New species of *Anelosimus* (Araneae: Theridiidae) from Africa and Southeast Asia, with notes on sociality and color polymorphism

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Abstract

The cobweb spider genus *Anelosimus* contains species showing various levels of social behavior. American *Anelosimus* are well known and several species have been described from Europe, China, Japan, and Madagascar. However, to date, only two behaviorally unknown species have been
described from continental Africa, Southeast Asia, and Australasia combined. In this paper we describe seven new \textit{Anelosimus} species, \textit{A. agnar} n. sp. (Malaysia), \textit{A. biglebowski} n. sp. (Tanzania), \textit{A. dude} n. sp. (Tanzania), \textit{A. linda} n. sp. (Malaysia), \textit{A. monskenyensis} n. sp. (Kenya), \textit{A. nelsoni} n. sp. (South Africa), and \textit{A. sulawesi} n. sp. (Sulawesi) from Africa and Southeast Asia. We also redescribe \textit{A. kohi} Yoshida, 1993 and provide evidence for subsocial behavior in that species. \textit{Anelosimus kohi} shows a marked color polymorphism that is apparently habitat-related, both in populations in Malaysia and in Singapore. Several of the undescribed species were included in previous phylogenetic analyses, and the likely phylogenetic placement of each species is discussed. Based on new behavioral information we discuss the phylogenetic and geographical distribution of temporary and permanent sociality in \textit{Anelosimus}.

\textbf{Key words:} Cladistics, morphology, sociality, subsocial, taxonomy

\section*{Introduction}

The cosmopolitan cobweb spider genus \textit{Anelosimus} Simon, 1891 (Theridiidae) is unique for the social behavior of nearly all its species. With species ranging from extensive maternal care (e.g. \textit{A. pacificus} Levi, 1956, I. A. pers. obs), to temporary social, e.g. \textit{A. arizona} Agnarsson, 2006 (see Avilés & Gelsey 1998; Bukowski & Avilés 2002; Powers & Avilés 2003) to permanently social, e.g. \textit{A. eximius} (Keyserling, 1884) (for review see Avilés 1997) the genus plays an important role in understanding the evolution of sociality in spiders, and other animals (for reviews see Kullmann 1972; Buskirk 1981; Avilés 1997). Knowledge of \textit{Anelosimus} species in different geographic regions is highly asymmetric (see distribution listings in Platnick 2005). New World species are intensely studied both taxonomically (Levi 1956, 1963; Agnarsson 2005, 2006) and behaviorally (reviewed in Avilés 1997). A number of species have been described from China and Japan (Bösenberg & Strand 1906; Yoshida 1986; Zhu 1998; Song \textit{et al}. 1999), Europe (Walckenaer 1802; Koch 1836) and Madagascar and the Seychelles (Roberts 1983; Agnarsson & Kuntner 2005) including some basic behavioral observations on some of the species. However, to date only one species has been described from each of mainland Africa (see Miller 2004), and Southeast Asia (see Yoshida 1993), although based on limited sampling the genus is widespread in these areas and probably many species are yet to be discovered.

This paper describes seven new \textit{Anelosimus} species from Southeast Asia (Malaysia, Singapore, Sulawesi) and Africa (Tanzania, Kenya, South Africa) based mostly on recently collected specimens. \textit{Anelosimus kohi} Yoshida, 1993 from Singapore and Malaysia is also redescribed. The paper provides basic behavioral information on two of the species, and discusses a remarkable example of color polymorphism in \textit{A. kohi}. The phylogenetic placement of each species is discussed based on both morphological (Agnarsson 2004, 2005, 2006), and preliminary molecular data (Agnarsson unpublished).
Material and methods

For details of methodology see Agnarsson (2004, 2005, 2006). Specimens were examined and illustrated using a Leica MZ Apo dissecting microscope and a Leica DMRM compound microscope, both with a camera lucida. Photographs were taken in the field with a Canon EOS digital camera with a ring-flash, and micrographs in the lab using a Leo 1430VP scanning electron microscope.

All measurements are in millimeters and were made using a micrometer eyepiece. Prosoma and opisthosoma length 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 prosoma and are thus approximations. Female genitalia were excised using micro-knives and sharp needles. The epigyna were then rendered transparent using KOH. Genitalia were drawn in ethanol using a compound microscope with a camera lucida.

In text ‘Fig.’ refers to figures herein, while ‘fig.’ refers to figures published elsewhere.

Material is deposited in the following institutions: California Academy of Sciences, San Francisco (CAS), Museum of Comparative Zoology, Harvard, Cambridge (MCZ), National Museum of Natural History, Smithsonian Institution, Washington DC (NMNH).

Results and discussion

Phylogenetics

Based on Agnarsson (2004, 2005, 2006), and preliminary molecular data (Agnarsson unpublished) the Anelosimus species described here belong to four lineages: the ‘kohi group’ (A. kohi), the filiform embolus clade [=‘Tanzania group’ in Agnarsson 2006] (A. biglebowski n. sp., A. dude n. sp., A. monskenyensis n. sp., and A. sulawesi n. sp.), the ‘agnar group’ (A. agnar n. sp., and A. linda n. sp.), and the ‘basal cymbial hood clade’ (A. nelsoni n. sp.) (see Fig. 1 and legend).

Sociality

Anelosimus kohi appears to show typical subsocial behavior. The webs are dome-shaped sheet with aerial flight intercepting threads (Fig. 2), and each colony is founded by a single female where she raises her offspring. Several webs were encountered with juveniles and egg sac present, indicating that females may often lay more than one egg sac. The young stay in the mother’s web at least until close to adulthood, nests were observed with juveniles estimated to belong to fourth or fifth instar. No webs were found with more than one adult female, and sex ratios appear to be approximately equal, hence these species apparently show level of sociality comparable to the well studied A. arizona (Avilés & Gelsey 1998; Bukowski & Avilés 2002; Powers & Avilés 2003, Klein et al. 2005). There is indirect evidence that A. monskenyensis may also be subsocial (see taxonomy), while behavioral information on other species is as yet lacking. None of the
collection data indicate the occurrence of large colonies, or female biased sex ratios, hence permanent sociality can be all but ruled out for all of the species. The discovery of subsociality in two old world lineages (and its presence in the European A. vittatus, F. Vollrath and P. Jaeger pers. comm.) increases the likelihood that subsociality is ancestral for the genus. To date, only A. pacificus from Central America (Agnarsson unpublished) and A. crassipes from Japan (Ito and Shinkai 1993) have been shown to be solitary although showing extended maternal care, a behavior that given the phylogenetic placement of the species well within the genus, seems to represent a reversal from subsociality.

