

Systematics of new subsocial and solitary Australasian *Anelosimus* species (Araneae : Theridiidae)

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Abstract. Species of the cobweb spider genus *Anelosimus* range from solitary to subsocial to social, and sociality has evolved repeatedly within the genus. Thus, this genus allows studies of the traits that play a role in social evolution. However, taxonomic knowledge of *Anelosimus* is geographically narrow and nearly all sociobiological studies have been done in the Americas. Only one behaviourally unknown species has been described from all of Australasia. Here, I describe seven new *Anelosimus* from Papua New Guinea (*Anelosimus potmosbi*, sp. nov., *Anelosimus pomio*, sp. nov., *Anelosimus eidur*, sp. nov. and *Anelosimus luckyi*, sp. nov.), Bali (*Anelosimus bali*, sp. nov.), Australia (*Anelosimus pratchetti*, sp. nov.) and an unknown locality (*Anelosimus terraincognita*, sp. nov.), ranging from solitary to subsocial. A phylogenetic analysis supports the inclusion of these species in *Anelosimus*, and suggests that solitary Papuan species represent a second reversal from subsocial behaviour. Both solitary species inhabit the beachfront, a habitat that appears not to be conducive to social behaviour in spiders. Subsocial species, as in other parts of the world, are found in montane tropical forests of Papua New Guinea, and at relatively high latitudes in Australia. Thus, a global ecological pattern of sociality in *Anelosimus* is emerging as taxonomic, phylogenetic and ethological knowledge extends beyond the Americas.

Additional keywords: Australia, Bali, evolution of sociality, New Britain, Papua New Guinea, social ecology, taxonomy.

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Introduction

The origin and evolution of social behaviour, and the ecological and evolutionary causes and consequences of inbreeding, are two prominent and fundamental biological questions addressed by hundreds of papers annually. Many of these use model organisms, both species and clade-based (for recent examples see Fox and Reed 2010; Delbarco-Trillo *et al.* 2011; Fox *et al.* 2011; Hirsch and Maldonado 2011; Okada *et al.* 2011; Rousselle *et al.* 2011; Simmons 2011; Yagi and Hasegawa 2011). Social spiders are an excellent model system to address questions regarding the origin and evolution of social behaviour, and the consequences of inbreeding, primarily because similar levels of sociality have arisen independently several times, nearly always associated with a switch to inbreeding (e.g. Avilés 1997, 2000; Bilde *et al.* 2005, 2007a, 2007b, 2009; Agnarsson *et al.* 2006a, 2010b; Avilés *et al.* 2006; Johannesen *et al.* 2007, 2009a, 2009b; Lubin and Bilde 2007; Schneider and Bilde 2008; Lubin *et al.* 2009; Ruch *et al.* 2009a, 2009b; Smith *et al.* 2009). Such evolutionary replications are particularly valuable in fields such as comparative biology where sample size is often prohibitively small (e.g. Pagel 1997). Nevertheless, current global understanding of the taxonomy and ethology of social spider lineages is rather poor, limiting the potential of this study system. For example, the cosmopolitan genus *Anelosimus* Simon, 1891 contains the highest number of

social species of any spider genus and is the subject of many studies of social behaviour and evolution, yet practically all such studies are limited to species that occur in the Americas. In contrast, species in other parts of the world are poorly studied and many, perhaps most, remain to be discovered and described (Agnarsson and Kuntner 2005; Agnarsson and Zhang 2006; Agnarsson 2006, 2012; Agnarsson *et al.* 2010a). Discovering and describing new species that vary in their social structure adds not only evolutionary behavioural replicates, but in a global perspective will facilitate intercontinental comparisons of, for example, the ecological factors that contribute to social evolution (Avilés *et al.* 2007; Guevara and Avilés 2007, 2009; Purcell and Avilés 2007, 2008; Yip *et al.* 2008; Guevara *et al.* 2011). The importance of ‘basic’ taxonomic work is thus obvious in facilitating ‘big’ research on fundamental questions, but is often underappreciated.

To date, a single *Anelosimus* species has been reported from Australasia, the behaviourally unknown *A. sulawesi* Agnarsson, 2006 (Agnarsson and Zhang 2006). Here, I describe and phylogenetically place seven species of *Anelosimus* recently discovered from Papua New Guinea, Bali and Australia. Basic information on social structure is available for many of these species, which include both solitary coastal, as well as subsocial montane forest species. Along with a recently discovered

radiation on Madagascar (Agnarsson and Kuntner 2005; Agnarsson *et al.* 2010a), the current taxonomic and phylogenetic work greatly enlarges the pool of potential study species and thus enhances the power of comparative analyses. However, lack of sampling, not absence of the genus, still characterises most regions outside the Americas, and the currently described species represent the only samples available from Indonesia and Australasia. Global sampling effort is certain to unravel many new *Anelosimus* species (see Fig. 1).

Materials and methods

Taxonomy

Taxonomic methodology was detailed in Agnarsson (2006). Specimens were examined under an Olympus SZX16 dissecting microscope (Olympus, Center Valley, PA). Illustrations were prepared using a visionary digital imaging system, the core components being a Canon 5D digital camera body (Canon, Tokyo) and a K2 Infinity microscope (Boulder, CO) equipped with Olympus metallurgical objectives. Successive images were combined with Helicon Focus 4.0 (Kharkov, Ukraine), and thereafter minimally processed with Photoshop CS3 (Adobe, San Jose, CA) to adjust contrast, brightness and to remove background blemishes. For photography, anatomical preparations were temporarily mounted in hand sanitiser, a 65–70% ethanol gel, and the specimen then covered with 70% ethanol. This allows precise manipulation of the specimen, without introducing unwanted background distractions, such as when using sand or glass spheres. Measurements, all given in mm, were made using an Infinity K2 long distance microscope, images processed in Photoshop CS3 and plates assembled in Illustrator CS3 (Adobe).

Phylogenetics

Specimens were fixed in 95% ethanol in the field. Voucher specimens were deposited at the National Museum of Natural History, Smithsonian Institution, Washington, DC. I obtained sequences of mitochondrial (16S, ND1 and COI) and nuclear (ITS2 and 28S) loci from *A. potmosbi*, *A. pomio*, *A. eidur*, *A. luckyi*, *A. pratchetti* and *A. bali* using standard primers described in Agnarsson *et al.* (2007). The sequences were interpreted through Phred (Green and Ewing 2002) and Phrap (Green 1999) via Mesquite (Maddison and Maddison 2011b) and subsequently proofread using the Chromaseq module (Maddison and Maddison 2011a). These data were then added to the existing molecular species level *Anelosimus* phylogeny (Agnarsson *et al.* 2007, 2010a; Agnarsson 2012). I did not attempt to extract DNA from the new *A. terraincognita*, as it is known from a single and apparently old specimen. GenBank accession numbers of new sequences JQ480119–JQ480151. The total dataset contained 98 terminal taxa representing 31 *Anelosimus* species. The data matrix and trees will be submitted to Treebank and are available upon request from the author. I aligned and analysed the molecular data using the same methods and settings as in previous studies (Agnarsson *et al.* 2007, 2010a; Agnarsson 2012). In summary, I aligned sequences in ClustalW (Thompson *et al.* 1994) with gap opening and extension costs of 24/6 (for justification see Agnarsson *et al.* 2007). Protein

coding sequences align unambiguously, and no sequences contained stop codons. For non-coding genes, the Clustal alignment was followed by minor manual adjustments, as described in Agnarsson *et al.* (2007). I then concatenated the genes into a single five-gene matrix in Mesquite (Maddison and Maddison 2011b) and exported them for model selection and analyses. The matrix was partitioned by gene, and for protein coding genes (COI and ND1), additionally by codon position, for a total of nine 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 analysed the concatenated matrix in MrBayes (Huelsenbeck and Ronquist 2001; Ronquist and 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 'burn-in', after which stationarity had been reached.

Results

Phylogeny

Other than the placement of the new species, the new phylogeny (Fig. 1), unsurprisingly given that the same genes are used, closely mirrors prior *Anelosimus* phylogenies (Agnarsson 2006, 2010, 2012; Agnarsson *et al.* 2007, 2010a). The analysis recovers the 'Old World clade' (Agnarsson 2012) containing four of the newly described species (*A. pomio*, *A. potmosbi*, *A. eidur* and *A. bali*) and all other Asian species (*A. kohi*, *A. chonganicus*, *A. linda* and *A. agnar*) except the Papuan *A. luckyi*. The three species from Papua New Guinea form a grade in a clade containing also *A. bali* from Bali, and *A. chonganicus* from China. As in prior phylogenies, the American *rupununi*-group is sister to the remaining *Anelosimus* species, and here *Anelosimus luckyi* branches off next. The new species *A. pratchetti* from Australia is placed as sister to the 'Madagascar clade'. The solitary and coastal *A. pomio* and *A. potmosbi*, the behaviourally unknown *A. bali*, and *A. chonganicus*, nest within the Old World clade, which appears to be primitively subsocial. Hence, this putatively represents a second reversal from subsociality to solitary behaviour in a coastal habitat, as shown for *A. pacificus* and relatives in the Americas (Agnarsson *et al.* 2006b). Unlike the case in Madagascar where solitary and subsocial species arrived independently to the island, the relationships among species in Papua, other than *A. luckyi*, are consistent with the colonisation of Papua by a subsocial ancestor, and subsequent diversification into the coastal 'solitary niche'.

