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A new phylogeny of *Anelosimus* and the placement and behavior of *Anelosimus vierae* n. sp. from Uruguay (Araneae: Theridiidae)

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Abstract. Available evidence suggests that sociality in the spider genus *Anelosimus* Simon has evolved as a gradual transition from short-term maternal care to permanent sociality. The discovery and description of new species displaying various intermediate levels of sociality deepens our understanding of this transition. Here I use five molecular loci (28S, ITS2, COI, 16S, ND1) to phylogenetically place specimens of an intermediate-social population from Uruguay, previously and tentatively identified as the widespread and common *A. studiosus* (Hentz 1850). The Chinese *A. chonganicus* Zhu 1998 is also phylogenetically placed for the first time, and new sequences from four additional *Anelosimus* species and two theridiid genera (*Audifia* Keyserling, *Tekellina* Levi) are all combined with previously published data to reconstruct a novel phylogeny of *Anelosimus* spiders. This phylogeny recaptures previously well-established groups and reiterates well-known themes such as the multiple origin of sociality. The Uruguayan specimens nest outside of *A. studiosus*, and I therefore describe these as a new species, *Anelosimus vierae* sp. n. and summarize existing data on its behavior in the context of social evolution. I also synonymize *A. tungurahua* Agnarsson 2006 with *A. studiosus* new synonymy. Finally, I define the subfamily Anelosiminae, containing *Anelosimus* and *Kochiura* Archer; Anelosiminae is sister to the diverse Theridiinae.

Keywords: Cobweb spiders, intermediate social, social evolution, subsocial

Only a few of the over 41,000 described spiders (Platnick 2010) are social, and most of them occur in a few clusters of phylogenetically closely-related species (Avilés 1997; Agnarsson et al. 2006a; Avilés et al. 2006; Lubin & Bilde 2007; Johannesen et al. 2007, 2009). The cobweb spider genus *Anelosimus* Simon 1891, for example, contains the majority of all cooperative spiders, and recent work has uncovered many new *Anelosimus* species (Agnarsson 2005, 2006; Agnarsson & Kuntner 2005; Agnarsson & Zhang 2006; Agnarsson et al. 2010). *Anelosimus* species display a range of social behavior from solitary with short-term maternal care (Agnarsson et al. 2006b) to permanent, highly social behavior (Vollrath 1986; Avilés 1997; Avilés et al. 2001). The majority of *Anelosimus* species are subsocial with single-female nests, involving sibling cooperation until adulthood, followed by dispersal and outbreeding, and equal sex ratios (Avilés 1997). Eight species are permanently social with multi-female nests showing adult cooperation and successive generations remaining in the natal nests, with inbreeding and interdemic selection resulting in strongly female-biased sex ratios (Avilés 1993, 1997; Avilés et al. 2007). The phylogenetic relationships among these species suggest multiple, gradual, transformations from subsocial to permanently social (Agnarsson et al. 2006a, 2007a), as also seen in the distantly related eresid spiders, genus *Stegodyphus* Simon 1873 (Bilde et al. 2005; Johannesen et al. 2007, 2009). This transition presumably occurs via the various intermediate social stages (occurrence of multi-female nests, partial outbreeding, intermediate sex ratio bias) (Powers & Avilés 2003; Avilés & Bukowski 2006) that are displayed by a few existing species, such as *A. jabaquara* Levi 1956, *A. dubiosus* (Keyserling 1891) and certain populations of *A. studiosus* (Hentz 1850) (Marques et al. 1998; Vasconcelos-Netto & Mello 1998; Jones & Parker 2000, 2002; Gonzaga & Vasconcellos-Neto 2001, 2002; Jones et al. 2007). Thus the discovery and phylogenetic placement of further species with intermediate social structures will deepen the understanding of social evolution in spiders.

