not been reported for *Anelosimus* species elsewhere. Old World *Anelosimus* are poorly known, both behaviourally and taxonomically, and no *Anelosimus* species have yet been described from sub-Saharan Africa or Madagascar. Based on a preliminary phylogenetic analysis we predicted sociality in an undescribed Madagascar species because it grouped among social New World species. An expedition to Madagascar then found no less than five undescribed periodic-social (subsocial) *Anelosimus* species in Périnet reserve. A sixth species from the same locality is known from museum specimens and the *Anelosimus* diversity of Périnet is comparable with the most diverse single locality in the Americas. Subsocial species play a key role in understanding the evolution of permanent sociality (quasisociality). This increased pool of available subsocial study species demonstrates the utility of phylogenies as predictors of traits in species thus far unstudied. Here, *A. andasibe* sp.n., *A. may* Agnarsson sp.n., *A. nazariani* sp.n., *A. sallee* sp.n., *A. salut* sp.n. and *A. vondrona* sp.n. are described. *Anelosimus locketi* Roberts, 1977 from Aldabra Atoll is a junior synonym of *A. decaryi* (Fage, 1930) comb.n. from Madagascar. Preliminary data on the behaviour of the new species are given, indicating a level of sociality similar to the American *A. 'arizona'*¹. The phylogenetic analysis supports the monophyly of the Madagascar group and places it as sister to a clade containing the *eximius* lineage from the Americas, and a pair of undescribed Tanzanian species.

Introduction

The vast majority of the over 38 000 described spider species (Platnick, 2004) are aggressive and solitary (Coddington & Levi, 1991). However, a few species show either periodic or permanent sociality (for reviews, see Kullmann, 1972 and Avilés, 1997). Periodic-social or subsocial species groups consist of a mother and her offspring, co-operating in nest maintenance, prey capture, and feeding. The siblings disperse before reaching maturity. In permanent social or quasisocial

species, individuals belonging to multiple clutches remain in their natal nest throughout their lives and mate with each other to produce successive generations. In this case, co-operation also involves communal brood care and sex ratios are strongly female biased (Avilés & Maddison, 1991; Avilés, 1993, 1997; Avilés *et al.*, 2000). The majority of social spiders belong to the family Theridiidae, or cobweb spiders, with most belonging to the genus *Anelosimus* Simon.

Anelosimus species are model organisms in the study of spider sociality and its evolution (see, e.g. Kullmann, 1972; Avilés, 1997; Avilés & Gelsey, 1998; Furey, 1998; Avilés *et al.*, 2000, 2001; Jones & Parker, 2000, 2002; Saffre *et al.*, 2000; Agnarsson, 2002; Bukowski & Avilés, 2002; Powers & Avilés, 2003), but based entirely on *Anelosimus* representatives from the New World. The discovery of social *Anelosimus* elsewhere will add to the research tools available and may advance understanding on the short-term (ecological) and long-term (evolutionary) causes and consequences of

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spider sociality (Avilés, 1997). *Anelosimus* contains more than forty described species, found world-wide, mostly in tropical to warm temperate areas (Agnarsson, unpublished data). All New World *Anelosimus* species for which behavioural data exist are social (either sub- or quasisocial), but social behaviour is unreported previously for *Anelosimus* species from other areas. As the American *Anelosimus* have been presumed to be monophyletic, and at least some non-American *Anelosimus* (e.g. *A. vittatus* in Europe) appear solitary, no previous prediction of social behaviour has been made for species on other continents.

In a preliminary phylogenetic analysis, an undescribed species from Madagascar nested within the social American *Anelosimus*. As a result, social behaviour could be predicted in these new, but behaviourally unknown, species. This prediction seemed controversial, as no social theridiids have ever been reported from Madagascar, despite recent arachnological expeditions and monitoring efforts there (Smithsonian Institution 1993, California Academy of Sciences 1993–present), which have collected specimens of several *Anelosimus* species. Nevertheless, in a pilot expedition by the authors seeking these spiders based on the above prediction we found no less than five undescribed species of social *Anelosimus* at a single locality, in Périnet Reserve, Madagascar. This find is particularly interesting as the social webs are very conspicuous (containing up to nearly 100 individuals) and Périnet Reserve is one of the most visited of all in Madagascar. Their sociality may have been overlooked by previous workers as the spiders are solitary for a part of the year, including when males are adult.

This paper provides original descriptions of six species from Périnet. We present preliminary data on their natural history, comparing them with species from the Americas. Agnarsson's (2004) genus-level theridiid phylogeny contained ten *Anelosimus* exemplars. To evaluate the phylogenetic placement of the new species we added two exemplars to his data matrix and re-ran the analysis.

Materials and methods

Expedition

Our pilot field expedition to Madagascar sought to test the above prediction by seeking the undescribed Madagascar *Anelosimus* and documenting its behaviour. Fieldwork focused on as many different ecosystems in Madagascar as feasible within a limited time and budget. We visited and exhaustively searched ten habitats (collections) in five sites (Fig. 10) during April and May 2001, ranging in ecology from the eastern Madagascar rain forest to southwestern and southern arid spiny desert. These collections are listed chronologically below, with exact locality and time, and basic ecological information. Collections were made by the authors and all material from this expedition is deposited in the National Museum of Natural History, Smithsonian Institution (NMNH). We made extensive spider collections

in all areas, but found *Anelosimus* spp. only in Périnet Special Reserve (referred to hereafter as Périnet).

1. Fianarantsoa Province, Parc National (P.N.) Ranomafana. Research station at Namorona River and surrounding forest. 1000 m. 21°15'S 47°25'E. 21–25.iv.2001. Secondary rain forest, rocky river bank and around buildings.
2. Fianarantsoa Province, P.N. Ranomafana. Vatoharana camp and surrounding forest. 1200 m. 21°17'S 47°25'E. 23.iv.2001. Primary (montane) rain forest.
3. Fianarantsoa Province, Ranomafana Village. 21°15'S 47°26'E, 24.iv.2001. Anthropogenic environment.
4. Fianarantsoa Province, Isalo Ranch. 22°35'S 45°23'E. 28.iv.2001. Arid environment.
5. Fianarantsoa Province, Isalo at Hotel Relais de la Reine. 22°38'40"S 45°19'53"E. 28.iv.2001. Gallery forest.
6. Fianarantsoa Province, 20 km west of Ilakaka. 1000 m. 22°46'35"S 45°01'32"E. 29.iv.2001. Dry forest on a volcanic hill.
7. Toliary Province, Ifaty. 23°05'33"S 43°36'32"E. 29–30.iv.2001. Arid spiny forest.
8. Toliary Province, Berenty Reserve. 25°00'S 46°18'E. 2–4.v.2001. Dry secondary forest and anthropogenic environment.
9. Toliary Province, Berenty Reserve, spiny forest. 25°01'04"S 46°18'29"E. 3.v.2001. Arid spiny forest.
10. Toamasina Province, Périnet Special Reserve (P.N. Andasibe Mantadia). 900–1000 m. 18°56'S 48°25'E. 7–8.v.2001. Primary rain forest.

Other collections

Further museum work subsequent to our field trip found additional *Anelosimus* specimens in the California Academy of Sciences, San Francisco (CAS) collection, from Périnet, Ranomafana and the following two areas (labelled 11 and 12 in Fig. 10):

11. Toamasina Province, 50 km west of Moramanga. 18°54'35"S 47°53'37"E. 1300 m. 1.vii.1992 (V. Roth) (CAS).
12. Antananarivo Province, Réserve Spéciale d'Ambohitanetly, Forêt d'Ambohitanetly. 18°13'31"S 47°17'13"E. Montane rain forest. 1410 m. 17–22.iv.2001 (J. J. Rafanomezantsoa et al.) (CAS).

Biological observations

Colonies of *Anelosimus* were located in the forest along trails and rivers in Périnet. Spider behaviour was observed over a period of approximately 10 h. Colonies were then measured and each entire colony (both silk and plant material in or associated with the web) collected and placed in a plastic bag. The contents of each colony (including other spiders and nonspider arthropods) were separated into vials in the laboratory. Animals from each colony

were identified and counted, and instars distinguished by plotting a histogram of tibia plus patella length of the first leg. Tibia length is more useful in distinguishing between instars than, for example carapace length/width (Toft, 1976) and tibia plus patella length has become a standard in *Anelosimus* literature (e.g. Avilés & Gelsey, 1998; Avilés & Salazar, 1999). The relationship of web size with both the number of individuals and the number \times size (tibia plus patella length) of individuals was analysed using linear regression.

Morphological examination

Morphological methods are described in detail in Agnarsson (2004, unpublished data). Specimens were examined and illustrated using a Leica MZ APO dissecting microscope and a Leica DMRM compound microscope, both with a camera lucida. Microscope images were taken using a Nikon DXM 1200 digital camera, and assembled with the Syncroscope Automontage software. Additional photographs were taken on a Leo 1430VP scanning electron microscope at the Department of Biological Sciences, George Washington University.

All measurements are in millimetres and were made using a micrometer eyepiece. Prosoma and abdomen length and height were measured in lateral view, the width in dorsal view, all measured at widest points. Leg segments were measured without the detachment of legs from the prosoma and are thus approximations. The position of metatarsal trichobothria and of tarsal organs is expressed as linyphiid metatarsal trichobothria in Roberts (1985). Temporary mounts of palps (Coddington, 1983) were made in methyl salicylate (Holm, 1979) and then photographed and drawn using a compound microscope with a camera lucida. Female genitalia were excised using microknives and sharp needles. The epigyna were made transparent in methyl salicylate (Holm, 1979). The internal genitalia were photographed and illustrated in ethanol. Most illustrations were rendered in Adobe Photoshop based on digital photographs; line drawings of internal epigyna were inked on Vellum paper. All plates were assembled and labelled in Adobe Illustrator.

Phylogenetics

We added two species to Agnarsson's (2004) analysis of theridiid genera (see also Agnarsson, 2003) containing 242 morphological characters. The two (*A. may* and *A. sallee*) were chosen as the best known of the six new species, from both sexes and with behaviour documented and photographed (Fig. 1).

