J. Insect Biodivers. Syst. 11 (in press) *Paper in Press, Proofed, Available online 11 October, 2024* *https://jibs.modares.ac.ir*

OPEN ACCESS

Tarbiat Modares University Press | Research Article | ISSN: 2423-8112
Entomological Society of Iran | Phylogeny | https://zoobank.org/urn:lsid:zoobank.org:2FABAAD1-AA11-4BE6-81C3-99099E3111A4

Phylogenetic position and redescription of *Orchestina manicata* Simon, 1893 (Araneae: Oonopidae)

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ABSTRACT. The goblin spider *Orchestina manicata* Simon, 1893 (Araneae: Oonopidae) has remained taxonomically unrevised and has not been phylogenetically placed until now. In this study, *O. manicata* is redescribed based on newly collected specimens from Sri Lanka. The habitus and genital morphology of both males and females are illustrated and described, with photographs provided for the first time. *Orchestina manicata* is recognised by the embolus which has a triangular bifid tip and a swollen palpal tibia. The abdomen in males and females is rounded. Through a phylogenetic analysis of 51 morphological characters, combined with molecular data from two target genes (28S, 18S), we present the first hypothesis regarding the phylogenetic placement of this species within the genus.

Keywords: biodiversity, Ceylon, cladistics, conservation, morphology

Received: *April 05, 2024*
Accepted: *September 26, 2024*
Available online: *October 11, 2024*
Subject Editor: *Alireza Zamani*

Citation: Ranasinghe, S. & Benjamin, S.P. (2025) Phylogenetic position and redescription of *Orchestina manicata* Simon, 1893 (Araneae: Oonopidae). *Journal of Insect Biodiversity and Systematics*, 11 (in press).

INTRODUCTION

The Oonopidae Simon 1890, commonly known as goblin spiders, is a large family currently comprising 1,890 described extant species (WSC, 2024) of minute spiders, typically ranging from 1 to 2 mm in size. These spiders inhabit leaf litter and forest canopies worldwide. Despite their small size, they exhibit significant variation in carapace shape and ornamentation, eye arrangement and number, leg spination, copulatory structures, and the degree of body sclerotization. Body sclerotization ranges from soft-bodied taxa (i.e., lacking scuta) to heavily sclerotized taxa (armoured "loricati" with abdominal scuta) (Grismado et al., 2011; Eichenberger et al., 2012; Henrard & Jocqué, 2012; Baehr et al., 2013; Busschere et al., 2014; Brescovit et al., 2019; see also Platnick et al., 2011, 2012; Thoma et al., 2014; Izquierdo & Ramírez, 2017). It has been shown that most soft-bodied genera are more basal within the Oonopidae phylogeny and are thus hypothesized to be the most primitive oonopids (Busschere et al., 2014). Based on this observation, it has been postulated that a low degree of body sclerotization is a plesiomorphic trait, while a higher degree of body sclerotization is a derived characteristic within Oonopidae (Busschere et al., 2014).

Orchestina Simon, 1882 is an example of a species-rich soft-bodied goblin spider genus, currently including 162 species with a worldwide distribution (WCS, 2024). These spiders are canopy-dwelling jumpers, easily identified by their elongated and enlarged fourth femora (likely an adaptation for jumping), H-shaped eye arrangement, and enlarged male palpal tibia (Saaristo, 2001; Henrard & Jocqué, 2012). Based on extensive cladistic analysis by Henrard and Jocqué (2012), *Orchestina* species are classified into two groups: the *macrofoliata* group and the *probosciformis* group. The *probosciformis* group is characterized by the ovoid male carapace, which is clearly longer than wide, a labium that is larger medially, strongly modified and sclerotized endites with serrula, and a thicker embolus. In contrast, the

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macrofoliata group is mainly defined by the presence of modified, flattened, leaf-shaped labial setae in males. All species in the *macrofoliata* group possess a strongly enlarged palpal tibia, except for *O. saaristoi* Henrard & Jocqué, 2012 (*prosociformis* group).

Four *Orchestina* species were described from Sri Lanka over a century ago (Simon, 1893a): *O. dentifera* Simon, 1893, *O. pilifera* Dalmas, 1916, *O. tubifera* Simon, 1893, and *O. manicata* Simon, 1893. Since then, however, the *Orchestina* fauna of Sri Lanka has remained taxonomically unrevised and has never been phylogenetically studied. Here, we examine some recently collected *Orchestina* specimens from Sri Lanka, all identified as *O. manicata* based on available literature (Simon, 1893b; Dalmas, 1916; Saaristo, 2001; Henrard & Jocqué, 2012). As this species has not undergone a detailed description in over a century, we redescribe *O. manicata*, providing illustrations of habitus and copulatory organs, and investigate its phylogenetic placement for the first time.

MATERIAL AND METHODS

This study is based on a total of 26 specimens collected between 2010 and 2014. Fieldwork was conducted across all climatic regions of Sri Lanka (Koelmeyer, 1958), sampling over 100 sites throughout the island. However, *Orchestina* specimens were found only at seven localities in the central highlands. Spiders were collected by beating vegetation and through general hand collection. The specimens were preserved in either 70% or 100% ethanol. The collected specimens were examined using an Olympus SZX7 stereomicroscope and initially identified to the generic level. Species-level identification was conducted by examining drawings of male palps and female genitalia. Drawings and photographs followed the methodology described by Ranasinghe and Benjamin (2016a). All measurements are provided in millimeters, and leg measurements are given in the order of femur, patella, tibia, metatarsus, and tarsus. Voucher specimens are deposited at the National Institute of Fundamental Studies (NIFS).

