

Check for updates

Three new species of *Aprusia* (Araneae: Oonopidae) from Sri Lanka with a phylogenetic analysis of the genus

U.G.S.L. Ranasinghe and Suresh P. Benjamin D

Evolution, Ecology and Biodiversity Project, National Institute of Fundamental Studies, Kandy, Sri Lanka

ABSTRACT

The South Asian goblin spider genus Aprusia Simon, 1893 currently consists of five species. All species are narrow endemics with very restricted distributions. In this paper, the Sri Lankan species are revised and three new species described from both sexes: Aprusia koslandensis n. sp., Aprusia rawanaellensis n. sp. and Aprusia vankhedei n. sp. We also provide some notes on the poorly known species A. strennus and A. vestigator. In addition, we present a key to adult Aprusia and a distribution map of the Sri Lankan species, highlighting their diversity in the highly fragmented forests of the island. To test the monophyly of Aprusia and infer relationships among its species, a matrix of 49 morphological characters scored for 11 taxa (seven ingroup and four outgroup) was assembled and analysed. The monophyly of Aprusia is recovered and supported by three unambiguous synapomorphies: the presence of smooth male endites, the presence of leg spines on the prolateral side of the femur I and the procurved ridge of the postepigastric scutum.

www.zoobank.org/urn:lsid:zoobank.org:pub:40352A9B-F455-4F41-B293-FF57BACA2997

ARTICLE HISTORY

Received 7 March 2017 Accepted 19 February 2018

KEYWORDS

Biodiversity; Sri Lanka; indicator species; conservation; leaf litter; Ceylon; taxonomy

Introduction

The spider family Oonopidae Simon, 1890 currently consist of 1775 described species placed in 114 genera (World Spider Catalogue 2017). These spiders are widely distributed throughout the world and are a common component of the leaf litter-dwelling fauna of tropical forests. Several species are pantropical, e.g. *Brignolia parumpunctata* (Simon, 1893b), *Heteroonops spinimanus* Simon, 1892, *Ischnothyreus peltifer* Simon, 1892, *Opopaea apicalis* Simon, 1893a, *Pelicinus marmoratus* Simon, 1892 and *Triaeris stenaspis* Simon (1892). However, many other species and even some genera are restricted to relatively small areas. These micro-distributed taxa can be used as indicators of environmental change (Saaristo 2002; Bolzern and Platnick 2013). Examples are the species of the West African genus *Antoonops* Fannes and Jocqué, 2008, the South-East Asian genus *Aposphragisma* Thoma et al., 2014 and the South American genus *Gradunguloonops* Grismado *et al.*, 2015.

CONTACT Suresh P. Benjamin Suresh.benjamin@gmail.com

Another example is the South Asian genus *Aprusia*, Simon, 1893a which currently consists of five species from Sri Lanka and south-western India (Grismado et al. 2011). Four species are endemic to Sri Lanka: the type species *A. strenuus*, Simon, 1893a, *A. kataragama* Grismado et al., 2011, *A. veddah* Grismado et al., 2011 and *A. vestigator* (Simon, 1893b). The identity of *A. strenuus* is doubtful, as it was originally based on juvenile specimens (Simon 1893a; Grismado et al., 2011) and has not been found since.

Aprusia is characterized by a unique combination of characters, such as the relatively small to medium-sized dorsal scutum, the presence of strong spines on leg I and II, the anteriorly directed receptaculum and the male palpal bulb fused to cymbium and a small slightly sclerotized embolus (Grismado et al. 2011). They are easily recognized even in the field due to their relatively large size comparative to other oonopids. Grismado et al. (2011) revised *Aprusia*, describing several new species. Here, we report an additional three new species from Sri Lanka, highlighting its diversity in the highly fragmented forests of the island. This paper is part of an ongoing survey of Sri Lankan Oonopidae and is the fourth in a projected series (Ranasinghe and Benjamin 2016a, 2016b, 2016c).

Materials and methods

Sample collection

Field visits were conducted at selected locations across Sri Lanka. Specimens were collected by sifting litter and leaving the residue overnight in a Winkler extractor or by hand-sorting the residue. The collected specimens were examined using an Olympus SZX7 stereomicroscope. Specimens were preserved in 70% ethanol and identified using recently published studies (Grismado et al. 2011, www.research.amnh.org/oonopidae). Specimen examination: left male palps were dissected and immersed in Kaiser's glycerol gelatine (Merck KGaA, Darmstadt, Germany), slide mounted, observed and illustrated with the aid of an Olympus BX51 compound microscope equipped with a drawing tube. The female epigastric region was dissected, digested in a pancreatin solution (Álvarez-Padilla and Hormiga 2008) for about three to seven days, slide mounted and illustrated. Digital images of the specimens were taken with a Leica MC170 HD camera mounted on a Leica M205C stereomicroscope using the software package Leica Application Suite, LAS version 4.6.2 (Leica Microsystems Ltd, Wetzlar, Germany). Acquired image stacks of different depths (15–50 images per stack) were assembled using Helicon Focus (version 6, Helicon Soft Ltd) to create a single image with the entire specimen in focus. Species descriptions follow the format of Grismado et al. (2011). All measurements are given in millimetres. Body length was considered as carapace length + abdomen length (excluding spinnerets).

Cladistic analysis

Mesquite (version 2.72; Maddison and Maddison 2009) was used to construct and edit the character matrix (Table 1). A total of 49 characters were scored for 11 taxa (seven ingroup and four outgroup). Parsimony analysis of the morphological data matrix was performed using TNT 1.1 (Goloboff et al. 2008) under equal weights and implied weights. For implied weights K-values of 3–10 were used. Ambiguous character optimizations were resolved to favour early

gains of features with subsequent reversals (Farris optimization or ACCTRAN). All multistate characters were treated as non-additive (unordered or Fitch minimum mutation model; Fitch 1971) as no transformation series could be inferred. Maxtrees was set to 10,000. In TNT, the traditional search (heuristic search) mode was used with 10,000 random addition sequence replicates, and the tree bisection reconnection (TBR) swapping algorithm saving one tree per replication. Character evolution was assessed using WinClada (version 1.00.08; Nixon 2002). Symmetric resampling (Goloboff et al. 2008) was performed to assess branch stability using TNT (1000 replicates). Bremer support and relative Bremer support (Bremer 1994; Goloboff et al. 2008) were also assessed using TNT.

Abbreviations

Institutional abbreviations

MNHN, Muséum National d'Histoire Naturelle, Paris, France; NIFS, National Institute of Fundamental Studies, Kandy, Sri Lanka; ZFMK, Zoological Research Museum Alexander Koenig, Bonn, Germany.

Character abbreviations

ALE, anterior lateral eyes; ar, anterior receptaculum; co, conductor; cp, conical projection; em, embolus; lap, lateral apodemes; PLE, posterior lateral eyes; PME, posterior median eyes; pr, posterior receptaculum; ss, semicircular sclerotization.

Additional abbreviations

FR, Forest Reserve; SNR, Strict Nature Reserve.

Taxonomy

Family **OONOPIDAE** Simon, 1890 Genus *Aprusia* Simon, 1893a

Aprusia Simon, 1893a: 295. Type species by original designation *A. strenuus* Simon, 1893a. Not examined, see Grismado et al. (2011) for a description of the types.

Diagnosis

Aprusia differ from related genera *Camtoscaphiella* and *Ischnothyreus* by the following characters: presence of smooth male endites, presence of leg spines on the prolateral side on the femur I and presence of procurved ridge of the postepigastric scutum. Further, males are recognized by the pale-coloured, ovoid to fusiform palpal bulb, with short, sclerotized, embolus, sometimes united with the conductor (Figures 2(b), 4(b)), cymbium which is completely fused to the bulb (Figures 2(a), 4(a)). Females are recognized by a strongly procurved anterior margin in the epigyne area and with anterior receptaculum, which vary in the size and shape among species. See Grismado et al. (2011) for a detailed diagnosis.