If subsociality is ancestral in Anelosimus, it remains unknown why permanent sociality is only known from Neotropical species, where it has evolved independently from subsocial ancestors several times (Agnarsson 2006). Most likely this reflects simply asymmetry in knowledge, the discovery of permanent sociality in many of the species is recent, and largely due to the work of Leticia Avilés and coworkers in Ecuador. We predict that with increased research effort permanently social Anelosimus species will be discovered in the African or Asian tropics.

Color polymorphism

Many Anelosimus species are known to show some variation in coloration, especially in the intensity of the opisthosoma coloration (Agnarsson 2006). However, some species examined here show a more extreme color polymorphism than any examined by Agnarsson (2005, 2006) or Agnarsson & Kuntner (2005), e.g. Anelosimus kohi (Fig. 3). The pattern of coloration is typical of Anelosimus worldwide, carapace and legs brownish with darker cephalic region and tips of some leg segment, opisthosoma grey to yellow with red longitudinal notched folium centrally on the opisthosoma, bordered by a narrow whitish band (e.g. Agnarsson & Kuntner 2005, fig. 1C, see also Fig. 4). In A. kohi the coloration ranges from relatively uniformly dark (Figs 3A–C), to bright and highly contrasting coloration with bright red central folium on the opisthosoma (Figs 3D–H). The most common color morphs are at the opposite end of the range (Figs 3A–H), but ‘intermediate’ color morphs are also found (e.g. Fig. 3I). In A. biglebowski and A. dude variation in coloring was also profuse (see Taxonomy), but specimens were only observed after being preserved in alcohol and thus having lost some pigments.

Color polymorphism is common and widespread in spiders and can be caused by various factors ranging from diet to genes (see Oxford & Gillespie 1998 for review). Perhaps the most spectacular example of color polymorphism is in the Hawaiian ‘happy face spider’, Theridion grallator Simon, 1900 (e.g. Oxford & Gillespie 2001). In T. grallator similar morphs appear to have evolved independently on different islands, seemingly in response to characteristics of the habitat and potential predators (Oxford and Gillespie 1998, 2001). In A. kohi most individuals can be roughly categorized into two morphs (see above) and based on our (I. Agnarsson, J. X. Zhang, W. P. Maddison) limited
FIGURES 2A–E. Photographs of webs of *A. kohi*. A–C, colonies of different sizes; A, web containing female with large juveniles; B, female with small juveniles; C, female with egg sac. D–E, female guarding egg sac. The leaves are taken from a small web the female typically attaches two leaves (D) to form a retreat, one or both leaves may also be folded (E). Inside the retreat the spider guards the egg sac surrounded by a thin silk envelope (E).

field observations these seemed to correspond to habitat with the brightly colored morph found primarily on the very edge of the forest on the beachfront, while the rather uniformly dark morph was almost exclusively found further inside the forest in more shaded areas. The absolute distance between these habitats was only a few meters, but they differed distinctly in exposure to sun. Whether these morphs may represent adaptations to different conditions in these microhabitats is an open question.
FIGURES 3A–I. *Anelosimus kohi*, color polymorphism. A, female, dark morph from Singapore; B, female, dark morph from Malaysia; C, male, dark morph from Singapore; D, male light morph from Malaysia; E–G, female with egg sac, light morph from Malaysia, note how egg sac is clasped with the cheliceral fangs and palpal claws; H, female with egg sac, light morph from Singapore; I, female unusual pale morph from Singapore.

FIGURES 4A–B. *Anelosimus agnar* n. sp., female with egg sac.
**Taxonomy**

*Anelosimus* Simon, 1891


Detailed diagnosis and circumscription of the genus *Anelosimus* including a list of generic synapomorphies can be found in Agnarsson (2006). Textual descriptions of species in the present paper are brief as they do not include general *Anelosimus* characteristics that are invariable. However, some figures are included to demonstrate general *Anelosimus* features such as the type and arrangements of spigots on the spinnerets (Figs 9G, 13D, 16G), shape and hirsuteness of carapace and sternum (Figs 9C, 13C, 17A–C), reduced stridulatory pick row in females (Figs 7D, 9D, 16D), irregular male stridulatory ridges on prosoma (Fig. 7E), opisthosoma texture and hirsuteness (Fig. 17F) and type of tarsal claws (Figs 13G, 17D).

Unusual aspects of some species here described include the egg sacs of *Anelosimus kohi* and *A. agnar* which are brightly white (Figs 2E, 3E–H, 5A–B), unlike the dull grey egg sacs known in the American species, and species from Madagascar (Agnarsson 2005, 2006; Agnarsson & Kuntner 2005). All the species here described have a robust male femur I compared to other femora (Figs 3C–D, 7G, 9F), as in most of the species in the *ethicus* group (Agnarsson 2005) but only in some of the *eximius* lineage (Agnarsson 2006).

**Species descriptions**

*Anelosimus biglebowski* Agnarsson n. sp.

(Figs 5A–C, 6A–F, 7A–G)

**Types**

Male holotype and paratypes (4♂, 4♀) from Tanzania, Iringa, Mufindi District, Uzungwa Scarp Forest Reserve, 8°30’S 35°52’W, 1515 m, 3.iii.1996, J. Coddington, N. Scharff et al., deposited in NMNH.

Additional material examined

7♂, 18 ♀; Same data as holotype. 27♂, 62♀: Tanzania, Tanga, Lushoto District, Mazumbai Forest Reserve. 4°49’S 38°29’E, 1650–1730 m, 18.ix.1995.