Details of phylogenetic methods are described in Agnarsson (2004). Cladistic analyses were performed in NONA (Goloboff, 1993) through the WINCLADA shell (Nixon, 2002) using the mult*1000 command and the ratchet 'island hopper' (Nixon, 1999) with 1000 replications, holding ten trees and selecting twenty-five characters for each, and in PAUP* (Swofford, 2002) with 1000 random stepwise additions, and subtree pruning and regrafting branch swapping algorithm (all searches carried out with both amb – and

amb = in NONA) searching for minimal length trees under the criterion of parsimony. These search algorithms are heuristic because exact algorithms (e.g. branch and bound) are not computationally feasible for matrices of this size.

To evaluate nodal support, bootstrapping percentages (Felsenstein, 1985) and Bremer support values (Bremer, 1988, 1994) were calculated.

Two new characters, diagnostic for the Madagascar group (see detailed descriptions in Taxonomy), were added to the character matrix and scored for all taxa (all but *A. may* and *A. sallee* receiving zero score for both characters):

243. *Epigynal pendulumlike septum*: (0) absent; (1) present (e.g. Fig. 8A).

Uniquely in the Madagascar *Anelosimus*, a distinct pendulum-shaped septum arises from the dorsal wall of the epigynum. In other *Anelosimus* the dorsal wall is entire.

244. *Hooked proximal embolic sclerite*: (0) absent; (1) present (e.g. Fig. 7D, E).

Character codings for *A. may* and *A. sallee* are as follows:

Anelosimus may: 00110000-000011111100000110
01-111—010200000000-00001111?00001000001
00000000-11000100001000000111000001001100
00000000001000000-00001000101010101101111
000100101011101001?1-01000111110011000001
100011000011?0?00?0111?10?03?01???00??-
100??????11

Anelosimus sallee: 00110000-00001111110000011
001-111—010200000000-00001111?0000100000
100000000-1100010000100000011100000100110
00000000001000000-0000100010101010110111
1000100101011101001?1-0100011111001100000
1100011000011?0?00?0111?10?03?01???00??-
?100??????11

The full data matrix is provided in the Supplementary material on Synergy. It is also available at: <http://www.gwu.edu/~clade/spiders/cladograms.htm> and from the authors. The matrix will also be submitted to treebase (<http://www.treebase.org>).

The new taxon name *A. 'arizona'* referred to in this article follows Agnarsson (unpublished data); it is here disclaimed and unavailable for nomenclatural purposes (ICZN Art. 8.3). Agnarsson (unpublished data) will provide diagnosis, description, type designation, and formal synonymy for *A. 'arizona'*.

List of abbreviations

Under 'Additional material examined', each collection is followed by a code in square brackets (e.g. '[IA0101]'). This refers to a unique identification number generated for all collections examined and placed in each specimen vial. Each specimen examined here should, therefore, be located easily, facilitating future work. The following abbreviations are used in the figures: AC, aciniform gland spigot(s); C, conductor; CD, copulatory duct(s); CO, copulatory opening; CY, cylindrical gland spigot(s); E, embolus; Eb, embolic division b; ES, epigynal septum; FD, fertilization duct(s); FL, flagelliform gland spigot(s); MA, median apophysis; mAP, minor ampullate gland spigot(s); PES, proximal embolic sclerite; PI,

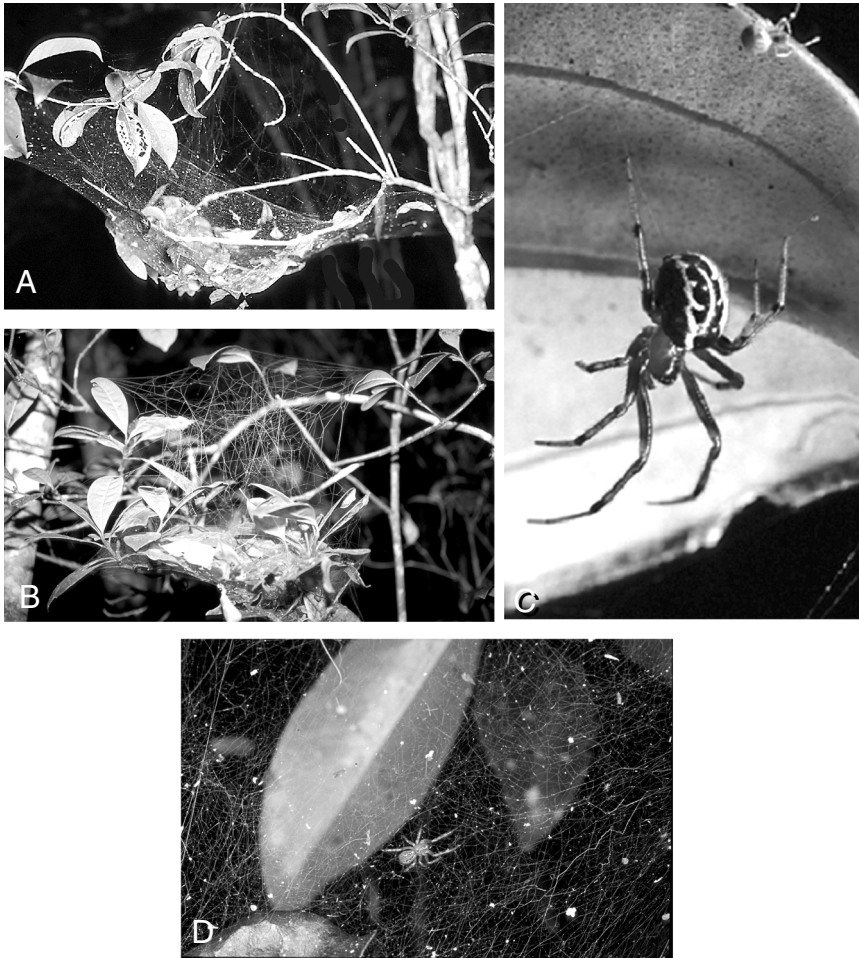


Fig. 1. Field photographs. A, *Anelosimus may* nest; B, *A. sallee* nest; C, *A. may* female habitus; D, *A. sallee* female on sheet web.

piriform gland spigot(s); S, spermathecae; SC, subconductor; t, trichobothrium; T, tegulum; TH, tegular hook; TTA, theridiid tegular apophysis; TO, tarsal organ.

Results

Biological observations

During the brief time available, our sampling strategy was far from optimal as we did not realize that we were dealing with multiple species. Complete nests of four *A. may* sp.n., five *A. nazariani* sp.n., two *A. vondrona* sp.n., one *A. sallee* sp.n., and one *A. andasibe* sp.n. colonies were collected. Additional partial samples were taken from two nests of *A. may*, and one nest of *A. sallee*, *A. andasibe*, and *A. salut*. Pooling all species, the complete nests contained between twenty-two and seventy individuals (mean = 41, standard deviation = 14.3). Nest size (length × width) was not correlated with the number of individuals within it ($r^2 = 0.06$, $P = 0.48$, d.f. = 1). However, when the size of the spiders was taken into account, nest size and content (number of individuals × within-nest average tibia plus patella length) were strongly correlated (linear regression

$r^2 = 0.80$, $P < 0.001$, d.f. = 1) (Fig. 2). Adult females were present in thirteen out of the seventeen nests examined, but no adult males were encountered. Due to the limited sample size

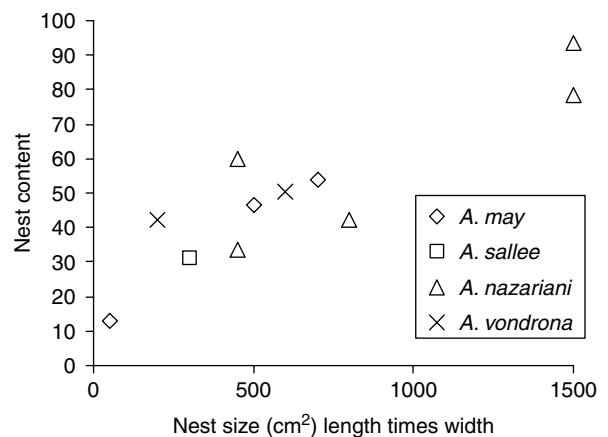


Fig. 2. The relationship of nest size and nest content (size × number of individuals per nest) for the four species with relevant data collected.

for each species, identifying instars involved some guesswork. However, using published data from other *Anelosimus* species allows fairly clear understanding. The five species seem to differ both in phenology (which instars were present at time of collection) and the size of instars. All six sampled colonies of *A. may* (three entire nests, three partial samples) contained only small juveniles (in addition to the mother), believed to represent instars I and II (postegg sac) (Fig. 3). Adult females of this species are comparable in size to *A. 'arizona'* (see Agnarsson, in press), and instars I and II are slightly larger than those of *A. 'arizona'* (Avilés & Gelsey, 1998). Both *A. vondrona* nests contained instars II and III only, being slightly larger than those of *A. may*. *Anelosimus nazariani* nests contained instars II–V, the majority of individuals being instars IV or V (Fig. 3). Adult females of *A. nazariani* reach the greatest size of any described *Anelosimus* species, and correspondingly the instars are large. The tibia plus patella length of antepenultimate *A. nazariani* was about equal to that found in penultimate *A. 'arizona'*. In two out of three of the *A. nazariani* nests with a high number of instar V (antepenultimate) the mother was absent. In *A. 'arizona'*, the mother typically dies (or is killed by her offspring) at the time her offspring reach the antepenultimate instar (Avilés & Gelsey, 1998). Only one complete nest of *A. sallee* was encountered, but seemed to contain instars II–V, whereas the partially sampled nest sample contained instars III and IV. This species is by far the smallest of the six, the antepenultimate instar being only slightly larger than the third instars of *A. nazariani* and *A. vondrona*. The single entire nest of *A. andasibe* contained an adult female, a subadult female and juveniles probably of instar III. This species is similar in size to *A. sallee* and the juveniles found match those of instar III of *A. sallee*. The partial *A. andasibe* sample likewise contained instars III. A single individual of *A. salut* was collected, but no data on the nest were taken.