I recently revised the American *Anelosimus* species (Agnarsson 2005, 2006) based on an examination of material from all major museums worldwide containing American material. Concurrently, behavioral data were being collected for some of the potentially new species (by L. Avilés and coworkers) which greatly helped species delimitation. Nevertheless, I concluded that these revisions were incomplete, not only because future sampling would likely uncover new species, but also because, in some cases, examination of morphology alone seemed insufficient to adequately delimit species from existing material (Agnarsson 2006). The first molecular phylogeny (Agnarsson et al. 2007a) showed good congruence with morphological taxonomy in general, especially for taxonomic decisions that were based on morphological and behavioral data combined, but this study also pointed to some potential problems. For example, *A. tungurahua* Agnarsson 2006 had seemed subtly distinct from *A. studiosus* morphologically, but nested within *A. studiosus* in gene trees of multiple loci (Agnarsson et al. 2007a). Further, a specimen from Uruguay tentatively identified as '*A. studiosus*' did not group close to *A. studiosus* in preliminary analyses (I. Agnarsson unpublished data). Now, several studies on the behavior of this Uruguayan population have been conducted, demonstrating some differences from the behavior of *A. studiosus*, and have highlighted that this population shows an intermediate social structure (Albo et al. 2007; Viera et al. 2006, 2007a, b, c; Viera & Albo 2008). For example, in the Uruguayan population multi-female nests are not uncommon, and primary sex ratios are female-biased 2:1 (Viera et al. 2007a).

Here, I add three specimens of the Uruguayan population and additional sequences from five other *Anelosimus* species (*A. analyticus* (Chamberlin 1924), *A. chonganicus* Zhu 1998, *A. ethicus* (Keyserling 1884), *A. octavius* (Agnarsson 2006), *A. rupununi* Levi 1956), and two new outgroups (*Audifia* Keyserling 1884 and *Tekellina* Levi 1957) to the molecular phylogenetic analyses of Agnarsson et al. (2007a, 2010) and, following the phylogenetic results, describe the Uruguayan

population as a new species. Finally, I summarize what is known about its behavior, in the context of social evolution.

METHODS

Phylogenetics.—Specimens were collected in the field (from Montevideo, Uruguay, 34°53′15″S, 56°08′33″W) by C. Viera and collaborators, and fixed in 95% ethanol. I obtained sequences of mitochondrial (16S, ND1, COI) and nuclear (28S, ITS2) loci from three individuals of *A. vierae*, using primers and settings as described in Agnarsson et al. (2007a) and Agnarsson (2010). I also obtained for the first time sequences from three specimens of *A. chonganicus* and additional sequences from three specimens of *A. analyticus* and *A. octavius*, two specimens of *A. rupununi*, and one specimen of *A. ethicus* and species of the genera *Audifia* sp. and *Tekellina* sp. I then combined these new sequences with previously published sequences from Agnarsson et al. (2007a, 2010). Genbank accession numbers of new sequences are not yet available. The total dataset contains 86 terminals, comprising 18 outgroups from across Theridiidae and 68 individuals representing 25 out of the 54 currently recognized *Anelosimus* species. Most of the missing *Anelosimus* species are outside the '*eximius* lineage' (Agnarsson 2006), which contains most of the American species, including *A. studiosus* and relatives, and thus are not critical to the placement of the Uruguayan population. The data matrix is available from the author and will be submitted to the Dryad database (online at http://datadryad.org/).

I aligned and analyzed the molecular data using the same methods and settings as in previous studies (Agnarsson et al. 2007a, 2010). In summary, I aligned sequences in Clustal W (Thompson et al. 1994) with gap opening and extension costs of 24/6, followed by minor manual adjustments. I then concatenated the genes into a single five-gene matrix in Mesquite (Maddison & Maddison 2010) and exported them for model selection and analyses. The matrix was partitioned by gene, and for protein coding genes (COI, ND1), additionally by codon position, for a total of 9 partitions. The appropriate model for each partition was chosen in jModeltest 0.1.1 (Posada 2008), selecting only among the 24 models implemented in MrBayes. Final model choice for each partition was thus as follows: 28S, COI^{1st}, COI^{2nd}, 16S, $ND1^{2nd}$ = GTR+I+Γ; COI^{3rd}, ITS2 = GTR+Γ; $ND1^{1st}$ = HYK+Γ; $ND1^{3rd}$ = HYK+I+Γ. I then analyzed the concatenated matrix in MrBayes (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003). The Bayesian analysis was run for 10,000,000 generations, with all base frequencies estimated from the data and parameter estimates unlinked (''unlink statefreq = (all) revmat = (all) shape =(all) pinvar = (all)''). The first 5,000,000 were then discarded as 'burnin', after which stationarity had been reached.