**Etymology**

The species epithet is a noun in apposition, after the movie “The Big Lebowski” of Joel and Ethan Coen.
FIGURES 5A–F. A–C, *Anelosimus biglebowski* n.sp. A, male pedipalpus, ventral (C conductor, E embolus, MA median apophysis, ST subtegulum, T tegulum, TTA theridiid tegular apophysis); B, epigynum ventral; C, epigynum cleared, dorsal (CD copulatory duct, FD fertilization duct, S spermathecae). D–F, *A. dude* n. sp. D, male pedipalpus, ventral; E, epigynum ventral; F, epigynum cleared, dorsal. Scale bars (upper for pedipalpi, lower for epigyna): 100 µm.
Males can be distinguished from most *Anelosimus* species by the narrow spiraling embolus, and from other species of the filiform embolus clade by its long embolus spiral (except *A. sulavesi* which is longer), and the shape of embolus base (Figs 5A, 6B–C). Females are readily separated from most *Anelosimus* by the large size of the spermathecae relative to the epigynal plate. Very similar to *A. dude*, but the opisthosoma is generally more sharply pigmented, with much contrast between the dark gray and white patterns. The epigynum is slightly more sclerotized, thus the spermathecae are not as clearly visible through the cuticle as in *A. dude*, furthermore the genital opening is narrower in respect to spermathecae than in *A. dude* (Figs 5B–C, E–F). To reliably separate these species it is best to clear the epigynum and look at the details of the copulatory ducts. In *A. biglebowski*
the copulatory ducts are longer have more complicated pathways than in *A. dude* which has relatively short ducts.

**FIGURES 7A–G.** *Anelosimus biglebowski* n. sp. A, epigynum, ventral; B, epiandrous gland spigots, ventral; C, male opisthosoma, stridulatory picks; D, female opisthosoma, left stridulatory pick row, ventral; E, male prosomal stridulatory ridges, dorsal; F, colular setae (arrow); G, male femur I. Scale bars A–B, D, 20 μm; C, G 100 μm; D–E, 10 μm.

**Description**

**Male** (holotype): Total length 1.90. Prosoma 0.95 long, 0.80 wide, brown, cephalic area and a narrow rim around the edge of prosoma slightly darker. Sternum 0.55 long, 0.50 wide, light brown with a narrow darker rim. Opisthosoma 1.00 long, 0.80 wide, with *Anelosimus* pattern, a dark dorsal longitudinal notched fovea, bordered by white. Colular setae smaller than in most other *Anelosimus* and may be difficult to see under a dissecting
microscope. Eyes subequal in size about 0.07 diameter. Clypeus height about 2.6 times AME diameter. Leg I femur 1.25, patella 0.30, tibia 1.10, metatarsus 0.80, tarsus 0.50. Femur I about 5 times longer than wide. Legs pale yellow with distal half of femur I and distal tip of tibia I darker. Tips of femur and tibia of other legs slightly darkened. 2–5 trichobothria dorsally on tibia, 2–4 on tibia I–III, 4–5 on tibia IV. 2 prolateral and 1 retrolateral trichobothria on palpal tibia. Stridulatory pick row on opisthosoma nearly straight, consisting of approximately eight modified setal bases (Fig. 7C). Epiandrous gland spigots in two clearly separate groups of 6–7 fusules (Fig. 7B).

Palpal organ as in Figures 5A, 6A–F.

**Female** (paratype): Total length 2.00. Prosoma 0.90 long, 0.75 wide, brown, cephalic area and a narrow rim around the edge of prosoma slightly darker. Sternum 0.60 long, 0.50 wide, brown, slightly darker than male, with a narrow darker rim. Opisthosoma 1.20 long, 0.95 wide, dark gray with a dorsal longitudinal notched fovea, bordered by white. Colular setae smaller than in most other *Anelosimus* and may be difficult to see under a dissecting microscope. Eyes subequal in size about 0.07 diameter. Clypeus height about 2.6 times AME diameter. Leg I femur 1.05, patella 0.25, tibia 0.90, metatarsus 0.75, tarsus 0.45. Femur I about 5 times longer than wide. Legs pale brown with distal half of femur I and II darker brown and distal tip of femur III and IV and tibia I–IV also darker. 2–5 trichobothria dorsally on all tibia, 2–4 on tibia I–III, 4–5 on tibia IV. 2 prolateral and 1 retrolateral trichobothria on palpal tibia.

Epigynum as in Figures 5B–C, 7A.

**Variation**

Variation in coloration of opisthosoma of both sexes (in alcohol) is large and ranges from grayish with a dull fovea to dark gray with a fovea bordered with sharp white. Similarly prosoma may be pale orange to darkish brown. Leg coloration ranges from yellow to brownish. Male total length from 1.80–2.10, femur I from 1.15–1.40, female total length from 1.85–2.15, femur I from 0.95–1.20. Embolus varies considerably in length, orientation of embolus base, how tightly it spirals and the exact location within the palpus. Generally if the embolus is fairly short it will be tightly coiled and embolus base oriented upwards, if embolus is long it is often more tightly coiled and base is facing downwards. This variation seems to be continuous and although extremes are easy to separate, intermediates of all kinds exist indicating an intraspecific variation rather than the existence of two (or more) species. Both extremes were frequently found in the same sample. Similarly, in the female genitalia the size of the genital opening and in particular the size of the spermathecae is very variable. However the pathways of the copulatory ducts are similar in all specimens and different than in *A. dude*.

**Distribution**

Only known from the type locality.
Natural history

Most specimens were collected by canopy fogging, but a few by sweeping vegetation, in a mid elevation rainforest (about 1500–1730 m). The species was more common in samples from 1650–1730 m than samples from 1515 m and was absent in samples from 1370 m. Although sympatric with *A. dude* over part of its range this species seems to prefer slightly higher altitude than *A. dude*. Although weak evidence, the sex ratio of collected specimens (about 2.5 female per male) does not suggests these animals have strongly skewed sex ratios, and are thus unlikely to be permanently social.

Phylogenetics

*Anelosimus biglebowski* has been included in several phylogenetic analyses, as *Anelosimus* sp. 1 (Agnarsson 2003, 2004) and *Anelosimus* sp. 2 Tanzania (Agnarsson 2005, 2006). All analyses place *A. biglebowski* sister to *A. dude*, together sister to a large clade of species from the Americas, Europe, South Africa and Madagascar (Fig. 1). This large clade is termed the ‘curved SPR clade’ in Agnarsson (2006), referring to one of its most conspicuous synapomorphies, distinctly curved row of stridulatory picks on the male opisthosoma (compare Figs 7C, 9E of *A. biglebowski* and *A. dude* to Figs 13F, 16E–F of *A. kohi* and *A. nelsoni*, two members of the curved SPR clade.