Natural history

Although quite variable, the most typical webs of the subsocial montane *Anelosimus eidur* are similar to most subsocial and social *Anelosimus* species, a dome-shaped sheet reinforced with leaves and above the sheet, non-sticky aerial threads that intercept insects in flight.

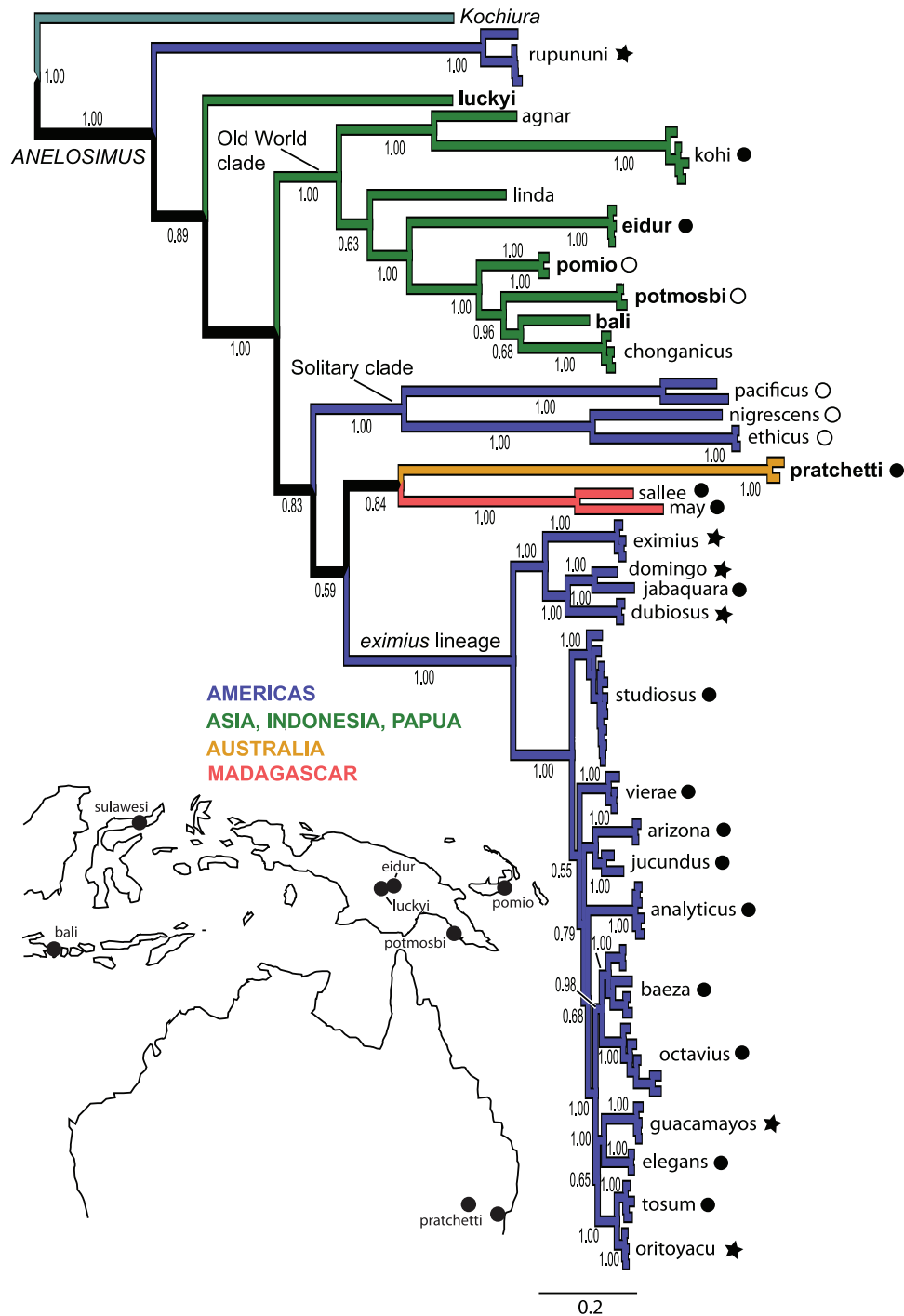


Fig. 1. A phylogeny of *Anelosimus* based on Bayesian analyses of the concatenated molecular matrix, colour coded according to distribution. Branches are proportional to length as estimated in MrBayes, outgroups are omitted for clarity, see Fig. 9 for the full phylogeny. New species are indicated in bold. Social species are indicated with a star, subsocial with a closed circle, solitary with an open circle and species with missing data lack a symbol. Numbers on nodes are posterior probability support values, shown for species and higher level nodes only – see Fig. 9 for the full phylogeny and support for each clade. The inset schematic map shows the distribution of the new species, which occur in the only areas where, to my knowledge, *Anelosimus* has been looked for. This map thus highlights the potential for species discovery in the region, through structured sampling. Scale shows expected substitutions per site.

Webs of *A. eidur* typically contained a female with her egg sac or spiderlings, ranging from estimated instar II to VI (subadult). Webs were also collected containing only spiderlings, including webs with multiple subadults. The ages or instars of juveniles were estimated based on their size, based on comparison of the instars to other *Anelosimus* species with similarly sized adult females (Agnarsson and Kuntner 2005). Furthermore, subadult males were readily recognised by their swollen palps. Spiderlings were observed feeding together, and together with their mother, and older spiderlings participated in prey capture, as typical of subsocial *Anelosimus* species. The new *A. pratchetti* also appear to be subsocial based on preliminary field observations (H. M. Smith, pers. comm.). Webs of *A. potmosbi* and *A. pomio*, in contrast, were encountered at the tips of branches of small-leaved mangrove species at the beachfront; *A. potmosbi* near Port Moresby in the capital district of Papua; and *A. pomio* near Pomio village at the coast of New Britain. These webs closely resemble webs of other solitary *Anelosimus* species, a three-dimensional silk mesh surrounding vegetation, with sticky droplets distributed throughout the mesh (Agnarsson *et al.* 2006b, 2010a). When a retreat was present, it consisted of two leaves sandwiched together using silk, or a silk-enforced rolled leaf.

In the field, mostly solitary webs contained an adult female, an adult male or a single juvenile. I estimated that the solitary juveniles found represented instars III or IV. Two webs contained a female and her young, but the young were very small, estimated to be instars I or II. These observations, while admittedly sparse, imply dispersal from the natal nest at an early ontogenetic stage, like in *A. pacificus*. As juveniles in social *Anelosimus* species typically start to contribute to the common tasks of the colony only after reaching instar III (Vollrath 1986), cooperative behaviour is likely absent in *A. potmosbi* and *A. pomio*.

Discussion

Phylogeny and biogeography

The new phylogeny supports the monophyly of *Anelosimus* and thus the placement the new species within the genus. Many of the new species belong to the Old World clade (see Agnarsson 2012), which includes other Asian species, and according to morphological evidence, several African species as well (Agnarsson 2006). Most species in the Old World clade are behaviourally unknown. However, among the behaviourally known species the subsocials are relatively 'basal' while the solitary ones form a 'distal' clade.

The phylogeny also supports, as has all prior work, a large clade of purely New World species, the 'eximius-group' (Agnarsson 2006). All of the species of the *eximius*-group are either subsocial or social. However, the current phylogeny is rather puzzling in other aspects in reference to the geographical distribution of species. First, as previously found, there are two additional New World clades (the solitary *ethicus* clade and the social *rupununi* clade) that nest among Old World taxa (Agnarsson 2005). Second, the new Australian species is sister to the Madagascar clade, suggesting long distance dispersal in either direction. This clade contains subsocial species only. Third, the new and behaviourally unknown species *A. luckyi*

from Papua New Guinea nests sister to the clade containing all *Anelosimus*, except the *rupununi*-group, with unclear biogeographical implications. Better global taxonomic knowledge of *Anelosimus* species outside the Americas, and a phylogeny containing a higher percentage of *Anelosimus* species and more loci is necessary before conclusive biogeographical analyses can be conducted. Fourth, the three remaining species from Papua New Guinea form a grade in a clade that contains species from China and Bali, suggesting dispersal out of Papua as a route of colonisation for China and Bali. The potential colonisation of continents from islands, in this case Asia from Papua New Guinea, so-called 'reverse colonisation' (Heaney 2007; Bellemain and Ricklefs 2008) is a recently recognised biogeographical pattern that is understudied, yet seemingly important. However, as stated above, any biogeographical interpretations at this stage are necessarily preliminary due to the many species not yet placed phylogenetically. These include both known species on which work is ongoing, and as yet undiscovered species, which can be expected to be many. For example, except for the highly isolated Mascarene Islands in the Indian Ocean, most Old World tropical landmasses I have recently visited or received samples from (east Africa, South Africa, Madagascar, Comoros, Papua New Guinea, New Britain, Australia and Bali) have contained as yet undescribed *Anelosimus* species. Similarly, Zhang *et al.* (2011) recently discovered new species on Hainan Island, China.