Key to adult Aprusia (A. strenuus known only from juveniles)

1.	Males (those of A. veddah unknown)2Females (those of A. kerala unknown)
2.	Conductor present (Figures 2(b), 4(b))3Conductor absent (Figures 7(b), 9(b))5
3.	Conical projection present (Figure 4(b), fig. 55 in Grismado et al. 2011)
4.	Conductor shorter than embolus (Figure 4(b)) <i>A. rawanaellensis</i> n. sp. Conductor about same length as embolus (fig. 55 in Grismado et al. 2011) <i>A. kerala</i> (India)
5.	Embolus nearly straight (Figure 9(a))
6.	Bulb slender and elongated (fig. 43 in Grismado et al. 2011)
7.	Anterior receptaculum longer than lateral apodemes (Figures 4(c), 7(d), 9(c)) 8 Anterior receptaculum shorter than lateral apodemes (Figure 2(c))
8.	Posterior receptaculum present (Figure 4(c), fig. 21 in Grismado et al. 2011) 9 Posterior receptaculum absent (Figure 7(d))
9.	Posterior receptaculum rounded (fig. 21 in Grismado et al. 2011) A. vestigator Posterior receptaculum undulated (Figure 4(c)) A. rawanaellensis n. sp.
10.	Procurved ridge of the postepigastric scutum thick and visible as a double line (fig. 42 in Grismado et al. 2011)
11.	Tip of anterior receptaculum slightly widened (fig. 44 in Grismado et al. 2011) A. kataragama Tip of anterior receptaculum not widened (Figure 2(c)) A. koslandensis n. sp.

Aprusia koslandensis n. sp. (Figures 1, 2)

Type material

Holotype. 1 ♂ (IFS_Oon_137): Sri Lanka: Badulla District, 189th mile post, between Koslanda and Beragala, 06°44′48.4″N 80°57′56.3″E, 1370 m, 1 January 2012, S. P. Benjamin *et al.*, litter. Deposited in ZFMK. *Paratypes.* 3 ♀ (IFS_Oon_134–136): same locality and data as holotype.

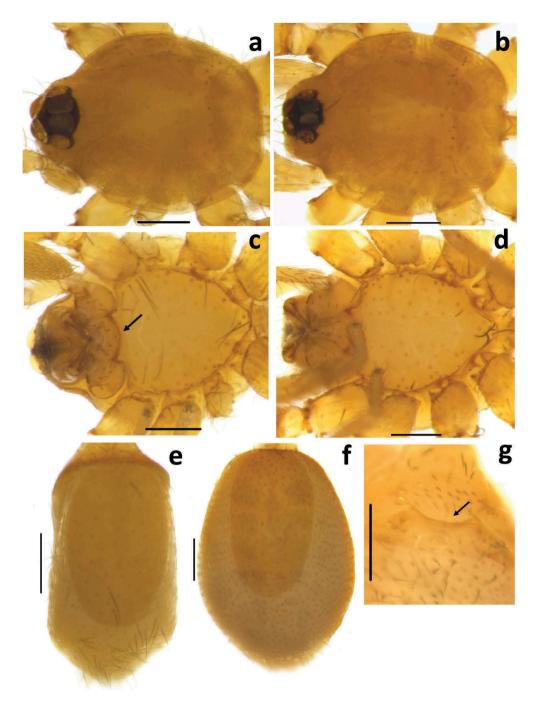


Figure 1. Aprusia koslandensis **n. sp.** male (a, c, e) and female (b, d, f, g) from forest between Koslanda and Beragala. (a, b) carapace, dorsal view; (c, d) sternum, ventral view; (e, f) abdomen, dorsal view; (g) abdomen, ventral view. Scale bars = 0.2 mm (a–g).

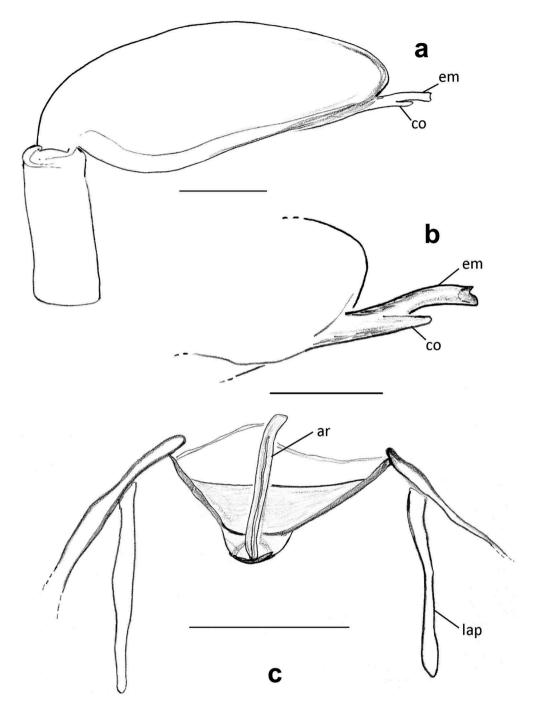


Figure 2. Aprusia koslandensis **n. sp**. from forest between Koslanda and Beragala. Male: (a) left palp, prolateral view; (b) details of the distal part of the bulb. Female: (c) epigastric region, dorsal view. Abbreviations: ar, anterior receptaculum; co, conductor; em, embolus; lap, lateral apodemes. Scale bars = 0.1 mm (a, c), 0.05 mm (b).

Other material examined. 5 Q (IFS_Oon_138–142): same locality and data as holotype. 1 Q (IFS_Oon_207): Sri Lanka: Badulla District, Namunukula, along Passara/Ella road, 06° 52'N 81°7'E, 1838 m, 22 January 2014, leg. S. P. Benjamin and N. Athukorala; 27 February 2015, leg. S. P. Benjamin, N. Athukorala, litter. 1Q (IFS_Oon_142): Sri Lanka: Badulla District, Bandarawela, 06°50'59.5"N 81°00'48.1"E, 1042 m, 31 December 2011, S. P. Benjamin *et al.*, litter. Deposited in ZFMK.

Diagnosis

Males can be identified by the narrowed, elongated bulb, without tiny conical projection, the slightly curved embolus with a bifid end and a conductor (Figure 2(b)). Females are recognized by a relatively short anterior receptaculum (Figure 2(c)).

Description

Male. Body length: 1.72. Cephalothorax as in Figure 1(a), pars cephalica strongly elevated, surface of elevated portion of pars cephalica smooth sides smooth. Eyes (Figure 1(a)), all eyes subequal, circular, ALE-ALE and PME-PME touching, ALE-PLE separated by less than their radius. Sternum longer than wide (Figure 1(c)), without radial furrows between coxae I–II, II–III, III–IV, surface smooth, with small hairs and few small pits, continuous margin (see arrow in Figure 1(c)), anterior margin concave, posterior margin extending posteriorly of coxae IV, distance between coxae I–II, II–III, III–IV, approximately equal.

Abdomen as in Figure 1(e). Dorsal scutum sclerotized, pale orange, without colour pattern, covering about 3/4 of abdomen (Figure 1(e)), more than 1/2 to most of abdomen width, not fused to epigastric scutum. Postepigastric scutum sclerotized, pale orange, almost rectangular, covering about 1/2 of abdominal length, fused to epigastric scutum. Two brown patches located above the spinnerets. Legs strong spines on leg I and II present, leg I: femur, pv0–0–1–1–1; tibia, v2–2–2–2–0; metatarsus, v2–2–0; leg II: femur, pv0–0–1–1, tibia, v2–2–2–2–0, metatarsus, v2–2–0, claw like setae present on leg III and IV.

Genitalia. Sperm pore large, circular, situated at level of anterior spiracles. Palp not strongly sclerotized, femur more than two times longer than patella, three trichobothria on tibia. Cymbium pale orange, completely fused with bulb, no seam visible, with distal patch of setae, distal part without tiny conical projection (Figure 2(a)). Bulb narrowed, elongated (Figure 2(a)). Embolus slightly curved with a conductor which is shorter than (3/4 of) the embolus (Figure 2(a), 2(b)).

Female. Body length: 2.04. As in male except as noted. Female palpal claws and spines absent, tarsus smooth. Abdomen ovoid, posterior spiracles connected by groove. Dorsal scutum covering 3/4 of abdomen (Figure 1(f)). Postepigastric scutum only around epigastric furrow, not fused to epigastric scutum.