Cladistic analysis. The character matrix used in the present study is the same matrix found in Henrard and Jocqué (2012) with 21 taxa (including the addition of *O. manicata* to the matrix) and 51 characters being assessed in total. Mesquite, version 3.04 (Maddison & Maddison, 2011) was used to construct and edit the character matrix. The analysis was carried out with TNT 1.1 (Goloboff et al., 2008) using implicit enumeration to find the most parsimonious trees. Bootstrap and Bremer's supports were calculated as measures of robustness.

Molecular analysis. Genomic DNA was extracted from 96% ethanol-preserved leg tissue using the DNeasy® Blood and Tissue Kit (Qiagen, Hilden, Germany) following the manufacturer's protocol from three selected specimens. Four promising primer pairs (18Sa2.0/9R (650 bp), 18S3F/18Sbi (850 bp) 18S1F/18S5R (820 bp) and 28SZX/28SC (1200 bp) for three overlapping regions of *18S* and a partial fragment of *28S* were selected for downstream application. The PCR protocol followed as in Busschere et al. (2014). Purified PCR products were Sanger sequenced in both directions by MACROGEN (Seoul, South Korea). Additional sequences of Oonopidae (n=20; [*Orchestina* n=16; outgroup n=4]) were obtained from GenBank; the total data set was assembled and aligned using Mesquite. Based on Busschere et al. (2014) we selected *Oonops placidus* Dalmas, 1916, *O. pulcher* Templeton, 1835 and *Tapinesthis inermis* (Simon, 1882) as outgroups. They are also compatible with the morphological matrix. Maximum likelihood (ML; Felsenstein, 1973) searches were performed in IQ-TREE version 1.6.12 (Nguyen et al., 2015) under the (GTR+F+I+G4) model of nucleotide substitution that was inferred as the best-fit model by ModelFinder (Kalyaanamoorthy et al., 2017). A total of 1000 ultrafast bootstrap (Hoang et al., 2018) replicates were performed to assess branch supports.

Abbreviations. *Institutional abbreviations:* NIFS, National Institute of Fundamental Studies, Kandy, Sri Lanka. *Character abbreviations:* ALE, anterior lateral eyes; ARe, anterior receptacle; AUS, anterior uterine sclerite; Ch, character; L, length; PLE, posterior lateral eyes; PME, posterior median eyes; Pp, posterior plate; Pr, lateral protrusion; W, width.

RESULTS

Cladistic analysis. We added *O. manicata* to the existing morphological matrix of 51 characters by Henrard and Jocqué (2012). The thus modified matrix analysed under implied weights, recovered four most parsimonious trees, each with a length (L) of 92. The strict consensus of these four trees is given in Figure 1. Bootstrap values (1000 replicates), Bremer support and relative Bremer support were calculated in TNT with implicit enumeration and are shown in Figure 1. Results verified that *O. manicata* belongs to the *prosbosciformis* group and is resolved as sister to other available members in the same group. As *O. manicata* showed key characters of the particular group such as an ovoid male carapace, clearly longer than wide, the labium larger in its median part strongly modified endites (with serrula) and sclerotized and thicker embolus. While a widened male endite base (Ch 23) and strongly enlarged palpal bulb (Ch 40) differentiated the species from other members of the group. However, *O. manicata* bears a strongly enlarged palpal tibia (Ch 38), which is also characteristic of the *macrofoliata* members. Both these species are in the *prosbosciformis* group, but not as sister-species.

