

<https://doi.org/10.15517/rev.biol.trop..v72i1.61426>

A new type of nest in the genus *Quindina* (Opiliones: Nomoclastidae) with hypotheses about its origin and a new species for Colombia

Héctor Lancheros*¹;  <https://orcid.org/0000-0002-0632-5151>

Daniel Arias Cuellar¹;  <https://orcid.org/0000-0001-8486-6319>

Ricardo Pinto-da-Rocha²;  <https://orcid.org/0000-0002-3959-2205>

1. Programa de Biología, Universidad El Bosque, Bogotá, Colombia; lancheroshector@unbosque.edu.co (*Correspondence); dsarias@unbosque.edu.co
2. Departamento de Zoología/Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil; ricrocha@usp.br

Received 06-VIII-2024. Corrected 24-IX-2024. Accepted 27-IX-2024.

ABSTRACT

Introduction: Parental care is a phenomenon that has been recorded for several clades of the order Opiliones, but nest building has only been reported in the Neotropical genus *Quindina* Roewer, 1914 (Nomoclastidae).

Objective: To describe a new type of nest used in parental care by a new species of *Quindina* and determine its placement in the phylogenetic tree of the genus, to propose hypotheses about the origin of the two types of nests reported so far.

Methods: Specimens and nests were collected in La Calera, Cundinamarca, Colombia. Observations of parental care were made both in the field and in terrariums. A new species was described based on somatic characters and penis structure. A phylogenetic analysis was carried out, consensus methods with equal weights, implicit weighting, and successive weighting were used.

Results: We describe a new case of parental care with a new type of disc-shaped nest, which we call “pendular disc nest”. The nest is built by males of *Quindina pendula* sp. nov.; this species can be recognized externally by the absence of white spots, the presence of a mushroom-shaped set of patches in the middle part of the prosoma, and the presence of a dark yellow background around most of the tubercles. Results of the phylogenetic analysis showed *Q. pendula* sp. nov. is sister to all *Quindina* species except *Quindina marginata*. Based on the tree, obtained by successive weighting, seven phylogenetic hypotheses, related to the possible origin of the two types of nests recorded in the genus *Quindina*, were proposed.

Conclusions: This study presents a new case of egg guarding and the building of nests in arthropods, which is not very common in nature.

Key words: Nomoclastinae; egg guarding; paternal care; pendular disc nest; open mud nest; Andean Forest.

RESUMEN

Un nuevo tipo de nido en el género *Quindina* (Opiliones: Nomoclastidae) con hipótesis sobre su origen y una nueva especie para Colombia

Introducción: El cuidado parental es un fenómeno que se ha registrado para varios clados del orden Opiliones, pero la construcción de nidos solo se ha reportado en el género neotropical *Quindina* Roewer, 1914 (Nomoclastidae).

Objetivo: Describir un nuevo tipo de nido utilizado en el cuidado parental, por una nueva especie de *Quindina*, y determinar su ubicación en el árbol filogenético del género, con el fin de proponer hipótesis sobre el origen de los dos tipos de nidos reportados hasta el momento.



Métodos: Los especímenes y nidos fueron recolectados en La Calera, Cundinamarca, Colombia. Se observó el cuidado parental, en el campo y en terrarios, de una nueva especie descrita con base en caracteres somáticos y en la estructura del pene. Se realizó un análisis filogenético, se utilizaron métodos de consenso con pesos iguales, ponderación implícita y ponderación sucesiva.

Resultados: Describimos un nuevo caso de cuidado parental con un nuevo tipo de nido, denominado “nido disco pendular”, el cual es construido por machos de *Quindina pendula* sp. nov.; esta especie se reconoce externamente por la ausencia de manchas blancas, la presencia de un conjunto de manchas en forma de champiñón en la parte media del prosoma y la presencia de un fondo amarillo alrededor de los tubérculos. Los resultados del análisis filogenético mostraron a *Q. pendula* sp. nov. como hermana de todas las especies de *Quindina*, excepto *Quindina marginata*. Con base en el árbol obtenido, por ponderación sucesiva, se propusieron siete hipótesis filogenéticas, relacionadas con el origen de los dos tipos de nidos registrados.

Conclusiones: Este estudio presenta un nuevo caso de protección de los huevos para el género *Quindina*, que implica la construcción de nidos en artrópodos, lo cual es poco común en la naturaleza.

Palabras clave: Nomoclastinae; protección de huevos; cuidado paterno; nido disco pendular, nido abierto de barro; bosque andino.

INTRODUCTION

Nomoclastidae Roewer, 1943, is a family of Neotropical species of harvestmen distributed from Costa Rica to Northern Brazil, it includes the subfamilies Zamorinae Kury, 1997 and Nomoclastinae Roewer, 1943, the first including the monotypic genus *Zamora* Roewer, 1927 and the second comprising the genera *Callcosma* Roewer, 1932, *Globitarsus* Roewer, 1913, *Kichua* Pinto & Bragagnolo, 2015, *Liomma* Roewer, 1959, *Lisarea* Roewer, 1943, *Meridanatus* Roewer, 1943, *Micropachylus* Roewer, 1913, *Napostygnus* Roewer, 1929, *Nomoclastes* Soerensen, 1932, *Quindina* Roewer, 1914 and *Troya* Roewer, 1914 (Kury et al., 2024; Kury & Villarreal, 2015; Pinto-da-Rocha & Bragagnolo, 2017; Villarreal & Kury, 2023). The family is defined by the following characters: no sexual dimorphism in its chelicerae and pedipalps (except *Liomma*); low, elliptical ocularium, with a median depression; ventral plate of the penis sub-rectangular to trapezoidal in shape; no lamellar setae on the ventrodorsal margin of the ventral plate; short, stout stylus with a rounded head, mounted on a long, columnar glans; glans without processes except in *Napostygnus* (Pinzón-Morales & Pinto-da-Rocha, 2020). Nomoclastidae currently includes 12 genera (8 monotypic) and 29 species, including the one herein described (Kury et al., 2024;

Pinto-da-Rocha & Bragagnolo, 2017; Pinzón-Morales & Pinto-da-Rocha, 2020; Villarreal & Kury, 2023).

The genus *Quindina*: *Quindina* is characterized by a type of body armor similar to that of *Callcosma* and *Kichua*, with a pair of long spines on area III and free tergites with a pair of spines each. It differs from other genera of the family by most species having a row of tall tubercles separated from each other on the lateral margins of dorsal scutum, very elongated tubercles on area III of dorsal scutum, absence of lateral margin elevation, and the presence of an apical prodorsal projection on femur IV (Pinto-da-Rocha & Bragagnolo, 2017; Pinzón-Morales & Pinto-da-Rocha, 2020). It is distributed in Costa Rica, Panama, Colombia and Ecuador. Eleven species had previously been described in this genus, four of which from Colombia: *Q. bella* Roewer, 1914 (type species) and *Q. marginata* (Roewer, 1963), from the Andean region; *Q. discolor* Pinzón-M. & Pinto-da-Rocha, 2020 and *Q. hermesi* Pinzón-M. & Pinto-da-Rocha, 2020, from the Caribbean region (Pinto-da-Rocha & Bragagnolo, 2017; Pinzón-Morales & Pinto-da-Rocha, 2020).

Parental care and nest building: Exclusive paternal care evolved independently in fifteen arthropod lineages, which include

approximately 1 500 species. This is a very small fraction of the diversity of this group (with more than 1.2 million species), making it probably the rarest form of postzygotic parental care investment (Requena et al., 2014). Egg guarding behavior is observed in most orders of the class Arachnida, but paternal investment in postzygotic care is restricted to members of the order Opiliones. For example, in Gonyleptidae, adult males of *Ampheres leucopheus* (Mello-Leitão, 1922) protect batches of eggs, attached by a mucous substance to the underside of leaves, and newly hatched nymphs (Hara et al., 2003). Three species of Progonyleptoidellinae Soares & Soares, 1985 show a similar behavior, with eggs being laid on the underside of leaves, covered by a thick mucous layer, while two species of Gonyleptinae Sundevall, 1833 lay eggs in natural cavities, in trunks or on the ground. In all these cases, eggs can be found in different stages of development with males taking care of them (Machado et al., 2004). Maternal care is also present in the order Opiliones and has been reported for at least five families of the suborder Laniatores Thorell, 1876. There are cases of maternal care in which females care for eggs in cavities and leaves or for example, two species of Cranidae, belonging to the genus *Phareicranaus* Roewer, 1913, have females that protect groups of eggs in cavities found between the roots of trees. The same type of behavior has been observed in females of the Gonyleptidae subfamily Goniosomatinae (Machado & Warfel, 2006).

The aforementioned cases imply paternal or maternal care of the eggs in surfaces or cavities, but without the construction of complex structures to protect the eggs. Rodríguez and Guerrero (1976) provided the first description of harvestmen nests for *Quindina albomarginis* (Chamberlin, 1925). The authors indicated that the construction of each nest corresponded to a single male, and that the material used came from the outer bark or outer bark remains of the trunk on which it was built, or from logs and debris from the vicinity. Mora (1990) complemented these observations and indicated that, for the construction, the males use bark

removed with the chelicerae and mixed with mud collected from the crevices of the trunk. She also noted that material could be collected from the forest floor, combined with salivary secretions and later applied on the substrate to assemble the nest, with a mud wall then applied to the edges, with an average nest diameter of 33 mm and an average nest wall height of 8.3 mm. Pinto-da-Rocha and Bragagnolo (2017) described four species of *Quindina* from Panama, three with the same type of nest (*Q. morae* Pinto-da-Rocha & Bragagnolo, 2017, *Q. burbayar* Pinto-da-Rocha & Bragagnolo, 2017 and *Q. kuna* Pinto-da-Rocha & Bragagnolo, 2017), which they called “open mud nest” or “reproductive arena”. Quesada-Hildalgo et al. (2019) and Rojas et al. (2019) also reported this type of nest for *Q. limbata* (Roewer, 1943) in Costa Rica, calling it “mud-nest” or “cup-like mud nest”.