Phylogeny, natural history and evolution of sociality

Based on the field data on webs and their contents, though few, I hypothesise that the montane *A. eidur* and the lowland Australian *A. pratchetti* are subsocial, while the beachfront *A. pomio* and *A. potmosbi* are solitary.

Solitary behaviour in *Anelosimus* was first documented only recently, in *A. pacificus* (Agnarsson *et al.* 2006b). Preliminary data suggest solitary behaviour also occurs in its close relatives, the South American *A. ethicus* and *A. nigrescens* (Guevara *et al.* 2011), as well as in *A. decaryi* and *A. ameliae* from Madagascar (Agnarsson *et al.* 2010a). All these solitary species hitherto described belong to this same solitary lineage. However, my findings here indicate a second reversal to solitary behaviour in the New Guinea clade, interestingly, also in species occurring in beachfront habitat.

Behavioural evolution in *Anelosimus* spiders seems to have a strong geographic and climatic component (Avilés *et al.* 2007), a pattern seen across terrestrial arthropods (Purcell 2011). Social *Anelosimus* species have evolved in lowland to mid-elevation tropical forests in the Americas (Avilés 1997; Avilés *et al.* 2007), with higher elevation populations and species showing lower levels of sociality (Purcell and Avilés 2007; Avilés and Purcell 2011). Subsocial species occur most commonly at mid-high elevation montane forests in the Americas (Agnarsson 2006; Avilés *et al.* 2007), Madagascar (Agnarsson and Kuntner 2005), possibly Malaysia (Agnarsson and Zhang 2006) and now Papua New Guinea, and are also found at higher latitudes in lowlands, in the Americas (Agnarsson 2006; Guevara *et al.* 2011), Singapore and Malaysia (Agnarsson and Zhang 2006), and now in Australia. Solitary species occur at the highest latitudes, e.g. in northern Europe (Roberts 1989)

and southern South America (Guevara *et al.* 2011). In the tropics they are confined to beachfront habitats, in the Americas (Agnarsson *et al.* 2006b), Madagascar (Agnarsson *et al.* 2010a), and now Papua New Guinea and New Britain. The evolution of sociality in lowland forests has been related to the larger sizes of prey and more intense rain disturbances in these habitats, while subsocials live in environments with high abundance of smaller prey, and in areas with less rain disturbance (Guevara and Avilés 2007; Purcell and Avilés 2007, 2008; Guevara and Avilés 2009). Solitary species at high latitudes presumably occur in areas with lower prey size and abundance. The occurrence of at least two independently solitary clades in beachfront habitats in the tropics remains to be explained. However, one can predict based on the above patterns that these beachfront habitats will tend to have relatively small available prey. The beachfront is also a stressful habitat, combining intense solar radiation and salt from ocean spray.

Taxonomy

All holotypes, except *A. terraincognita*, are deposited in the National Museum of Natural History, Smithsonian Institution. Abbreviations: CD, copulatory ducts; FD, fertilisation ducts; E, embolus; MA, median apophysis; *t*, tegulum; ST, subtegulum; CH, cymbial hood.

Family **THERIDIIDAE** Sundevall, 1833

For diagnosis see Agnarsson (2004).

Genus ***Anelosimus*** Simon, 1891

For diagnosis and synonymies see (Agnarsson 2005, 2006; Agnarsson *et al.* 2010a). All species described herein share typical features of *Anelosimus*, such as the characteristic abdominal pattern (e.g. Fig. 2A, B), though unusual in *A. pratchetti* (Fig. 6D), and robust and curved femur I (Fig. 8G). As with other *Anelosimus*, the species described here lack a visible colulus but have a pair of colular setae. As in many theridiids, there is a distinct row of stridulatory ridges on the male abdomen around the pedicel (Fig. 8E), prosoma is unmodified (Fig. 8C, D), epiandrous gland spigots are in two distinct pockets (Fig. 8B) and spinnerets are typical for theridiids (Fig. 8F). Many of the species have secondarily simplified palps that are otherwise unusual in *Anelosimus*. The embolus is prominent in these species, often ‘corkscrew-like’ or spiralled (e.g. Figs 2D–F, 4D–F). Median apophysis is small in most species, though it presumably still works to lock the unexpanded palp in the cymbium through interacting with the cymbial hood, visible, e.g. in Figs 2F and 7F. In most of these species the theridiid tegular apophysis and the conductor appear to be absent, these species thus resemble the also secondarily simplified palps of the theridiid genus *Theridula*.

Anelosimus potmosbi, sp. nov.

(Fig. 2A–H)

Material examined

Holotype male, and a male and two female paratypes from PAPUA NEW GUINEA: National Capital District, Baruni Village, just west of Port

Moresby, 9°25′38″S 147°07′59″E, trees on beach, 0 m elevation, 17.iv.2009, coll. I. Agnarsson.

Diagnosis

Anelosimus potmosbi habitus resembles most other *Anelosimus* species (Fig. 2A–C), but it can be distinguished from all other *Anelosimus* species by the shape of the embolus, a very elongated ‘corkscrew’ in the male (Fig. 2D–F), and by the internal female genitalia, including details of the copulatory duct trajectory in the female, which are very simple in this species (Fig. 2H).

Description

Male (holotype)

Total length 2.65. Prosoma 1.40 long, 1.10 wide, yellowish-orange, grey markings in centre and on rim. Abdomen 1.45 long, 1.16 wide, 1.22 high, pattern as in Fig. 2A–C. Eyes subequal, diameter ~0.08. Leg I femur 2.15, patella 0.60, tibia 1.90, metatarsus 1.45, tarsus 0.75. Femur I thickened, little over four times longer than wide, curved. Leg formula 1243. Leg base colour light, distal half of femur I and tips of joints dark orange-brown, most distinctly on leg I. Palp as diagnosed (Fig. 2D–F).

Female (same data as male)

Total length 3.00. Prosoma 1.55 long, 1.15 wide, yellowish-brown, centre and rim darker. Abdomen 1.80 long, 1.40 wide, 1.40 high, pattern as in male. Eyes subequal, diameter ~0.10. Leg I femur 2.15, patella 0.65, tibia 1.70, metatarsus 1.25, tarsus 0.70. Femur thickened, I about five times longer than wide, curved. Leg formula 1423. Leg colour as in male. Epigynum as diagnosed (Fig. 2G, H), paired weakly sclerotised openings. Copulatory and fertilisation ducts simple.

Natural history

Web structure similar to that of *A. pacificus* from Costa Rica (Agnarsson *et al.* 2006b; Fig. 1A, B) and lack of webs with juveniles cohabiting suggests this species is solitary, as are most other coastal *Anelosimus* species.

Etymology

The species epithet, a noun in apposition, is named after the Papua New Guinea capital Port Moresby, on the outskirts of which it was collected, following the spelling of Tok Pisin, an official creole language of Papua New Guinea: Pot Mosbi.

Anelosimus pomio, sp. nov.

(Fig. 3A–G)

Material examined

Holotype male, and a male and two female paratypes from PAPUA NEW GUINEA: New Britain, East New Britain Province, outside Pomio village, 5°31′20″S 151°31′0″E, trees on beach, 0 m elevation, 15.iv.2009, coll. I. Agnarsson.