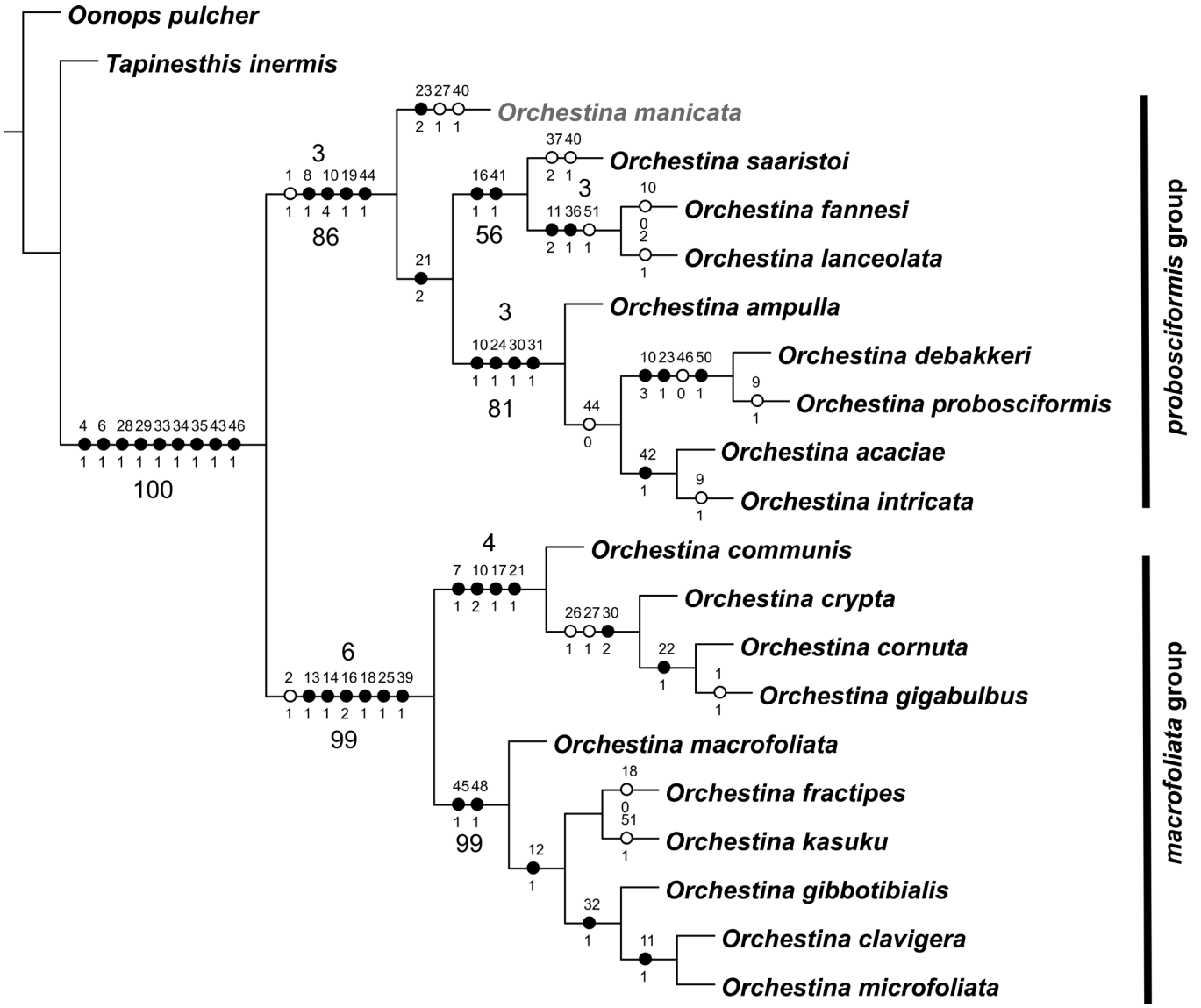

Figure 1. Phylogenetic placement of *O. manicata* obtained by the analysis of 51 morphological characters. The strict consensus of the 4 MPT trees found when the character matrix was analysed using implied weights (K=3 to 10). Unambiguous character state changes, Bremer support (values higher than 1; above branches) and bootstrap support are given (values above 40; below branches).

Molecular analysis. The genus *Orchestina* is represented in the combined *18S+28S* (2782bp) (*18S* (1582bp) +*28S* (1200bp) analysis by 19 specimens from different continents (Africa, Asia, and South America) (Busschere et al., 2014). Here we obtained contrasting results compared to the morphological analysis and previous results obtained by Busschere et al. (2014). In the phylogenetic tree (Fig. 2), the two main groups of *Orchestina* (*macrofoliata* and *probosciformis*) are not recovered as monophyletic. Instead, three distinct clades were recovered. Compared to the morphological tree the *macrofoliata* group formed two separate clades (clade 1 and clade 2). Clade 1 includes (*O. fractipes* Henrard & Jocqué, 2012, *O. macrofoliata* Henrard & Jocqué, 2012) from Congo and two *Orchestina* specimens from Singapore, clade 2 includes *O. crypta* Henrard & Jocqué, 2012, *O. communis* Henrard & Jocqué, 2012 from Congo and *O. cornuta* Henrard & Jocqué, 2012 from Cameroon. The *probosciformis* group can be visualized as three clades (clades 3, 4 and 5), which also included Sri Lankan *O. manicata* specimens in clade 4. South American specimens formed another distinct clade which is compatible with the previous study. Compared to the morphological tree, the latter clade belongs to the *probosciformis* group. Interestingly, the three Sri Lankan *O. manicata* specimens formed a well-supported clade with *O. saaristoi* as its sister species.