In a monitored *A. nazariani* nest, the spiders showed typical *Anelosimus* behaviour, including collaborative prey catching and communal feeding. As in other *Anelosimus*, the spiders spent most of their time underneath the leaves embedded in the sheet.

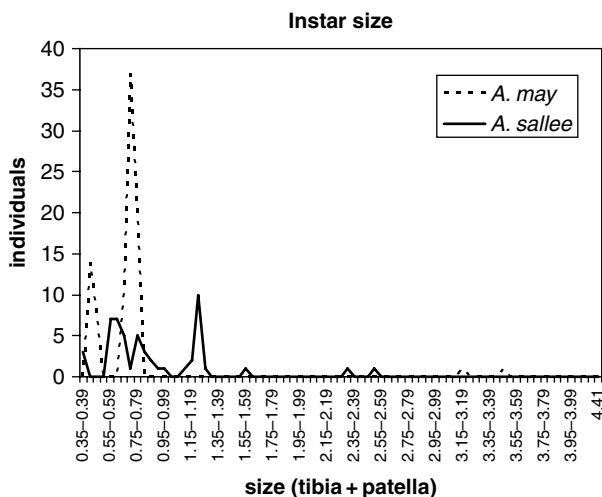
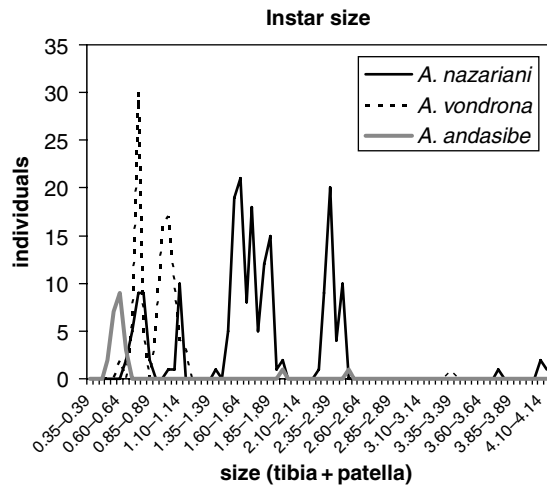


Fig. 3. Instar size and counts for each of the five species in the entire nests that were collected. The five species differ in instars present and instar size.

Taxonomy

Theridiidae Sundevall, 1833

Anelosimus Simon, 1891

Anelosimus Simon, 1891, Ann. Soc. Ent. France, 60: 11. Type species: *Anelosimus socialis* Simon, 1891 (= *Anelosimus eximius* (Keyserling 1884)).

See Agnarsson (2004, unpublished data) for taxonomic treatment of the genus.

The Madagascar group

Diagnosis

Males differ from all other *Anelosimus* in having a large and distally rugose embolic division b (Fig. 7B–F) and a hooked proximal embolic sclerite nesting in between the tegulum and the embolus, hooking with the subconductor (Fig. 7D, E). The proximal embolic sclerite is not present in any other examined theridiids. The sperm duct pathway of the male palps is furthermore unlike any other *Anelosimus* or theridiid examined. The complex ducts have multiple (nine to ten) switchbacks (vs. two in most *Anelosimus*, see Agnarsson (2004) for a discussion on theridiid sperm duct trajectories), starting immediately after the fundus. In all other *Anelosimus* (and typically in theridiids) the duct travels nearly a complete loop in the tegulum before any switchbacks occur. The females from Madagascar uniquely possess a pendulumlike epigynal septum (Figs 5E–J, 8A) and the copulatory duct follows the septum edge (Fig. 6A, B, D, E) except in *A. nazariani* (Fig. 6C).

Phylogenetics

Six unambiguous synapomorphies support the monophyly of the Madagascar group (character number followed by state number): reverse switchbacks in the sperm duct trajectory (57–1), presence of switchback III (58–1), a branched theridiid tegular apophysis (81–1), short leg IV (female) (185–0), a pendulumlike epigynal septum (243–1), and a hooked embolic sclerite (244–1). The exceptionally complex sperm duct trajectory will probably provide further synapomorphies.

Composition

In addition to the six new species described here, the Madagascar group of *Anelosimus* contains numerous undescribed species from other Eastern Madagascar montane rain forest localities (own data). *Anelosimus decaryi* (Fage) (see also Roberts, 1983), currently the only *Anelosimus* recognized from the region (see below), apparently does not belong in the same group; the males lack the hooked proximal embolic sclerite and the females lack an epigynal septum.

Distribution

Montane rain forests of Eastern Madagascar.

Natural history

The group shows typical subsocial behaviour, with nests including a single mother and her offspring. The mother dies when juveniles approach maturity, and the juveniles presumably disperse prior to mating. Nests range from about 10 × 10–30 × 30 cm and contain at most a few dozen individuals. Most nests encountered were 1–2 m above the ground, typically at tips of branches.

Anelosimus may Agnarsson, sp.n. (Figs 1A, C, 4A–C, 5A, E, 6A, 7A–F, 8A–F)

Types

Holotype ♂ [IA50121], MADAGASCAR: Antananarivo Province, Réserve Spéciale d'Ambohitantely, Forêt d'Ambohitantely, 18°13'31'S, 47°17'13'E, montane rain forest 1410 m, 17–22.iv.2001 (J. J. Rafanomezantsoa *et al.*) (CAS). Paratype ♀ [IA50101], MADAGASCAR: Toamasina Province, Périnet Special Reserve (P.N. Andasibe Mantadia), 900–1000 m, 18°56'S, 48°25'E, 7–8.v.2001 (I. Agnarsson and M. Kuntner) (NMNH).

Etymology

The species epithet is a noun in apposition; a patronym after Laura May-Collado, the senior author's wife. It was discovered in May 2001 on her birthday.

Diagnosis

Males are diagnosed easily from other species by the theridiid tegular apophysis with two equal sized distal projections (Fig. 5A). Females differ from others of the Madagascar group by the anchor-shaped septum (Fig. 5E).

Description

Male (holotype). Total length 3.25. Cephalothorax 1.63 long, 1.27 wide, 0.99 high, brown. Sternum 0.99 long, 0.84 wide, extending between coxae IV, light brown, darkest near rim. Abdomen 1.69 long, 1.32 wide, 1.40 high. Pattern as in Fig. 4(A), dorsal band orange-red in live specimens. Eyes subequal in size, about 0.10 in diameter. Clypeus height about 3.0× one anterior median eye diameter. Chelicerae with one large and two small prolateral teeth, four to five denticles retrolaterally. Leg I femur 2.67, patella 0.65, tibia 2.54, metatarsus 1.98, tarsus 0.81. Femur about 7× longer than wide, metatarsus I about 22× longer than wide. Leg formula 1243. Leg base colour as carapace, light brown, with distal tip of femora and tibia darkened. Tarsal organs slightly distal (0.55–0.60) on tarsi I and II, proximal (0.35–0.40) on III–IV. Numerous (five to six) small trichobothria dorsally on all tibia, five to six on tibia III, five to six on tibia I. Trichobothria on metatarsi I–III proximal (about 0.35–0.40), absent on metatarsus IV. Four to five dorsal trichobothria on female palpal tibia. Palp as in Figs 5(A) and 7(A–F).

Female (paratype). Total length 5.01. Cephalothorax 2.28 long, 1.82 wide, 1.45 high, brown. Sternum 1.35 long, 1.16 wide, extending halfway between coxae IV, brown. Abdomen 2.93 long, 2.44 wide, 2.52 high. Pattern as in Figs 1(C) and 4(B). Eyes subequal in size about 0.12 in diameter. Clypeus height about 2.4× one AME diameter. Chelicerae with one large and two small prolateral teeth, three denticles retrolaterally. Leg I femur 2.89, patella 0.98, tibia 2.70, metatarsus 2.57, tarsus 0.94. Femur about 5× longer than wide, metatarsus I about 16× longer than wide. Leg formula 1243, with leg II very slightly longer than leg IV. Leg base colour as carapace, light orange-brown, with distal tip of tibia darkened, and metatarsus/tarsus junction dark. Tarsal organs slightly distal (0.55–0.60) on tarsi I and II, central (0.5) on III, slightly proximal (0.45) on IV, distal (0.85) on female palp, positions vary slightly between specimens. Numerous (seven to eight) small trichobothria dorsally on all tibia, seven on tibia III, eight on tibia I. Trichobothria on metatarsi I–III central or slightly proximal (about 0.45–0.50), absent on metatarsus IV. Four to five dorsal trichobothria on female palpal tibia. Epigynum with anchor-shaped septum, juxtaposed spermathecae and the copulatory ducts following the septum edge (Figs 5E, 6A, 8A).