Genitalia. Ventral view: anterior margin of postepigastric scutum with a thin, procurved sclerotized ridge (see arrow in Figure 1(g)). Dorsal view: short anterior receptaculum, with a narrow lumen, without bracket-shaped semicircular sclerotized ridges, apparently without posterior receptaculum (Figure 2(c)).

Etymology

The specific name is taken from the type locality.

Distribution

Koslanda, Beragala, Namunukula and Bandarawela (Figure 11).

Aprusia rawanaellensis n. sp. (Figures 3, 4)

Type material

Holotype. 1 of (IFS_Oon_223): Sri Lanka: Badulla District, Rawana Ella, forest around cave, 06°51′52.4″N 81°03′01.3″E, 990 m, 31 December 2011, leg. S. P. Benjamin *et al.*, litter. Deposited in ZFMK.

Paratypes. 1 ♂ (IFS_Oon_224) and 2 ♀ (IFS_Oon_225–226): same locality and data as holotype. Deposited in ZFMK.

Diagnosis

Males resemble those of *A. kerala* in having a pale coloured, narrowed, elongated bulb and a conical projection (Grismado et al. 2011) but differ in having a straight embolus and a conductor (Figure 4(b)). Females can be recognized by the thin, sclerotized, procurved ridge of the postepigastric scutum, the long anterior receptaculum and the undulated posterior receptaculum (Figure 4(c)).

Description

Male. Body length: 1.84. Cephalothorax as in Figure 3(a), pars cephalica only slightly elevated, surface of elevated portion of pars cephalica smooth with randomly distributed small rounded pits, sides smooth. Eyes; all eyes subequal, circular, ALE-ALE and PME-PME touching, ALE-PLE separated by less than their radius. Sternum longer than wide (Figure 3(b)), without radial furrows between coxae I–II, II–III, III–IV, surface smooth, with small hairs and few small pits, continuous margin (see arrow in Figure 3(b)), anterior margin concave, posterior margin extending posteriorly of coxae IV, distance between coxae I–II, II–III, III–IV approximately equal.

Abdomen as in Figure 3(a). Dorsal scutum sclerotized, pale orange, without colour pattern, covering about 3/4 of abdomen, more than 1/2 to most of abdomen width (Figure 3(a)), not fused to epigastric scutum. Postepigastric scutum sclerotized, pale orange, almost rectangular, covering about 1/2 of abdominal length, fused to epigastric scutum(Figure 3(b)). Two light brown patches located above the spinnerets (Figure 3(b)). Legs; strong spines on leg I and II present, leg I: femur, pv0-0-1-1-1-1; tibia, v2-2-2-2-2-0; metatarsus, v2-2-0; leg II: femur pv0-0-0-1-1; tibia v2-2-2-2-0; metatarsus, v2-2-0, claw like setae present on legs III and IV.



Figure 3. Aprusia rawanaellensis **n. sp.** male (a, b) and female (c, d) from Badulla, Rawana Ella. (a) habitus, dorsal view; (b) habitus, ventral view; (c) habitus, dorsal view; (d) habitus, ventral view. The arrow in (d) points to the thin, procurved, sclerotized ridge of the postepigastric scutum. Scale bars = 0.5 mm (a, b), 1 mm (c, d).

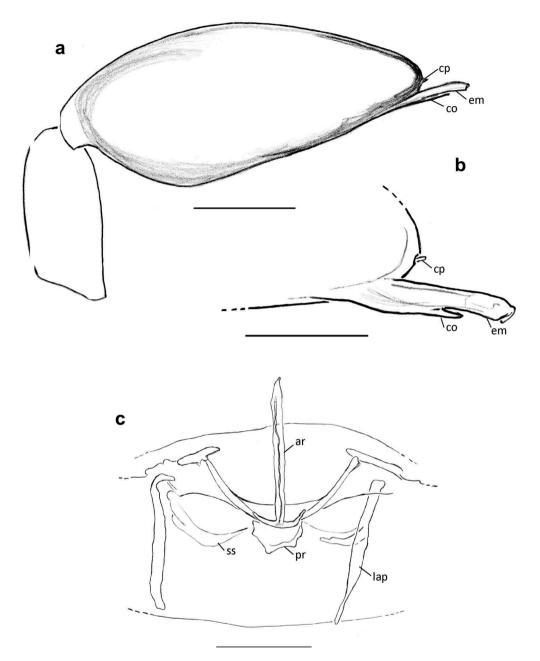


Figure 4. Aprusia rawanaellensis **n. sp.** from Badulla, Rawana Ella. Male: (a) left palp, prolateral view; (b) details of the distal part of the bulb. Female: (c) epigastric region, dorsal view. Abbreviations: ar, anterior receptaculum; co, conductor; cp, conical projection; em, embolus; lap, lateral apodemes; pr, posterior receptaculum; ss, semicircular sclerotization. Scale bars = 0.1 mm (a, c), 0.05 mm (b).

Genitalia. Sperm pore large, circular, situated at level of anterior spiracles (Figure 3(b)). Palp not strongly sclerotized, femur longer than patella. Cymbium pale orange, completely fused with bulb, no seam visible, with distal patch of setae, distal part with a tiny conical projection (Figure 4(b)). Bulb narrowed, elongated, slightly tapering apically

without ventral concavity (Figure 4(a)), Embolus pale, straight, conductor shorter than embolus (Figure 4(b)).

Female. Body length: 2.38. As in male except as noted. Female palpal claws and spines absent, tarsus smooth. Posterior spiracles connected by groove. Dorsal scutum covering 1/4 of abdomen (Figure 3(c)). Postepigastric scutum only around epigastric furrow, not fused to epigastric scutum (Figure 3(d)).

Genitalia. Ventral view: anterior margin of postepigastric scutum with a thin, procurved, sclerotized ridge (see arrow in Figure 3(d)). Dorsal view: long anterior receptaculum with narrow lumen and slightly pointed tip; bracket-shaped, slightly sclerotized semicircular ridge on either side of the procurved ridge; posteriorly directed lateral apodemes: posterior receptaculum small with undulated surface (Figure 4(c)).

Etymology

The specific name is taken from the type locality.

Distribution

Known only from the type locality (Figure 11).

Aprusia strenuus Simon, 1893a (Grismado et al. 2011, figs. 1–5)

Aprusia strenuus Simon, 1893a: 295. Two immature syntypes from Nuwara Eliya, Sri Lanka, 06°58'N, 80°47'E (MNHN 1502). See Grismado et al. (2011) for a detailed description and diagnosis.

Remarks

During a recent revision of *Aprusia*, Grismado et al. (2011) redescribed *A. strenuus* based on the original juvenile specimens. Although they mentioned the possibility that *A. strenuus* might be conspecific with one of the other described species, they could not unambiguously match any of their specimens to the original types or description of *A. strenuus*. We conducted extensive fieldwork in Nuwara Eliya and the surrounding forests. However, we did not find any *Aprusia* specimens in the area. Further, none of our specimens can be unambiguously matched to the original types or the recent redescription of Grismado et al. (2011) of the species. As we continue to search for *A. strenuus*, we refrain from effecting any taxonomic changes at this juncture.

Aprusia vankhedei n. sp. (Figures 5–7)

Type material

Holotype. 1 of (IFS_Oon_100): Sri Lanka: Kandy District, Udawattakele FR, 07°17'57"N 80°38'29"E, 580 m, 21 August 2012, leg. S. P. Benjamin, litter. Deposited in ZFMK.

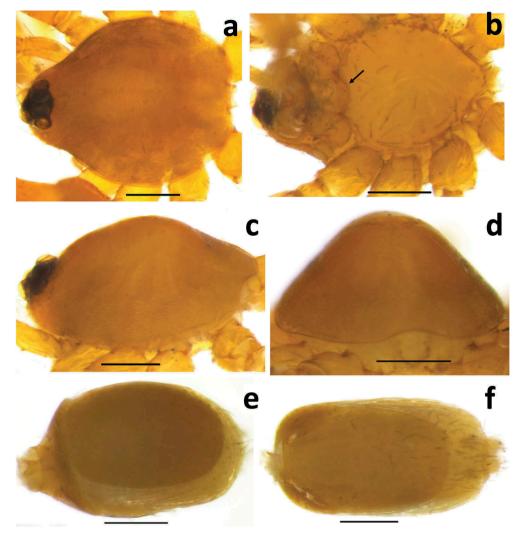


Figure 5. Aprusia vankhedei **n. sp.** male from Udawattakele FR. (a) carapace, dorsal view; (b) sternum, ventral view; (c) carapace, lateral view; (d) carapace, posterior view; (e) abdomen dorsal view; (f) abdomen, ventral view. Scale bars = 0.2 mm.