Our aim in this study is to describe a new species of the genus *Quindina*, which builds a new type of nest. In addition, we strive to determine the position of the species in the phylogenetic tree of its respective genus and hypothesize about the origins for the two nest types recorded in this group.

MATERIALS AND METHODS

Collection and conservation of specimens: We collected the male specimens in the vereda Mundo Nuevo and females in the vereda El Líbano, in the municipality of La Calera, Cundinamarca, Colombia. The specimens were gathered at the site where the nests were found, by direct observation of the tree branches, the underside of trunks and the interior of an abandoned hut. After locating the nests, we waited until nightfall to collect the male individuals coming back to the nests. Two male individuals were fixed in 70 % ethanol; two others were transported alive, in order to observe their nest building in terrariums. Females were collected under logs and rocks near a road in the vereda El Líbano. The two female specimens collected were fixed in 70 % ethanol. All specimens were



deposited in the collection of the “Museo de Ciencias de la Universidad El Bosque (MCUB)”.

Measurement and description of the specimens: We observed the general characters of the body and appendages under a stereoscope, with magnifications of 10-180X. The penis was observed under an optical microscope, with magnifications of 400X and 1 000X. In both cases, photographs were taken with a digital camera attached to one of the eyepieces. In the photographs taken from the stereoscope, a millimeter scale was included. In the microscope photographs, dimensions were calculated using the millimeter scale recorded at 4X magnification. These scales were used to measure the parts with ImageJ software (Rueden et al., 2017).

All measurements are given in millimeters. Illustrations were made with LibreOffice Draw (The Document Foundation, 2022) and Gimp software (Kimball et al., 2022). The delineation of the parts was drawn following the contour of the digital photographs. Descriptions and terminology follow the ones proposed by Pinto-da-Rocha and Bragagnolo (2017) and Pinzón-Morales and Pinto-da-Rocha (2020). Description of genitalia follows the findings of Kury and Villarreal (2015) and Kury (2016). Indications for nomenclature of the structures, measurements and relative positions of structures, follow Acosta et al. (2007).

Distribution records: At the type locality (vereda Mundo Nuevo, municipality of La Calera) a photographic record of the vegetation type was taken using a drone. The collection records of the type specimens was complemented by previous observations made by Héctor Lancheros in the rural area of the Bogotá, Capital District, and other new records made in the municipalities of Choachí (Department of Cundinamarca), Saboyá (Department of Boyacá) and Une (Department of Cundinamarca), by biologists Daniel Arias Cuellar, Christian Franco García and Osvaldo Villarreal, respectively. The distribution map was assembled using QGIS software (QGIS.org, 2021), based

on the coordinates recorded with Viking software (Battaglia et al., 2021).

Description of the nests: The fresh weight of twelve nests was recorded in the field, using an electronic scale with 3-digit precision. Length and width dimensions for each one were measured using ImageJ software (Rueden et al. 2017), based on photographs taken on the scale plate, using its diameter as a point of reference. Thickness was recorded using a digital caliper. The dry weight of eight nests was recorded after drying them in a hot air circulation oven at 30 °C. Four nests were used for behavioral observations in the laboratory, where we paid special attention to the care provided by adult males and egg development and hatching. These four nests were also used to analyze the materials that compose them. In each nest, the type of plant material from which it hung was identified. The remains of liverworts present in nests were identified down to genus level.

Observations of parental care and development: The first observations of parental care were made directly in the field, from the beginning of the day until the early evening hours (from 18:00 to 20:30). For observations under controlled conditions in the laboratory, two terrariums were prepared, each containing a section of branch from which hung a nest in a plastic box, with the respective adult male. Observations were made in each terrarium for two weeks. For developmental observations (i.e. changes in egg coloration, hatching and nymph development), two complementary set-ups were made on absorbent paper in Petri dishes, each with only one nest. Observations for each petri dish lasted between 20 days and one month, until hatching ceased. Adults and nymphs were fed using cooked rice with peas and carrots, cooked spaghetti and dead fruit flies, in both terrariums and petri dishes.

Phylogenetic analysis: The matrix used for the phylogenetic analysis was originally published by Kury and Villarreal (2015), including 77 morphological characters and 38 taxa

(26 from the clade Laminata). It was later modified by Pinto-da-Rocha and Bragagnolo (2017) who added 13 species in Nomoclastidae, adjusted the coding of characters 11 and 12, and added 16 new characters (78 to 93), two of which originated from the subdivision of the original character 13 (characters 78 and 82). To this, Pinzón-Morales and Pinto-da-Rocha (2020) added two new species of the genus *Quindina*. With the addition of the new species, the matrix now comprises 93 characters and 54 taxa (Table 1), all belonging to the suborder Laniatores. The taxa comprise 48 species of the superfamily Gonyleptoidea (infraorder Grassatores), of which 42 belong to the clade Laminata, which is divided into 20 species of Nomoclastidae and 22 of Microsetata. Outgroups comprise five species from three other superfamilies of the infraorder Grassatores (Samooidea, Epedanoidea and Assamioidea) and the root is one species from the superfamily Triaenonychoidea of the infraorder Insidiatores (the latter is the first outgroup) (Kury & Villarreal, 2015). The description of the characters can be found in Pinzón-Morales and Pinto-da-Rocha (2020). Species of the most recently added genera to Nomoclastidae (*Globitarsus*, *Liomma*, *Lisarea*, *Meridanatus*, *Micropachylus* and *Troya*) were not included due to lack of reproductive data and several morphological data for matrix. The parsimony analysis was carried out using the software TNT v.1.5 (Goloboff & Catalano, 2016). The heuristic method (“traditional search”) was applied with the tree bisection-reconnection (TBR) option with equal weights. From the trees with maximum parsimony, two cladograms were obtained, one using the strict Nielsen consensus method and another using majority consensus, with 50 % cutoff. Subsequently, the implicit weighting method was applied, which decreases the weight value of homoplastic characters in the analysis based on a concavity constant (k), the value of this constant is negatively related to the decrease in the weight of these characters in the analysis (Goloboff, 1993). To obtain the “optimal” value of the constant k for our data set, the TNT script setk.run was used (Goloboff et al., 2008; Villarreal &

García, 2021). Finally, the successive weighting method was applied with the rescaled consistency index rc (Farris, 1989), using the script rew.t.run. The latter is a technique that decreases the weight of homoplastic characters after obtaining a cladogram and repeats the process until successively equal trees are obtained (Farris, 1969). Relative Bremer supports were calculated for the trees obtained with the four methods, which provide an approximate measure of the amount of favorable/contradictory evidence for each group (Giribet, 2003; Goloboff & Farris, 2001), and the tree with the highest support values was chosen. Sensitivity plots (Navajo rugs) were used to compare the coincidence of the groups obtained with the different methods and hypotheses.

Hypotheses of the origin of the nests: To propose hypotheses of origin of the nests, the most parsimonious reconstructions method was used (Goloboff, 2022, Chapter 3), with the TNT Characters/Reconstructions option in the optimize menu. For this, the genus *Quindina* section of the chosen tree was used, with an external group and the character nest presence with three unordered states: 0 = absent, 1 = pendular disc nest, 2 = open mud nest, ? = nest construction unknown. The reconstructions obtained were stored in the display buffer. The frequency with which each nest type occurred in a reference group (each group is one of the main clades that make up the genus *Quindina*) was tabulated for each possible “condition” (ancestral, derived or in an internal group). The combination of each nest type with the reference group was called “characteristic”, and for each characteristic, the condition with the highest frequency was listed. This is an illustrative method to indicate the possible nodes of origin of each nest type, as unknown data for most species of *Quindina* does not allow for making a complete reconstruction of the evolution of the nest type and its origin.

All figures (illustrations, map, photographs and cladograms) were diagrammed using LibreOffice Draw graphics editing software (The Document Foundation, 2022).



Table 1
Data matrix (93 characters, 54 taxa) used for the phylogenetic analysis of Nomoclastidae.