Variation

Female total length 4.75–5.5, cephalothorax 2.25–2.54, femur I 2.73–3.50. Male total length 3.15–3.35, cephalothorax

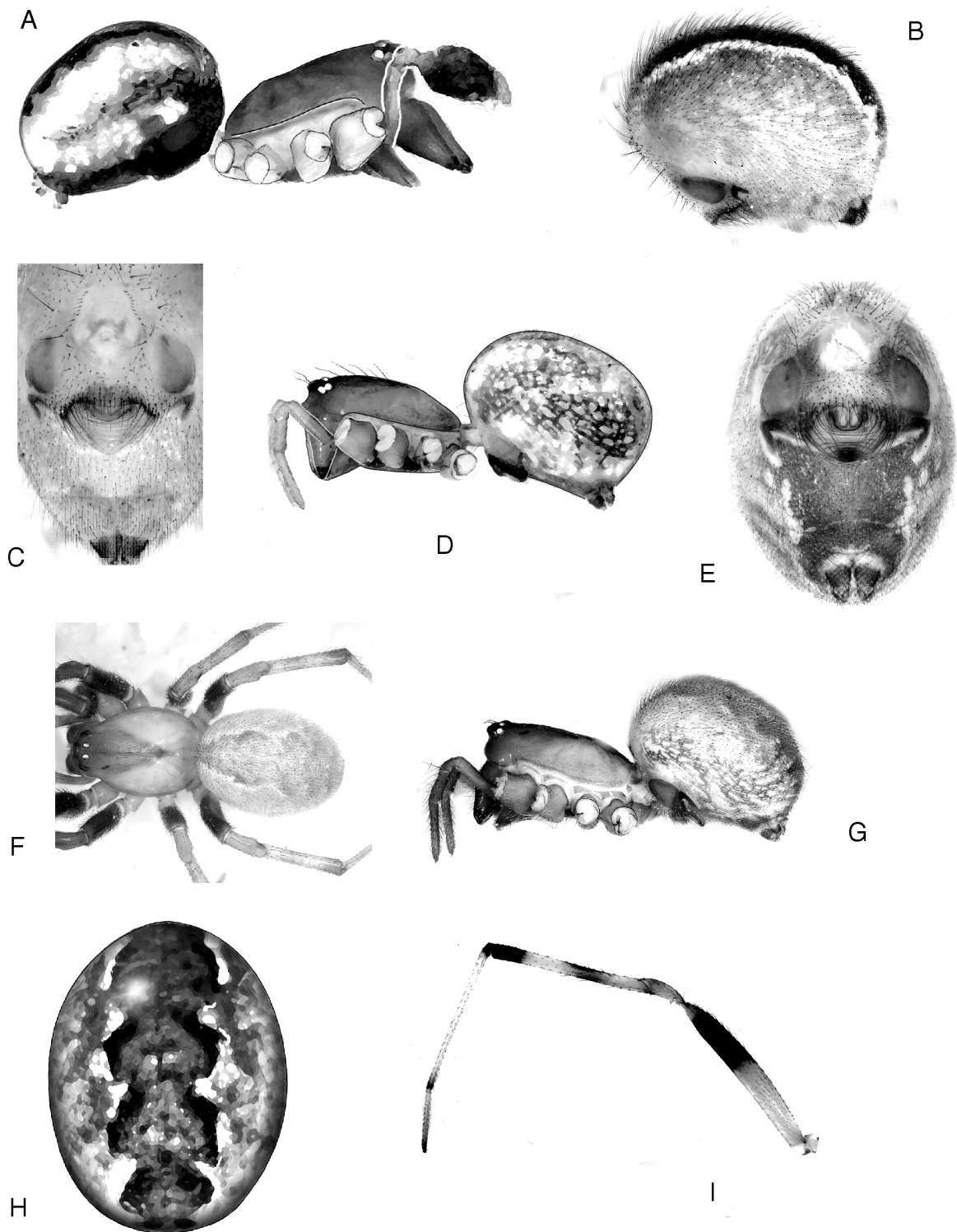


Fig. 4. New *Anelosimus* species somatic morphology. A–C, *Anelosimus may*; A, male, lateral; B, female abdomen, lateral; C, same, ventral; D, *A. sallee*, female, lateral; E–G, *A. nazariani*, female; E, abdomen, ventral; F, habitus, dorsal; G, same, lateral; H, *A. vondrona*, female abdomen, dorsal; I, *A. salut*, female leg I, retrolateral.

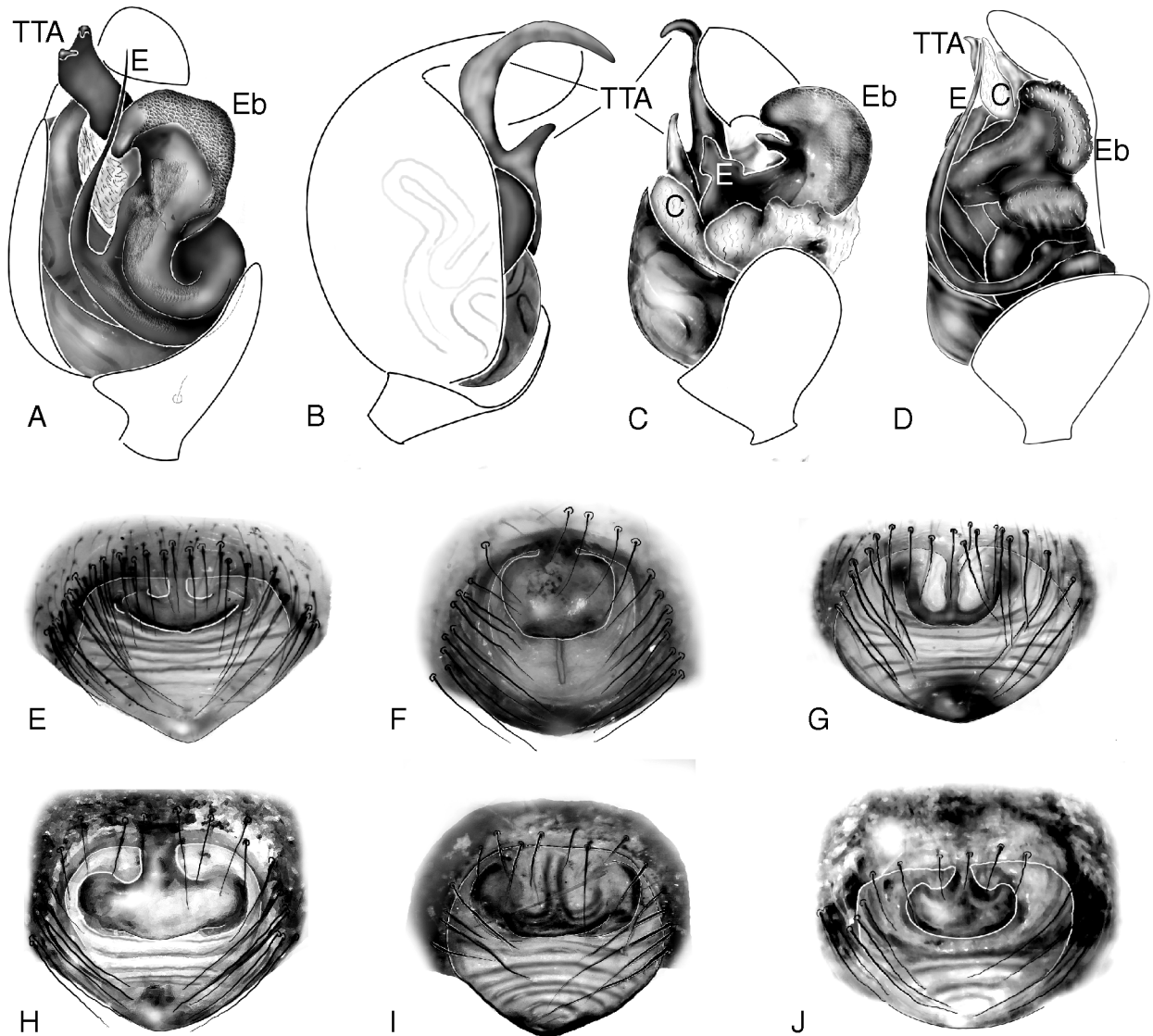


Fig. 5. New *Anelosimus* species genitalic morphology. A, *Anelosimus may*, holotype pedipalp, ventral; B, *A. sallee* holotype, pedipalp, mesal; C, same, ventral; D, *A. salut*, pedipalp, ventral; E–J, epigyna, ventral; E, *A. may* paratype; F, *A. sallee* paratype; G, *A. nazariani*; H, *A. vondrona*; I, *A. andasibe* holotype; J, *A. salut*.

1.55–1.70, femur I 2.61–2.73. Specimens from Ranomafana are generally larger than those from Périnet and the sclerotized epigynal edges are more concave.

Natural history

Subsocial. In early May 2001, I and II instars (postegg sac) were present in nests, and a female with an egg sac had been collected about 2 weeks earlier in P.N. Ranomafana (see material examined). The largest nest contained seventy individuals. Two species of hemipterans were collected with

the nests and may be commensal, as are the *Ranzovious* mirid hemipterans in America (Henry, 1984, 1999).

Additional material examined

Sixty-nine juveniles [with paratype ♀ IA50101], 51 juveniles [IA50102], 1 ♀ [IA50103], 18 juveniles [IA50104], 1 ♀ [IA50105], 1 ♀, 1 juvenile [IA50106], 1 ♀ [IA50107], same locality, 7–8.v.2001 (I. Agnarsson and M. Kuntner) (NMNH).