*Anelosimus dude* Agnarsson n. sp.

(Figs 5D–F, 8A–F, 9A–G, 18E)

Types

Male holotype and paratypes (4♂, 4♀) from Tanzania, Iringa, Mufindi District, Uzungwa Scarp Forest Reserve, 8°30′S 35°52′W, 1515 m, 3.iii.1996, J. Coddington, N. Scharff et al., deposited in NMNH.

Additional material examined

10 ♂, 15 ♀: Same data as holotype. 20 ♂, 60 ♀: Same data as holotype, except 1370 m. 2 ♂: Tanzania, Tanga, Lushoto District, Mazumbai Forest Reserve, 4°49′S 38°29′E, 1650–1730 m, 18.ix.1995.

Etymology

The species epithet is a noun in apposition, after “The Dude” a character in the movie “The Big Lebowski” by Joel and Ethan Coen.

Diagnosis

*Anelosimus dude* males can be distinguished from all other *Anelosimus*, except *A. kohi* and *A. monskenyensis* by the simple and short embolus and unmodified embolus base, and from *A. kohi* and *A. monskenyensis* by the voluminous tegulum (Figs 5D, 8C–F). Females
are readily separated from other *Anelosimus*, except *A. biglebowski* by the large size of the spermathecae relative to the epigynal plate. Females differ from *A. biglebowski* in that the epigynum is usually very lightly sclerotized so that spermathecae are seen very clearly through the cuticle (Fig. 18E), the genital opening is wide in relation to spermathecae, and copulatory ducts are shorter (Figs 5E–F).

**FIGURES 8A–F.** *Anelosimus dude* n. sp., male pedipalpus (C conductor, E embolus, MA median apophysis, ST subtegulum, T tegulum, TTA theridiid tegular apophysis). A, dorsal; B, prolateral; C, prolateral-ventral; D, ventral, note a distinct groove in the tegulum (arrow); E, retrolateral; F, details of embolus and distal sclerites, caudoventral. Scale bars: A–E, 100 µm; F, 50 µm.

**Description**

*Male* (holotype): Total length 1.85. Prosoma 0.90 long, 0.70 wide, brown, cephalic area and a narrow rim around the edge slightly darker. Sternum 0.55 long, 0.45 wide, light brown with a narrow darker rim. Opisthosoma 1.00 long, 0.90 wide, with *Anelosimus*
pattern, dull gray with a dorsal longitudinal notched fovea, bordered by bands of white. Colular setae are smaller than in most other *Anelosimus* and may be difficult to see under a dissecting microscope. Eyes subequal about 0.07 diameter. Clypeus height about 2.4 times AME diameter. Leg I femur 1.30, patella 0.25, tibia 0.95, metatarsus 0.70, tarsus 0.45. Legs pale yellow with distal half of femur I slightly darker. Femur I about 5 times longer than wide. 2–5 trichobothria dorsally on all tibia, 2–4 on tibia I–III, 4–5 on tibia IV. 2 prolateral and 1 retrolateral trichobothria on palpal tibia. Stridulatory pick row on opisthosoma nearly straight, consisting of approximately seven to eight modified setal bases (Fig. 9E). Epiandrous gland spigots in two clearly separate groups of 6–7 fusules (Fig. 9B).

FIGURES 9A–G. *Anelosimus dude* n. sp. A, epigynum, ventral; B, epiandrous gland fusules; C, female prosoma, dorsal; D, female stridulatory pick row; E, male left stridulatory pick row; F, male first leg; G, female left spinning field (ALS anterior lateral spinneret, PLS posterior lateral spinneret, PMS posterior median spinneret). Scale bars: C–D, F, 100 μm; A, 50 μm; B, 50 μm; G, 20 μm; E, 10 μm.
Palpal organ as in Figures 5D, 8A–F.

**Female** (paratype): Total length 2.10. Prosoma 0.95 long, 0.70 wide, brown, cephalic area and a narrow rim slightly darker. Sternum 0.60 long, 0.50 wide, brown, slightly darker than male, with a narrow darker rim. Opisthosoma 1.25 long, 1.10 wide, pattern as in male. Colular setae are smaller than in most other *Anelosimus* and may be difficult to see under a dissecting microscope. Eyes subequal about 0.07 diameter. Clypeus height about 2.3 times AME diameter. Leg I femur 1.15, patella 0.30, tibia 0.95, metatarsus 0.85, tarsus 0.50. Legs brownish yellow with distal half of femur I darker and distal tip of femur IV and tibia I and IV also slightly darker. 2–5 trichobothria dorsally on all tibia, 2–4 on tibia I–III, 4–5 on tibia IV. 2 prolateral and 1 retrolateral trichobothria on palpal tibia. Epigynum as in Figures 5E–F, 9A.

**Variation**

Variation in coloration (in alcohol) of opisthosoma of both sexes is large and ranges from grayish with a dull folium to dark gray with a folium bordered with sharp white. The light gray coloration is more common. Leg coloration ranges from yellow to brownish. Male total length from 1.80–2.10, femur I from 1.15–1.40, female total length from 1.85–2.15, femur I from 0.95–1.20.

**Distribution**

Only known from two localities in Tanzania, the Uzungwa Scarp Forest Reserve (type locality) and the Mazumbai Forest Reserve.

**Natural history**

Most specimens were collected by canopy fogging but a few by sweeping vegetation. Habitat was mid elevation rainforest (1370–1730 m). The species was most common in samples from 1370 m, abundant in samples from 1515 m, but very rare in samples from 1650–1730 m. The sex ratio of collected specimens of about 2.6 females per male, while weak evidence, does not suggest that these animals are permanently social, while the phylogenetic position predicts subsociality.

**Phylogenetics**

*Anelosimus dude* has been included in several phylogenetic analyses, as *Anelosimus* sp. 2 (Agnarsson 2003, 2004) and *Anelosimus* sp. 3 Tanzania (Agnarsson 2005, 2006). For the phylogenetic position see under *A. biglebowski*.