Diagnosis

Anelosimus pomio (Fig. 3A, B) can be distinguished from other *Anelosimus* species by the shape of the embolus in the male (Fig. 3C–E), which during the first spiral circulates around its own

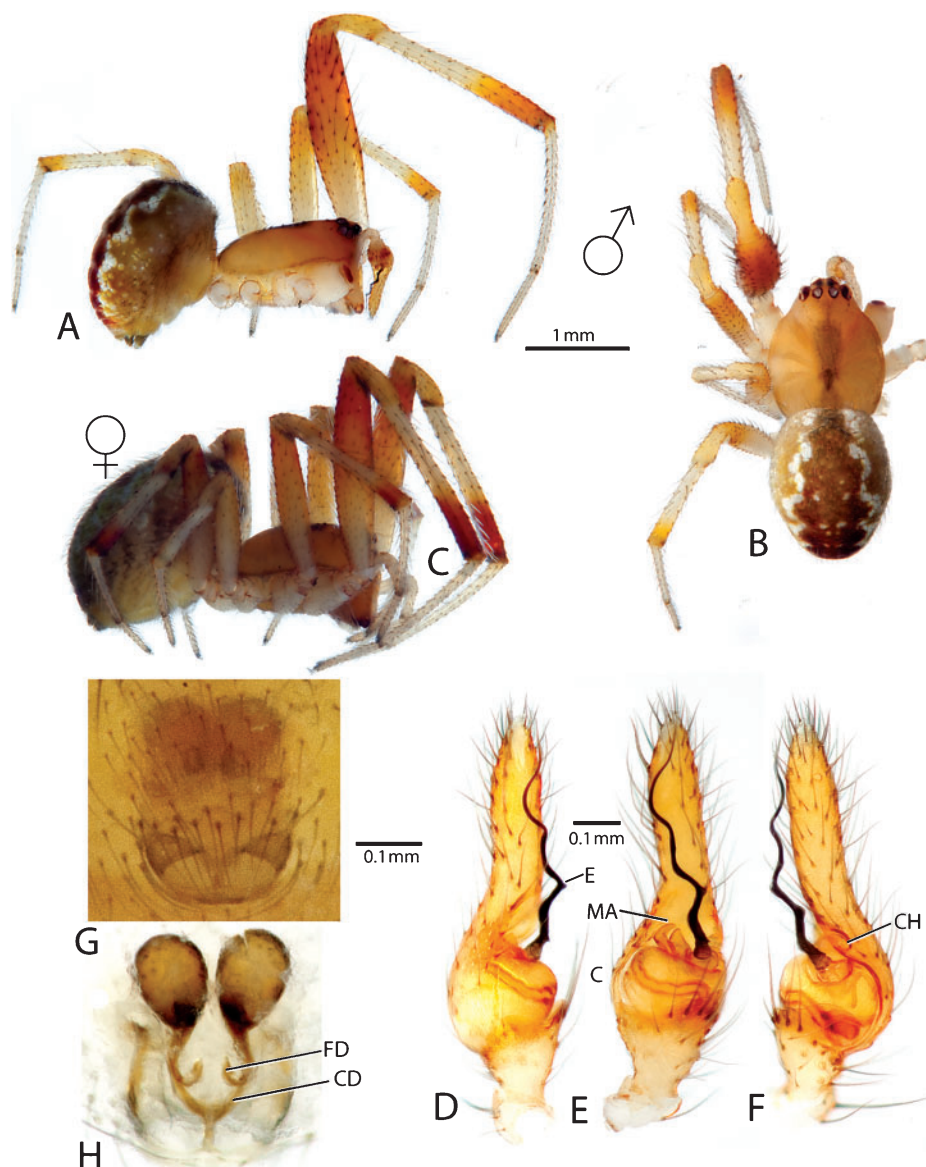


Fig. 2. *Anelosimus potmosbi*, sp. nov. Male habitus: (A) ectal; (B) dorsal. (C) Female habitus ectal. Male palp: (D) mesal; (E) ventral; (F) ectal. Female epigynum: (G) ventral; (H) dorsal, cleared. 1 mm scale bar refers to all habitus photographs; 0.1 mm scale bar on left to epigynum, on right to palp.

base. The male is similar to the Chinese *A. chonganicus* Zhu, 1989 and *A. membranaceus* Zhang, Liu & Zhang, 2011 (Zhang *et al.* 2011), but the embolus has fewer spirals than the former, and spirals closer to the embolus base than the latter. *Anelosimus pomio* differs from other *Anelosimus* by the external and internal female genitalia, including the shape of the copulatory plate (Fig. 3F).

Description

Male (holotype)

Total length 3.25. Prosoma 1.75 long, 1.40 wide, light yellowish, faint grey markings in centre and on rim. Abdomen 1.80 long, 1.50 wide, 1.10 high, pattern as in female (Fig. 3A, B).

Eyes subequal, diameter ~ 0.12 . Leg I femur 3.10, patella 0.85, tibia 2.60, metatarsus 2.50, tarsus 0.75. Femur I thickened, about five times longer than wide, curved. Leg base colour light yellowish, distal tips of joints of legs slightly darkened. Palp as diagnosed (Fig. 3B–D) with a spiralling embolus encircling its own base before extending towards the cymbial tip.

Female (paratype)

Total length 3.80. Prosoma 1.80 long, 1.50 wide, orange, centre and rim with faint grey markings. Abdomen 2.40 long, 1.70 wide, 1.70 high, pattern as in Fig. 3A, B. Eyes subequal, diameter ~ 0.11 . Leg I femur 2.45, patella 0.75, tibia 2.35, metatarsus 1.90, tarsus 0.80. Femur I thickened, about five

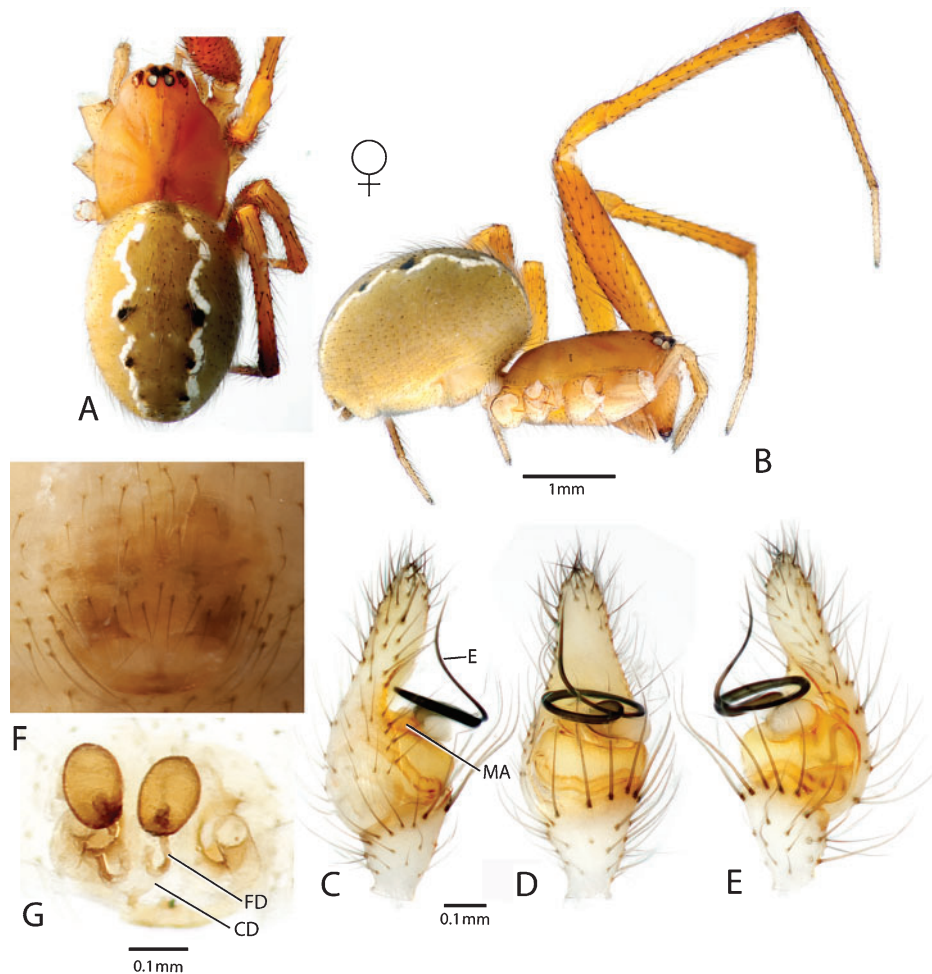


Fig. 3. *Anelosimus pomio*, sp. nov. Female habitus: (A) dorsal; (B) ectal. Male palp: (C) mesal; (D) ventral; (E) ectal. Female epigynum: (F) ventral; (G) dorsal, cleared. 1 mm scale bar refers to habitus photograph; 0.1 mm scale bar on left to epigynum, on right to palp.

times longer than wide, curved. Leg formula 1423. Leg base colour orange, distal tibial joints slightly darkened, especially leg I. Epigynum as diagnosed (Fig. 3F, G), paired weakly sclerotised openings. Copulatory and fertilisation ducts very simple and short.

Natural history

As for *A. potmosbi*, the preliminary data available suggest that this species is solitary.