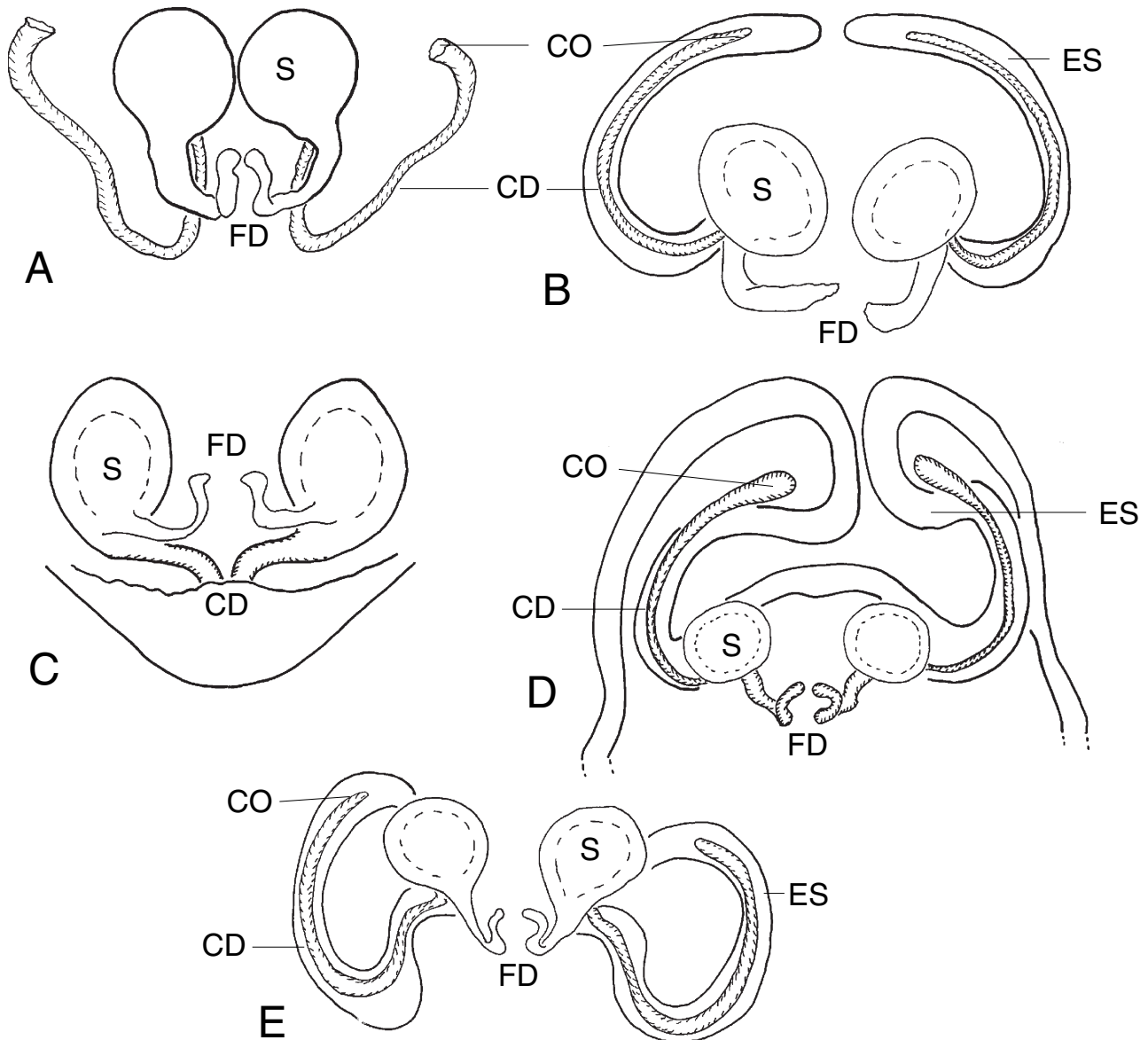


Fig. 6. Epigynal anatomy, schematic and interpretive illustrations from the dorsal view. Note that in all species but *Anelosimus nazariani* the copulatory ducts appear to follow the septum sclerotization. A, *Anelosimus may* (septum omitted); B, *A. sallee*; C, *A. nazariani* (septum omitted); D, *A. vondrona*; E, *A. andasibe*.

Four ♂, 2 ♀ [with paratype ♂ IA50121], 2 ♂, 10 ♀ [IA50128], MADAGASCAR: Antananarivo Province, Réserve Spéciale d'Ambohitantely, Forêt d'Ambohitantely, 18°13'31'S, 47°17'13'E, montane rain forest 1410 m, 17–22.iv.2001 (J. J. Rafanomezantsoa *et al.*) (CAS).

One ♀ [IA50130], MADAGASCAR: Fianarantsoa Province, P.N. Ranomafana, Vohiparara, Piste Touristique, 21°13'6'S, 47°24'0'E, c. 1000 m, 23.iv.1998 (C. E. Griswold *et al.*) (CAS).

One ♀ [IA50131], MADAGASCAR: Fianarantsoa Province, P.N. Ranomafana, Vohiparara village, 21°12'8'S,

47°23'0'E, c. 1100 m, 24–25.iv.1998 (C. E. Griswold *et al.*) (CAS).

One ♀ [IA50170], MADAGASCAR: Fianarantsoa Province, 7 km west of P.N. Ranomafana, 21°12'S, 47°27'E, 1100 m, 8–21.x.1998 (W. E. Steiner) (NMNH).

Distribution

Northeastern Madagascar, in montane rain forest (c. 1000–1500 m).

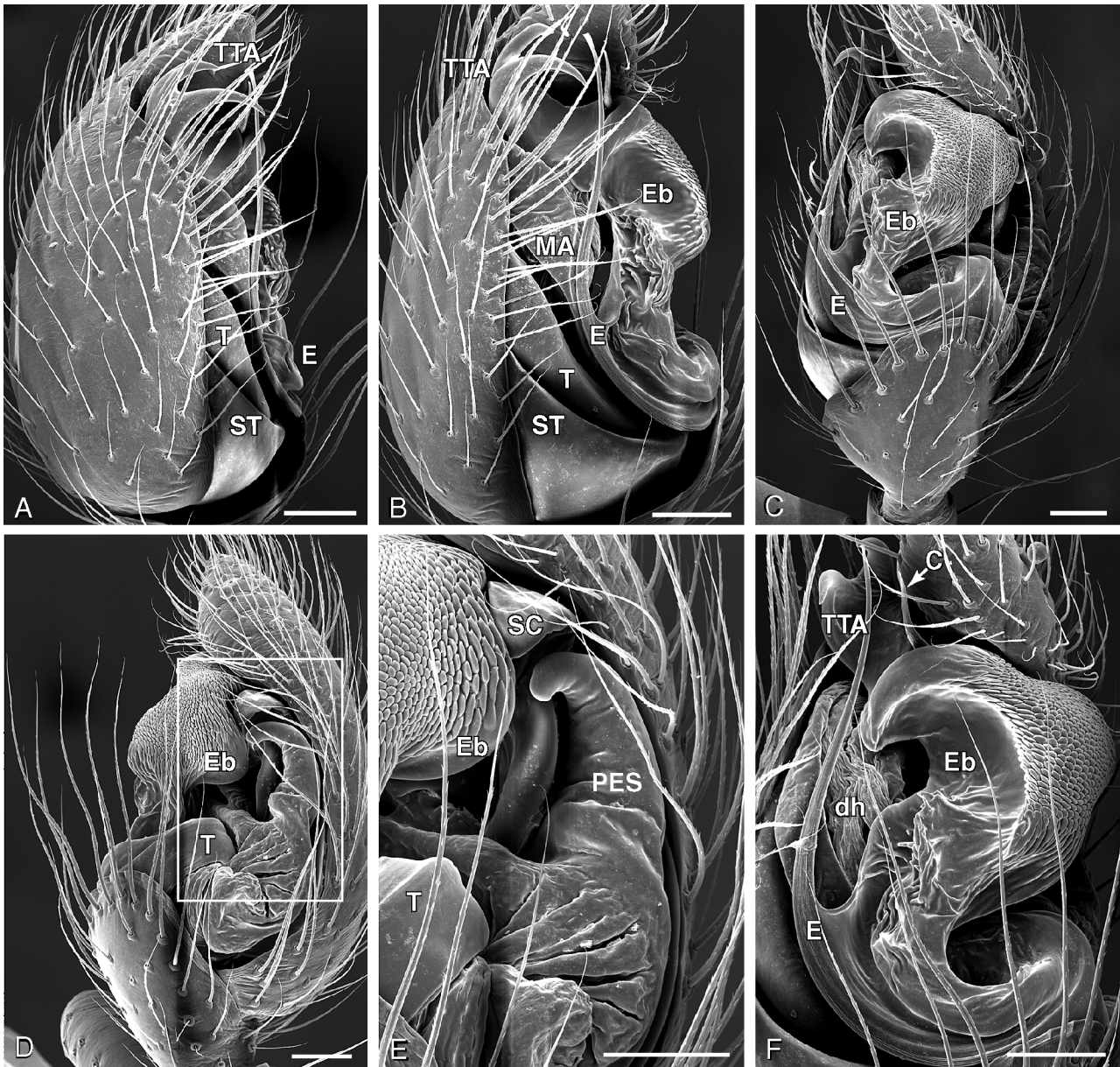


Fig. 7. *Anelosimus may*, male pedipalp: A, mesal; B, submesal; C, ventral; D, ectal, box delimits area of image E; E, detail (note the hooked proximal embolic sclerite, PES, uniquely present in all known males of Madagascar *Anelosimus*); F, details of embolus. Scale bars: 100 μ m.

***Anelosimus sallee* Agnarsson & Kuntner, sp.n. (Figs 1B, D, 4D, 5B, C, F, 6B)**

Types

Holotype δ , paratype f [IA50126], MADAGASCAR: Toamasina Province, Périnet Special Reserve (P.N. Andasibe Mantadia), 900–1000 m, 18°56'S, 48°25'E, 24.xii.1999 (M. E. Irwin *et al.*) (CAS).

Paratype f [IA50110], same locality, 7–8.v.2001 (I. Agnarsson and M. Kuntner) (NMNH).

Etymology

The species epithet is a noun in apposition after the Sallee Charitable Trust, whose contribution made the collecting trip to Madagascar possible.