Taxonomy.—Morphological methods were described in detail in Agnarsson (2004, 2006). Nomenclature of the male palpal organ follows Agnarsson et al. (2007b). All measurements are in millimeters and made using an Infinity K2 long-distance microscope. Prosoma and abdomen length and height are measured in lateral view, and widths in dorsal view are all measured at widest points. Leg segments are measured without the detachment of legs from the prosoma. Illustrations are prepared using a Visionary Digital imaging system, the core components being a Canon 5D digital camera body and a K2 Infinity microscope equipped with Olympus metallurgical objectives. Successive images are combined with Helicon Focus 4.0, and thereafter minimally processed with Photoshop CS3 to adjust for both contrast and brightness and to remove background blemishes. For photography, anatomical preparations are temporarily mounted in alcohol-based hand sanitizer jelly (62% ethanol) and the specimen then covered with 70% ethanol. I deposited type specimens at the National Museum of Natural History, Smithsonian Institution, Washington, D.C.; additional voucher specimens were lodged in the Zoological Museum, University of Puerto Rico, Río Piedras.

RESULTS AND DISCUSSION

Phylogenetics.—The new phylogeny in most details mirrors that of Agnarsson et al. (2007a, 2010), except in the placement of some species of the sclerotized CD clade, and in higher posterior probability support inferred for many nodes (Fig. 1). *A studiosus* (including specimens of *A. tungurahua*) plus the three Uruguayan specimens form a grade sister to other species of the sclerotized CD clade. Hence, the Uruguayan specimens are here described as a new species, *A. vierae* n. sp., and *A. tungurahua* is synonymized with *A. studiosus* (see below).

The newly added Chinese species *A. chonganicus* nests sister to species from Malaysia and Singapore within a clade, which, based on morphological evidence, also contains many African and Southeast Asian species; this clade is thus referred to as the 'Old World clade' (Fig. 1). Other newly added specimens of four additional *Anelosimus* species group as expected with their previously sequenced conspecifics, and all species here represented by multiple specimens are monophyletic (Fig. 1). The newly added genus *Audifia* (Hadrotarsinae) is used here as the primary outgroup, and its placement is thus not tested. However, the other newly added genus *Tekellina* does not group within the Theridiinae, unlike previously hypothesized (Agnarsson 2004). Further investigation of the placement of these two genera is necessary and will be facilitated by the sequences made available here.

Spiders of two genera, *Anelosimus* and *Stegodyphus*, are the major models in the study of spider sociality and its evolution (e.g., Avilés 1997; Avilés et al. 2000, 2001; Jones & Parker 2000, 2002; Bukowski & Avilés 2002; Johannesen et al. 2002, 2007, 2009; Powers & Avilés 2003, 2007; Bilde et al. 2005, 2007; Jones et al. 2007; Lubin & Bilde 2007; Purcell & Avilés 2007; Yip et al. 2008; Pruitt et al. 2008, 2010; Pruitt & Riechert 2009; Duncan et al. 2010). Discovery and phylogenetic placement of new species in these genera will deepen our understanding of social evolution and its causes and consequences. Because many aspects of the behavior of *A. vierae* are already studied, describing and phylogenetically placing this new species will contribute to the phylogenetic ancestral character reconstruction of the various components of social behavior in spiders. Furthermore, *A. vierae* is a close relative of the socially polymorphic *A. studiosus* and will thus represent a good model to complement recent studies on social polymorphism and its origin and consequences (Jones and Parker 2000, 2002; Jones et al. 2007; Pruitt et al. 2008, 2010; Pruit & Riechert 2009; Duncan et al. 2010).

