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'. 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, cooperation 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 & Gelse, 1998; Furey, 1998; Avilés et al., 2000, 2001; Jones & Parker, 2000, 2002; Safré 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
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).

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.

**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).

**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 x 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 Syncroscopy 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 cylindrical gland spigot(s); PES, proximal embolic sclerite; MA, median apophysis; mAP, minor ampullectomy duct(s); E, embolus; Eb, embolic division b; 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 ampullectomy gland spigot(s); PES, proximal embolic sclerite; PI, embolic division b.

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: 00010000-00001111110000101010101010101010100110100000000-110001000010000001110000010011000000000000-00001111?00001000001

Anelosimus sallee: 00110000-000011111100000100000000-1100010000100000011100000100110

The full data matrix is provided in the Supplementary material on Syntropy. 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 ampullectomy gland spigot(s); PES, proximal embolic sclerite; PI,
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 \times 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 \times 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. 1. Field photographs. A, *Anelosimus may* nest; B, *A. sallee* nest; C, *A. may* female habitus; D, *A. sallee* female on sheet web.](image)

![Fig. 2. The relationship of nest size and nest content (size \times number of individuals per nest) for the four species with relevant data collected.](image)
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.

### Taxonomy

**Theridiidae Sundevall, 1833**

*Anelosimus* Simon, 1891


Type species: *Anelosimus socialis* Simon, 1891 (= *Anelosimus eximius* (Keyserling 1884)).


### 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 epignyal 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 pendulunlike 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


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. 4A, 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 5A and 7A–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...

1.55–1.70, femur I 2.61–2.73. Specimens from Ranomafana are generally larger than those from Pépinet 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 ♀ IAS50101], 51 juveniles [IAS50102], 1 ♀ [IAS50103], 18 juveniles [IAS50104], 1 ♀ [IAS50105], 1 ♀, 1 juvenile [IAS50106], 1 ♀ [IAS50107], same locality, 7–8.v.2001 (I. Agnarsson and M. Kuntner) (NMNH).

**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. nazarianii*; H, *A. vondrona*; I, *A. andasihe* holotype; J, *A. salut.*
Four ♂, 2 ♀ [with paratype ♂ IA50121], 2 ♂, 10 ♀ [IA50128], MADAGASCAR: Antananarivo Province, Réserve Spéciale d’Ambositra, Forêt d’Ambositra, 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, 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).

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

Types

Holotype ♂, paratype ♀ [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 ♀ [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.

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**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 × 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 × longer than wide, metatarsus I about 16 × 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 × 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 × longer than wide, metatarsus I about 11 × 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. sallie* 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, Périté 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 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 × 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 × longer than wide, metatarsus I about 17 × 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 sparassid, a mysmenid, and an Argyrodexes 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′33″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, Pénet 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 retrolaterally. 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 sparassid 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 ♀ [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, 1.12 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 retrolatetally. 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 palp 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 regular 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 Nephenthes madagascariensis; ‘le Sainte-Marie (Mocquary); Diégo-Suarez (Alluaud), sur les buissons’.

*Anelosimus locketi* Roberts, 1977, syn.n. Types: A vial (1878.11.22) 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).
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 Pe`rinet 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 Pe`rinet 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 knockdown 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 (subsocial) 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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