**Anelosimus monskenyensis** Agnarsson n. sp.

(Figs 10A–C)

**Types**

Male holotype and paratypes (1 ♂, 3 ♀) from Kenya, Mount Kenya, Bulgurst Trail, lower West side, 1.–2.x.1992, V. and B. Roth, deposited in CAS.
Etymology

The species epithet is a Latin adjective and refers to the type locality of Mount Kenya.

Diagnosis

_{Anelosimus monskenyensis_} n. sp. males differ from all other _Anelosimus_ except _A. dude_ n. sp. and _A. kohi_ by the short and simple, undivided embolus (Fig. 10A), lacking an ‘embolic division b’ (see Agnarsson 2006). It differs from _A. kohi_ by a simpler embolus base, lacking any folds, and from _A. dude_ by a shorter embolus tip. Females differ from other _Anelosimus_ by the pathways of the copulatory and fertilization ducts (Fig. 10C).

Description

**Male** (holotype): Total length 1.80. Prosoma 0.90 long, 0.75 wide, light brown, center and narrow rim darker. Sternum 0.60 long, 0.50 wide, light brown. Opisthosoma 0.95 long, 0.80 wide. Pattern as in other _Anelosimus_, dark notched dorsal folium, edged by white. Eyes subequal in size about 0.07 in diameter. Clypeus height about 1.9 times AME diameter. Leg I femur 1.35, patella 0.35, tibia 1.15, metatarsus 1.00, tarsus 0.50. Femur I about 5 times longer than wide. Leg formula 1243. Leg pale yellowish, femur I distinctly darkened, except at base. 3–5 small trichobothria dorsally on all tibia, 3–4 on tibia I–III, 5 on tibia IV. 2 prolateral and 1 retrolateral trichobothrium on palpal tibia. Stridulatory pick row on opisthosoma, under light microscopy, appears nearly straight, consisting of less than 10 modified setal bases. Epiandrous gland spigots in two clearly separate groups, number of fusules difficult to estimate under light microscopy. Palpal organ as in Figure 10A.

**Female** (paratype): Total length 1.90. Prosoma 0.90 long, 0.65 wide, light to dark brown, center and narrow rim darker. Sternum 0.55 long, 0.45 wide, light to dark brown. Opisthosoma 1.25 long, 1.05 wide. Pattern as in male. Eyes subequal in size about 0.07 in diameter. Clypeus height about 2.1 times AME diameter. Leg I femur 1.15, patella 0.35, tibia 0.95, metatarsus 0.75, tarsus 0.45. Femur I about 6 times longer than wide. Leg formula 1243. Leg pale yellowish, femur I distinctly darkened, except at base, tibia I darkened distally. 3–5 small trichobothria dorsally on all tibia, 3–4 on tibia I–III, 4–5 on IV. 3 dorsal trichobothria on palpal tibia.

Epigynum as in Figures 10B–C.

Variation

Male total length from 1.80–1.90, femur I from 1.35–1.40. Female total length from 1.90–2.55, femur I from 1.15–1.30. Coloration appears to vary somewhat, with one of the three female paratypes darker than the others, and with tips of all tibia darkened.

Distribution

Only known from the type locality.
Natural history

The collection label states: “♀ theridiids in social agelenid web (among leaves) ♀’s carrying egg sacs”. Based on this description it would seem that *A. monskenyensis* lives as a kleptoparasite in agelenid webs. However, kleptoparasitic living in *A. monskenyensis* would be unique among *Anelosimus*. We feel it is more likely that the web(s) was confused with those of social agelenids that are common in the area, and rather represented social (subsocial) *Anelosimus* web(s). In Madagascar several subsocial *Anelosimus* species were recently discovered in a small forest plot where the most common social spider was an agelenid (Agnarsson & Kuntner 2005). The webs of these unrelated social spiders were so similar that we in some cases collected agelenid webs (without seeing the habitants) and brought back to the lab by mistake, thinking they were *Anelosimus*. Agnarsson & Kuntner (2005) speculated that the late discovery of this diverse group of Madagascar *Anelosimus* was in part due to collectors overlooking their webs, assuming they belonged to the common agelenids.

One egg sac in the vial with the type material contained 13 eggs.

Phylogenetics

*Anelosimus monskenyensis* n. sp. has not been placed phylogenetically, but its morphology clearly indicates it belongs to the ‘filiform embolus’ clade (Fig. 1).

*Anelosimus sulawesi* Agnarsson n. sp.
(Figures 10D–F)

Types

Male holotype from Sulawesi, Dumoga Bone National Park, 1984, A. Russel–Smith, no. 5/5, canopy fogging, lowland forest, plot C, deposited in MCZ.

Additional material examined

1 ♀: same locality data as holotype

Etymology

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

Diagnosis

*Anelosimus sulawesi* n. sp. males differ from all other *Anelosimus* by the extremely elongate embolus, completely covering other sclerites in ventral view (Fig. 10D). Females differ from all other *Anelosimus* by the unusual trajectory of the copulatory ducts (Fig. 10E) and the elongate spermathecae with fertilization ducts arising from the dorsobasal margin (Fig. 10F).
**Description**

**Male** (holotype): Total length 2.00. Prosoma 1.00 long, 0.75 wide, brown. Sternum 0.70 long, 0.55 wide, brown. Opisthosoma 1.10 long, 0.80 wide. Pattern rather faint, but appears to be fairly typical for *Anelosimus*: dark notched dorsal folium, edged by white, albeit centrally the white ‘edges’ touch. Eyes subequal in size about 0.08 in diameter. Clypeus height about 1.5 times AME diameter. Leg I femur 1.35, patella 0.45, tibia 1.30, metatarsus 0.95, tarsus 0.50. Femur I about 4 times longer than wide. Leg formula 1243. Leg pale yellowish, femur I distinctly darkened, except at base. 3–5 small trichobothria dorsally on all tibia, 3–4 on tibia I–III, 5 on IV. 2 prolateral and 1 retrolateral trichobothria on palpal tibia. Stridulatory pick row on opisthosoma, under light microscopy, appears nearly straight, consisting of less than 10 modified setal bases. Epiandrous gland spigots in two clearly separate groups, number of fusules difficult to estimate under light microscopy.