Paratypes. 1 \circ (IFS_Oon_101) and 6 \circ (IFS_Oon_102–107): same locality and data as holotype. Deposited in ZFMK.

Other material examined. 1 of (IFS_Oon_ 276) and 16 \bigcirc (169–181, 278–279, 301), 29 December 2011, 24 April 2015, N. Athukorala *et al.*; 8 June 2015, Ranasinghe *et al.* All same locality as holotype. 1 \bigcirc (IFS_Oon_024): Sri Lanka, Dunumadalawa FR, 07°17'00"N 80°37'49"E, 600 m, 22 April 2010, S. P. Benjamin and S. Batuwita. Deposited in ZFMK.

Diagnosis

Males resemble *A. kerala* in having a pale-coloured, stout bulb, a tiny conical projection and a sinuous embolus but differ in lacking a conductor, and having a

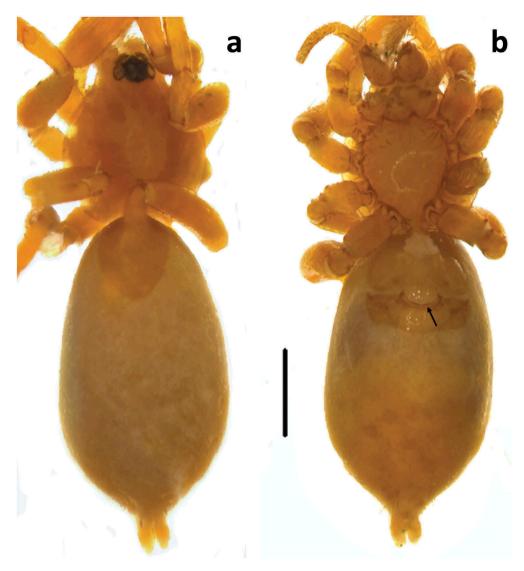


Figure 6. Aprusia vankhedei **n. sp.** female from Udawattakele FR. (a) habitus, dorsal view; (b) same, ventral view. The arrow in (b) points to the thick, procurved, sclerotized ridge of the postepigastric scutum. Scale bar = 0.5 mm (a, b).

membranous connection just below the embolus (Figure 7(b)). Females can be recognized by having a thick, sclerotized, procurved anterior margin of the postepigastric scutum and two semicircular sclerotized ridges lying close to the lateral apodemes (Figures 6(b), 7(d)).

Description

Male. Body length: 1.92. Cephalothorax as in Figure 5(a), pars cephalica only slightly elevated (Figure 5(c)), surface of elevated portion of pars cephalica smooth, sides reticulate. Eyes; all eyes circular; ALE largest, PME subequal, ALE separated by less than

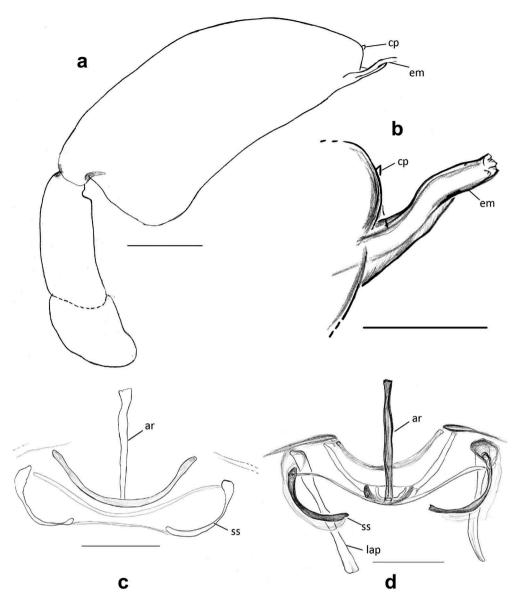


Figure 7. Aprusia vankhedei **n. sp.** from Udawattakele FR. Male: (a) left palp, prolateral view; (b) details of the distal part of the bulb. Female: (c) epigastric region, ventral view; (d) epigastric region, dorsal view. Abbreviations: ar, anterior receptaculum; cp, conical projection; em, embolus; lap, lateral apodemes; ss, semicircular ridges. Scale bars = 0.2 mm (a), 0.05 mm (b), 0.1 mm (c, d).

their radius, ALE-PLE separated by less than ALE radius, PME touching throughout most of their length, PLE-PME separate less than PME radius. Sternum longer than wide (Figure 5(b)), without radial furrows between coxae I–II, II–III, III–IV, surface smooth, with small hairs, continuous margin (see arrow in Figure 5(b)), anterior margin concave, posterior margin extending posteriorly of coxae IV, distance between coxae I–II, II–III approximately equal, but distance between coxae III–IV greater than them.

Abdomen as in Figure 5(e). Dorsal scutum sclerotized, pale orange, without colour pattern, covering about 3/4 of abdomen, more than 1/2 to most of abdomen width (Figure 5(e)), not fused to epigastric scutum. Postepigastric scutum sclerotized, pale orange, almost rectangular, covering about 3/4 of abdominal length, fused to epigastric scutum (Figure 5(f)). Two light brown patches located above the spinnerets (Figure 5(f)). Legs; strong spines on leg I and II present, leg I: femur, pv0–0–1–1–1–1; tibia, v2–2–2–2–0; metatarsus v2–2–0; leg II: femur, pv0–0–0–1–1; tibia v2–2–2–2–0; metatarsus, v2–2–0 claw like setae present on legs III and IV.

Genitalia. Sperm pore large, circular, situated at level of anterior spiracles (Figure 5(f)). Palp not strongly sclerotized femur two times as patella. Cymbium pale orange, completely fused with bulb, no seam visible, with distal patch of setae, distal part with a tiny conical projection (Figure 7(a)). Bulb stout, slightly tapering apically with small ventral concavity (Figure 7(a)), Embolus pale, slightly sinuous with membranous connection just below the embolus (Figure 7(b)). Conductor absent.

Female. Body length: 2.10. As in male except as noted. Palp claws and spines absent, tarsus smooth. Posterior spiracles connected by groove. Dorsal scutum covering 1/4 of abdomen (Figure 6(a)). Postepigastric scutum only around epigastric furrow, not fused to epigastric scutum (Figure 6(b)).

Genitalia. Ventral view: anterior margin of postepigastric scutum with a thick, procurved, sclerotized ridge (see arrow in Figure 6(b)); a bracket-shaped, sclerotized, semicircular ridge on either side of the procurved ridge. Dorsal view: long anterior receptaculum, with a narrow lumen and a slightly widened tip, bracket-shaped, semicircular sclerotized ridge on either side of the procurved ridge, posteriorly directed lateral apodemes; apparently without posterior receptaculum (Figure 7(c), 7(d)).

Etymology

Named for Dr Ganesh Vankhede (17 August 1951 to 1 July 2016), friend, professor of zoology and former president of the Indian Society of Arachnology.

Distribution

Udawattakele FR, Dunumadalawa FR (Figure 11)

Aprusia vestigator (Simon, 1893b) (Figures 8, 9; figs. 6–21, 64, 65 in Grismado et al. 2011)

Ischnothyreus vestigator Simon, 1893b: 302 Aprusia vestigator Grismado, Deeleman and Baehr, 2011: 7, figs. 6–21, 64–65.

Material examined

1 m c (IFS_Oon_090), Sri Lanka, Ritigala SNR, Kodigala Summit, 08°06'33"N 80°39'16"E, 716 m, 28 June 2011, S. P. Benjamin *et al.* litter; 1 m c (IFS_Oon_089), Padaviya, 08°48'0"N 80°45'0"E, 51 m, 10 January 2012, N. Athukorala, litter; 1 m c (IFS_Oon_240), Meemure, 07°25'51"N 80° 50'44"E, 636 m, 20 October 2014, leg. N. Athukorala, S. Ranasinghe and C. Clayton, litter; 1 m c (IFS_Oon_271), Ethagala, 07°28'17"N 80°22'30"E, 190 m, 8 April 2015, S. P. Benjamin *et al.*, litter. Deposited in ZFMK.