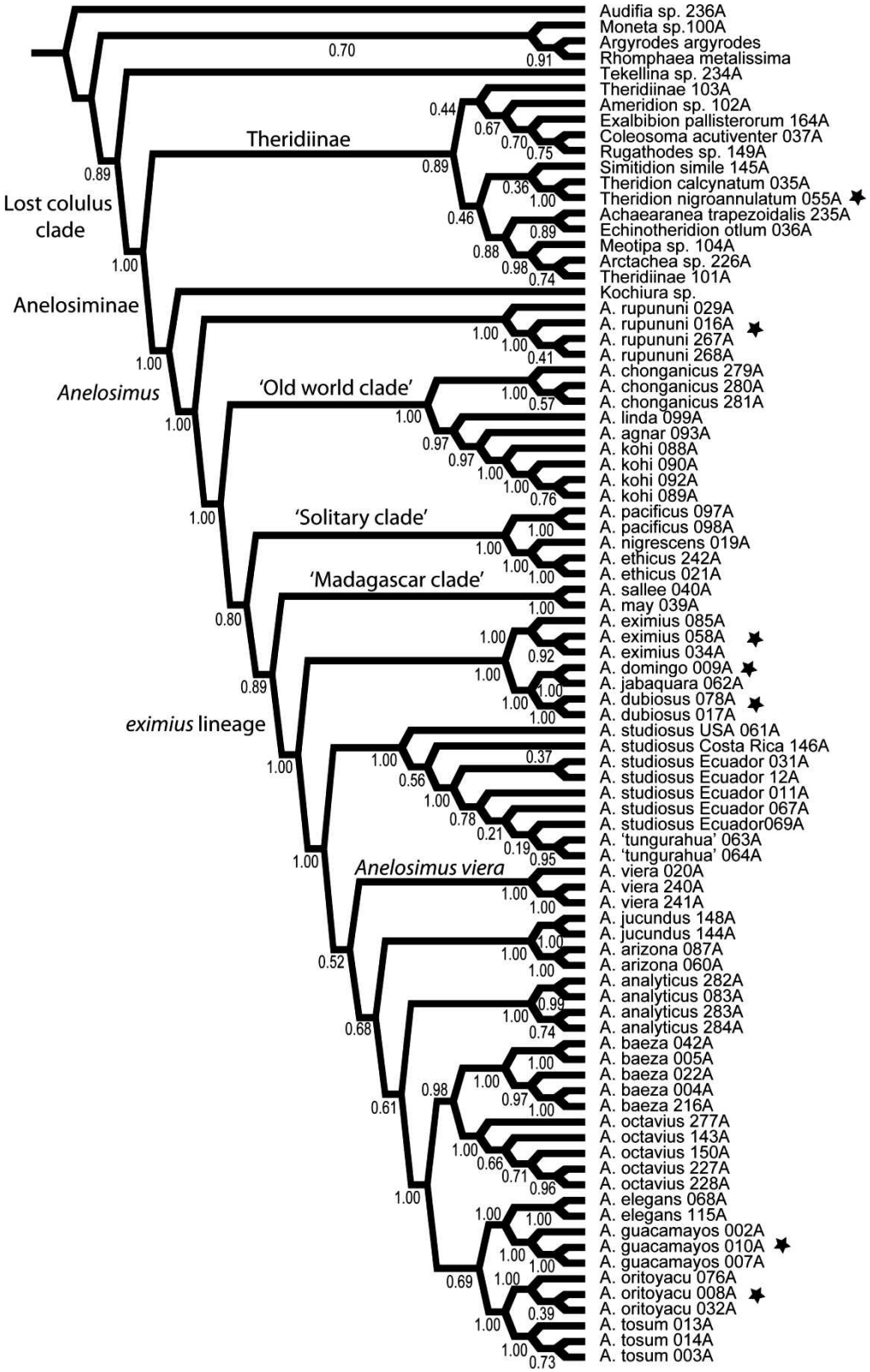


Figure 1.—Results of Bayesian phylogenetic analysis of the concatenated dataset for the genus *Anelosimus*. The new species *A. vierae* does not group with *A. studiosus*, where the Uruguayan specimens were tentatively placed before. Permanently social species are marked with ★.

All recent studies corroborate the 'maternal care route to sociality' (Avilés 1997; Agnarsson 2002, 2004; Bilde et al. 2005; Johannesen et al. 2007, 2009; Agnarsson et al. 2010), 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. see Powers & Avilés 2003).