Palpal organ as in Figure 10D.

**Female** (data as holotype): Total length 2.05. Prosoma 0.95 long, 0.75 wide, brown. Sternum 0.70 long, 0.55 wide, brown. Opisthosoma 1.25 long, 0.95 wide. Pattern very faint, but appears as in male. Eyes subequal in size about 0.08 in diameter. Clypeus height about 1.7 times AME diameter. Leg I femur 1.30, patella 0.45, tibia 1.20, metatarsus 0.95, tarsus 0.45. Femur I about 5 times longer than wide. Leg formula 1423. Leg pale yellowish, femur I distinctly darkened, except at base. 3–6 small trichobothria dorsally on all tibia, 3–4 on tibia I–III, 4–6 on tibia IV. 3 dorsal trichobothria on palpal tibia.

Epigynum as in Figures 10E–F.

**Distribution**

Only known from the type locality

**Natural history**

Unknown; the specimens were collected by canopy fogging.

**Phylogenetics**

*Anelosimus sulawesi* n. sp. has not been placed phylogenetically, but its morphology clearly indicates it belongs to the ‘filiform embolus’ clade (Fig. 1).

**Taxonomic note**

The matching of sexes is based primarily on the two specimens having been collected together. While both are clearly congeners, the match between the genitalia seems poor. The extremely long male embolus is not matched by elongate copulatory ducts in the female. For that reason the matching is only tentative and therefore the female is not designated as a paratype, as is done in the other species.
Anelosimus kohi Yoshida, 1993
(Figs 2A–E, 3A–I, 11A–H, 12A–F, 13A–G)

Anelosimus kohi Yoshida, 1993: 8, figs 1–3.

Types
Male holotype (NSMT–Ar 2966) and a paratype (1♀, NSMT–Ar 2967) from Singapore, deposited in the collection of the Department of Zoology, National Science Museum, Tokyo, examined.

Additional material examined

Diagnosis
This species differs from all other Anelosimus in lacking colular setae. Anelosimus kohi males differ from those of all other Anelosimus species by the simple, short embolus, lacking an elaborate ‘embolic division b’ (Agnarsson 2006). Females differ from all other Anelosimus by having two pairs of spermathecae (or a pair of accessory sacs, in addition to the spermathecae), see Figures 11E–G, 11H–F.

Description
Male (Singapore, Palau Ubin, Chek Jawa, N 1.407°, E 103.991°, 30.iv.2005, W. Maddison, D. Li, I. Agnarsson, J.X. Zhang): Total length 2.50. Prosoma 1.30 long, 1.30 wide, light or dark brown, center darkest. Sternum 1.00 long, 0.80 wide, pale yellowish. Opisthosoma 1.65 long, 1.30 wide. Pattern as in Figures 3C–D. Eyes subequal in size about 0.10 in diameter. Clypeus height about 1.8 times AME diameter. Leg I femur 1.80, patella 0.65, tibia 1.70, metatarsus 1.70, tarsus 0.70. Femur I about 4 times longer than wide. Leg formula 1243. Leg pale to dark brown, femora and distal tip of tibia darker. 3–5 small trichobothria dorsally on all tibia, 3–4 on tibia I–III, 5 on tibia IV. 2 prolateral and 1 retrolateral trichobothria on palpal tibia. Stridulatory pick row on opisthosoma distinctly curved, with distal setae compressed, consisting of approximately 16–19 modified setal bases (Fig. 13F). Epiandrous gland spigots in two separate groups with approximately 8–9 fusules, but less tightly arranged than in many other Anelosimus (Fig. 13B).
FIGURES 12A–F. Anelosimus kohi Yoshida, 1993, male pedipalpus (C conductor, dh distal haematodocha, E embolus, MA median apophysis, ST subtegulum, T tegulum, TTA theridiid tegular apophysis). A, prolateral; B, ventral, note size of tibia compared to the pedipalpal bulb; C, retrolateral; D, details of sclerites, prolateral-ventral; E, details or bulb, ventral; F, details of bulb, retrolateral-ventral. Scale bars: A–E, 100 µm; F, 50 µm.

Palpal organ as in Figures 11A–D, 12A–F.

Female (data as male): Total length 3.80. Prosoma 1.80 long, 1.45 wide, light or dark brown, center darkest. Sternum 1.10 long, 0.95 wide, pale yellowish. Opisthosoma 2.30 long, 1.75 wide. Pattern as in Figures 3A–B, E–I. Eyes subequal in size about 0.10 in diameter. Clypeus height about 2.1 times AME diameter. Leg I femur 2.40, patella 0.80, tibia 2.10, metatarsus 2.10, tarsus 0.80. Femur I about 5 times longer than wide. Leg formula 1423. Leg pale to dark brown, femora and distal tip of tibia darker. 3–5 small trichobothria dorsally on all tibia, 3–4 on tibia I–II, 4–5 on tibia III–IV. 3 dorsal trichobothria on palpal tibia.
Epigynum as in Figures 11E–H, 13A.

**FIGURES 13A–G.** *Anelosimus kohi* Yoshida, 1993. A, epigynum, ventral; B, epiandrous gland fusules; C, female prosoma, dorsal; D, female posterior lateral and posterior median spinnerets, left side (AC aciniform spigots, AG aggregate spigots, CY cylindrical spigots, FL flagelliform spigots; mAP minor ampullate spigots); E, female anterior lateral spinnerets and colular area (arrow), uniquely in *A. kohi* no colular setae are present. F, male stridulatory pick row; G, female pedipalpal claw, lateral. Scale bars: C, E, 100 µm; A–B, 50 µm; D, F–G, 10 µm.
Variation

The color variation is striking in this species, mostly representing two rather distinct color morphs, uniformly reddish brown with dark brown dorsal folium on the opisthosoma (Figs 3A–C), or a morph with contrasting colors, a gray opisthosoma, and red dorsal folium bordered by a broad, bright yellow band (Figs 3D–H). Some lightly colored, less contrasty forms also exist (Fig. 3I). Male total length from 2.40–3.40, femur I from 1.70–2.40, Female total length varies from 3.70–4.40 and femur I from 2.30–2.80. The genitalia of both sexes are quite variable also (Figs 11A–H, 12A–F, 13A). The shape of the embolus base, and the length of the embolus tip differ considerably between specimens. The length versus the width of the palpal organ varies with some palps appearing rather long and narrow, others short and stubby. The epigyna also vary in the shape of the epigynal bursa, and of the spermathecae. None of these morphological variations seem to correlate clearly with the color morphs, or localities.