Diagnosis

Males can be recognized by the pale coloured, stout bulb, without tiny conical projection and the nearly straight embolus, without a conductor (Figure 9(a), 9(b), fig. 20 in Grismado et al. 2011). Females can be recognized by the long anterior receptaculum, rounded posterior receptaculum and semicircular ridges (fig. 21 in Grismado et al. 2011).

Results and discussion

Cladistic analysis

A phylogenetic analysis was performed to examine the inter-relationships of *Aprusia* species. The character matrix included 11 taxa. Ingroup taxa include: *A. kataragama, A. kerala, A. veddah, A. vestigator, A. koslandensis* n. sp., *A. rawanaellensis* n. sp. and *A. vankhedei* n. sp. As outgroup taxa four species that are morphologically similar to *Aprusia* were selected: *lschnothyreus peltifer* Simon 1892, *I. velox* Jackson 1908, *Camptoscaphiella simoni* Baehr and Ubick, 2010 and *C. fulva* di Caporiacco, 1934. Grismado *et al.*, 2011 notes the morphological similarly of *Camptoscaphiella* and *lschnothyreus* to *Aprusia*. Further, Sri Lankan *Aprusia* and *Camptoscaphiella* were added to the matrix of de Busschere et al. (2014) and reanalysed. In the recovered tree *Camptoscaphiella, lschnothyreus* and *Aprusia* formed a well-supported clade, further validating our selection of outgroups. The 49 characters that form the matrix are described below.

Characters and character states

Somatic morphology

- Ch 1: Carapace, shape, dorsal view. (0) oval (fig. 1 in Platnick et al. 2012), (1) broadly oval (Figures 1(a), 3(a), 5(a)).
- Ch 2: Carapace, pars cephalica, elevation in lateral view. (0) slightly elevated (Figure 5(c)), (1) strongly elevated (fig. 48 in Grismado et al. 2011).
- Ch 3: Carapace, sides, surface. (0) smooth (Figures 1(a), 3(a)), (1) finely reticulate (Figure 5 (c)), (2) strongly reticulate (fig. 336 in Baehr and Ubick 2010, see PBI website, https:// research.amnh.org/oonopidae).
- Ch 4: Carapace, lateral margin. (0) straight, rebordered, (1) undulate, rebordered (fig. 34 in Baehr and Ubick 2010), (2) straight, smooth (Figure 1(a), 3(a), 5(c)).
- Ch 5: Carapace, dark brown oval patches behind eyes. (0) absent, (1) present (fig. 76 in Platnick et al. 2012).
- Ch 6: Carapace, colour in alcohol. (0) yellow-brown (fig. 200 in Baehr and Ubick 2010, see PBI website), (1) olive green (fig. 88 in Platnick et al. 2012, see PBI website), (2) pale orange (Figures 1(a), 3(a), 5(a)).
- Ch 7: Carapace, eyes. (0) all eyes subequal (Figure 1(a)), (1) ALE largest, others subequal.
- Ch 8: Male chelicerae. (0) unmodified, (1) with large protuberance on the base of the fang (figs. 5–8, 83 in Platnick et al. 2012).
- Ch 9: Male endites, anterior-median part. (0) with strong tooth-like projection (fig. 9 in Platnick et al. 2012), (1) with brush-like scopula (brush-like setae in fig. 32 of Baehr and Ubick 2010), (2) smooth.

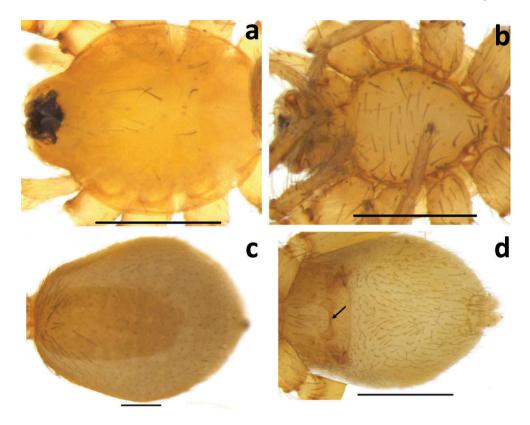


Figure 8. Aprusia vestigator (Simon, 1893b) female from Meemure. (a) carapace, dorsal view; (b) sternum, ventral view; (c) abdomen, dorsal view; (d) abdomen, ventral view. Scale bars = 0.5 mm (a, b, d), 0.2 mm (c).

- Ch 10: Sternum. (0) longer than wide (Figures 1(b), 3(b), 5(b)), (1) as long as wide (Figure 8(b), fig. 17 in Grismado et al. 2011).
- Ch 11: Sternum anterior margin. (0) straight, (1) curved (Figure 1(c)), (2) with continuous transverse groove (fig. 89 in Platnick et al. 2012).
- Ch 12: Sternum, radial furrows. (0) absent, (1) with radial furrows between coxae I–II, II–III, III–IV (fig. 37 in Baehr and Ubick 2010).
- Ch 13: Postepigastric scutum shape. (0) widely hexagonal in (fig. 217 in Baehr and Ubick 2010), (1) rectangular (Figures 3(b), 5(f)), (2) oval (fig. 7 in Grismado et al. 2011, see PBI website).
- Ch 14: Book lung covers, shape. (0) ovoid (fig. 337 in Baehr and Ubick 2010, see PBI website), (1) elliptical (Figures 3(b), 5(f)).
- Ch 15: Abdomen, patches anterior to the spinnerets. (0) absent, (1) present (Figures 3(b), 5(f)).
- Ch 16: Legs, spines on the prolateral side of femur I. (0) two, (1) three (figs. 24, 38, 46 in Grismado et al. 2011), (2) four (fig. 7 in Grismado et al. 2011, see PBI website).
- Ch 17: Legs, claw-like setae on leg III and IV. (0) absent (fig. 62 in Grismado et al. 2011), (1) present (figs. 64, 66 in Grismado et al. 2011).

- Ch 18: Dorsal scutum in males. (0) covering ½ of the abdomen (fig. 22 in Grismado et al. 2011), (1) covering ½ to ¾ of the abdomen (fig. 6 in Grismado et al. 2011), (2) covering more than ¾ of the abdomen (Figures 1(f), 5(e)).
- Ch 19: Postepigastric scutum in males. (0) covering about ½ of abdominal length (Figure 3(b)), (1) covering about ¾ of abdominal length.
- Ch 20: Postepigastric scutum in females. (0) covering less than ¼ of abdominal length (Figure 3(d)), (1) covering more than ¼ but less than ½ of abdominal length (Figure 6 (b)), (2) covering about ½ of abdominal length (fig. 14 in Grismado et al. 2011), (3) covering about ¾ of abdominal length.
- Ch 21: Postepigastric scutum, ventral view, ridges. (0) absent, (1) present (Figures 3(d), 6 (b), 8(d)).
- Ch 22: Pedicel tube. (0) unmodified, (1) ribbed (fig. 206 in Baehr and Ubick 2010).
- Ch 23: Spinneret scutum. (0) absent (Figures 3(a), 5(f), 6(b)), (1) present (fig. 126 in Platnick et al. 2012).