Species	Characters												
	0000000000	1111111111	2222222222	3333333333	4444444444	5555555555	6666666666	7777777777	8888888888	999			
<i>Acumonia succinea</i>	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	012			
<i>Stygonomma fultrimanni</i>	0000000000	2-0?000000	0200000200	0000000000	0300-0000-	000000-000	00-0-----	-?-000000	0000000000	0??			
<i>Santobius annulipes</i>	000-100000	2-0?100100	0010000?00	0000000010	1001-0000-	0000000-000	00-0-----	-?-010000	0000000000	0??			
<i>Pungica simoni</i>	3101001000	000?001002	01?0100000	0010000012	1001-0000-	0002000000	00-0-00010	-?-0110??	?0?0?0?0?0?	???			
<i>Dibunus similis</i>	810-100100	0200100000	1200000100	0010000010	1001-0000-	0002000000	00-0100001	00-01100??	?0?0?0?0?0?	???			
<i>Sorensenius pygmaeus</i>	5100000000	000?000000	12?0000000	0010200010	1001-0000-	0002000000	00-0150010	00001110??	?0?0?0?0?0?	???			
<i>Paramitraceras granulatum</i>	5000000000	020?200000	12?0000200	0-10210010	1001-0000-	0002000000	00-0100025	300011?000	0000000000	0??			
<i>Globibunus rubrofemoratus</i>	1100001000	0001000003	1200000001	0010010110	1102-00000	0201000000	00-01000--	300011?000	0000000000	000			
<i>Ricstygnum quineti</i>	511-101100	020?200000	0020000100	0002111111	1102-00000	0101000000	00-010001?	1301111000	0000000000	0??			
<i>Stenostygnellus macrochelis</i>	101-101100	030?200000	0020000100	1002111111	1102-00000	0001000000	00-0100020	1000111000	0000000000	000			
<i>Taquaara bicoloripes</i>	6100010000	0000001000	0300100000	1010010110	1102-00000	0021000000	00-0100020	110011?000	0000000000	000			
<i>Gerdésius mapinguari</i>	6100010000	0301001000	0000000000	1012210111	1102-00000	0001000000	1100100022	?00111?000	0000000000	000			
<i>Cajamarca affinis</i>	2101001100	000?000000	1200000001	1000010110	1203000210	0101010110	10-0040025	141111?000	0000000000	0??			
<i>Chacoikeontius clavifemur</i>	3101001100	130?000000	1200000001	1000010110	1203000210	0101010110	10-0040025	141111?000	0000000000	0??			
<i>Incasarcus dianae</i>	2101011100	1001000000	1200000201	0010010110	1203000210	0001010110	1131040025	141111?000	0000000000	0??			
<i>Toito juruensis</i>	3101002000	2-00011011	0121010401	1012010111	1203000200	0101000210	1122040025	1411111000	0000000000	0??			
<i>Cynortia conspersa</i>	3101002100	2-00011011	0121010400	0000000111	1203000200	0101000210	1102040025	1411111000	0000000000	0??			
<i>Cosmetus variolosus</i>	3101002200	2-0?011011	0121010400	0000000111	1203000200	0101000210	10-2040025	1411111000	0000000000	0??			
<i>Syncranus cribrum</i>	3101001100	2-00001000	1020000310	1002000111	1203000100	0001010000	1121040025	231111?000	0001100000	0??			
<i>Saramacia lucasae</i>	3101001100	2-00001000	1020000310	1002000111	1203000100	0001010000	10-1040025	2311111000	0000000000	0??			
<i>Heterocranias chlorogaster</i>	3011013100	2-00200000	0210001200	1002010111	1213100202	0001111001	1201041125	131111?000	0000000000	0??			
<i>Chiriboga albituber</i>	6011001100	2-00200000	0200001200	1002010111	1213100202	0001111001	1201041125	131111?000	0000000000	0??			
<i>Zanmicranus monolomius</i>	4011013100	2-00202000	0220001200	1002010111	1213100202	0001111001	1201041025	131111?000	0000100000	0??			
<i>Phaetocranias giganteus</i>	3101003100	1000002000	0300001200	1002010111	1213100202	0001111001	1201041025	?3111110000	0001100000	0??			
<i>Phalangodus</i> sp.	2101003100	0000002000	0310000200	1000010111	1213100202	0001011000	1200040025	?31111?000	0000000000	0??			
<i>Licornus tama</i>	4101011110	0311001000	0000000300	1111121111	120300?002	0101210000	?0?0040025	?30111?100	0100000000	000			
<i>Hütamaia caramaschii</i>	4101011020	031?001000	0000000300	1111121111	1203000002	0001210000	00-0040025	230111?100	0100000000	000			
<i>Ampycus telfer</i>	2100011111	2-11001000	0000000300	1112211111	12030000302	1001210000	1210040025	230111?100	0000000000	000			

Species	Characters									
	0000000000	1111111111	2222222222	3333333333	4444444444	5555555555	6666666666	7777777777	8888888888	999
<i>Nesopachylus monoceros</i>	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	012
<i>Glysterus metatarsalis</i>	2101011001	030?001000	0000000300	1112211111	1203000302	1001210000	1210040025	230111?000	0000000000	000
<i>Neopachylodes</i> sp.	2101011011	030?001000	0000000300	1112211111	1203000302	1001210000	0000040025	230111?000	0000000000	000
<i>Discocorytus crenulatus</i>	4201011100	0301001000	1000000303	1110211111	1203000202	0011000000	12100?0025	210111?000	0000000000	000
<i>Gonyleptes horridus</i>	4201011100	2-01001000	1000000303	1112-1111	1203000202	0011000000	1101030025	1411111110	0000000000	000
<i>Acanthopachylus aculeatus</i>	4101011000	0101001000	1000000303	1110211111	1203000202	0011000000	1200040025	1411111110	0000000000	000
<i>Zamora granulata</i>	5010001000	0200200000	0200000000	0002110111	120301040-	0001410000	00-00-20123	147111?000	0000000000	000
<i>Nomoclastes quasimodo</i>	50--102000	2-0?300000	0010000000	0000200111	1203011000	0001410000	00-00-0125	020111?000	0000000000	000
<i>Nepostygnus bispinosus</i>	?201011011	0000001000	0020000000	0000000112	1203011000	0101410000	0--4030125	?111?1?000	0000000000	000
<i>Kichua rheimsae</i>	3101001100	2-00001000	1020000000	0000000111	1203011000	0001410000	0--00-0125	020111?000	0000000000	000
<i>Callcosma cofan</i>	3101001100	0300001000	1020000000	0000000111	1203011000	0001410000	0--?0-1125	02-?11?000	0020100000	001
<i>Callcosma gracillima</i>	3101001100	0300001000	1020000000	0000000111	1203011000	0001410000	0--?0-1125	020111?000	0020101000	001
<i>Callcosma abrapatricia</i>	3101001100	1300001000	1000000000	0000000111	1203011000	0001410000	0--40-1125	020111?000	0000111000	001
<i>Callcosma barasana</i>	3101001100	0300001000	1020000000	0000000111	1203011000	0001410000	0--?0-1125	020111?000	0020111000	001
<i>Quindina marginata</i>	3101001100	2-20011000	0000000000	0000000111	1203011000	0001410000	0--?0-1125	?2??11?200	0100000100	000
<i>Quindina albomarginis</i>	3101001100	1220011000	1000000000	0000000111	1203011000	0001410000	00-40-1125	020111?200	0210100101	011
<i>Quindina albociliaria</i>	3101001100	0320011000	1000000000	0000000111	1203011000	0001410000	0--40-1125	020111?210	0011100111	111
<i>Quindina limbata</i>	3101001100	2-20011000	1000000000	0000000111	1203011000	0001410000	0--40-1125	020111?211	1011100101	111
<i>Quindina burbayar</i>	3101001100	0320011000	1000000000	0000000111	1203011000	0001410000	0--40-1125	020111?200	0011100101	011
<i>Quindina morae</i>	3101001100	0120011000	1000000000	0000000111	1203011000	0001410000	0--40-1125	020111?200	0011100101	011
<i>Quindina bimaculata</i>	3101001100	0-20011000	1000000000	0002000111	1203011000	0001410000	0--?0--125	02??11?201	0100100111	011
<i>Quindina bella</i>	3101001100	0320011000	1000000000	0000000111	1203011000	0001410000	13100-1125	020111?211	0101100111	111
<i>Quindina kuma</i>	3101001100	0120011000	1000000000	0000000111	1203011000	0001410000	0--40-1125	020111?211	0110110111	111
<i>Quindina hermesi</i>	3101001100	0220011000	1000000000	0000000111	1203011000	0001410000	???061125	020111?211	1000010111	101
<i>Quindina discolor</i>	3101001100	2-20011000	1000000000	0000000111	1203011000	0001410000	1130060125	020111?210	0101101101	011
<i>Quindina pendula</i> sp. nov.	3101001100	0320011000	0000000000	0000000111	1203011000	0001410000	10-0061025	020111?200	0000100100	001

Based on Kury and Villarreal (2015), Pinto-da-Rocha and Bragnolo (2017) and Pinzón-Morales and Pinto-da-Rocha (2020).



RESULTS

***Quindina pendula* Lancheros, Arias-Cuellar & Pinto-da-Rocha sp. nov.** zoobank.org:act:69BE1437-BEA0-4006-9528-329D725401DF

Etymology: The specific epithet, *pendula*, is a Latin term meaning “pendant” and refers to the pendular disc nest, contrasting with the open mud nest attached to the substrate.

Type material: Holotype (MCUB-R-AR-000938) adult male preserved in 70 % ethanol, the nest is preserved dry, Colombia, Cundinamarca, La Calera, vereda Mundo Nuevo (4°39'55.7" N & 73°51' 16.9" W; 2 693 m elevation), 16.II.2019, Daniel Arias Cuellar leg. Paratypes: two males (MCUB-R-AR-000936), from the same locality as the holotype, 19.XII.2020, Daniel Arias Cuellar leg.; two females (MCUB-R-AR-000939), Colombia, Cundinamarca, La Calera, vereda El Libano (4°39'44" N & 74°0'31" W; 3 006 m elevation), 27.III.2021, Nicolás Briceño Avellaneda leg.

Diagnosis: Ocularium with a group of 3-6 tubercles near each eye, towards the center. Prosoma with dark yellow background on most tubercles both dorsally and ventrally. Area I with a group of uniformly tubercles forming a triangle on each side. Area III with two or three pale yellow patches on each side. Area IV with one pale yellow patch on each side. Dorsal scutum areas and tergites without white spots. Free tergites predominantly black on the sides and yellow in the center.