Distribution

Only known from Singapore and Malaysia.

Natural history

*Anelosimus kohi* builds *Anelosimus* ‘basket webs’ (see Agnarsson 2006), which were encountered at the tips of branches of trees along the beach in Singapore and Malaysia. Based on observing a number of webs and examining their content, *Anelosimus kohi* appears to be a subsocial species, similar to *Anelosimus arizona* (e.g. Avilés & Gelsey 1998), with webs founded by single females, and colonies consisting of a female and her offspring persisting until the spiderlings disperse close to adulthood.

Taxonomic note

Considering the extensive variation in habitus color and genitalia morphology it is certainly possible that what we here circumscribe as one, may represent two, or even more species. However, we prefer the current taxonomical hypothesis because genitalia morphology seems to vary continuously, and genital variation does not seem to correlate with coloration, or geographic locality. Furthermore, preliminary molecular data (Agnarsson unpublished) indicates that ‘contrasty’ vs. ‘uniform’ color morphs are not distinct (or respectively monophyletic). The current taxonomical hypothesis makes testable predictions about the expected gene flow and ease of breeding between ‘morphs’ and the hypothesis that all these morphs represents a single species could be rejected by e.g. demonstrating inability of morphs to interbreed.

Phylogenetics

*Anelosimus kohi* was included in the phylogenetic analyses of Agnarsson (2005, 2006) as “A. sp. 4 Singapore”. In those analyses *A. kohi* was sister to a large clade (termed the E b clade for a conspicuous synapomorphy, the ‘embolic division b’, see Agnarsson 2006) of
European, African and American species including the ‘filiform embolus clade’ (see Fig. 1) and the Madagascar group plus the eximius lineage. Preliminary molecular data suggests a similar placement (Agnarsson unpublished).

*Anelosimus nelsoni* Agnarsson n. sp.
(Figs 14A–C, 15A–F, 16A–G, 17A–F)

**Types**
Male holotype and paratype (1 ♀) from South Africa, KwaZulu Natal St. Lucia Estuary, Fanies Island, 5 km S of Cape Vidal, 28°06’41"S,32°25’51"E 5.iv. 2001, I. Agnarsson et al., deposited in NMNH

**Etymology**
The species epithet, a noun in genitive case, is a patronym in honor of Nelson Mandela.

**Diagnosis**
*Anelosimus nelsoni* n. sp. males can be separated from other *Anelosimus* by the shape of the large and bifurcate ‘embolic division b’, and the conspicuous hook on the distal portion of the embolus base (Figs 14A, 15B–D). Females differ from all other *Anelosimus* by the copulatory duct wrapping the spermathecae (Fig. 14C).

**Description**

**Male** (holotype): Total length 2.08. Prosoma 1.20 long, 0.90 wide, pale yellowish, center and a narrow rim dark. Sternum 0.75 long, 0.60 wide, pale yellowish, lightest in center. Opisthosoma 1.10 long, 0.90 wide, 0.90 high. Pattern other *Anelosimus*. Eyes subequal in size about 0.07 in diameter. Clypeus height about 2.3 times AME diameter. Leg I femur 1.60, patella 0.50, tibia 1.55, metatarsus 1.40, tarsus 0.62. Femur about 6 times longer than wide. Leg formula 1423. Leg pale yellowish, narrow dark rings near all joints (except coxae–trochanter). 4–7 small trichobothria dorsally on all tibia, 5–6 on tibia I, 6 on tibia III. 2 prolateral and 1 retrolateral trichobothrium on palpal tibia. Stridulatory pick row on opisthosoma distinctly curved, with distal setae compressed, consisting of approximately 27–32 modified setal bases (Figs 16E–F). Epiandrous gland spigots in two distinctly separate groups with approximately 6–7 fusules (Fig. 16C).

Palpal organ as in Figures 14A, 15A–F.

**Female** (paratype): Total length 2.60. Prosoma 1.40 long, 1.00 wide, pale yellowish, center and a narrow rim dark. Sternum 0.90 long, 0.65 wide, pale yellowish, lightest in center. Opisthosoma 1.45 long, 1.25 wide. Pattern as in other *Anelosimus*. Eyes subequal in size about 0.07 in diameter. Clypeus height about 2.5 times AME diameter. Leg I femur 1.60, patella 0.50, tibia 1.35, metatarsus 1.25, tarsus 0.60. Femur about 6 times longer than wide. Leg formula 1423. Leg pale yellowish, narrow dark rings near all joints (except
coxae-trochanter). 5–6 small trichobothria dorsally on all tibia, 5–6 on tibia I, 5 on tibia III. 4 dorsal trichobothria on palpal tibia on one side (Fig. 17E), 3 on the other.

Epigynum as in Figures 14B–C, 16A–B.

Distribution

Only known from the type locality.

Natural history

This species was collected beating bushes and trees during day. Webs were not seen. The habitat was a small, open, forest patch, situated on a small river island.

Phylogenetics

Anelosimus nelsoni n. sp. was included in the phylogenetic analyses of Agnarsson (2005, 2006) as Anelosimus sp. 5 South Africa. In these analyses A. nelsoni n. sp. was sister to the ‘epigynal scape clade’ (see Agnarsson 2006), together these form a clade here termed the ‘basal cymbial hood clade’ (Fig. 1), referring to a synapomorphy shared by all species in it (Fig. 15F).