Etymology

The species epithet, a noun in apposition, is named after Pomio village, where it was collected.

Anelosimus eidur, sp. nov.

(Fig. 4A–I)

Material examined

Holotype male, and 20 male and female paratypes from PAPUA NEW GUINEA: Enda Province, in and around Porgera, 5°27'48"S 143°08'42"E,

in ornamental trees in town and in natural vegetation NE of Porgera, 2200 m elevation, 15.xi.2009, coll. I. Agnarsson. Ten females from Porgera, Suyan camp, 5°28'59"S 143°08'01"E, 2300 m elevation, 28–29.vii.2008, coll. W.P. Maddison. Four females and one male from Enda Province, Kaingri, 5°34'26"S 143°02'52"E, 3315 m elevation, 5–8.vii.2008, coll. W.P. Maddison. Two females and one male from Eastern Highland Province, Mt Gahavisuka Provisional Park, 6°00'53"S 145°24'43"E, 2325 m elevation, 1–2.viii.2008, coll. W.P. Maddison.

Diagnosis

Anelosimus eidur can be distinguished from all other *Anelosimus* species by the shape of the embolus in the male (Fig. 4D–F), an extremely elongated spiral, and by the female genitalia, including the complex trajectory of the copulatory duct, encircling the spermathecae many times (Fig. 4G–I).

Description

Male (holotype)

Total length 2.90 (range: 2.75–3.10). Prosoma 1.50 long, 1.15 wide, brown (Fig. 4A). Abdomen 1.60 long, 1.20 wide,

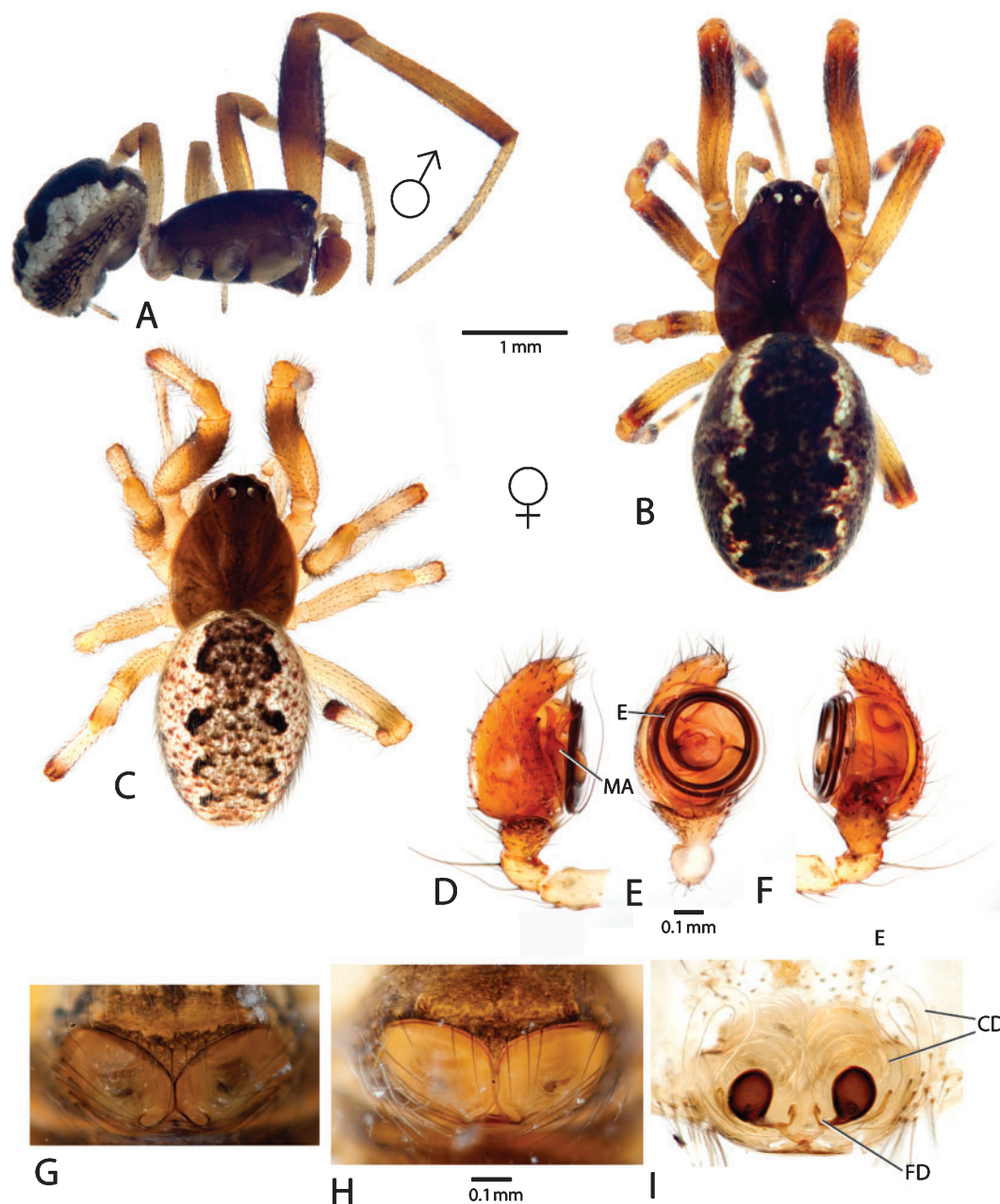


Fig. 4. *Anelosimus eidur*, sp. nov. (A) Male habitus ectal. Female habitus: (B) 'dark' morph; (C) 'light' morph. Male palp: (D) mesal; (E) ventral; (F) ectal. Female epigynum: (G) ventral; (H) ventral, variation; (I) dorsal, cleared. 1 mm scale bar refers to all habitus photographs; 0.1 mm scale bars to genitalia, upper male, lower female.

1.10 high, pattern as in Fig. 4A–C. Eyes subequal, diameter ~0.09. Leg I femur 1.90, patella 0.60, tibia 1.75, metatarsus 1.10, tarsus 0.70. Femur I thickened, about five times longer than wide, curved. Leg base colour light yellowish, distal half of femur I, and tips of joints of other legs slightly darkened, patella and tibia of leg I darker than metatarsus and tarsus. Palp as diagnosed (Fig. 4D–F), with a very elongated spiralling embolus completing five to six spirals.

Female (paratype)

Total length 3.90 (range: 3.30–4.00). Prosoma 1.75 long, 1.30 wide, brown (Fig. 4B, C). Abdomen 2.45 long, 1.75 wide, 1.60 high, variable colour, pattern as in Fig. 4B, C. Eyes subequal, diameter ~0.10. Leg I femur 2.00, patella 0.60, tibia 1.45, metatarsus 1.10, tarsus 0.75. Femur I about six times longer than wide, curved. Leg formula 1423. Leg base colour light, distal

tibial joints darkened, brown or red, sometimes a red band on proximal part of tibia. Epigynum as diagnosed (Fig. 4G–I), paired distinctly sclerotised openings and part of copulatory ducts visible through the cuticle. Copulatory ducts extremely long and circling (Fig. 4J).

Natural history

The available data, though they are sparse, suggest that this species is subsocial, similar to the North American *A. arizona* Agnarsson, 2006 (e.g. Avilés and Gelsey 1998; Bukowski and Avilés 2002) and several montane species from Madagascar (Agnarsson and Kuntner 2005), with single female colonies, and juveniles cohabiting in their natal nest until near adulthood. *Anelosimus eidur* was abundant in scrubby high elevation forest in Southern Highland province of Papua New Guinea, as well as in and around the mining town of Porgera (Enga Province, 5°26'S 143°08'E, 2300 m, 15.ix.2009, coll. I. Agnarsson). Webs of *A. eidur* were variable; they were generally built by connecting several leaves of relatively small-leaved trees, including conifers. Webs often had the 'basket web' shape typical of subsocial and social *Anelosimus* species, with a three-dimensional basket from which aerial knock-down threads radiated upwards. However, many webs were poorly defined three-dimensional meshes lacking aerial knock-down threads. Webs typically contained an adult

female, a female with an egg sac, or a female with spiderlings ranging from estimated instar II–VI. Webs were also collected containing only spiderlings, including webs with multiple subadults. The ages or instars of juveniles were estimated based on their size, based on comparison of the instars to other *Anelosimus* species with similarly sized adult females (Agnarsson and Kuntner 2005).

Etymology

The species epithet, a noun in apposition, is a patronym for my son Eiður Francis.

Anelosimus luckyi, sp. nov.

(Fig. 5A–C)

Material examined

Holotype male from PAPUA NEW GUINEA: Western Province, Muller Range, Sawetau camp, 5°39'4"S 142°18'3"E, 1587 m elevation, 11.ix.2009, coll. A. Lucky.