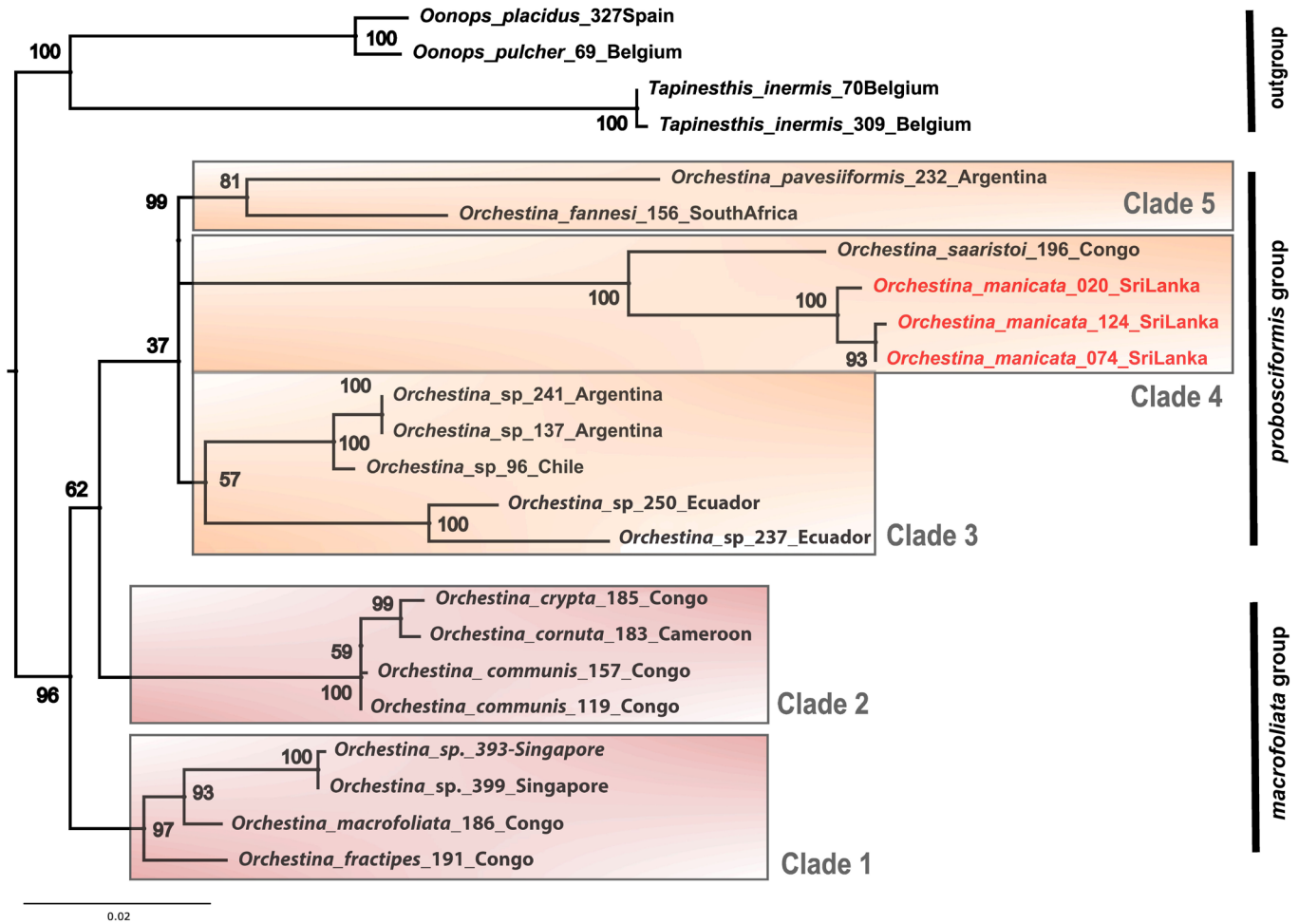

Figure 2. Phylogeny of *Orchestina* species based on the concatenated *28S* and *18S* sequence data (2782bp). Maximum likelihood tree with the best-fit model of nucleotide substitution (GTR+F+I+G4). *Oonops placidus* Dalmas, 1916, *O. pulcher* Templeton, 1835 and *Tapinesthis inermis* (Simon, 1882) as outgroups to root the tree. Bootstrap supports (%) >50 are shown next to the branches.

Taxonomy

Class Arachnida Lamarck, 1801

Order Araneae Clerck, 1757

Family Oonopidae Simon, 1890

Genus *Orchestina* Simon, 1882

Orchestina manicata Simon, 1893

Orchestina manicata Simon, 1893b:248. Lectotypes ♂, ♀. Sri Lanka: Kandy, Galle, Maturata, Nuwara-Eliya. – Muséum National d'Histoire Naturelle in Paris, France (MNHN); *Orchestina manicata* Dalmas, 1916:228, fig 20.

Material examined. 1♀ (IFS_Oon_002): Sri Lanka, Central Province, Kandy District, Deltota, Loolcondera, 07°08'5"N, 80°41'53"E, 1480 m, 11-V-2010, leg. S. Batuwita, N Athukorala; 1♂ (IFS_Oon_020): Loolcondera, 07°08′45"N, 80°41′53"E, 1480 m, 13-VII-2010, leg. S.P. Benjamin, S. Batuwita et al.; 1♀ (IFS_Oon_039): 30-VI-2011, leg. S.P. Benjamin; 1♀ (IFS_Oon_040): 30-V-2011, leg. S.P. Benjamin; 1♀ (IFS_Oon_029): Corbett's Gap, Knuckles range, 07°21'40"N, 80°50'00"E, 1360 m, 12-VIII-2010, leg. S.P. Benjamin, S. Batuwita; 2♂♂, 6♀♀ (IFS_Oon_074–075, 124–129): Nuwara Eliya District, Upcot, 06°046'N, 80°036'E, 14-II-2012, leg. S.P. Benjamin, N. Athukorala; 1♀ (IFS_Oon_145): Uva Province, Badulla District, Bandarawela, 6°50'59.5"N, 81°00'48.1"E, 1042 m, 31-XII-2011, leg. S.P. Benjamin et al.; 1♂, 2♀♀ (IFS_Oon_066–068): Ohiya, 06°50'32"N, 80°53'05"E, 26-V-2012, leg. S.P. Benjamin, N. Athukorala; 1♂, 8♀♀ (IFS_Oon_195–202, 206, Namunukulla peak, along Passara / Ella Road, 6°52'N 81°7'E, 1337 m, 22-I-2014, leg. S.P. Benjamin, N. Athukorala.