Natural history.—This section summarizes previous work on the natural history and behavior of this species (Viera et al. 2006, 2007a, b, c; Albo et al. 2007; Viera & Albo 2008). *Anelosimus vierae* is a subsocial species, the mother of which cares for her young, and the juveniles show a lack of conspecific aggression, but rather cooperate in the natal nest until dispersal, near or at adulthood (Albo et al. 2007). Absence of aggression is nearly complete for motile instars; females cannibalize some eggs, but never eat larvae or nymphs (Viera et al. 2007c). Maternal care involves many elements, starting with egg-sac guarding and then opening the egg sac to release the young. The larvae are not able to break out of the egg sac by themselves (Viera et al. 2007c). Mothers open the egg sac based on time since laying the egg (21 days), but the mothers' actions are also triggered by the movement of nymphs within the egg sac (Viera et al. 2007c). The mother then feeds her offspring via regurgitation (Viera et al. 2005). The mother dies as the juveniles reach instars IV–VI. A very interesting feature of this species is that the juveniles then continue to feed each other via regurgitation (Viera et al. 2005). As a result of these altruistic acts, there is an equalizing of food distribution among colony members, which may prevent starvation and result in more individuals reaching adulthood. Although this remains to be observed in other species, it seems likely that juvenile food sharing may represent an evolutionary 'stepping-stone' towards permanent sociality.

In general, males of *A. vierae* mature earlier and consistently disperse, while females mature asynchronously and may or may not disperse from the natal nest. The consequence of this dispersal pattern is the formation of some multi-female nests. The occurrence of multi-female nests, in turn, implies a somewhat intermediate social structure, or social polymorphism, as seen in certain populations of *A.studiosus* in North America (Jones & Riechert 2008; Pruitt et al. 2008). In fact, the primary sex ratio in this species is also slightly female biased (2:1) (Viera et al. 2007a), implying some interdemic selection (Avilés 1993, 1997). Hence, *A. vierae* could be characterized as an intermediate social species, showing levels of sociality somewhere close to *A. jabaquara* (Marques et al. 1998).

The early-maturing males court and guard both subadult and adult females and fight other males, indicating competition for paternity among males (Albo et al. 2007). Fights can be repeated and males winning first fights may eventually lose to other males. Males court females using vibration, silk thread plucking, and touching the female until she adopts a copulation position. Males that lose fights may still remain as satellites around the nest and opportunistically mate with her later. This implies that strict first male priority need not be the rule in *A. vierae*, and this implication was recently confirmed through a gamma radiation sterilization experiment, showing that first and second males have about equal levels of paternity success (Lorieto et al. 2010).

TAXONOMY

Remarks.—Agnarsson (2004) established a classification of theridiid spiders, placing most of the genera into subfamily-level clades. However, *Anelosimus* and *Kochiura* remained unplaced. Here I find a well-supported clade including *Anelosimus* and *Kochiura,* which together form a clade sister to the subfamily Theridiinae. Therefore, the subfamily Anelosiminae is established to accommodate *Anelosimus*, *Kochiura*, and possible relatives of these taxa (Fig. 1). While naming well-supported clades is certainly useful, establishing many fixed ranks in between genera and families can be problematic (Kuntner & Agnarsson 2006), and authors should be careful not to treat theridiid subfamilies as 'comparable' taxonomic units; fair comparisons are between sister clades.

Family Theridiidae Sundevall 1833

Subfamily Anelosiminae subfam. nov.

Remarks.—Anelosiminae currently includes *Kochiura* and *Anelosimus*. A putative synapomorphy of this clade is the characteristic abdominal pattern (Figs. 6–8). These genera also have a unique combination of characters with colulus highly reduced (*Kochiura*) or absent (*Anelosimus*), but with two small colular setae usually present. This character combination, however, does not represent a synapomorphy, as the two taxa have different states of colular reduction, and the retention of two colular setae is primitive, which may explain why there is little support for this arrangement in morphological data. Furthermore, the character-rich palpal organ is extremely variable within this subfamily such that Anelosiminae synapomorphies are not evident. Anelosiminae is readily diagnosed from the sister subfamily Theridiinae, as in the latter all species lack colular setae.

Genus *Anelosimus* Simon 1891

Type species.—*Anelosimus socialis* Simon 1891 [= *Anelosimus eximius* (Keyserling 1884)].

Remarks.—See Agnarsson (2004, 2006) for taxonomic treatment of the genus.