Comparison: Comparison: Resembles *Q. bella*, *Q. bimaculata*, *Q. discolor*, *Q. hermesii*, and *Q. marginata*, by the lack of enlarged tubercles on the lateral margins of the dorsal scutum. It can be distinguished from *Q. bella* by the presence of only small yellow tubercles on the lateral margin of the dorsal scutum (a group of larger, white tubercles on each side of the lateral margin in *Q. bella*); from *Q. bimaculata* by the presence of dark yellow background around

most of the tubercles on the dorsal and ventral body, and in free tergites I-III (yellowish white tubercles and a white patch with three tubercles in each side of the lateral margin of the dorsal scutum in *Q. bimaculata*); from *Q. discolor* by the dark yellow background of the prosoma with black areas (presence of a white patch on the posterior half of the prosoma in *Q. discolor*); from *Q. hermesii* by presence of only yellow and black coloration (anterior margin tubercles white and a white spot on each side of the lateral margin near the back of the dorsal scutum in *Q. hermesii*); and from *Q. marginata* by the smaller number of tubercles in the ocularium and the absence of these in the posterior part of the prosoma, the presence of only yellow, brown and black coloration and a pair of parallel spines in the free tergite III (presence of 18 tubercles in the center of the ocularium and 23 behind of this, silver tubercles and absence of a pair of parallel spines in the free tergite III in *Q. marginata*).

Description, Male Holotype (MCUB-R-AR-000938)

Measurements: Carapace length: 1.4; carapace width: 2.2; dorsal scutum length: 3.1; dorsal scutum width: 2.8; femur: 1.6, 3.6, 2.4, 3.3; patella: 0.6, 1, 0.9, 1.1; tibia: 1.1, 2.5, 1.6, 2.1; metatarsus: 1.9, 3.2, 2.5, 3.6. Variation in male measurements (Table 2).

Live color (Fig. 1A): Dorsal shield with brown background, ocularium with black patches on the lateral areas, middle part of the prosoma with a mushroom-shaped set of brown patches. Black patches in 49 % of the prosoma, the other 51 % of the prosoma brown. Areas I and II with dark yellow dots. Spines of area III black with two bright yellow patches on each side. Most of the dorsal and ventral tubercles have dark yellow patches. Lateral areas with small irregular black patches. Lateral edges of the shield are dark yellow. Free tergites black with light yellow lateral patches. Legs light yellow with a pattern of irregular black patches. Pedipalps and chelicerae are dark yellow with

Table 2
Variation in body and appendage size in *Quindina pendula* sp. nov.

	Males (n = 3)			Females (n = 2)		
	Max.	Min.	Mean	Max.	Min.	Mean
CL	1.6	1.4	1.5	1.2	1.2	1.2
CW	2.6	2.2	2.4	1.8	1.8	1.8
DSL	3.5	3.1	3.3	2.8	2.7	2.8
DSW	3.0	2.8	2.9	2.6	2.4	2.5
Fe I	1.7	1.6	1.7	1.1	1.1	1.1
Ti I	1.1	1.1	1.1	0.8	0.7	0.8
Fe II	3.6	3.3	3.5	2.1	2.1	2.1
Ti II	2.6	2.4	2.5	1.4	1.4	1.4
Fe III	2.5	2.2	2.4	1.5	1.5	1.5
Ti III	1.6	1.5	1.6	1.0	1.0	1.0
Fe IV	3.5	3.2	3.4	2.2	2.1	2.2
Ti IV	2.1	2.0	2.0	1.4	1.3	1.4

Abbreviations: CL = carapace length, CW = carapace width, DSL = dorsal scutum length, DSW = dorsal scutum width, Fe = femur length, Ti = tibia length, n = number of specimens measured.

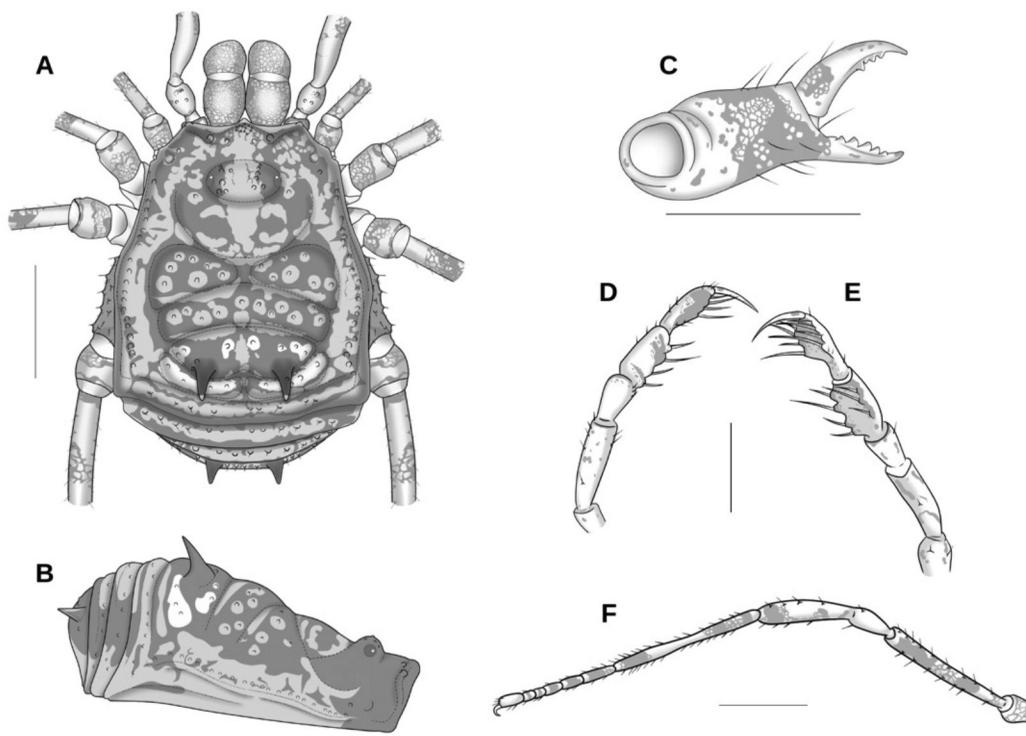


Fig. 1. *Quindina pendula* sp. nov. male holotype (MCUB-R-AR-000938). **A-B.** Habitus, A, dorsal view; B, lateral view. **C.** Chelicerae hand with fixed and movable fingers. **D-E.** Pedipalp, trochanter to tarsus, C, meso-dorsal view; D, ventral view. **F.** Leg I, trochanter to tarsus in ventral view. Scales: 1 mm.

black patches. Ventral body dark yellow with heterogeneous black patches. Free sternites with black lines and light yellow patches. UV fluorescence is observed in free tergites I to III (Fig. 2C and Fig. 2D).

Color in ethanol: Background of the dorsal scutum dark yellow. Ocularium with black patches on the lateral areas. Black patches in 49 % of the prosoma, the other 51 % of the prosoma dark yellow (Fig. 1A). Area I and II