Diagnosis

Anelosimus luckyi can be distinguished from all other *Anelosimus* species by the shape of the embolus in the male (Fig. 5B, C), a round base terminating in a short and stout 'corkscrew'.

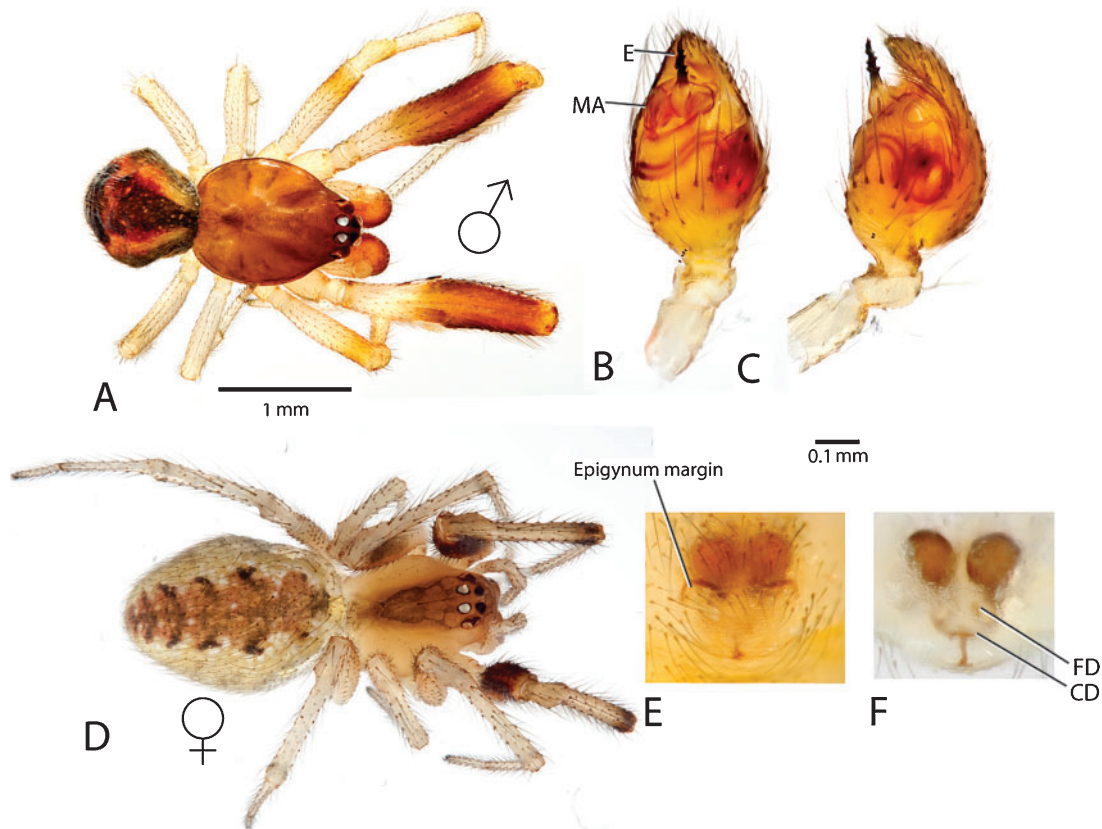


Fig. 5. *Anelosimus luckyi*, sp. nov. (A) Male habitus dorsal. Male palp: (B) ventral; (C) ectal. *Anelosimus bali*, sp. nov. (D) Female habitus dorsal; female epigynum: (E) ventral; (F) dorsal, cleared. 1 mm scale bar refers to both habitus photographs; 0.1 mm scale bar to all genitalia.

*Description**Male (holotype)*

Total length 2.05. Prosoma 1.30 long, 0.95 wide, light brown, slightly darker in head region (Fig. 5A). Abdomen 1.20 long, 0.90 wide, 0.75 high, pattern as in Fig. 5A. Eyes subequal, diameter ~0.08. Leg I femur 1.50, patella 0.50, tibia 1.20, metatarsus 0.80, tarsus 0.50. Femur I thickened, less than four times longer than wide, curved. Leg base colour light yellowish, distal half of femur I and tips of other joints on legs I and II darkened. Palp as diagnosed (Fig. 5B, C).

Female

Unknown.

Natural history

Unknown.

Etymology

The species epithet, a noun in the genitive case, is a patronym for Andrea Lucky, who collected the only known specimen.

***Anelosimus bali*, sp. nov.**

(Fig. 5D–F)

Material examined

Holotype female from INDONESIA: Bali, Sanur beach, 8°42'25"S 115°15'45"E, trees on beach, 6 m elevation, 24.vii.2010.

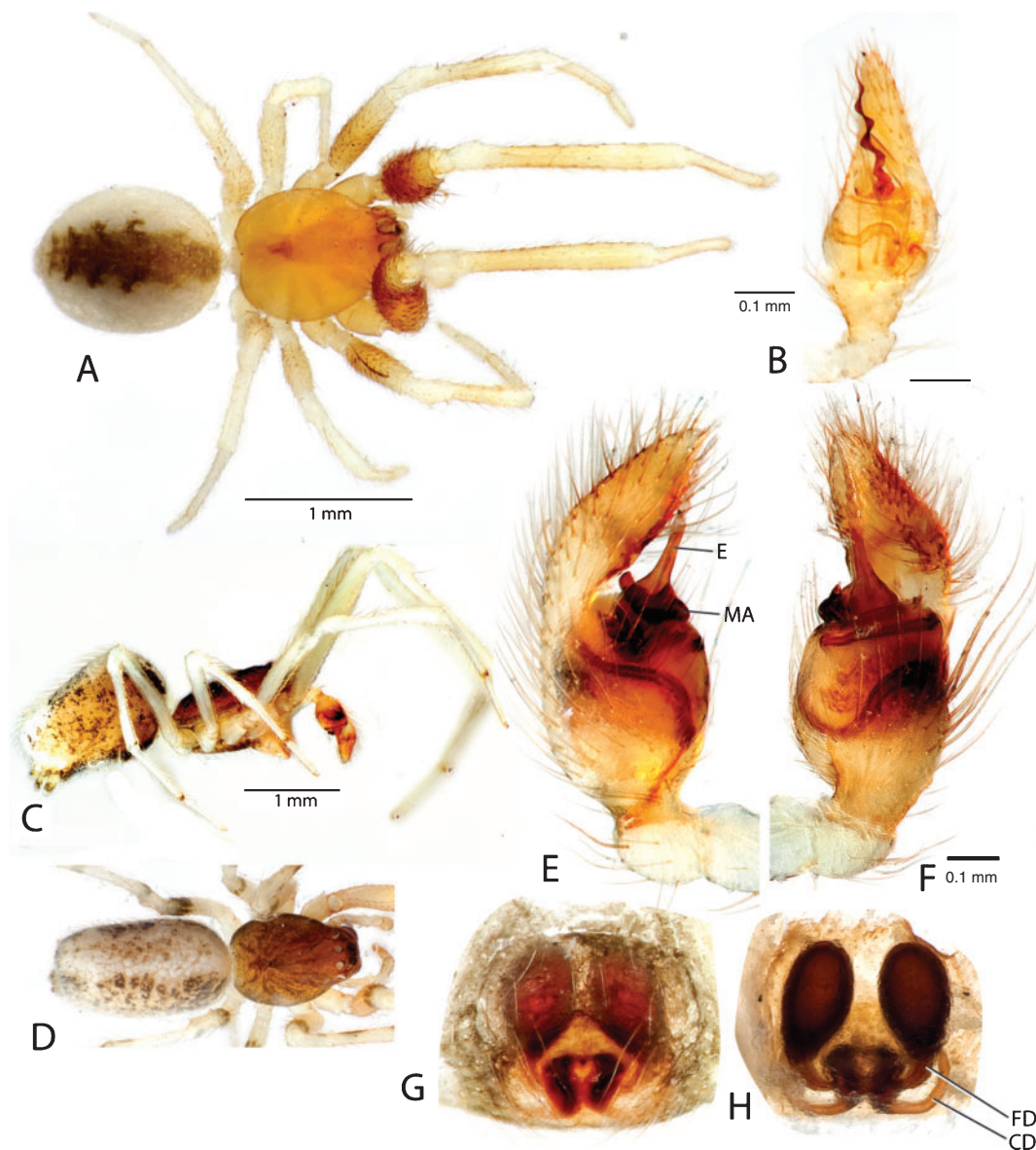


Fig. 6. *Anelosimus terraincognita*, sp. nov. (A) Male habitus dorsal. (B) Male palp ventral. *Anelosimus pratchetti*, sp. nov. (C) Male habitus ectal; (D) female habitus dorsal. Male palp: (E) mesal; (F) ventral. Female epigynum; (G) ventral; (H) dorsal, cleared. 0.1 mm scale bar refers to all genitalia.