Anelosimus studiosus (Hentz 1850)

Anelosimus tungurahua Agnarsson 2006:502, figs. 35K–Q, 42–43, 64D. **New Synonymy.**

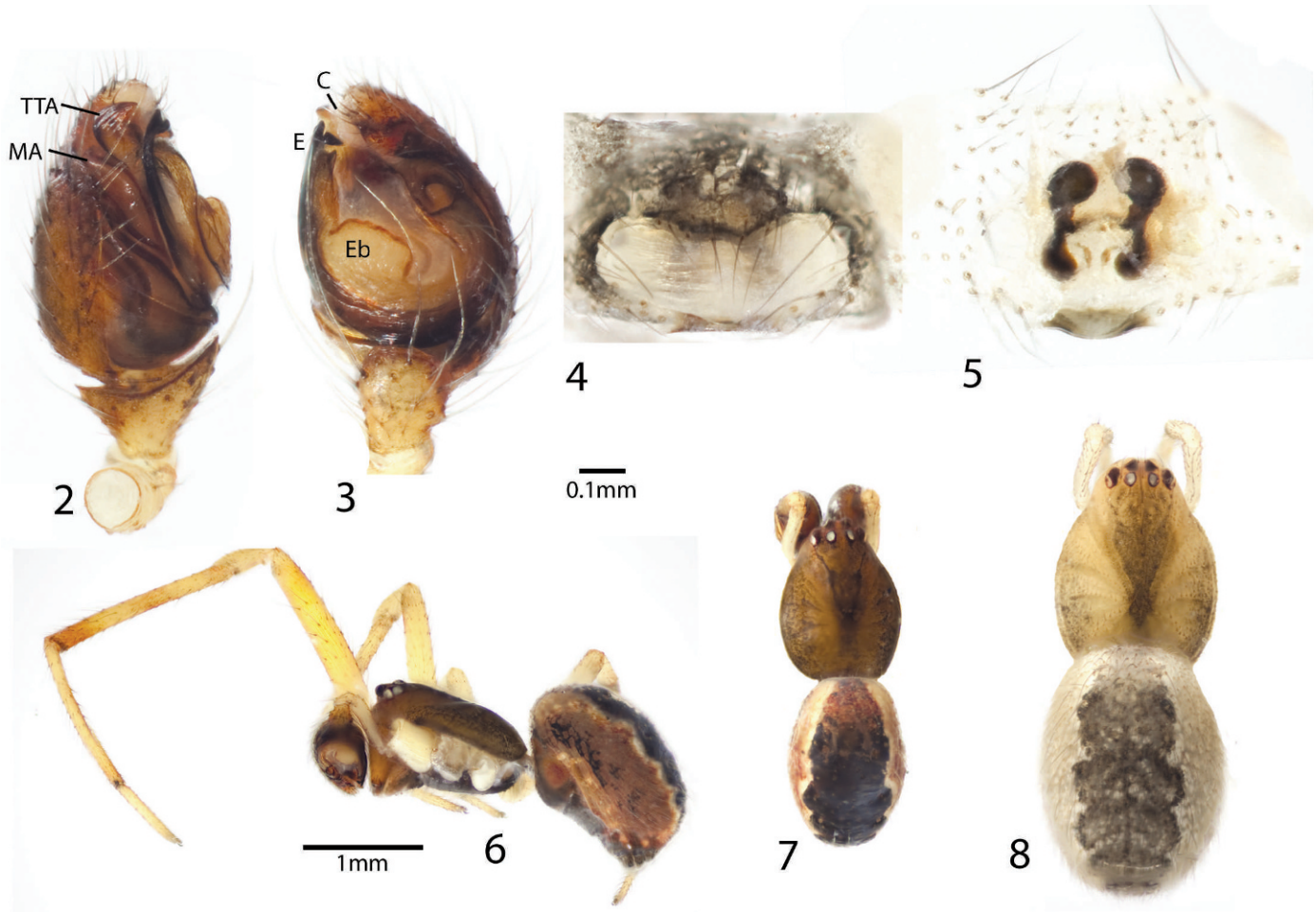
Synonymies.—See Agnarsson (2006) for detailed synonymies

Remarks.—Agnarsson's (2006) diagnosis was based on subtle morphological differences between *A. tungurahua* and *A. studiosus*, namely that males of the former had a flatter embolic division b (Eb), with a narrower and less rugose distal tip, and females had a larger epigynal lip. However, in light of the current results, these traits are now considered as intraspecific morphological variation of *A. studiosus*.