Diagnosis. Based on illustrations given in Dalmas (1916) the four Sri Lankan species differ as follows: the embolus is tapered in both *O. dentifera* and *O. pilifera* (Dalmas, 1916:figs 21, 22). However, the latter has a swollen, rounded palpal tibia (Dalmas, 1916:fig. 21). In females of *O. tubifera* the abdomen is a tube-like extension (hence its specific name; male unknown); see Dalmas (1916:fig. 26). In *O. manicata* the embolus has a triangular bifid tip (Fig. 3), palpal tibia is swollen, oval and the abdomen in males and females is rounded (Figs 3E, 3F). Further, in having a pyriform bulb, males of *O. manicata* are similar to those of *O. communis* and *O. cornuta*, but differ by having triangular bifid extensions in the embolus (Fig. 3D). The palpal tibia is twice as wide as femur, similar to that of *O. saaristoi*, but differs by the pyiform enlarged bulb. In having a bell-shaped pattern in the genital area, the females are similar to those of *O. saaristoi*, but differ by the stout, tube-shaped anterior uterine sclerite (AUS) with lateral protrusions (Pr) (Fig. 4B).

Re-description. — **Male**. Total length 1.04. Carapace L 0.44, W 0.36. *Cephalothorax*: Carapace light yellow, oval in dorsal view, pars cephalica slightly elevated in lateral view, anteriorly narrowed to 0.49 times at its maximum width or less, non-marginal pars cephalica setae absent at lateral side (Fig. 3A). Clypeus sloping forward in lateral view, very narrow in dorsal view. Eyes arrangement H-shaped, PMEs largest, squared; ALE-PLE touching, PLE-PME separated by less than PME radius (Fig. 3C). Sternum longer than wide, light-yellow, anterior margins curved, posterior margin extending posteriorly beyond anterior edges of coxae IV as single extension (Fig. 3D). *Mouthparts*: Chelicerae, endites and labium yellow. Chelicerae straight; retromargin with row of teeth. Labium anterior margin not indented at middle, spade-shaped, fused to sternum; slightly sclerotized, with strongly procurved, sclerotized posterior and lateral margins; anterior margin triangular ending in narrow with few setae. Endite serrula present in single row, anteromedian tip with one strong projection, much more heavily sclerotized than sternum. *Legs*: yellow; patella plus tibia I nearly as long as carapace. Legs aspinose. Length of leg segment: leg I: 1.32 (0.40, 0.08, 0.36, 0.28, 0.20); leg II: 1.32 (0.36, 0.08, 0.40, 0.32, 0.16). leg III: 1.06 (0.30, 0.06, 0.20, 0.30, 0.20); leg IV: 1.10 (0.30, 0.10, 0.28, 0.26, 0.16). Femur IV enlarged compared to femora of other legs. Abdomen: L 0.50, W 0.44, globular; dorsum soft portions pale white (Fig. 3E). Book lung covers small. Male palp as in Figure 4A; proximal segments pale yellow; femur not narrowed at base; patella attached to tibia basally; tibia 3 times as wide as femur; cymbium yellow, oval, tapered towards tip, setae densest on prolateral face; bulb pale-yellow, stout basally, pyriform with distal part leading to embolus gradually narrowed; embolus sclerotized, with triangular bifid extensions.