Diagnosis

Anelosimus bali (Fig. 5D) can be distinguished from all other *Anelosimus* species by the shape of the epigynum, a semi-heart-shaped depression (Fig. 5E, F).

*Description**Male*

Unknown.

Female (holotype)

Total length 2.90. Prosoma 1.35 long, 0.90 wide, light yellow, cephalic region brown. Abdomen 1.70 long, 1.20 wide, 1.25 high, pattern as in Fig. 5D. Eyes subequal, diameter ~0.08. Leg I femur 1.60, patella 0.50, tibia 1.30, metatarsus 1.20, tarsus 0.60. Femur I more than five times longer than wide, curved. Leg formula 1423. Leg base colour light yellow, distal half of femur I and tip of tibia I dark brown. Epigynum as diagnosed (Fig. 5E, F).

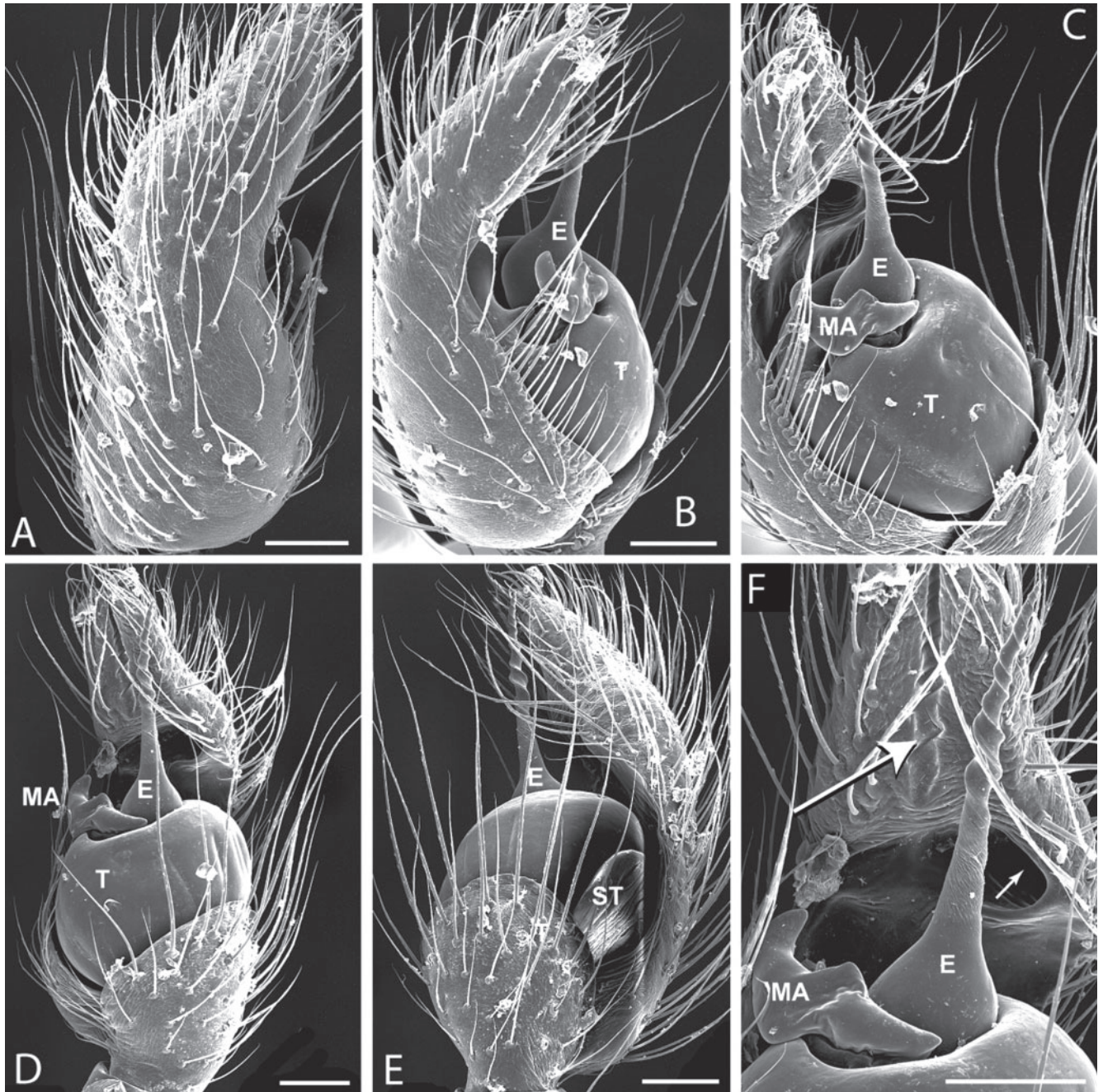


Fig. 7. *Anelosimus pratchetti*, sp. nov. Male palp: (A) dorsal; (B) mesal; (C) submesal; (D) ventral; (E) ectal. (F) Details of sclerites, cymbial embolic groove (upper arrow), and cymbial hood (lower arrow). Scale bars = 100 μ m.

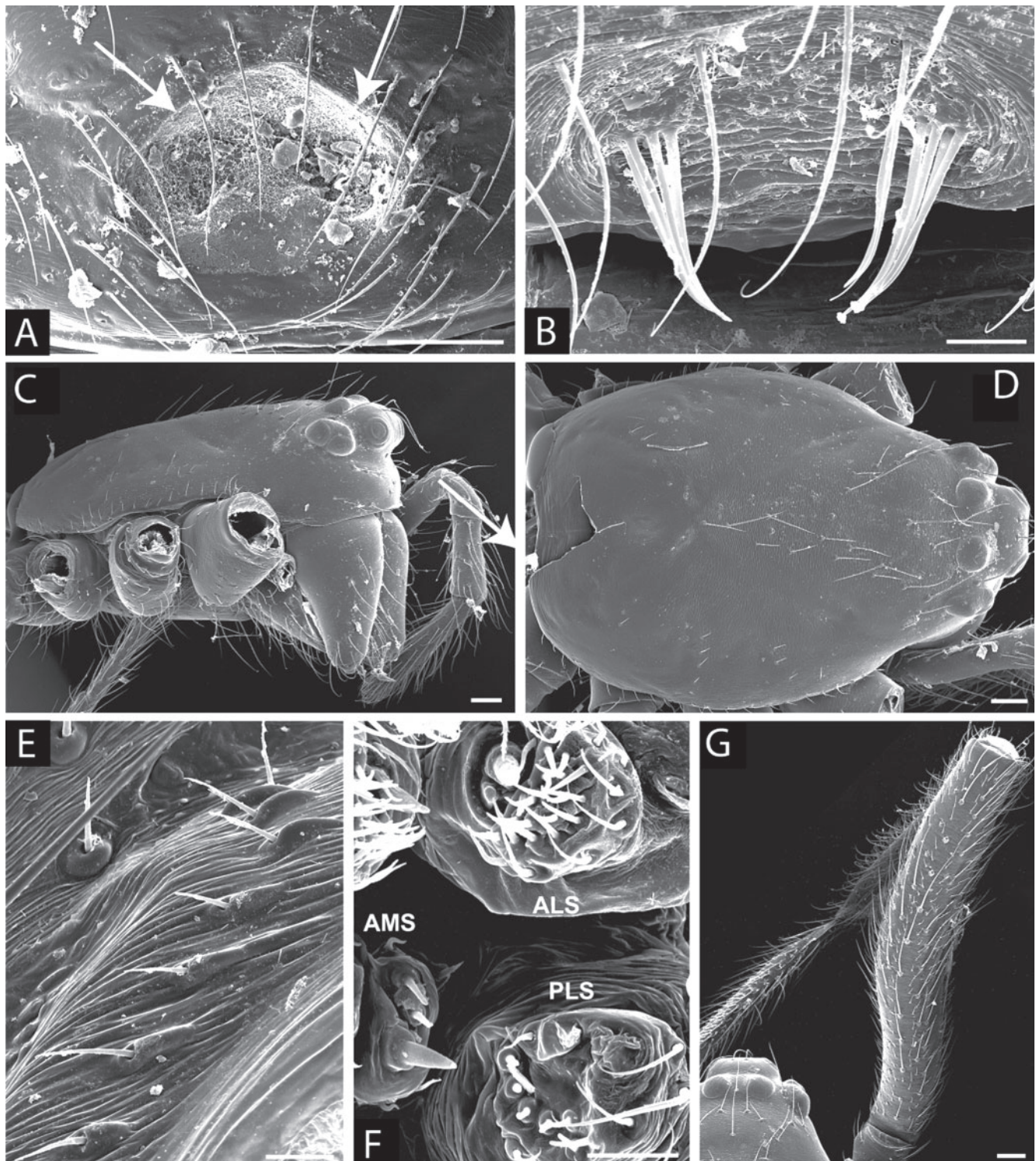


Fig. 8. *Anelosimus pratchetti*, sp. nov. (A) Epigynum, arrows indicate margins of the semi-triangular epigynal plate. (B) Epiandrous gland fusules. Female prosoma: (C) ectal; (D) dorsal. (E) Male stridulatory pick row. (F) Male spinnerets, left field. (G) Male femur I, the curvature is synapomorphic for *Anelosimus*. Scale bars: A, C, D, G = 100 µm; B, E, F = 20 µm.