Male genitalia

- Ch 24: Sperm pore position, ventral view. (0) at level of anterior spiracles (Figure 3(b)), (1) between anterior and posterior spiracles (fig. 47 in Grismado et al. 2011, see PBI website).
- Ch 25: Sperm pore size. (0) small, oval (fig. 337 in Baehr and Ubick 2010), (1) large, triangular with rounded angles (figs. 15, 16 in Platnick et al. 2012), (2) large, circular (Figure 3(b)), (3) small, circular (fig. 23 in Grismado et al. 2011).
- Ch 26: Palp sclerotization. (0) slightly sclerotized, lightly coloured (figs. 11, 26, 50 in Grismado et al. 2011), (1) heavily sclerotized, black (fig. 85 in Platnick et al. 2012), (2) heavily sclerotized, dark-orange (fig. 340 in Baehr and Ubick 2010, see PBI website).
- Ch 27: Bulb, shape. (0) stout, gradually tapering apically, obtusely bent before apex (figs. 34, 35 in Platnick et al. 2012), (1) stout, tapering apically, with a ventral concavity (Figure 7(a)), (2) slender, elongated (Figures 2(a), 4(a)), (3) stout, tapering apically, bulged ventrally (fig. 163 in Baehr and Ubick 2010), (4) stout, tapering apically, inverted T-shaped projection (fig. 169 in Baehr and Ubick 2010), (5) stout, tapering apically, rounded gradually (fig. 108 in Platnick et al. 2012), (6) stout, elongated (fig. 53 in Grismado et al. 2011).
- Ch 28: Bulb, ventral protuberances. (0) absent, (1) present (fig. 36 in Platnick et al. 2012).
- Ch 29: Male palp, embolus, distal part. (0) tapering to end (fig. 43 in Grismado et al. 2011), (1) widened (fig. 161 in in Baehr and Ubick 2010), (2) slightly bifurcate (Figure 2 (b)), (3) with multiple complex processes (fig. 34 in Platnick et al. 2012), (4) narrow, long extension (fig. 108 in Platnick et al. 2012), (5) blunt (Figures 4(b), 7(b)).
- Ch 30: Male palp, embolus, shape (0) small, nearly straight (Figure 4(b)), (1) small, sinuous (Figure 2(b)), (2) bifurcate ventrally (fig. 161 in Baehr and Ubick 2010), (3) multiple process without prolateral excavation (fig. 85 in Platnick et al. 2012), (4) clearly delimited, with ventral T-shaped extension within translucent ventral flange; apex with long, narrow extension (fig. 108 in Platnick et al. 2012) (5) widened, without prolateral excavation (fig. 169 in Baehr and Ubick 2010).
- Ch 31: Male palp, conductor. (0) absent, (1) present (Figures 2(b), 4(b)).

- Ch 32: Male palp, conical projection. (0) absent, (1) present (Figures 4(b), 7(b)).
- Ch 33: Male palp, proximal segments colour. (0) white (see PBI website), (1) black (figs. 85, 108 in Platnick et al. 2012), (2) orange-brown (fig. 207 in Baehr and Ubick 2010, see PBI website), (3) pale orange (fig. 340 in Baehr and Ubick 2010, see PBI website), (4) pale yellow (Figure 3(a)).
- Ch 34: Palp, cymbium. (0) not fused to the bulb (figs. 161, 168 in Baehr and Ubick 2010), (1) fused to the bulb (Figures 2(a), 4(a)).
- Ch 35: Palp, cymbium length, dorsal view. (0) not extending beyond distal tip of bulb, (1) extending beyond distal tip of bulb.
- Ch 36: Male palp, cymbium, distal patch of setae. (0) absent, (1) present.
- Ch 37: Male palp, patella. (0) unmodified, (1) enlarged (figs. 161, 167 in Baehr and Ubick 2010).
- Ch 38: Male palp, tibia, trichobothria. (0) absent, (1) present.
- Ch 39: Male palp, trochanter, ventral projection. (0) absent, (1) present (fig. 108 in Platnick et al. 2012).

Female genitalia

- Ch 40: Anterior receptaculum. (0) absent, (1) present (Figures 2(c), 4(c), 7(c), 9(c)).
- Ch 41: Anterior receptaculum, length (0) short (Figure 2(c)), (1) long (Figures 4(c), 7(c), 9(c)).
- Ch 42: Anterior receptaculum, shape (0) T-shaped (fig. 95 in Platnick et al. 2012), (1) cylindrical with slightly widened tip (Figure 7(c)), (2) cylindrical without widened tip (Figure 2(c)), (3) cylindrical with tapering tip (Figure 4(c)).
- Ch 43: Semicircular ridges. (0) absent, (1) present (Figures 4(c), 7(c)).
- Ch 44: Posterior receptaculum. (0) absent, (1) present (Figure 4(c), figs. 21, 45 in Grismado et al. 2011).
- Ch 45: Posterior receptaculum, shape. (0) rounded (fig. 21 in Grismado et al. 2011), (1) triangular (fig. 45 in Grismado et al. 2011), (2) undulate (Figure 4(c)).
- Ch 46: Lateral apodemes, ventral view. (0) short, not or only slightly exceeding connecting groove of posterior spiracles (Figure 2(c)), (1) long, clearly exceeding connecting groove of posterior spiracles (Figure 9(c)).
- Ch 47: Shape of ridges. (0) boat-shaped transverse ridge (fig. 130 in Platnick et al. 2012), (1) single procurved line (Figure 3(d)), (2) double procurved lines (Figure 6(b)).
- Ch 48: External copulatory opening. (0) not visible (fig. 19 in Grismado et al. 2011), (1) narrow, slit-shaped (fig. 73 in Platnick et al. 2012)
- Ch 49: Posterior genitalic ducts. (0) absent, (1) squiggled (figs. 96, 126 in Platnick et al. 2012), (2) short, drop-shaped (fig. 182 in Baehr and Ubick 2010).

Heuristic searches in TNT under equal weights produced five most parsimonious trees (length = 108). Reanalysis of the same matrix under implied weights (K = 3–10) resulted a single most parsimonious tree (Figure 10; length (L) = 108, consistency index (CI) = 75, retention index (RI) = 63). This tree was identical in topology to one of the trees produced in the unweighted analysis. A monophyletic *Aprusia* was recovered. The two *Camptoscaphiella* species are resolved as sister species. Both

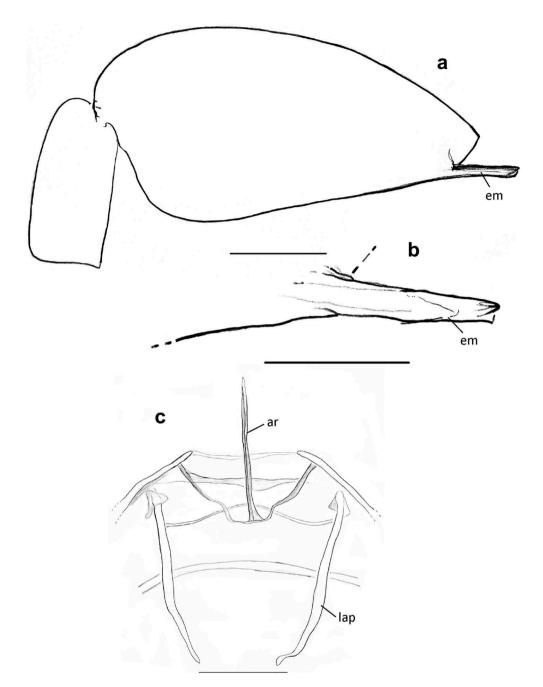


Figure 9. Aprusia vestigator (Simon, 1893b) from Ritigala SNR, Kodigala Summit. Male: (a) left palp, prolateral view; (b) details of the distal part of the bulb. Female from Meemure: (c) epigastric region, dorsal view. Abbreviations: ar, anterior receptaculum; em, embolus; lap, lateral apodemes. Scale bars = 0.1 mm (a, c), 0.05 mm (b).

genera shared eight unambiguous synapomorphies as resolved in the cladogram. These shared characters include: dark brown oval patches behind eyes (Ch 5, state 0), unmodified male chelicerae (Ch 8, state 0), straight sternum anterior margin (Ch 11,

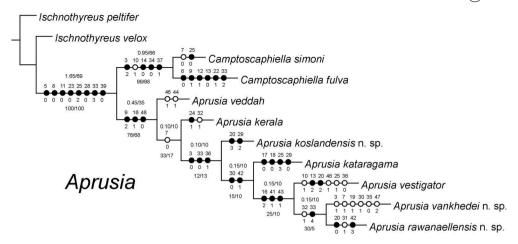


Figure 10. Phylogenetic tree of Aprusia spp. obtained by the analysis of 49 morphological characters under implied weights. The values above each node represent Bremer support/relative Bremer support, while the values below each node represent symmetric resampling frequencies/symmetric resampling frequency differences.

state 0), absence of spinneret scutum (Ch 23, state 0), large, circular sperm pore (Ch 25, state 2), absence of ventral protuberances on the bulb (Ch 28, state 0), proximal segments colour of male palp (Ch 33, state 3) and absence of ventral projection in trochanter (Ch 39, state 0). *Camptoscaphiella* species are characterized by carapace side surface (Ch 3, state 2), sternum as long as wide (Ch 10, state 1), ovoid book lung covers (Ch 14, state 0), fusion of cymbium with bulbus (Ch 34, state 0) and enlarged palpal patella (Ch 37, state 1).