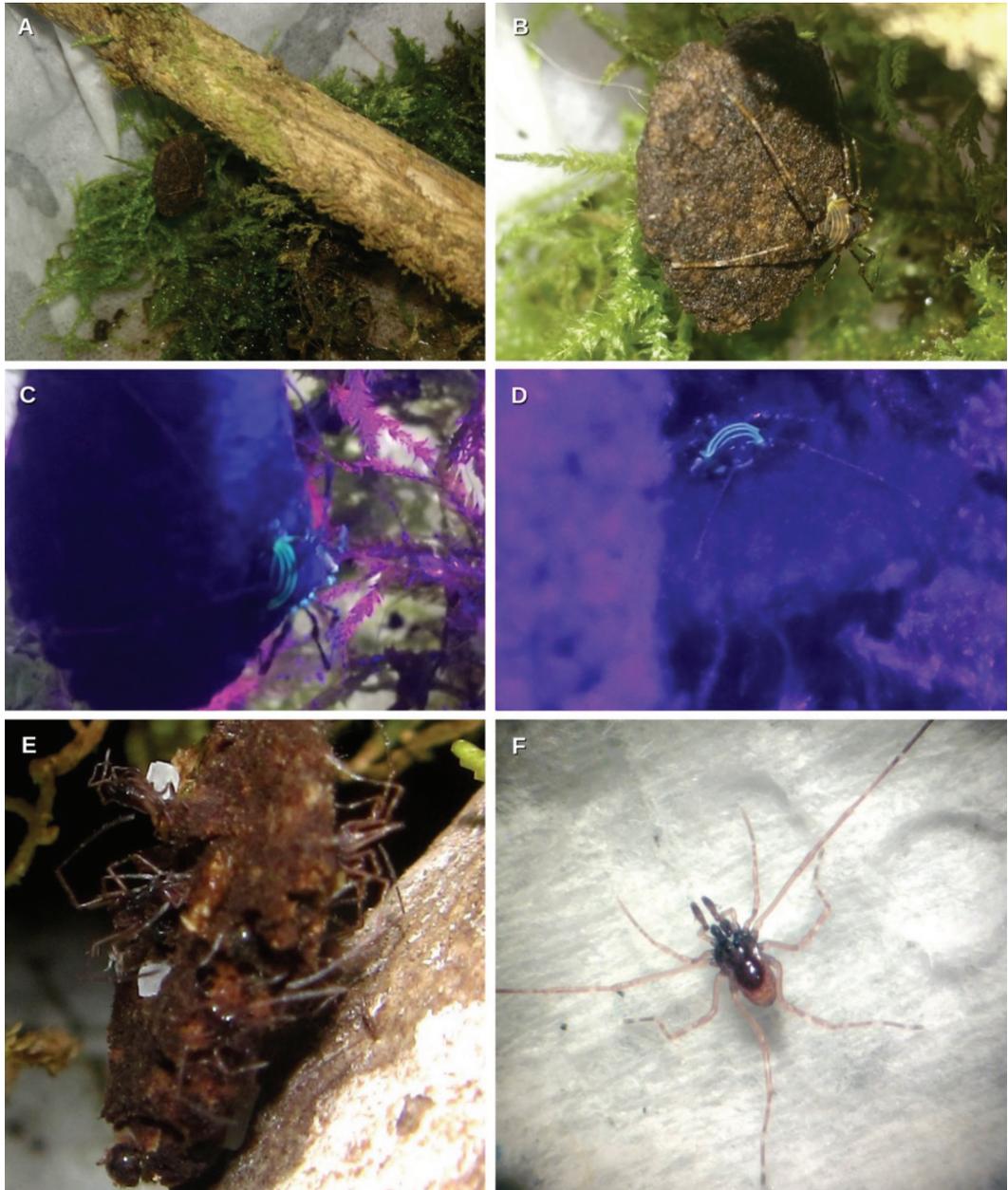


Fig. 2. Observations of the adult male and nymphs of *Quindina pendula* sp. nov. in the terrarium. **A-B.** Adult male tending the nest in the terrarium. **C-D.** UV observation for evidence of fluorescent areas. **E.** 2-day-old nymphs on the nest. **F.** 21-day-old nymph. Photos: A, B, C and D. Daniel Arias; E and F. Héctor Lancheros.

with dark yellow dots. Spines of area III black, each with two or three pale yellow patches forward on each side (Fig. 1A). Most of the dorsal and ventral tubercles have dark yellow patches. Lateral areas with small irregular black patches (Fig. 1B). Free tergites with black lateral patches. Yellow pedipalps with black patches. Chelicerae with a dark yellow background with heterogeneous black patches. Legs yellow with black patches. Ventral part is dark yellow with heterogeneous black patches. Free sternites with black lines and dark yellow patches.

Dorsal scutum (Fig. 1A): Type β dorsal scutum, anterior margin with one tubercle on each side. Preocular monticle with some granules. Carapace with one tubercle at each side of the preocular monticle, and one tubercle forward or behind of each ozopore. Ocularium with a small median depression, with two paramedial groups of 3-6 tubercles. Lateral margins with a row of 19-20 tubercles from center of coxa III to almost posterior margin, elevated posteriorly. Grooves of the dorsal scutum are well marked. Area I with 7-8 tubercles forming a triangle on each side. Area II with a row of eleven tubercles. Area III with a pair of sharp, slightly divergent spines, directed backwards; with four tubercles forward of each spine and one or two tubercles at the base or over these. Area IV with four tubercles on each side. Posterior margin with nine tubercles. Free tergites: I and II with a row of twelve tubercles; III with a pair of parallel spines directed backwards, with four tubercles between spines and four at each side. Anal plate with nine small-scattered tubercles.

Ventral: Coxa I with 13 scattered tubercles. Coxa II with 28 tubercles. Coxa III with 21 scattered tubercles. Coxa IV with more than 50 tubercles.

Legs (Fig. 1F): I and III with small tubercles on the front, II with one medium-sized and one large tubercle on the front. Trochanters: I-IV with small scattered setiferous tubercles in the dorsal, ventral and lateral parts. Femora

I-IV with rows of various setiferous tubercles; the apex of the femora II-IV presents two spiny lateral tubercles, the retrolateral larger than the prolateral. Tarsal articles: 6(3)/12-13(3)/7/8.

Chelicerae (Fig. 1C): Basal segment with a few small setiferous tubercles on the bulla. Movable finger with four teeth; fixed finger with five teeth.

Pedipalps (Fig. 1D and Fig. 1E): Trochanter with a few small dorsal tubercles, one ecto-lateral and one ventral setiferous tubercles. Femur with small scattered dorsal tubercles. Tibia: mesal iili, ectal ili; Tarsus: mesal liii, ectal liii.

Penis (Fig. 3): Ventral plate oval in shape, lateral margin with a basal constriction, half of the distal edge curved, three pairs of spatulate macrosetae C; one pair of spatulate macrosetae A directed towards the truncus, almost as long as macrosetae C; one pair of conical macrosetae D; three pairs of macrosetae E on ventral surface of ventral plate. Glans wide and conical, stylus long, slightly wide at apex, with submedian ventral process. Type 4 microsetae distributed in the ventral side of the ventral plate.

Female Paratype (MCUB-R-AR-000939)

Measurements: Carapace length: 1.2; carapace width: 1.8; dorsal scutum length: 2.8; dorsal scutum width: 2.5; femur: 1.1, 2.1, 1.5, 2.2; patella: 0.4, 0.6, 0.7, 0.7; tibia: 0.8, 1.4, 1.0, 1.4; metatarsus: 1.1, 1.8, 1.5, 2.3. Variation in female measurements (Table 2).

Females differ from males in several morphological aspects and have dark brown spots instead of black spots (Fig. 4). Anterior margin of the scutum with two tubercles on each side. Ocularium with two paramedial groups of tubercles. Lateral margins without a row of tubercles. Area III and free tergite III lacking a pair of spines. Free tergites II and III with sharper and larger tubercles (Fig. 4B).

The number of tubercles is different in areas I-IV of the dorsal scutum, the free tergites

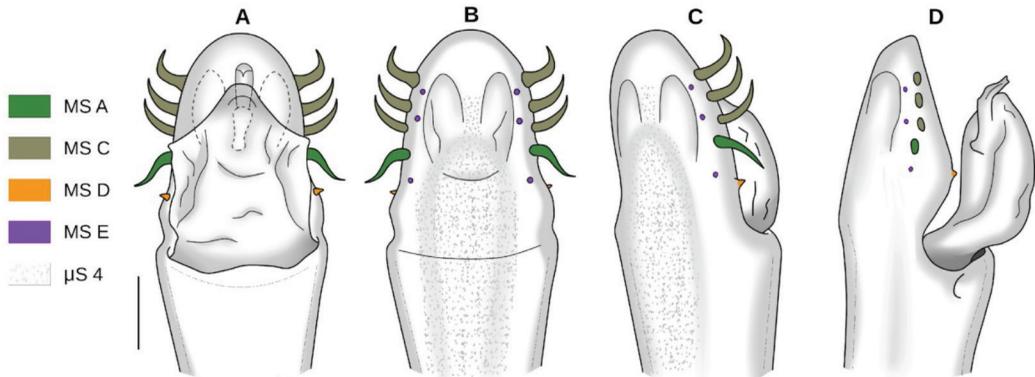


Fig. 3. Penis of *Quindina pendula* sp. nov., holotype (MCUB-R-AR-000938). **A.** dorsal view, **B.** ventral view, **C.** ventrolateral view, **D.** lateral view. MS = macrosetae, μ S 4= type 4 microsetae. Scale: 0.01 mm.

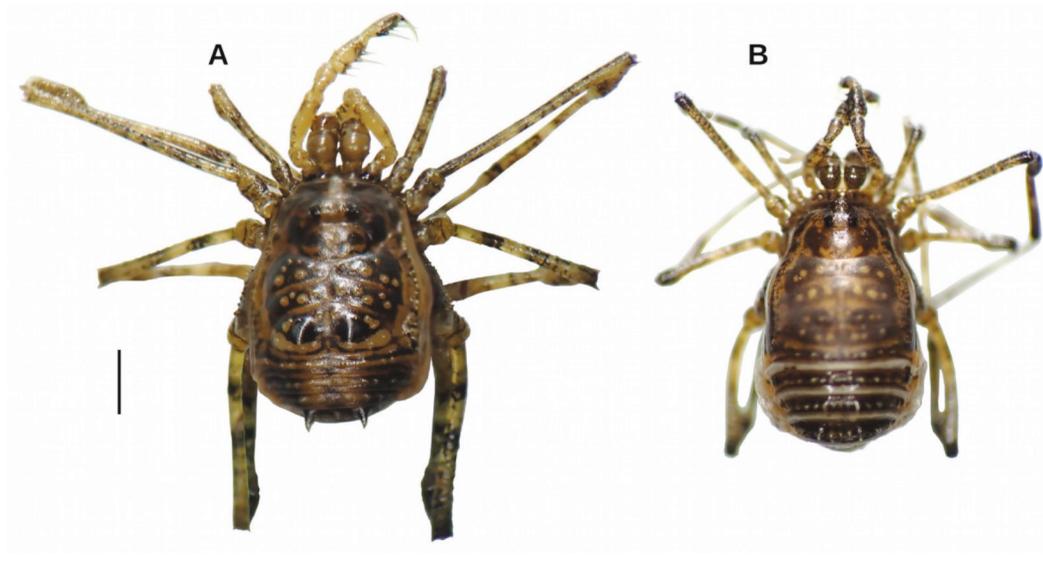


Fig. 4. Comparison of male and female of *Quindina pendula* sp. nov.. **A.** Dorsal view of the male holotype (MCUB-R-AR-000938), **B.** Dorsal view of a female paratype (MCUB-R-AR-000939). Scale 1mm. Photos: Héctor Lancheros.

and the anal plate. Area I with a row of two or four tubercles on each side. Area II with a row of three tubercles on each side. Area III with four to eight tubercles on each side. Area IV with three to four tubercles on each side. Posterior margin with ten tubercles. Free tergites: I with a row of ten tubercles; II with a row of 13 tubercles; III with eleven tubercles. Anal plate with two rows of four small tubercles. Tarsal counts smaller than males: 5(3)/8(3)/6/6.