FIGURES 14A–C. Anelosimus nelsoni n. sp. A, male pedipalpus, ventral (C conductor, E embolus, EB 'embolic division b', MA median apophysis, TTA theridiid tegular apophysis); B, epigynum, ventral; C, epigynum cleared, dorsal (CD copulatory ducts, FD fertilization ducts, S spermathecae), line sketch above shows trajectory of the copulatory ducts to the spermathecae. Scale bars (left for pedipalpus, right for epigyna): 100 µm.
FIGURES 15A–F. Anelosimus nelsoni n. sp., male pedipalpus, slightly expanded (C conductor, E embolus, Eb ‘embolic division b’, MA median apophysis, SC subconductor, ST subtegulum, T tegulum, TTA theridiid tegular apophysis). A, prolateral; B, prolateral-ventral; C, ventral; D, retrolateral-ventral; E, retrolateral; F, details of pedipalpus, retrolateral, showing basal cymbial hood (arrow), the saw-toothed edge may be a basal part of the TTA. Scale bars: A–E, 100 µm; F, 50 µm.

Anelosimus agnar Agnarsson n. sp.
(Figs 4A–B, 18A–B)

Types
Female holotype and paratype (1♀) from Malaysia, Johor, Teluk Mahkota, 1°54′0″N, 104°6′14.4″E, altitude 0–5 m, 25.–26.v.2005, W. Maddison, D. Li, I. Agnarsson, J. X. Zhang, deposited in NMNH.
Etymology

The species epithet is a noun in apposition, and is a patronym after my father Agnar Ingólfsson.

FIGURES 16A–G. Anelosimus nelsoni n. sp. A, epigynum, ventral; B, same, caudal; C, epiandrous gland fusules; D, female stridulatory pick row; E, male opisthosoma, pedicel area, ventral; F, male stridulatory pick row, left side; G, female left spinning field (ALS anterior lateral spinneret, PLS posterior lateral spinneret, PMS posterior median spinneret). Scale bars: A–B, D–E, G, 100 μm; C, F, 10 μm.
FIGURES 17A–F. *Anelosimus nelsoni* n. sp. A, female prosoma, dorsal; B, same, lateral; C, male sternum, ventral; D, male tarsus I tip, lateral; E, female pedipalpal tibia, dorsal, with four trichobothria (the other pedipalpal tibia of the same animal had only three); F, female opisthosoma surface, near center laterally. Scale bars: A–C, F, 100 μm; E, 50 μm; D, 10 μm.

**Diagnosis**

*Anelosimus agnar* n. sp. differs from all other *Anelosimus* females by the very long, flimsy, copulatory ducts (Figs 18A–B).

**Description**

*Female* (holotype): Total length 2.40. Prosoma 0.95 long, 0.80 wide, light brown, cephalic region darker. Sternum 0.60 long, 0.50 wide, light brown. Opisthosoma 1.30 long, 1.20 wide. Pattern as in other *Anelosimus*, dark (bright red in live specimens) dorsal
notched folium, edged by a narrow white rim. Eyes subequal in size about 0.08 in
diameter. Clypeus height about 1.8 times AME diameter. Leg I femur 1.20 patella 0.35,
tibia 1.05, metatarsus 0.85, tarsus 0.40. Femur I about 6 times longer than wide. Leg
formula 1243. Leg pale yellowish, femora I and II distinctly darkened (bright red in live
specimens), except at base, dorsally with yellowish longitudinal streaks. 3–5 small
trichobothria dorsally on all tibia, 3–4 on tibia I–III, 4–5 on IV. 3 dorsal trichobothria on
palpal tibia.

Epigynum as in Figures 18A–B.

Male: unknown.

Variation

Total length from 2.05–2.40, femur I from 1.00–1.20. The paratype is much paler than
the type specimen, with light dorsal folium on the opisthosoma, and only a small portion
of femur I darkened, lacking red coloration (Figs 4A–B).

Natural history

Type material was collected from small webs at tips of branches in a forest at the
beach. The paratype female was carrying an egg sac (Figs 4A–B) that contained 22 eggs.

Phylogenetics

Anelosimus agnar n. sp. has not been included in a phylogenetic analysis, but
preliminary molecular data suggests it forms a clade with A. linda n. sp., together in a
placement as indicated for the ‘agnar group’ in Fig. 1.

Anelosimus linda Agnarsson n. sp.
(Figs 18C–D)

Types

Female holotype and paratype (1 ♀) from Malaysia, Pahang, Cameron Highlands,
Arcadia, trail 3, 4°28′55.2″N, 101°23′16.8″E, 1550 m, 21.–23.v.2005, W. Maddison, D.
Li, I. Agnarsson, J. X. Zhang, deposited in NMNH. Paratype female in poor condition,
lacking legs I.

Etymology

The species epithet is a noun in apposition, and is a patronym after my mother Linda
Wendel.

Diagnosis

Anelosimus linda n. sp. differs from all other Anelosimus by the very short copulatory
ducts, and small hook–shaped epigynal openings (Figs 18C–D).
Figures 18A–E. A–B, A. agnar n. sp. A, epigynum, ventral; B, epigynum cleared, dorsal. C–D, A. linda n. sp. C, epigynum, ventral; D, epigynum cleared, dorsal (CD copulatory ducts, FD fertilization ducts, S spermathecae). E, Anelosimus dude n. sp., female opisthosoma ventral, showing setae around the pedicel and the transparency of the cuticle anterior to the epigynum. Scale bar for epigyna: 100 mm.

Description

Female (holotype): Total length 1.90. Prosoma 0.95 long, 0.75 wide, dark brown. Sternum 0.65 long, 0.60 wide, brown. Opisthosoma 1.05 long, 0.90 wide. Pattern as in other Anelosimus, dark dorsal notched folium, edged by a narrow white rim. Eyes subequal in size about 0.10 in diameter. Clypeus height about 2.1 times AME diameter.
Leg I femur 1.35, patella 0.35, tibia 1.15, metatarsus 0.95, tarsus 0.45. Femur I about 7 times longer than wide. Leg formula 1423. Leg pale yellowish, femur I distinctly darkened, except at base. 4–6 small trichobothria dorsally on all tibia, 4–5 on tibia I–III, 5–6 on IV. 3 dorsal trichobothria on palpal tibia.

Under light microscopy we could not detect the presence of colular setae, however, in these small spiders they could easily be overlooked.

Epigynum as in Figures 18C–D.

Male: unknown.

Natural history

The type material was collected by beating in a mid elevation forest.

Phylogenetics

See under A. agnar n. sp. and Figure 1.

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