The monophyly of *Aprusia* is well supported by three unambiguous synapomorphies: presence of smooth male endites (Ch 9, state 3), presence of two leg spines on the prolateral side on the femur I (Ch 16, state 1) and presence of copulatory opening (Ch 48, state 0). The first two characters might be plesiomorphic, as some female *Camptoscaphiella* and most *Ischnothyreus* have very strong spines in the same position (see figs. 260, 296 in Baehr and Ubick 2010; figs. 2c, 6c, 35a in Edward and Harvey 2014). However, the three characters taken together could be considered during diagnosis/ identification. Further, palpal sclerotization (Ch 26, state 0), fusion of cymbium with bulbus (Ch 34, state 1), presence of procurved ridge of the postepigastric scutum (Ch 47) and absence of posterior genitalic ducts (Ch 49, state 0) can also aid generic identification.

A. vankhedei n. sp. and A. rawanaellensis n. sp. are resolved as sister species by two synapomorphies: presence of conical projection (Ch 32, state 1) and proximal segments colour of male palp (Ch 33, state 4). Both species are sister to A. vestigator, forming a clade supported by three unambiguous synapomorphies: leg spination (Ch 16, state 2), length of anterior receptaculum (Ch 41, state 1) and presence of semicircular ridges (Ch 43, state 1). This clade is resolved as sister to A. kataragama with two unambiguous synapomorphies: embolus shape (Ch 30, state 0) and anterior receptaculum shape (Ch 42, state 1). Further, A. koslandensis n. sp. is sister to a clade consisting of A. kataragama + A. vestigator + A. vankhedei n. sp. + A. rawanaellensis n. sp. This clade is supported by smooth carapace sides (Ch 3, state 0), proximal

						-													, x	~									e									4				
Taxon\Character	1 2 3 4 5 6 7	56	2	∞	6	0	-	7	m	4	S	9	7 8	8	0	-	2	m	4	5	9	7	∞	6	0	-	3 S	4	S	9	7	∞	6	0	1	3	4	5	9	2	∞	6
Ischnothyreus peltifer	0 1 1 2	1	-	-	0	0	-	0	-	-	0	0	ļ_	[[0	0	-	0	-	-	0	-	m	- m			-	0	0	0	-	-	-	0	0	0	1	0	~`	-	–
Ischnothyreus velox	1 1 1 2 1 2 1	1 2	-	-	0	0	-	0	-	-	0	0	~.	-	-	-	0	-	0	-	-	ŝ	,	4	4	0	-	-	0	0	0	-	-	0	~:	~	0	1	0	0	~·	-
Camptoscaphiella simoni	1 0 2 1 0 2 0	0 2	0	0	0	-	0	0	-	0	0	0	~	2	~	~	0	0	0	0	7	4	0	,	5	0	3	0	0	0	-	~:	0	~.	~:	~`	ċ	~·	è.	~·	~·	~
Camptoscaphiella fulva		000	-	0	-	-	0	-	0	0	0	~:	~	0	-	0	-	0	0	2	2	m	0	-	2	0) 2	0	0	0	-	~:	0	0	~.	0 ~:	0	1	0	~·	-	2
Aprusia kataragama		0 2	0	0	2	0	0	0	-	-	0	-	0	0	-	-	0	0	0	m	0	2	0	0	0	0	0	-	-	-	0	~:	0	-	6	_	0	1	0	-	0	0
Aprusia veddah	10120210	0 2	-	0	2	0	0	0	-	-	0	-		نہ خ	-	-	0	0	<u>~</u> .	<u>~</u> .	~·	~·	~·	~:	~.	~	~	~-	~·	~·	<u>~</u> .	~:	~:	-	0	0	-	-	-	2	0	0
Aprusia vestigator		0 2	0	0	2	-	0	0	2	-	0	7	-	0	2	-	0	0	0	-	0	-	0	ŝ	0	0	0	-	-	0	0	~:	0	_	-	_	-	0	-	-	0	0
Aprusia vankhedei	1012021	0 2	-	0	2	0	0	0	-	-	-	7	-	2	-	-	0	0	0	2	0	-	0	S	-	0	4	-	0	-	0	-	0	_	-	_	0	1	0	2	0	0
Aprusia rawanaellensis	-	0 2	0	0	2	0	0	0	-	-	-	7	-	0	0	-	0	0	0	2	0	7	0	ŝ	0	-	4	-	-	-	0	-	0	_	- -	~	-	2	0	-	0	0
Aprusia koslandensis	-	0 2	0	0	2	0	0	0	-	-	-	-	-	2	~	-	0	0	0	2	0	7	0	2	-	-	0	-	-	-	0	-	0	-	0	0	0	1	0	-	0	0
Aprusia kerala	1 1 1 2 0 2 0	0 2	0	0	7	0	0	0	-	-	-	-	-	0	~ ~	~	0	0	-	7	0	9	0	5	, _	_	~ 	-	-	0	0	~:	0	~-	~	~.	÷	~·	~·	~·	~·	ć.
			ľ		١.		ľ	ŀ	ľ		ľ		1																													L

Table 1. Phylogenetic data matrix.

Notes: The first state is '0', followed by '1', etc.; '?' denotes missing data; - inapplicable.

segments colour of male palp (Ch 33, state 0) and presence of distal patch of setae on cymbium (Ch 36, state 1). *A. kerala*, a species from outside the island, retrieved as sister to a clade consisting of *A. koslandensis* n. sp. + *A. kataragama* + *A. vestigator* + *A. vankhedei* n. sp. + *A. rawanaellensis* n. sp. Further, *A. veddah* is sister to all six *Aprusia* species.

Male and female genitalia

All Aprusia species possess slightly sclerotized and light coloured palps with the bulb fused to the cymbium. The bulb of A. vestigator and A. vankhedei n. sp. is stout, tapering apically with a ventral concavity (Figures 7(a), 9(a), fig. 20 in Grismado et al. 2011), whereas A. kataragama, A. rawanaellensis n. sp. and A. koslandensis n. sp. have a slender, elongated bulb (Figures 2(a), 4(a), fig. 43 in Grismado et al. 2011) and A. kerala has a stout and elongated bulb (fig. 53 in Grismado et al. 2011). All of them are equipped with a tiny, slightly sclerotized embolus (Grismado et al. 2011). Aprusia kerala, A. vankhedei n. sp. and A. koslandensis n. sp. exhibit sinuous emboli (Figures 2(b), 7(b), fig. 55 in Grismado et al. 2011). However, A. vestigator, A. kataragama and A. rawanaellensis n. sp. bear nearly straight emboli (Figure 4(b), figs. 20, 43 in Grismado et al. 2011). The distal part of the embolus is slightly bifurcate in A. koslandensis n. sp. (Figure 2(b)), tapered in A. kataragama (fig. 43 in Grismado et al. 2011) and blunt in other species (Figures 4 (b), 7(b), 9(b)). The presence of a conductor and a conical projection are remarkable and variable among species: a conductor is present in A. kerala, A. rawanaellensis n. sp. and A. koslandensis n. sp. (Figures 2(b), 4(b), fig. 55 in Grismado et al. 2011), whereas a conical projection is present in A. kerala, A. vankhedei n. sp. and A. rawanaellensis n. sp. (Figure 4(b), 7(b), fig. 55 in Grismado et al. 2011).

In females the postepigastric scutum has a strongly procurved anterior margin (in ventral view). The margin is thicker in *A. veddah* and *A. vankhedei* n. sp. than in others (compare Figure 6(b) with Figures 3(d), 8(d)). An anterior receptaculum (ar) is present in all *Aprusia* species (Figures 2(c), 4(c), 7(d), 9(c)). However, the anterior receptaculum is short (shorter than the lateral apodeme; lap in Figure 2(c)) in *A. kataragama, A. veddah* and *A. koslandensis* n. sp., whereas it is relatively longer in *A. vestigator, A. vankhedei* n. sp. and *A. rawanaellensis* n. sp. Nevertheless, *A. vestigator, A. veddah* and *A. rawanaellensis* n. sp. bear a posterior receptaculum which is variable in size and shape (Figure 4 (c), figs. 21, 45 in Grismado et al. 2011).