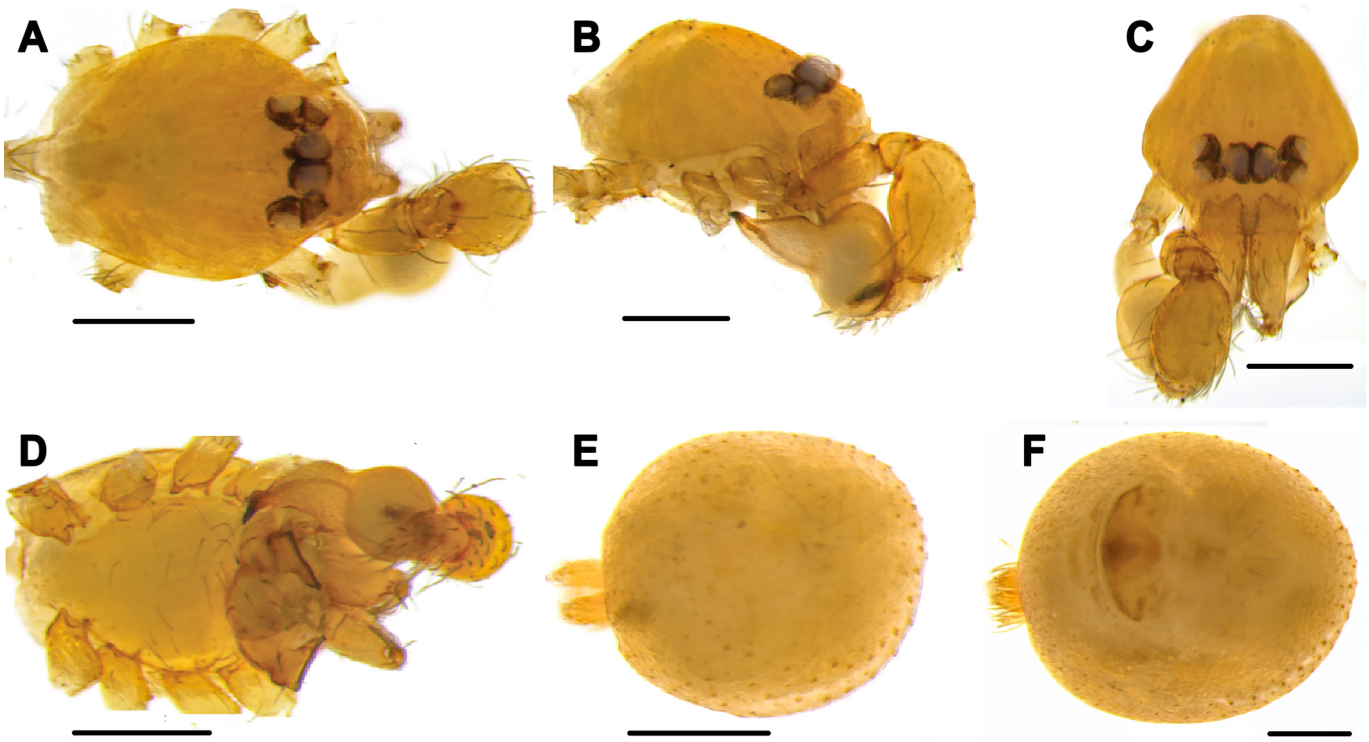

Figure 3. *Orchestina manicata* Simon, 1893, male (A–E) and female (F). **A.** Carapace, dorsal view; **B.** Carapace, lateral view; **C.** Carapace, anterior view; **D.** Sternum, ventral view; **E.** Abdomen, dorsal view; **F.** Abdomen, ventral view. Scale bars = 0.2 mm.

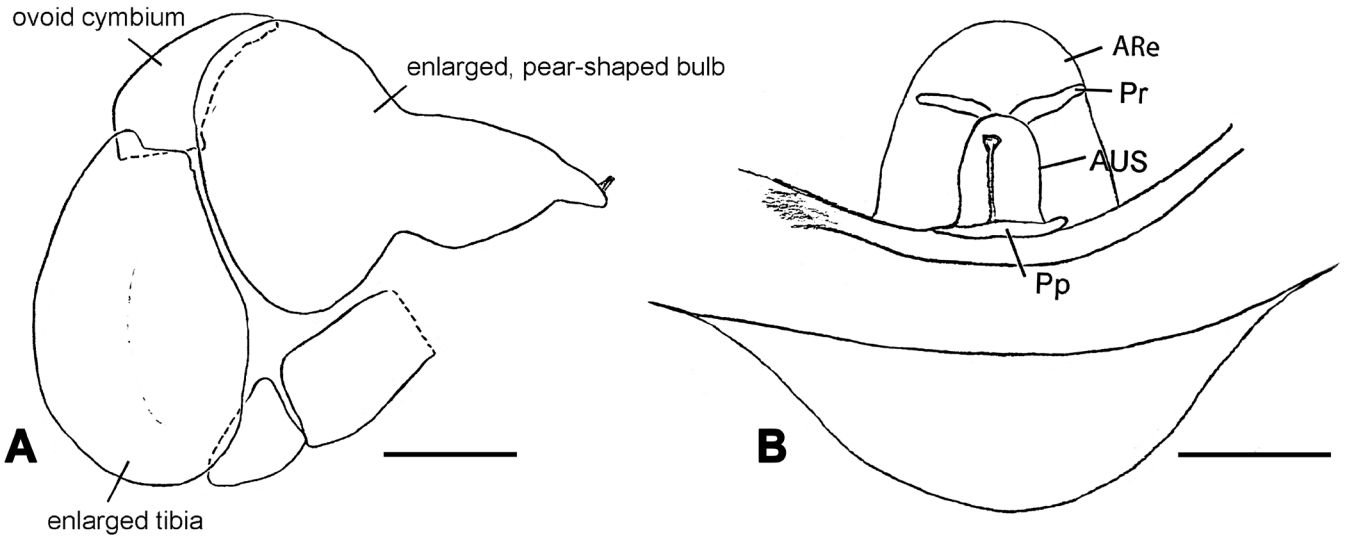

Figure 4. *Orchestina manicata* Simon, 1893. **A.** Male left palp, prolateral view; **B.** Female epigastric region, dorsal view. Are: anterior receptacle; AUS: anterior uterine sclerite; Pp: posterior plate; Pr: lateral protrusion. Scale bars = 0.1 mm.

Female. Total length 1.28. Carapace L 0.58, W 0.40. Other somatic characters as in males. Legs: Leg I: Total length 0.88. 0.28, 0.06, 0.12, 0.26, 0.16. Leg II: not measured. Leg III: Total length 1.20. 0.40, 0.10, 0.20, 0.32, Leg IV: Total length: 1.44. 0.44, 0.12, 0.32, 0.36, 0.20. Abdomen: L 0.70, W 0.68. Epigyne as in Figure 4B ventrally lightly sclerotized, ARe a bell-shaped structure, encloses AUS; dorsally ARe oval, without sclerotized pockets; AUS with lateral protrusions (Pr) well-developed, AUS stout, tubular, dark

anteriorly; Pr slightly curving laterally, close to apex of AUS; posterior plate (Pp) small, semicircular, anteriorly concave; dorsolateral extensions, sclerotized pockets, posterior receptacle absent (Fig. 4B).