Distribution (Fig. 5): Recorded in the department of Cundinamarca: municipalities of La Calera (Fig. 6), Choachí (Fig. 7A, Fig. 7B, Fig. 7C), Tena; and in the Distrito Capital locality of Chapinero (Bogotá). The elevation range is between 2 040 and 3 150 m and the observed vegetation corresponds to the Andean Forest formation. In addition, there are photographic records of the same type of nests of this species in the municipality of Saboyá (department

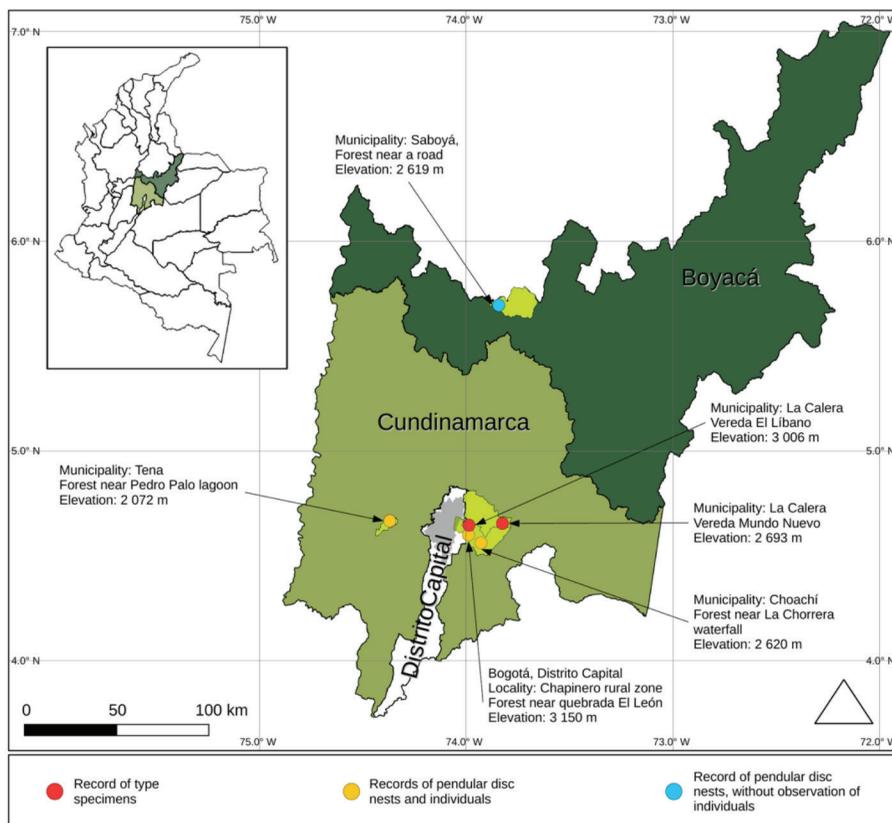


Fig. 5. Sites where *Quindina pendula* sp. nov. or pendular disc nests have been recorded in the departments of Cundinamarca and Boyacá. The color of the dots indicates the type of record; the blue dot represents the record of the nests without the individuals, so there is no certainty that it is the same species.

of Boyacá), at an elevation of 2 619 m, these could belong to the same species, but there is no record, of the individuals from this locality, deposited in scientific collections.

Nest characteristics: We report a new type of nest in *Quindina pendula* sp. nov. This species builds pendular disc-shaped nests in which the female lays the eggs that are cared for by the male. Most of these pendular disc nests were observed on tree branches in well-preserved Andean Forest areas, generally on branches colonized by foliose liverworts. Apparently, the nest is composed of mud. However, upon close examination, one can observe only plant fragments such as bark segments and bryophytes (Fig. 8), united by an adherent substance that is presumably secreted by the harvestmen.

A detailed examination of one of the nests revealed the presence of small arthropods on its surface: a Psocoptera nymph of the family Ectopsocidae and a mite, apparently of the order Mesostigmata (Fig. 8E and Fig. 8F).

The nests were found suspended from various structures such as sections of leafy liverworts (*Frullania atrata*, *F. cf. brasiliensis* and *Plagiochila* sp.), thin branches of trees, leaves of bromeliads, among others (Fig. 8B, Fig. 8C, Fig. 9 and Fig. 10). Seven nests were observed in a single tree, four of these on a branch. Two nests were observed (Fig. 10) in an abandoned hut in the forest of the vereda Mundo Nuevo, one hanging from the lower part of the sill beam (Fig. 10B and Fig. 10C) and the other inside near the roof, suspended from a blackberry plant that was growing partially inside the hut



Fig. 6. Municipality of La Calera, vereda Mundo Nuevo. Elevation: 2 693 m. **A.** General view of the vegetation cover in the area. **B.** Relief of the area. **C.** Abandoned hut where two nests were observed. **D.** Nest suspended from liverworts on a tree branch. **E.** Adult of *Quindina pendula* sp. nov. protecting the nest. Photos: A, B, C and D. Héctor Lancheros; E. Daniel Arias.



Fig. 7. A-C. Observations in the municipality of Choachí, Forest near La Chorrera waterfall, elevation: 2 620 m. **A.** High cover of liverworts on tree branches in the forest interior. **B.** Nest hanging from liverworts on a tree branch. **C.** Male harvestman found in the nest. **D-F.** Observations of juvenile individuals in the wild. **D-E.** Shortly after hatching the nymphs remain in the nest. **F.** Juvenile individual found on the ground under a log. Photos: A, B and C. Daniel Arias; D, E and F. Héctor Lancheros.



Fig. 8. Nest structure of *Quindina pendula* sp. nov. **A.** General view of the nest. **B-C.** Detail showing the elements from which it hangs, a thin branch and a leaf of *Tillandsia* sp., we observed that the nest is composed of small fragments of plant bark. **D.** Phyllidium of a liverwort that is part of the nest structure. **E-F.** Mite, probably of the order Mesostigmata, and Psocoptera nymph of the family Ectopsocidae found in the nest. Photos: Héctor Lancheros.



Fig. 9. Nests of *Quindina pendula* sp. nov. found in tree branches, suspended from different structures **A.** tree with high epiphytism of foliose liverworts. **B.** Nest built on the apex of an epiphyte of the genus *Tillandsia*. **C.** Nest built around a liverwort with two support points. **D.** Nest built around the middle part of a liverwort. **E.** Nest built on the terminal part of a slender branch. Photos: Héctor Lancheros.

(Fig. 10D and Fig. 10E). Nests generally hang from a single point, but occasionally hang from two (Fig. 9C and Fig. 10C); In most observations the nest was at the terminal part of the supporting element, but occasionally it was observed in the middle part, with a section of

the element protruding at the bottom (Fig. 9C, Fig. 9D and Fig. 7D).

The observed values of mass and dimensions were as follows: fresh mass 0.12-0.6 g; dry mass 0.08-0.01 g; length 16-20 mm, width 15-21 mm, average diameter 15-21 mm; thickness



Fig. 10. Nests of *Quindina pendula* sp. nov. found in an abandoned hut inside the forest of the vereda Mundo Nuevo. **A.** Hut hidden inside the forest. **B.** Nest hanging on the lower part of the sill beam. **C.** Detail of the nest hanging on the sill beam. **D.** Adult harvestman tending a nest on a blackberry plant. **E.** Nest suspended from the blackberry plant (*Rubus* sp.) inside the hut. Photos: Héctor Lancheros.

3.80–4.35 mm; surface area (sum of the two faces) 353–693 mm². The value of fresh mass is highly variable due to the different degree of hydration, which depends on the location of the nest and the precipitation before data collection. For dry mass $n = 8$, for the other variables $n = 12$.

Observations on parental care: Adults were not observed in the nests during the day. In the field, after 6:00 p.m., we observed that males remained constantly on or near the nest (Fig. 6E, Fig. 10D and Fig. 10E). In the lab, we observed that, at night, the male takes care of the nest, even if it is damaged, repairing the nest when it suffered minor damage (Fig. 2A, Fig. 2B, Fig. 2C and Fig. 2D). During the day the male remained hidden at the bottom of

branches. We also observed that, when the nest of another male is placed inside the box, the male continues to take care of it, even if it is not his own. We have not recorded any females in or near the nests.

Developmental stages from laying to hatching: Initially the eggs were completely covered by nest material, but as they developed and increased in size, they became partially exposed. It appears that deterioration of the nest due to rain also causes them to gradually become exposed. The fact of being partially uncovered does not cause direct changes in the color of the eggs, they only change color gradually as they advance in their development. Preliminary observations show four stages of development from egg laying to hatching: white

eggs with no visible differentiated structures; brown eggs with visible appendages; black eggs; emergence of the anterior part of the body (Fig. 11). At least 22 days elapse between laying and the second stage. Then, brown eggs take approximately 12 days to develop into black eggs and 10 to 12 days elapse between the third and fourth stages. In total, at least

45 days elapse from laying to the beginning of hatching (Fig. 11).