Distribution pattern

To date, *Aprusia* has been reported only from Sri Lanka and India (fig. 67 in Grismado et al. 2011). Among the >100 localities sampled in Sri Lanka, *Aprusia* specimens were found at only 14 sites (Figure 11). *A. vankhedei* n. sp. was found from Udawattakele FR and Dunumadalawa FR, secondary forests located within the Kandy city. *A. rawanaellensis* n. sp. was collected from Rawana Ella and *A. koslandensis* n. sp. was found from a small forest patch between Koslanda and Beragala Namunukula and Bandarawela. *A. vestigator* which was previously reported from Kandy and Sinharaja FR, is now reported from Anuradhapura, Meemure and

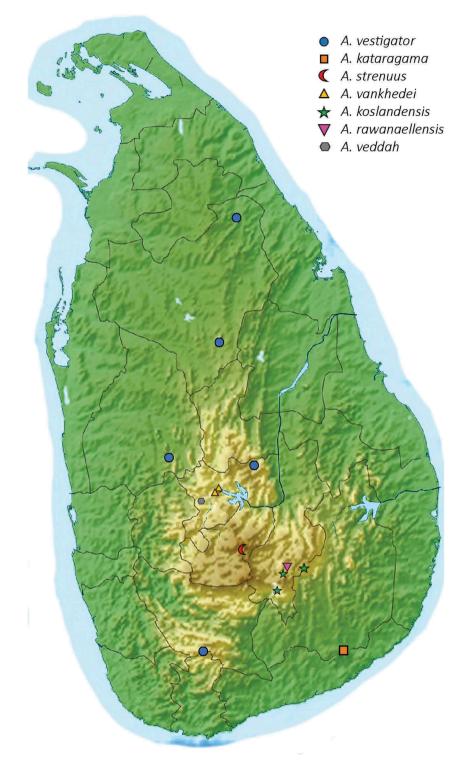


Figure 11. Map of Sri Lanka showing the known distribution of Aprusia. See text for details. ●A. vestigator, ■A. kataragama, 《A. strenuus, ▲A. vankhedei, ★A. koslandensis, ♥A. rawanaellensis, ●A. veddah.

Ethagala. Of the eight known species from the genus *Aprusia*, seven are now known from Sri Lanka. The three new species are endemic to forests in central highlands of the country.

Acknowledgements

We would like to thank N. Athukorala for assistance in the field and S. Batuwita, H. Sandamali, Z. Jaleel, C. Clayton, N. Kanesharatnam and I. Sandunika (all of NIFS) for collecting some of the described material. The Department of Wildlife Conservation and the Department of Forest Conservation of Sri Lanka provided permits for fieldwork. Thanks to S. Piyathissa for helping with the map. We are grateful to Dr Wouter Fannes, Mr Darrell Ubick and Dr Andrew Polaszek for reviewing this work for publication. The authors were funded by the National Institute of Fundamental Studies.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the National Institute of Fundamental Studies.

ORCID

Suresh P. Benjamin D http://orcid.org/0000-0003-4666-0330

References

- Álvarez-Padilla F, Hormiga G. 2008. A protocol for digesting internal soft tissues and mounting spiders for scanning electron microscopy. J Arachnology. 35:538–542.
- Baehr BC, Ubick D. 2010. A review of the Asian goblin spider genus *Camptoscaphiella* (Araneae: Oonopidae). Am Mus Novit. 3697:1–65.
- Bolzern A, Platnick NI. 2013. The Neotropical goblin spiders of the new genus *Varioonops* (Araneae, Oonopidae). Am Mus Novit. 3791:1–66.

Bremer K. 1994. Branch support and tree stability. Cladistics. 10:295–304.

- de Busschere C, Fannes W, Henrard A, Gaublomme E, Jocqué R, Baert L. 2014. Unravelling the goblin spiders puzzle: rDNA phylogeny of the family Oonopidae (Araneae). Arthropod Syst Phylogeny. 72(2):177–192.
- di Caporiacco L. 1934. Aracnidi dell'Himalaia e del Karakoram raccolti dalla Missione Italiana al Karakoram (1929-VII). Vol. 13. Genova: Memorie della Società Entomologica Italiana; p. 113–160.
- Edward KL, Harvey MS. 2014. Australian goblin spiders of the genus *lschnothyreus* (Araneae, Oonopidae). Bull Am Museum Nat Hist. 389:1–144.
- Fannes W, Jocqué R. 2008. Ultrastructure of *Antoonops*, a new, ant-mimicking genus of Afrotropical Oonopidae (Araneae) with complex internal genitalia. Am Mus Novit. 3614:1–30.
- Fitch WM. 1971. Towards defining the course of evolution: minimal change for a specific tree topology. Syst Zool. 20:406–416.
- Goloboff PA, Farris JS, Nixon KC. 2008. TNT, a free program for phylogenetic analysis. Cladistics. 24:774–786.

- Grismado CJ, Deeleman C, Baehr B. 2011. The goblin spider genus *Aprusia* Simon, 1893 (Araneae: Oonopidae). Am Mus Novit. 3706:1–21.
- Grismado CJ, Izquierdo MA, González MME, Ramírez MJ. 2015. The Amazonian goblin spiders of the new genus *Gradunguloonops* (Araneae: Oonopidae). Zootaxa. 3939:1–67.
- Jackson AR. 1908. On some rare arachnids captured during 1907. Trans Nat Hist Soc Northumberland (N.S.). 3:49–78.
- Maddison WP, Maddison DR. 2009. Mesquite: a modular system for evolutionary analysis. Version 2.72. http://mesquiteproject.org
- Nixon KC. 2002. WinClada. Ithaca (New York): Published by the author. http://www.cladistics.com/ about_winc.htm.
- Platnick NI, Berniker L, Kranz-Baltensperger Y. 2012. The goblin spider genus *lschnothyreus* (Araneae, Oonopidae) in the New World. Am Mus Novit. 3759:1–32.
- Ranasinghe UGSL, Benjamin SP. 2016a. A review of Sri Lankan *Brignolia* including the description of four new species (Araneae: Oonopidae). Zootaxa. 4144(4):451–476.
- Ranasinghe UGSL, Benjamin SP. 2016b. The goblin spider genus *Xestaspis* in Sri Lanka (Araneae: Oonopidae). Zootaxa. 4189(1):60–80.
- Ranasinghe UGSL, Benjamin SP. 2016c. New records of *Pelicinus* and *Xyphinus* from Sri Lanka (Araneae: Oonopidae). Indian J Arachnol. 5:71–78.
- Saaristo MI. 2002. New species and interesting new records of spiders from Seychelles (Arachnida, Araneaea [sic]). Phelsuma. 10(suppl. A):1–31.
- Simon E. 1890. Etudes arachnologiques. 22e Mémoire. XXXIV. Etude sur les arachnides de l'Yemen. Annales de la Société Entomologique de France. 10(6):77–124.
- Simon E. 1892. On the spiders of the island of St. Vincent. Part 1. Proc Zool Soc London. 59(4, for 1891):549–575.
- Simon E. 1893a. Histoire naturelle des araignées. Vol. 1. Paris: Roret; p. 257-488.
- Simon E. 1893b. Études arachnologiques. 25e Mémoire. XL. Descriptions d'espèces et de genres nouveaux de l'ordre des Araneae. Annales de la Société Entomologique de France. 62:299–330.
- Thoma M, Kranz-Baltensperger Y, Kropf C, Graber W, Nentwig W, Frick H. 2014. The new Southeast Asian goblin spider genus Aposphragisma (Araneae, Oonopidae): diversity and phylogeny. Zootaxa. 3798:1–86.
- World Spider Catalog. 2017. World spider catalog. version 18.5. Bern: Natural History Museum. [accessed 2017 Aug 3]. http://wsc.nmbe.ch.