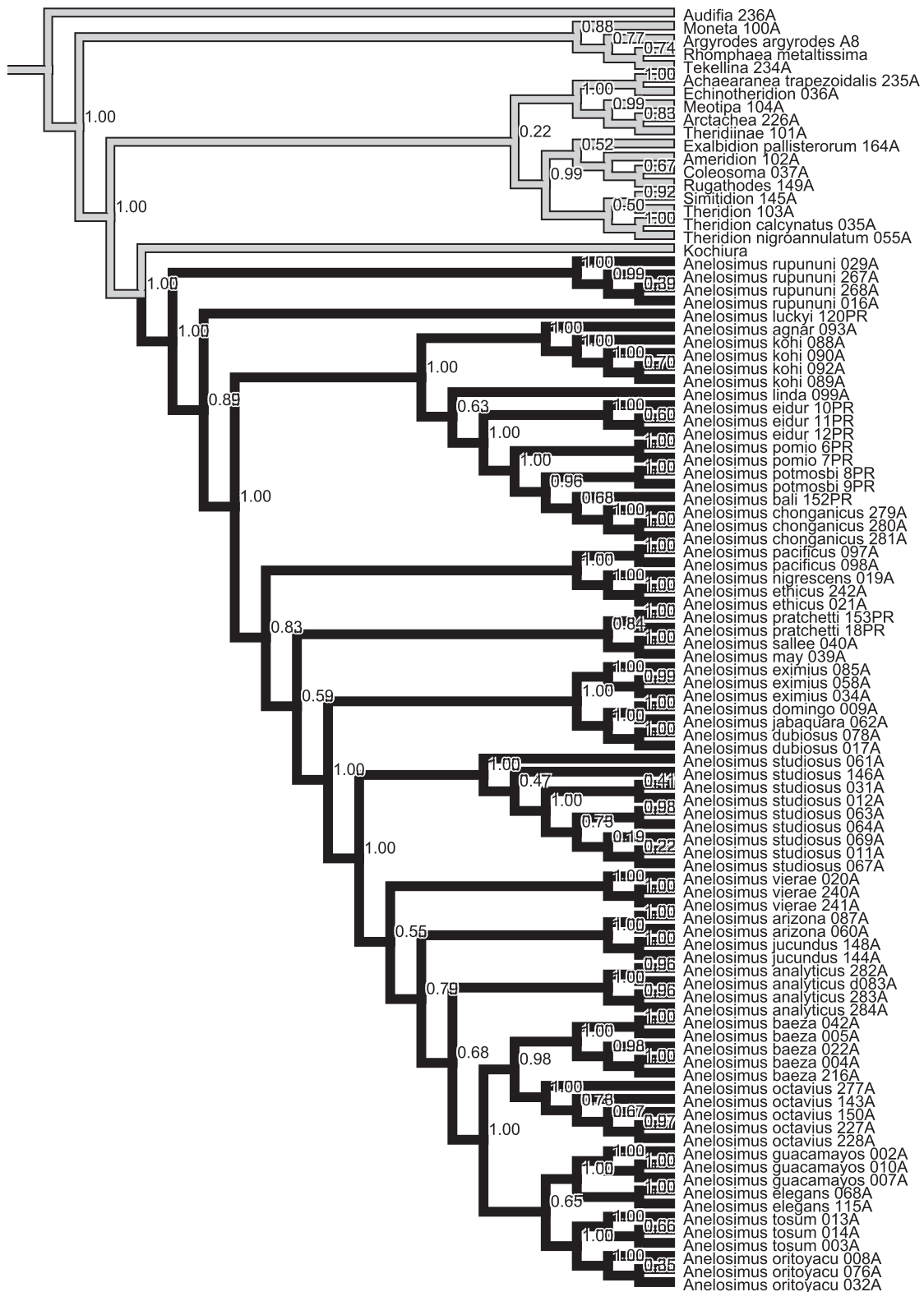


Fig. 9. The full phylogeny including all outgroups and posterior probability support for each clade.

Natural history

Unknown.

Etymology

The species epithet, a noun in apposition, is named after the Indonesian island of Bali, where it was collected.

***Anelosimus terraincognita*, sp. nov.**

(Fig. 6A, B)

Material examined

Holotype male from an unknown locality, collector unknown, type deposited in RMNH, Leiden, Netherlands.

Diagnosis

Anelosimus terraincognita can be distinguished from all other *Anelosimus* species by the shape of the embolus (Fig. 6B), a ‘corkscrew’ that is intermediate in length between that of *A. luckyi* and *A. potmosbi*.

*Description**Male (holotype)*

Total length 2.20. Prosoma 1.00 long, 0.80 wide, light yellowish, faint darker markings in centre. Abdomen 1.80 long, 1.50 wide, 1.10 high, pattern as in Fig. 6A. Eyes subequal, diameter ~0.09. Leg I femur 1.40, patella 0.40, tibia 1.20, metatarsus 0.90, tarsus 0.55. Femur I thickened, about four times longer than wide, curved. Leg base colour light yellowish, femur I darker yellow, tibia of legs I and II slightly darkened. Palp as diagnosed (Fig. 6B).

Female

Unknown.

Natural history

Unknown.

Comments

The morphology of the male palp suggests that this species is Australasian. ‘Corkscrew’ palps in *Anelosimus* spiders have only been reported from that region (this paper).

Etymology

The species epithet, a noun in apposition, refers to the unknown collecting locality of the specimen. *Terra incognita* is Latin for unknown or uncharted land.

***Anelosimus pratchetti*, sp. nov.**

(Figs 6C–H, 7A–F, 8A–G)

Material examined

Holotype male, and a male and two female paratypes from AUSTRALIA: New South Wales, Berowra Valley Regional Park, Blue Gum Walk, 33°42'S 151°06'E, 29.xii.2000, ~100 m elevation, G. Millidge and H. Smith, in NMNH. An additional male and two females from AUSTRALIA: New South Wales, Toolijooa, 0–5 m elevation, 34°45'S 150°46'E, 0–5 m elevation, 18.xi.2008, coll. K. Simpson.

Diagnosis

Anelosimus pratchetti can be distinguished from all other *Anelosimus* species by the shape of the embolus in the male (Figs 6E, F, 7B–F), a ‘corkscrew’ that is much longer than that in *A. luckyi* and that is accommodated by a groove on the cymbium (Fig. 7C, D, F). Females differ from all other *Anelosimus* by strong sclerotisation of the copulatory ducts near the genital opening, and the triangular shape of the epigynal plate (Fig. 6G, H).

*Description**Male (holotype)*

Total length 2.95 (range: 2.40–3.10). Prosoma 1.35 long, 0.95 wide, light yellowish, with greyish striae from the fovea. Abdomen 1.65 long, 0.95 wide, 1.05 high, pattern as in Fig. 6D. Eyes subequal, diameter ~0.09. Leg I femur 1.80, patella 0.45, tibia 1.50, metatarsus 1.10, tarsus 0.75. Femur I not thickened, about six times longer than wide, curved (Fig. 8G). Leg base colour light whitish. Palp as diagnosed (Figs 6E–G, 7A–F).

Female (paratype)

Total length 3.40 (range: 2.80–3.60). Prosoma 1.40 long, 1.00 wide, light yellowish, with greyish striae from the fovea. Abdomen 2.00 long, 1.05 wide, 0.70 high, pattern as in male. Eyes subequal, diameter ~0.09. Leg I femur 1.70, patella 0.55, tibia 1.40, metatarsus 1.20, tarsus 0.74. Femur I not thickened, about seven times longer than wide, curved. Leg formula 1423. Leg base colour whitish, distal femoral and tibial joints darkened. Epigynum as diagnosed (Figs 6G, H, 8A).

Natural history

Anelosimus pratchetti is likely subsocial given preliminary field observations (H. Smith, pers. comm.).

Etymology

The species epithet, a noun in the genitive case, is a patronym in honour of Sir Terence David John ‘Terry’ Pratchett, the wonderful writer ‘sometimes accused of literacy’, a comic genius and the creator of the Discworld series.

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