In the field, the nymphs remain in the nest shortly after hatching (Fig. 7D and Fig. 7E). They can fall to the ground when hit by raindrops or can take shelter again in the holes on the nest that remain after hatching. This was observed once in the first nest recorded in the

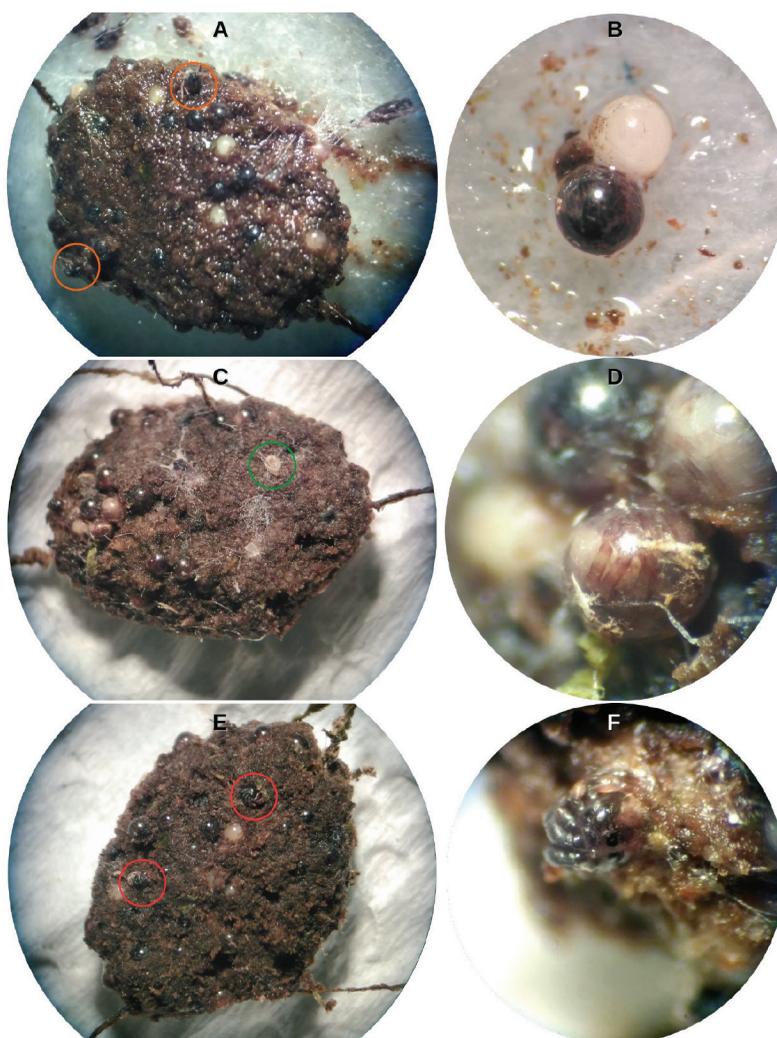


Fig. 11. Nest of *Quindina pendula* sp. nov. with eggs at different stages of development, the circles on the absorbent paper are 1 mm in diameter, the eggs have a diameter of 0.55 mm. **A-B.** 10 days after collection, with black and white eggs, two hatchings are also observed (orange circles). **C-D.** 22 days after collection, on one side of the nest there are eggs in the second and third stage of development, brown and black, respectively; also, an egg shell is observed after hatching (green circle). **E-F.** 22 days after collection, on the other side of the nest there are eggs in the first, third and fourth stage of development: white, black and initiating hatching (red circles), respectively. Photos: Héctor Lancheros.



vereda Mundo Nuevo during the day, when the adult male was absent. A juvenile individual was found on the ground, under a log; this may be the environment in which they remain before reaching maturity and initiate nest construction (Fig. 7F). As in the natural environment, in the terrarium, nymphs remained in the nest for the first few days (Fig. 2E and Fig. 2F).

Phylogenetic analysis: Using the equal weights method, we obtained 30 equally parsimonious trees with 380 steps. From these, we obtained a strict consensus tree of 416 steps and a majority consensus tree of 386 steps. Using the implicit weighting method, with $k = 9.2188$, obtained with the `setk.run` script, we obtained a tree of 381 steps. Using successive weighting, with the rc index, we obtained a tree of 381 steps. With all methods, we recovered Nomoclastidae as a monophyletic unit, sister to Microsetata; in the latter, the relative position of the species is similar to that obtained by Kury and Villarreal (2015), with the exception of the species in the *Ampycus telifer*, *Neopachyloides* sp., *Glysterus metatarsalis* and *Nesopachylus monoceros* clade, with the strict consensus, implicit weighting and successive weighting methods (Appendix 1A, Appendix 1B, Appendix 1C, Appendix 1D). The relative position of the other Gonyleptoidea families, as well as that of the outgroups, was the same as that obtained Kury and Villarreal (2015) using the successive weighting method but slightly different with the implicit weighting method, the latter differs in the position of *Sorensenius* and *Dibunus* (Appendix 1C, Appendix 1D).

Concerning the relative position of the genera within Nomoclastidae, the different methods showed *Zamora* as sister to the other genera. Nevertheless, the methods do not agree on their relative positions. The strict consensus tree with equal weights showed a polytomy between all species of *Callcosma* and the genera *Kichua*, *Napostygnus*, *Nomoclastes* and *Quindina* (Appendix 1A). The majority consensus tree with equal weights showed a polytomy between *Napostygnus*, *Nomoclastes* and the clade (*Kichua* (*Callcosma Quindina*)) (Appendix 1B). The

successive and the implicit weighting tree shows a well-defined topology, with *Nomoclastes* sister to the group ((*Kichua* (*Napostygnus Callcosma*)) *Quindina*) (Appendix 1C, Appendix 1D); in addition, the highest relative Bremer support values were obtained with the successive weighting method (Appendix 1D).

Regardless, the main object of this study is the genus *Quindina*, the topologies we obtained with the implicit and successive weighting methods show *Quindina marginata* as sister to the remaining species of the genus (including *Q. pendula* sp. nov.). Similarly, we recovered *Quindina pendula* sp. nov. as sister to the remaining 10 species of the genus. Sensitivity plots (Navajo rugs) indicate that the two topologies coincide in seven of the twelve species of the genus *Quindina*, the relative position varying within the clade formed by *Q. hermesii*, *Q. bella*, *Q. kuna*, *Q. limbata* and *Q. albiocularia*. We obtained the highest values of Bremer relative support with the topology recovered by the successive weighting method (values between 53 and 74 for each clade within the genus), so we chose this cladogram for the comparison with the other methods (with the sensitivity plots) and the approach of the possible hypotheses of the origin of the pendular disc-shaped and open mud nests (Fig. 12).

Hypotheses of the origin of the nests: We have obtained seven hypotheses for the origin of the two types of nests in the genus *Quindina* using the method of most parsimonious reconstructions with the tree obtained by the successive weighting (Fig. 13). The characteristics observed in the hypotheses are summarized in Table 3. For each characteristic (nest type for each reference group) we give the frequency of each condition (ancestral, derived or in an internal group), the sum being equal to seven. The last column shows the condition that we observed most frequently (in most hypotheses).

The obtained results differ on the origin of the nests and the type of nest that first appeared. The lack of data for other nomoclastid genera hindered us to know if these genera share nest construction (Fig. 13F, Fig. 13G)

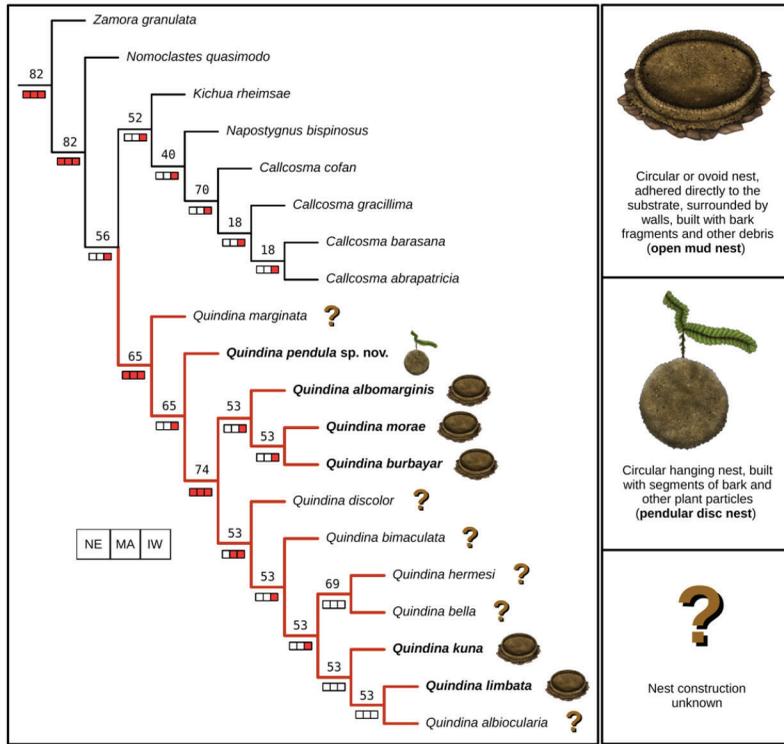


Fig. 12. Cladogram of Nomoclastidae obtained by successive weighting with *rc*, including the new species. Sensitivity plots (Navajo rugs) indicate, with red squares, agreement with groups obtained by other methods: strict Nelsen consensus (NE), majority consensus > 50 % (MA) and implicit weighting with *k* = 9.2188 (IW). Numbers in each branch indicate relative Bremer supports. Next to each species there are drawings indicating the type of nest observed in each; nest descriptions are presented in the boxes on the right. The other species of Gonyleptoidea have been omitted as they are not the subject of discussion in this paper (Appendix 1D).

Table 3

Characteristics present in the seven hypotheses with the frequency of occurrence of each condition.