Distribution. In Sri Lanka, *O. manicata* is known from the island's central montane wet evergreen forests: Badulla (663 m), Corbet's Gap (1360 m), Loolcondura (1480 m), Namunukula peak (1330 m), Nuwara Eliya (1887 m), Ohiya (1280 m) and Upcot (1199 m) (Fig. 5). Also reported from Vietnam (Dalmas, 1916). However, this conclusion was based on finding two female specimens from Vietnam in Simon's collection (Dalmas 1916). Females are difficult to be unambiguously assigned to species without studying their internal genitalia. Thus, we are doubtful of this record.

Remarks. It is noted that they are very common in the canopy of forest and savannah trees and tend to be very abundant in the crowns of trees (Fannes et al., 2008; Izquierdo & Ramírez, 2017).

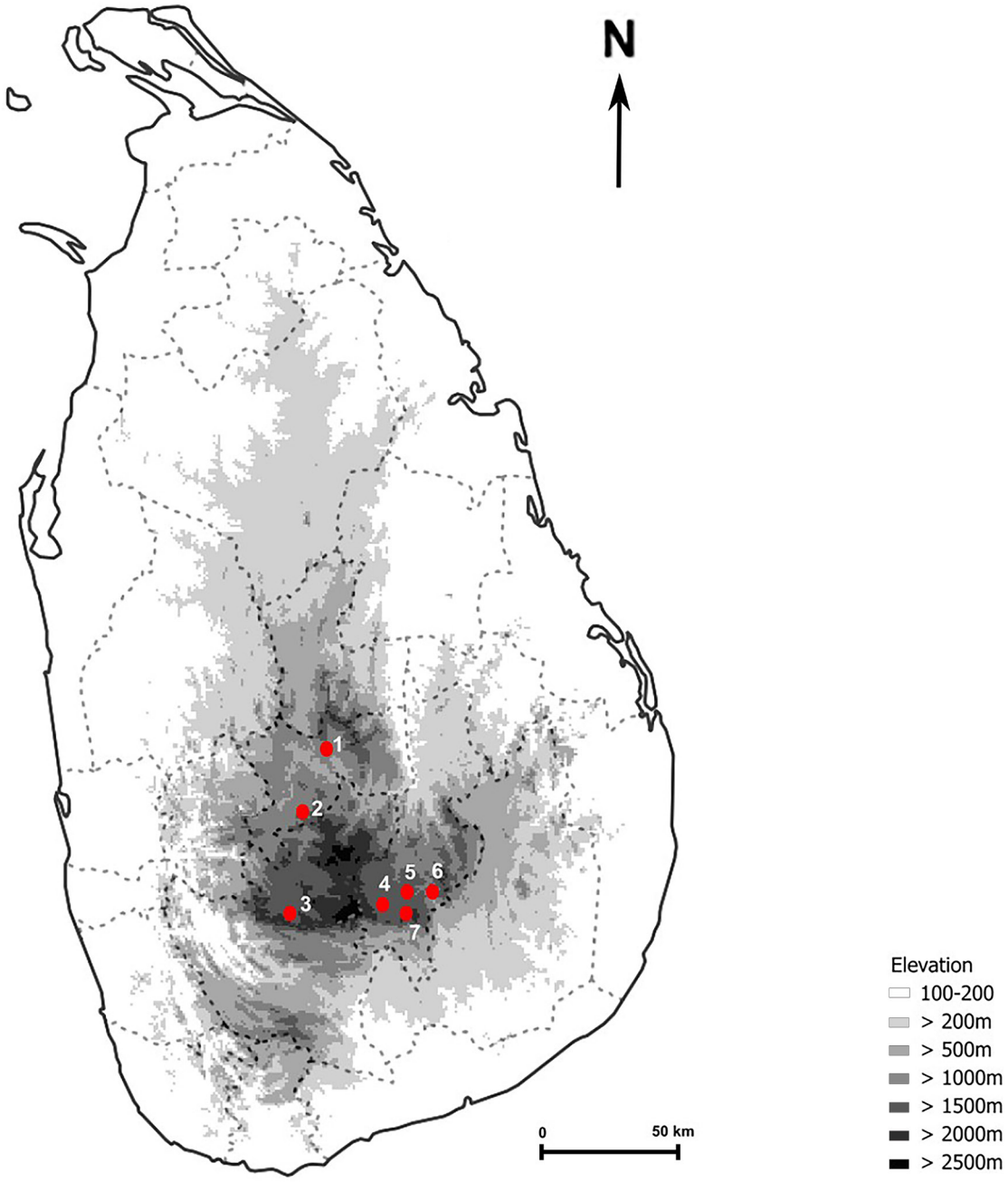

Figure 5. Distribution map of *Orchestina manicata* Simon, 1893 in Sri Lanka.