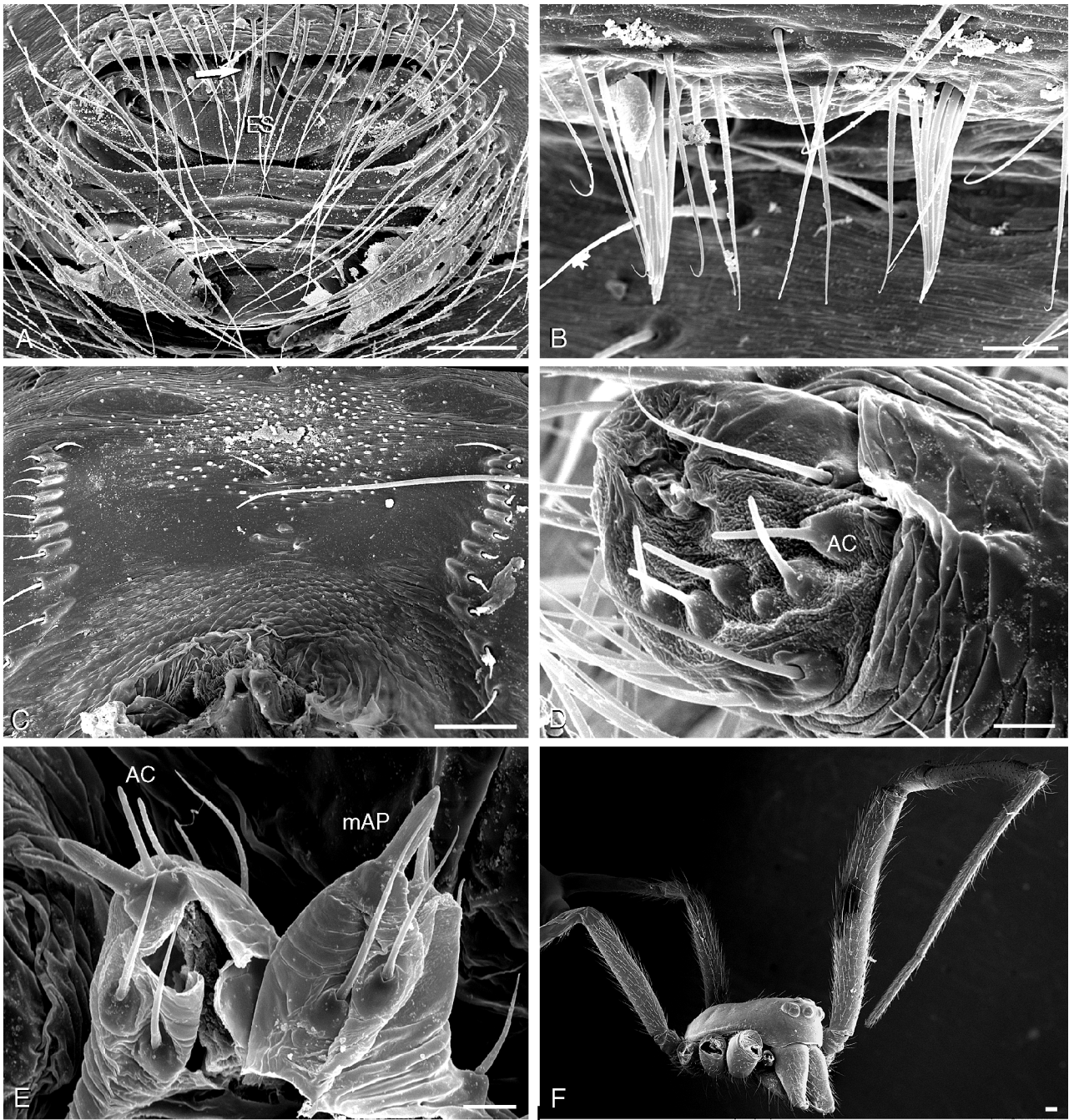


Fig. 8. *Anelosimus may*, epigynal and somatic morphology. A, Epigynum, ventral (note presumed position of copulatory opening, arrow); B, epiandrous gland spigots; C, male stridulatory pick row; D, male posterior lateral spinnerets; E, male posterior median spinnerets; F, male prosoma and leg I. Scale bars: A, F, 100 μ m; B, 20 μ m; C, 50 μ m; D, E, 10 μ m.

Diagnosis

Males are readily diagnosed from other species by the large apical theridiid tegular apophysis distal projections (Fig. 5B, C). Females differ from others of the Madagascar group by the semiquadrangular shape of the septum (Fig. 5F).

Description

Male (holotype). Total length 2.67. Cephalothorax 1.30 long, 0.99 wide, 0.81 high, light orange-brown. Sternum 0.79 long, 0.68 wide, extending between coxae IV, brown. Abdomen 1.50 long, 1.09 wide, 1.12 high. Pattern as in

female. Eyes subequal in size, about 0.08 in diameter. Clypeus height about $2.1 \times$ one AME diameter. Chelicerae with one large and two small prolateral teeth, three to four denticles retrolaterally. Leg I femur 1.79, patella 0.55, tibia 1.69, metatarsus 1.46, tarsus 0.68. Femur about $7 \times$ longer than wide, metatarsus I about $16 \times$ longer than wide. Leg formula 1243. Leg base colour as carapace, light orange-brown, with distal tip of femur IV darkened, and metatarsus/tarsus junction dark. Tarsal organs distal (0.55) on tarsus I central (0.5) on II, slightly proximal (0.45) on III and IV. Numerous (five to ten) small trichobothria dorsally on all tibia, five on tibia III, seven to ten on tibia I, variable between sides of the animal. Trichobothria on metatarsi I–III central or slightly distal (about 0.50–0.55), absent on metatarsus IV. Two prolateral and one retrolateral trichobothria on palpal tibia. Palp as in Fig. 5(B, C).

Female (paratype). Total length 3.51. Cephalothorax 1.56 long, 1.25 wide, 0.99 high, orange-brown. Sternum 1.01 long, 0.87 wide, extending halfway between coxae IV, light brown. Abdomen 2.15 long, 1.68 wide, 1.57 high. Pattern as in Fig. 1(D). Eyes subequal in size, about 0.07 in diameter. Clypeus height about $2.2 \times$ one AME diameter. Chelicerae with one large and two small prolateral teeth, four denticles retrolaterally. Leg I femur 1.89, patella 0.65, tibia 1.76, metatarsus 1.50, tarsus 0.72. Femur about $5 \times$ longer than wide, metatarsus I about $11 \times$ longer than wide. Leg formula 1243 with legs II and IV subequal. Leg base colour as carapace, light orange-brown, with distal tip of tibia darkened, and metatarsus/tarsus junction dark. Femur IV also darkened distally. Tarsal organs distal (0.65) on tarsus I central (0.5) on II, slightly proximal (0.40–0.45) on III and IV, distal (0.85) on female palp. Numerous (six to seven) small trichobothria dorsally on all tibia, six on tibia III, seven on tibia I. Trichobothria on metatarsi I–III slightly proximal (about 0.40–0.45), absent on metatarsus IV. Four dorsal trichobothria on palpal tibia. Epigynum with semiquadrangular septum and juxtaposed spermathecae; the copulatory duct is interpreted in Fig. 6(B) to follow the septum edge.

Natural history

Subsocial. The nests of *A. sallee* contained instars II–V in early May 2001, the larger nest contained a female and thirty juveniles. An uloborid spider was collected with one of the nests; uloborids commonly build their webs in association with *Anelosimus* nests in the Americas.

Additional material examined

Thirteen juveniles [with paratype ♀ IA50110], 1 ♀, 30 juveniles [IA50111], same locality, 7–8.v.2001 (I. Agnarsson and M. Kuntner) (NMNH).

Distribution

Known only from the type locality.

Anelosimus nazariani Agnarsson & Kuntner, sp.n. (Figs 4E–G, 5G, 6C)

Types

Holotype ♀ and paratype ♀ [IA50114], MADAGASCAR: Toamasina Province, Périnet Special Reserve (P.N. Andasibe Mantadia), 900–1000 m, $18^{\circ}56'S$, $48^{\circ}25'E$, 7–8.v.2001 (I. Agnarsson and M. Kuntner) (NMNH).

Etymology

The species epithet is a patronym after our mutual friend M. Javad Nazarian.

Diagnosis

Anelosimus nazariani differs from other species in being much larger (it is the largest *Anelosimus* species recorded to date) and darker in appearance. The epigynum differs from all but *A. andasibe* by the W-shaped septum, and from *A. andasibe* by the larger distance between the septum and the epigynal margin (Fig. 5G). Apparently unique in the group is the pathway of the short copulatory ducts, which open posteriorly and do not follow the septum edge (Fig. 6C).

Description

Male. Unknown.

Female (holotype). Total length 7.28. Cephalothorax 3.64 long, 2.06 wide, 1.98 high, orange-brown with cephalic region conspicuously darker. Sternum 1.77 long, 1.50 wide, extending halfway between coxae IV, light brown. Abdomen 3.90 long, 2.76 wide, 2.92 high. Pattern as in Fig. 4(E–G), darker than in other species. Eyes subequal in size, about 0.16 in diameter. Clypeus height about $2.3 \times$ one AME diameter. Chelicerae with one large and two small prolateral teeth, three large denticles retrolaterally. Leg I femur 3.25, patella 1.24, tibia 3.09, metatarsus 3.02, tarsus 1.17. Femur about $5 \times$ longer than wide, metatarsus I about $17 \times$ longer than wide. Leg formula 1243 with leg II slightly longer than IV. Leg base colour as carapace, orange-brown, with most of the femora and the distal tip of the tibia darkened, and metatarsus/tarsus junction dark. Tarsal organs distal (0.60–0.65) on tarsi I and II, central (0.5) on III, proximal (0.40) on IV, distal (0.90) on female palp, positions vary slightly between specimens. Numerous (seven to eight) small trichobothria dorsally on all tibia, seven on tibia III, eight on tibia I. Trichobothria on

metatarsi I–III central (about 0.50), absent on metatarsus IV. Five dorsal trichobothria on female palpal tibia. Epigynum with a W-shaped septum (Fig. 5G), copulatory ducts short and do not follow septum, rather they open posteriorly (Fig. 6C).

Variation

Female total length 6.75–7.50, cephalothorax 3.51–3.74, femur I 3.20–3.45. The caudal tip of the epigynum ranges from unicolorous to having a black tip (Figs 4E, 5G).

Natural history

Subsocial. Nests contained between twenty and fifty individuals, mostly of instars IV and V in early May 2001. The spiders spent most of their time underneath leaves imbedded in the sheet. In late afternoon, nest members collaborated on web construction (knock-down lines). Prey was attacked communally, larger juveniles (or mother) appeared to attack first. Juveniles fed communally on large prey items. Several arthropods were collected with the nests, including two hemipteran species and one coleoptera, and several spiders, two uloborid species, a salticid, a sparrassid, a mysmenid, and an *Argyrodes* species. Argyrodine and mysmenid spiders are common kleptoparasites of *Anelosimus* webs in Americas (e.g. Cangialosi, 1990a, b). *Anelosimus nazariani* is the largest *Anelosimus* species recorded to date.

Additional material examined

One ♀, 34 juveniles [IA50115], 1 ♀, 13 juveniles [IA50116], 41 juveniles [IA50117], 1 ♀, 46 juveniles [IA50118], 1 ♀, 31 juveniles [IA50119], 1 ♀, 21 juveniles [IA50120], same locality, 7–8.v.2001 (I. Agnarsson and M. Kuntner) (NMNH).