Anelosimus vierae new species
(Figs. 2–8)

Material examined.—*Type:* Holotype ♂, URUGUAY: *Montevideo*, Montevideo, Melilla, 34.90°S, 56.15°W, 30 m, November 2003, C. Viera and F. Costa (USNM).

Other specimens (not types).—3 ♂, 3 ♀, same data (USNM); 1 ♂, 1 ♀, URUGUAY, *Lavalleja*, Sierra de Minas, Parque de Vacaciones, 34.426°S, 55.195°W, December 2005, W. Maddison, G. Ruiz, M. Simó, M.E. Rodriguez (USNM).



Figures 2–8.—*Anelosimus vierae* sp. n. genitalia and habitus of specimens from Sierra de Minas, Lavalleja, Uruguay. 2, 3: Male palp, ectal, ventral; 4, 5: Female epigynum, ventral, dorsal cleared; 6, 7: Male habitus, ectal, dorsal; 8: Female habitus, dorsal. Upper scale bar for Figs. 2–5, lower scale bar for Figs. 6–8.

Etymology.—The species epithet is a noun in apposition; a patronym after Carmen Viera, whose work on this species has revealed some fascinating behaviors, and inspired further investigation into its phylogenetic placement.

Diagnosis.—Males can be diagnosed from other *Anelosimus* species except *A. studiosus* by the sharp constriction of the embolic division b (Eb) centrally (Fig. 3), and from *A. studiosus* by longer distal arm of the Eb, and wider lightly sclerotized area separating the Eb from the ectal tegular margin. Females differ from all other *Anelosimus* species, except others in the *studiosus* group, by having the strongly sclerotized portion of the copulatory duct (see Agnarsson 2006) directly ventral to the spermathecae (Fig. 5). However, females are difficult to diagnose from other species of the *studiosus* group, except using molecular data.

Description.—*Male* (Sierra de Minas, Uruguay)*:* Total length 2.80. Cephalothorax 1.35 long, 1.05 wide, 0.80 high, brown. Abdomen 1.45 long, 1.00 wide, 1.15 high. Pattern as in Figs. 6, 7. Eyes subequal in size about 0.08 in diameter. Chelicerae with one large and two small prolateral teeth, three to four denticles retrolaterally. Leg I femur 1.70, patella 0.45, tibia 1.65, metatarsus 1.35, tarsus 0.70. Femur not noticeably thickened, ventral thickened hairs on metatarsus one absent. Leg formula 1243. Leg base color yellowish, light brown, with distal tip of femora and tibia darker. Four to five small trichobothria dorsally on all tibia. Trichobothria on metatarsi I–III proximal (about 0.35–0.40), absent on metatarsus IV. Palp (Figs. 2, 3) as in other species of the *studiosus* group, smaller and with less voluminous sclerites than species of the *jucundus* group. Embolus spiral runs along mesal margin of palp terminating in a ridged bifurcation, embolus with a simple flat, embolic division b, which is narrow distally. The basal lobe of the embolus is oriented toward the subconductor, from which a small and translucent conductor arises. Median apophysis simple, without ducts, interacting with cymbial hood. TTA hooked and ridged distally.

Female (Sierra de Minas, Uruguay)*:* Total length 3.70. Cephalothorax 1.80, long, 1.40 wide, 1.00 high, brown. Abdomen 2.10 long, 1.55 wide, 1.30 high. Pattern as in Fig. 8. Eyes subequal in size, about 0.10 in diameter. Chelicerae with one large and two small prolateral teeth, three denticles retrolaterally. Leg I femur 2.10, patella 0.65, tibia 1.80, metatarsus 1.70, tarsus 0.90. Leg formula 1243. Leg base color light yellowish-brown, with distal tip of tibia darkened. Four to seven small trichobothria dorsally on all tibia. 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 externally a lightly ridged plate, internally with simple short copulatory and fertilization ducts, copulatory ducts strongly sclerotized and situated directly below the ectalmost margin of the spermathecae (Figs. 4, 5).

Variation.—Female total length 3.60–4.20, male total length 2.5–2.85.

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