DISCUSSION

Among the thirteen genera of goblin spiders reported in Sri Lanka (Ranasinghe & Benjamin, 2016a, 2016b, 2016c, 2018a, 2018b), only *Orchestina* represents the soft-bodied group. Four species of the genus, *O. dentifera*, *O. pilifera*, *O. tubifera,* and *O. manicata*, have been reported from the island. As per the descriptions by Henrard and Jocqué (2012), the two species *O. dentifera* and *O. pilifera* share some features in common with *O. communis* Henrard & Jocqué, 2012 from Africa, which include the presence of a group of strong setae on the apical part of the chelicerae, the palpal conformation, a strongly swollen palpal tibia, a sub basal patella attachment to the tibia, a rounded cymbium and a pyriform bulb with a slender, tubular embolus (figs 115, 116 in Henrard & Jocqué, 2012). The third species, *O. tubifera*, is similar to *O. probosciformis* Henrard & Jocqué, 2012 and *O. debakkeri* Henrard & Jocqué, 2012, due to its long trunk-shaped extension of the abdomen (figs 537, 542 in Henrard & Jocqué, 2012; see also Izquierdo & Ramírez, 2017; Brescovit et al., 2019). The fourth species, *O. manicata*, was redescribed by Dalmas in 1916. It resembles *O. saaristoi* by the bifid extensions in the embolus (figs 573–605, 607 in Henrard & Jocqué, 2012). However, it differs from *O. saaristoi* by pyriform enlarged palpal bulb, oval carapace without net-shaped pattern. All our recently collected specimens possess above diagnostic characters and are thus, identified as *O. manicata*.

Our phylogenetic trees reconstructed with morphological and molecular data show different topologies. In particular, the division of *Orchestina* into two main groups (*macrofoliata* and *probosciformis*) is not supported by the molecular data. Compared to the morphological tree, the *macrofoliata* group now formed two separate clades (clades 1 and 2), whereas clades 1 and 2 represent the 'brown clade' and 'orange clade' respectively as shown in fig. 610 in Henrard and Jocqué, 2012. Clade 3 can be visualized as three sub-clades, which also include Sri Lankan *O. manicata* specimens. Therefore, our morphological analysis suggests that *O. manicata* belongs to the *probosciformis* group. Furthermore, our molecular analysis strongly supports the close relationship of *O. manicata* with *O. saaristoi*, as the latter specimens formed a well-supported branch that is sister to *O. manicata*. However, these relationships should be further tested with the addition of more taxa, target genes, and morphological character systems.

Of the more than 100 localities sampled in Sri Lanka, several goblin spider species were found exclusively in a few sites whilst others were found only in a single forest patch and were absent even in the immediate surrounding forests (see Ranasinghe & Benjamin, 2016a, 2016b, 2016c, 2018a, 2018b). Here, specimens of *O. manicata* were collected from seven localities, all from high-altitude forests. The number of collected specimens is low. However, this might not be due to its rarity but due to our sampling method, since most species of the genus are reported to be found in the forest canopy (Fannes et al., 2008).

AUTHOR'S CONTRIBUTION

The authors confirm their contribution to the paper as follows: S. Ranasinghe: formal analysis, methodology, writing the original draft, writing, review & editing. S.P. Benjamin: supervision, field work, validation, writing, review & editing the manuscript. The authors read and approved the final version of the manuscript.

FUNDING

This research received no specific grant from any funding agencies.

AVAILABILITY OF DATA AND MATERIAL

The specimens listed in this study are deposited at the National Institute of Fundamental Studies (NIFS) and are available from the curator, upon request.

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This study only arthropod material, and all required ethical guidelines for the treatment and use of animals were strictly adhered to in accordance with international, national, and institutional regulations. No human participants were involved in any studies conducted by the authors for this article.

CONSENT FOR PUBLICATION

Not applicable.

CONFLICT OF INTERESTS

The authors declare that there is no conflict of interest regarding the publication of this paper.

ACKNOWLEDGMENTS

We would like to thank N. Athukorala and S. Batuwita for assistance in the field. We are grateful to Arnaud Henrard for his comments on *Orchestina* via personal communications. We are grateful to an anonymous reviewer for reviewing and improving this manuscript for publication. The Department of Wildlife Conservation and the Department of Forest Conservation of Sri Lanka provided permits for fieldwork.

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موقعیت فیلوژنتیک و توصیف مجدد *Orchestina manicata* Simon, 1893 (Araneae: Oonopidae)

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| **تاریخ دریـافت:** ۱۷ فروردین ۱۴۰۳ | **تاریخ پذیرش:** ۰۵ مهر ۱۴۰۳ | **تاریخ انتشار:** در حال چاپ |

چکیـده: عنکبوت کوتوله، *Orchestina manicata* Simon, 1893 (Araneae: Oonopidae) تاکنون از نظر طبقه‌بندی مورد بازنگری قرار نگرفته و جایگاه فیلوژنتیکی آن مشخص نشده است. در این مطالعه، *O. manicata* بر اساس نمونه‌های تازه جمع‌آوری‌شده از سری‌لانکا مجددا توصیف شد. شکل ظاهری و ریخت‌شناسی اندام‌های زادآوری در هر دو جنس نر و ماده به تصویر کشیده و توصیف شده است و برای اولین بار تصاویر آن‌ها ارایه شد. عنکبوت *Orchestina manicata* بر اساس دارا بودن بالشک دو دندانه و ساق پالپ متورم متمایز می‌شود. شکم در نرها و ماده‌ها گرد است. بر اساس تحلیل فیلوژنتیک مبتنی بر ۵۱ ویژگی مورفولوژیک، همراه با داده‌های مولکولی از دو ژن هدف (28S و 16S)، اولین فرضیه را در مورد موقعیت فیلوژنتیک این گونه درون جنس *Orchestina* ارایه شد.

واژگـان کلیدی: تنوع زیستی، سیلان، کلادیستیک، حفاظت، مرفولوژی