One ♀ [IA50123], 1 ♀ [IA50125], same locality, 24.xii.1999 (M. E. Irvin *et al.*) (CAS).

One ♀ [IA50124], MADAGASCAR: Toamasina Province: 50 km west of Moramanga, 18°54'35'S, 47°53'37'E, 1300 m, 1.vii.1992 (V. Roth) (CAS).

Distribution

Eastern tropical mid-elevation rain forest of Madagascar, may be limited to forest east of Antananarivo.

***Anelosimus vondrona* Agnarsson & Kuntner, sp.n. (Figs 4H, 5H, 6D)**

Types

Holotype ♀ [IA50112], MADAGASCAR: Toamasina Province, Périnet Special Reserve (P.N. Andasibe

Mantadia), 900–1000 m, 18°56'S, 48°25'E, 7–8.v.2001 (I. Agnarsson and M. Kuntner) (NMNH).

Etymology

The species epithet is a Malagasy word meaning 'group', reflecting the group living of the species.

Diagnosis

Anelosimus vondrona can be diagnosed by a very broad septum (Fig. 5H).

Description

Male. Unknown.

Female (holotype). Total length 5.14. Cephalothorax 2.21 long, 1.68 wide, 1.42 high, brown. Sternum 1.29 long, 1.16 wide, extending between coxae IV, brown. Abdomen 3.12 long, 2.89 wide, 2.64 high. Pattern as in Fig. 4(H). Eyes subequal in size, about 0.12 in diameter. Clypeus height about 2.4× one AME diameter. Chelicerae with one large and two small prolateral teeth, four to five denticles retro-laterally. Leg I femur 3.09, patella 0.98, tibia 2.70, metatarsus 2.60, tarsus 0.85. Femur about 5× longer than wide, metatarsus I about 15× longer than wide. Leg formula 1243. Leg base colour lighter than carapace, orange-brown, with femora I and IV, and the distal tip of tibia darkened, and metatarsus/tarsus junction dark. Tarsal organs distal (0.55–0.65) on tarsi I and II, slightly proximal or central (0.45–0.50) on III and IV, distal (0.85) on female palp. Numerous (seven to eight) small trichobothria dorsally on all tibia, seven on tibia III, seven to eight on tibia I. Trichobothria on metatarsi I–III slightly proximal or central (0.45–0.50), absent on metatarsus IV. Five dorsal trichobothria on female palpal tibia. Epigynum with a broad septum, widely separated spermathecae and the copulatory duct following the septum edge (Figs 5H, 6D).

Variation

Total length 5.14–5.33, abdomen colour different in the two specimens.

Natural history

Subsocial. The collected nests contained around fifty individuals of instars II and III. A sparrassid and a salticid spider were collected with the nests.

Additional material examined

Fifty-one juveniles [with holotype ♀ IA50112], 47 juveniles [IA50113], same locality, 7–8.v.2001 (I. Agnarsson and M. Kuntner) (NMNH).

One ♀ [IA50122], same locality, 24.xii.1999 (M. E. Irwin *et al.*) (CAS).

One ♀ [IA081301], MADAGASCAR: Fianarantsoa Province: P.N. Ranomafana, 21°17'0'S, 47°25'0'E, *c.* 1200 m, iv–v.1992 (V. & B. Roth) (MCZ).

One ♀ [IA50129], same locality, 5–18.iv.1998 (C. E. Griswold *et al.*) (CAS).

Distribution

Northeastern Madagascar, in montane rain forest (*c.* 1000–1500 m).

Anelosimus andasibe* Agnarsson & Kuntner, sp.n. (Figs 5I, 6E)Types*

Holotype ♀ [IA50108], MADAGASCAR: Toamasina Province, Périnet Special Reserve (P.N. Andasibe Mantadia), 900–1000 m, 18°56'S, 48°25'E, 7–8.v.2001 (I. Agnarsson and M. Kuntner) (NMNH).

Etymology

The species epithet is a noun in apposition after the type locality.

Diagnosis

Anelosimus andasibe differs from all but *A. nazariani* by the W-shaped septum, and from *A. nazariani* by the small distance between the septum and the epigynal margin (Fig. 5I), and by being smaller.

Description

Male. Unknown.

Female (holotype). Total length 3.77. Cephalothorax 1.76 long, 1.29 wide, 1.22 high, dark brown. Sternum 0.99 long, 0.86 wide, extending halfway between coxae IV, dark brown. Abdomen 2.15 long, 1.57 wide, 1.73 high. Pattern as in *A. vondrona* (Fig. 4H). Eyes subequal in size, about 0.09 in diameter. Clypeus height about 2.4× one AME diameter. Chelicerae with one large and two small prolateral teeth, three to four denticles retrolaterally. Leg I femur 1.98, patella 0.68, tibia 1.89, metatarsus 1.69, tarsus 0.75.

Femur about 5× longer than wide, metatarsus I about 11× longer than wide. Leg formula 1243. Leg base colour lighter than carapace, yellowish, distal tips of femora, patella and tibia darkened, and metatarsus/tarsus junction dark. Femora and tibia also with a ventral band centrally. Tarsal organs distal (0.55–0.60) on tarsi I and II, slightly proximal or central (0.40–0.45) on III and IV, distal (0.85) on female palp. Numerous (six to seven) small trichobothria dorsally on all tibia, seven on tibia III and I. Trichobothria on metatarsi I–III slightly proximal or central (0.45–0.50), absent on metatarsus IV. Four to five dorsal trichobothria on female palpal tibia. Epigynum with W-shaped septum (Fig. 5I) and separated spermathecae; the copulatory duct is interpreted in Fig. 6(E) to follow the septum edge.

Variation

Total length 3.60–4.55, cephalothorax 1.7–2.0, femur I 1.95–2.50.

Natural history

Subsocial. The single nest collected contained twenty-four individuals, mostly of instar III, in addition to one subadult, and one adult female.

Additional material examined

Twenty-three juveniles [with holotype ♀ IA50108], 1 ♀, 9 juveniles [IA50109], MADAGASCAR: same locality, 7–8.v.2001 (I. Agnarsson and M. Kuntner) (NMNH).

Two ♀ [IA50132], MADAGASCAR: Fianarantsoa Province, P.N. Ranomafana, Vohiparara village, 21°12'8'S, 47°23'0'E, *c.* 1100 m, 10–11.iv.1998 (C. E. Griswold *et al.*) (CAS).

Distribution

Northeastern Madagascar, in montane rain forest (*c.* 1000–1500 m).

Anelosimus salut* Agnarsson & Kuntner, sp.n. (Figs 4I, 5D, J)Types*

Holotype ♂ and paratype ♀ [IA50127], MADAGASCAR: Toamasina Province, Périnet Special Reserve (P.N. Andasibe Mantadia), 1000 m, *c.* 18°56'S, 48°25'E, 24.xii.2001 (M. E. Irwin, E. I. Schlinger, H. H. Rasolondalao) (CAS).

Etymology

The species epithet is an arbitrary combination of letters.

Diagnosis

Anelosimus salut males are readily diagnosed by small theridiid tegular apophysis distal projections, and by a bilobed embolic division b. Females differ from all but *A. vondrona* in having an 'inverted T-shape' septum, and from *A. vondrona* in the septum being narrower (Fig. 5J).

Description

Male (holotype). Total length 3.25. Cephalothorax 1.56 long, 1.19 wide, 1.02 high, brown. Sternum 0.92 long, 0.83 wide, extending between coxae IV, brown. Abdomen 1.82 long, 1.49 wide, 1.65 high. Pattern as in *A. vondrona* (Fig. 4H). Eyes subequal in size, about 0.11 in diameter. Clypeus height about 2.3× one AME diameter. Chelicerae with one large and two small prolateral teeth, four to five denticles retrolaterally. Leg I femur 2.76, patella 0.72, tibia 2.70, metatarsus 2.47, tarsus 0.98. Femur I about 6× longer than wide, metatarsus I about 12× longer than wide. Leg formula 1243. Legs unicolorous orange. Tarsal organs distal on tarsus I (0.65) and II (0.60), proximal (0.4–0.45) on III and IV. Five to eight small trichobothria dorsally on all tibia, five to six on tibia III, six to eight on tibia I. Trichobothria on metatarsi I–III proximal (about 0.40–0.45), absent on metatarsus IV. Two prolateral and one retrolateral trichobothria on palpal tibia. Palp as in Fig. 5(D).

Female (paratype). Total length 3.64. Cephalothorax 1.56 long, 1.24 wide, 0.96 high, dark brown. Sternum 0.92 long, 0.84 wide, extending between coxae IV, dark brown. Abdomen 2.15 long, 1.50 wide, 1.50 high. Pattern as in *A. vondrona* (Fig. 4H). Eyes subequal in size, about 0.09 in diameter. Clypeus height about 2.2× one AME diameter. Chelicerae with one large and two small prolateral teeth, four to five denticles retrolaterally. Leg I femur 2.76, patella 0.65, tibia 2.54, metatarsus 2.34, tarsus 0.91. Femur about 6× longer than wide, metatarsus I about 11× longer than wide. Leg formula 1243. Leg base colour pale yellow, with distal half of all femora and tip of tibia, patella and metatarsi darkened. Tarsal organs distal (0.70) on tarsus I, central (0.5) on II–III, proximal (0.45) on IV, distal (0.85) on female palp. Five to eight small trichobothria dorsally on all tibia, six on tibia III, five to six on tibia I. Trichobothria on metatarsi I–III proximal (about 0.40–0.45), absent on metatarsus IV. Four dorsal trichobothria on palpal tibia. Epigynum with a relatively narrow, 'inverted T-shape' septum (Fig. 5J); inner epigynum not examined due to the lack of specimens.

Variation

Known only from the type series.

Natural history

Unknown.

Anelosimus decaryi (Fage, 1930), comb.n.

Theridium decaryi Fage, 1930: 26–27, figs 1, 2. *Types*: Two vials in Musée National d'Histoire Naturelle, Paris (AR 2367), examined. One contains a male (presumably the holotype) and a female; another labelled 'type male' contains three females. Fage (1930: 26) reported the following localities: 'Madagascar: environs de Fort-Dauphin (Decary), sur les urnes du *Nepenthes madagascariensis*; 'le Sainte-Marie (Mocquary); Diégo-Suarez (Alluaud), sur les buissons'.

Anelosimus locketi Roberts, 1977, syn.n. *Types*: A vial (1878.11.1.22) in BMNH (examined) labelled 'Aldabra (woodland with mixed low scrub below Brown)', contains a single female, presumed to be the holotype, in poor condition, epigynum missing.

Anelosimus decaryi appears to belong to a different species group than the species described here, lacking the female epigynal septum, and the proximal embolic sclerite.

Phylogenetics

Cladistic analysis found the same single most-parsimonious cladogram under both 'amb-' and 'amb ='. This tree (Fig. 9) provides robust support for the monophyly of the Madagascar group (bootstrap = 99% and Bremer support index = 7), and places it within the 'curved SPR clade' of *Anelosimus* (see Agnarsson, 2004). The tree is otherwise identical to that found by Agnarsson (2004).

Discussion

The initial phylogenetic prediction was confirmed by finding social *Anelosimus* in Madagascar (the first outside the Americas). Understanding biodiversity and biogeography can therefore be augmented through phylogenies, for example to discover substantial pockets of unknown biodiversity. Phylogenies are a powerful predicting tool ideally suited to allocate research effort and resources parsimoniously. The late discovery of sociality in Malagasy *Anelosimus* is surprising as the nests are common and obvious in popularly visited areas. Three main explanations are possible: (1) previous workers may have collected them mostly during their solitary phase, (2) their social nests may have been overlooked, perhaps through the use of commonly used collecting methods such as beating vegetation, (3) they are

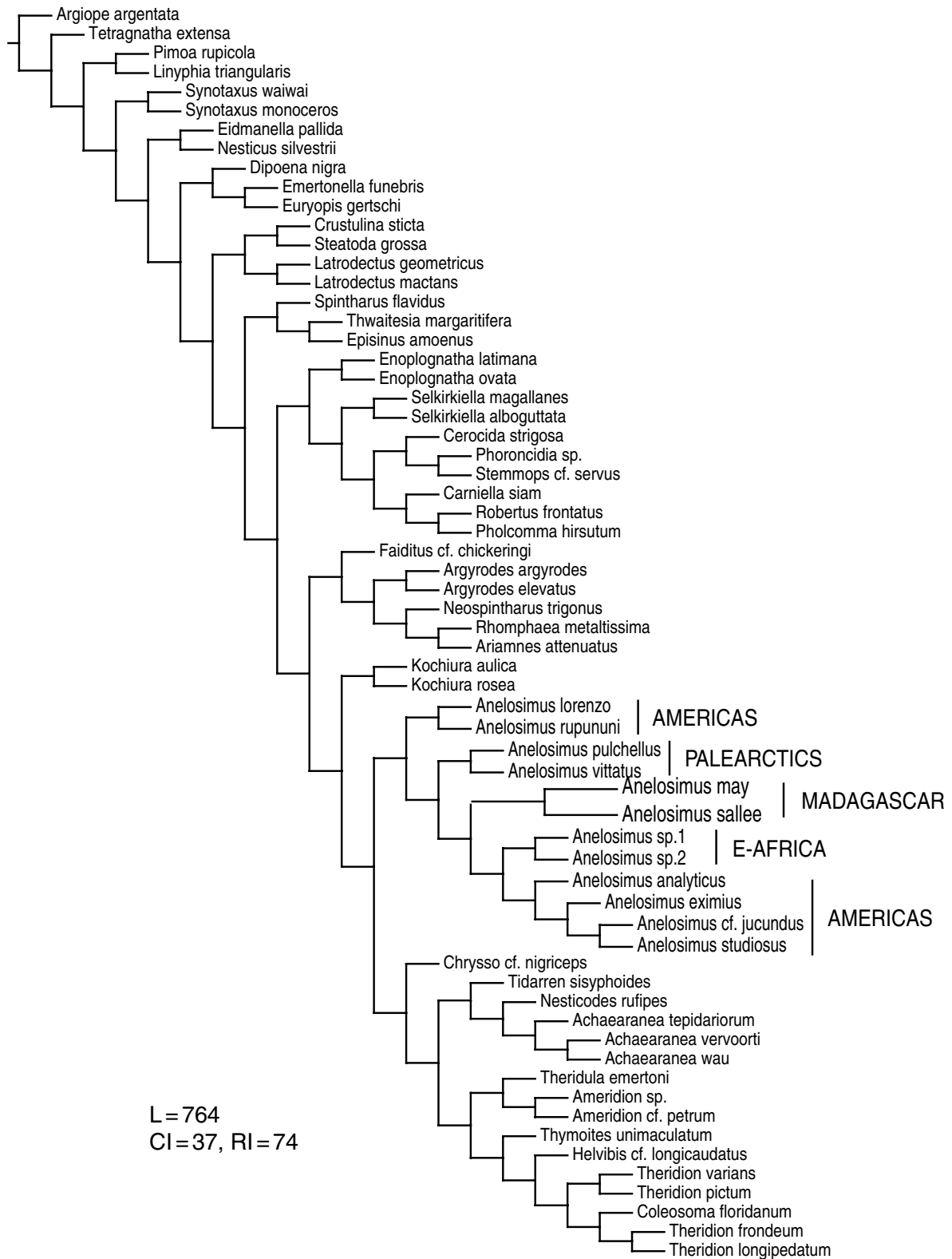


Fig. 9. The single most-parsimonious tree from the analysis of morphological data. Support for the Madagascar group is high (bootstrap = 99%; Bremer = 7). Apart from the Madagascar group, the tree is identical to that found by Agnarsson (2004) and support for all nodes is nearly identical (not shown).

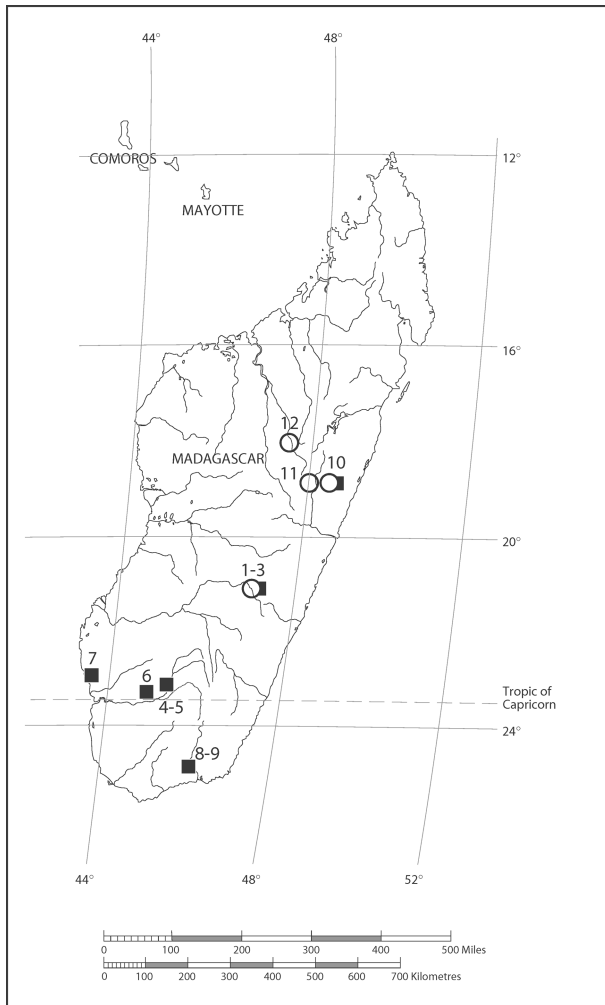


Fig. 10. Map of Madagascar with localities visited in 2001 (squares, 1–10, see text) and localities with the new species described (circles, see text).

commonly mistaken for the similar nests of unrelated social agelenid spiders that are ubiquitous in the area. All explanations find some support, several previous collections had males (collected during the solitary phase), no previous collection included juveniles (indicating that no entire nests have been collected), and the agelenid webs in Périnet are more common and reach greater size than the *Anelosimus* colonies – and previous workers had no reason to expect social webs in Madagascar to contain *Anelosimus* spiders. The key to our discovery was focused fieldwork, justified by the phylogenetic prediction of social *Anelosimus* where none had been reported previously.

Although previously unreported, the species richness in the small Périnet forest reserve, with at least six *Anelosimus* species living in sympatry, is similar to the most diverse parts of the Americas.

Given our meagre field data, a detailed comparison with behaviourally well-known American species is premature.

However, all five species encountered in the field appear typical subsocial *Anelosimus*. The nest is typical (Fig. 1A, B), a sheet embedded with leaves and with overlying knock-down threads. We never observed more than one adult female in a nest, suggesting that nests predominantly contain only a mother and her offspring. This is also indicated by the relatively low number of individuals per nest. As in many subsocial *Anelosimus*, the mother dies as the young near adulthood and the juveniles probably disperse before reaching adulthood (Avilés & Gelsey, 1998; Bukowski & Avilés, 2002; Powers & Avilés, 2003). In the few cases where instars could be sexed (antepenultimate and penultimate males are recognizable), juvenile sex ratios appear to be unbiased. Thus, the level of sociality shown by the new species seems similar to that of *Anelosimus 'arizona'* (Avilés & Gelsey, 1998; Bukowski & Avilés, 2002; Powers & Avilés, 2003).

All recent studies corroborate the 'maternal care route to sociality' (Avilés, 1997; Bukowski & Avilés, 2002; Agnarsson, 2002, 2004; Powers & Avilés, 2003; Miller & Agnarsson, in press) in which maternal care precedes subsociality, which in turn precedes quasisociality in evolutionary time. The study of intermediate social (subsocal) species is thus fundamental to understanding the evolution of quasisociality (e.g. Powers & Avilés, 2003); our finding has dramatically increased the pool size of subsocial species available for study.

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