Characteristic	Variable	Condition			Most common condition
		Ancestral	Derived	In an internal group	
1. Presence of pendular disc nest in the genus <i>Quindina</i> .	H F	F 1	D 1	E C A B G 5	In an internal group
2. Presence of pendular disc nest in the sister group of <i>Q. marginata</i> .	H F	D F 2	B 1	E C A G 4	In an internal group
3. Presence of pendular disc nest in <i>Q. pendula</i> .	H F	D B F 3	E C A G 4	0	Derived
4. Presence of open mud nests in the genus <i>Quindina</i> .	H F	G 1	E 1	C A D B F 5	In an internal group
5. Presence of open mud nest in the sister group of <i>Q. marginata</i> .	H F	E G 2	C 1	A D B F 4	In an internal group
6. Presence of open mud nest in the sister group of <i>Q. pendula</i> .	H F	E C G 3	A D B F 4	0	Derived

H = hypotheses in which this condition is met (Fig. 13); F = frequency (number of hypotheses in which it is met).

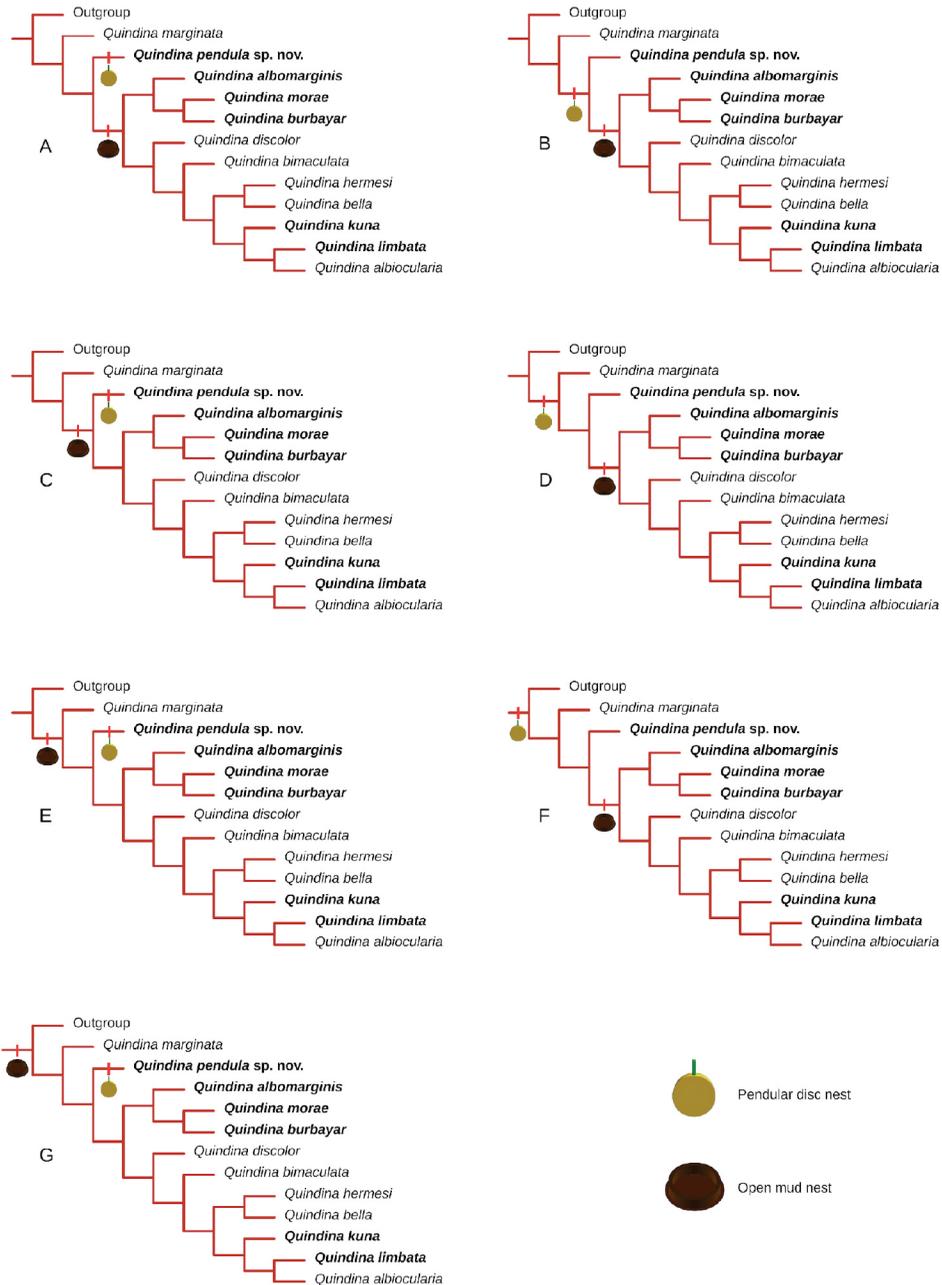


Fig. 13. Hypothesized origin of nests in the genus *Quindina*. **A.** Independent origin of the pendular disc nest in *Q. pendula* and the open mud nest in the sister group of this. **B.** Origin of the pendular disc nest in the common ancestor of the sister group of *Q. marginata* and modification to the open mud nest in the sister group of *Q. pendula*. **C.** Origin of the open mud nest in the common ancestor of the sister group of *Q. marginata* and modification toward the pendular disc nest in *Q. pendula*. **D.** Origin of the pendular disc nest in the common ancestor of *Quindina* spp. and modification to the open mud nest in the sister group of *Q. pendula*. **E.** Origin of the open mud nest in the common ancestor of all *Quindina* species and modification toward the pendular disc nest in *Q. pendula*. **F.** Origin of the pendular disc nest in an ancestor external to the genus *Quindina* with modification toward the open mud nest in the sister group of *Q. pendula*. **G.** Origin of the open mud nest in an ancestor external to the genus *Quindina* with modification toward the pendular disc nest in *Q. pendula*.

or if this is exclusive for *Quindina* spp. (Fig. 13A, Fig. 13B, Fig. 13C, Fig. 13D, Fig. 13E). The absence of reproductive data for the first derived species of *Quindina*, *Q. marginata*, is also an obstacle in understanding how nest construction evolved within the group. At this moment it is impossible to know if the pendular disc nest is exclusive for *Quindina pendula* sp. nov., or if it evolved first and then was replaced by an open mud nest. The only consensus among all hypotheses is that most species of *Quindina* share an open mud nest as a strategy to lay eggs and raise nymphs. Thus, this clade is composed of species for which we observed an open mud nest in the field (*Q. albomarginis*, *Q. morae*, *Q. burbayar*, *Q. kuna*, and *Q. limbata*) and other species that we hypothesize also build this kind of nest.

DISCUSSION

Previously described nest-building harvestmen are distributed across the territories of Costa Rica (*Q. limbata*) and Panama (*Q. albomarginis*, *Q. burbayar*, *Q. kuna* and *Q. morae*) (Pinto-da-Rocha & Bragagnolo, 2017), making *Q. pendula* sp. nov. the first nest-producing species recorded in Colombia. In addition, this new species represents the first record of a pendular disc nest, built with fragments of bark and other plant remains. The pendular disc nest differs significantly in shape, substrate type and substrate attachment, from the previously reported nest type, which is an open mud nest. This last kind of nest is totally attached to the substrate, surrounded by walls and built with bark fragments and other materials. Both nest types do share some similarities, specifically in the type of materials which compose them (Mora, 1990; Rodríguez & Guerrero, 1976). Nevertheless, the composition of the previously reported nests needs to be re-examined through detailed microscopic observations in order to verify its accuracy.

The presence of small arthropods on the surface of the pendular disc nest, such as psocids and mites, could be related to their use of the nest as a food source. Insects of the order

Psocoptera are mainly phytophagous, feeding on algae, fungi, pollen and fallen plant parts (Gillott, 2005, Chapter 8). On the other hand, Mesostigmata mites are mainly free-living predators, where some are phoretic on insects and some consume pollen, nectar and fungi (Dhooria, 2016, Chapter 5). The Ectopsocidae (Psocoptera) may roam the nest consuming plant debris or the mycelium of fungi growing on its surface. Meanwhile, the mites may also be in the nest to eat mycelium or, instead, act as a predatory species, consuming small arthropods such as psocoptera or harvestmen nymphs.

The addition of *Q. pendula* sp. nov. to the phylogenetic analysis result in great differences in the relationships within *Quindina* when compared with Pinzón-Morales and Pinto-da-Rocha (2020); the implicit and successive weighting methods coincide only in *Q. marginata* as sister group of the remaining species in the genus and in the clade (*Q. albomarginis* (*Q. morae* *Q. burbayar*)). However, the topology of the different nomoclastid genera is identical between our findings with these two methods and the previous study.

Aside from *Quindina*, no reproductive studies have tackled other nomoclastid genera. Field observations did not find nests in the area of occurrence for *Kichua rheimsae* Pinto-da-Rocha & Bragagnolo 2017, *Callcosma abra-patricia* Pinto-da-Rocha & Bragagnolo 2017 or *C. gracilima* Roewer 1932 (Cabra, Rheims, pers. comm.; Pinto-da-Rocha pers. obs.). However, the lack of observation of nests in these other species is not sufficient evidence of their absence, given that the respective field trips lasted only a few days. It is more likely that all or at least most of the species of the genus *Quindina* build nests, since this behavior has been observed in half of the known species. Furthermore, the ones that have no records (*Q. marginata*, *Q. discolor*, *Q. bimaculata*, *Q. hermesii*, *Q. bella* and *Q. albiocularia*) have few observations (Pinto-da-Rocha & Bragagnolo, 2017; Pinzón-Morales & Pinto-da-Rocha, 2020). The fact that we did not find the nestless species on the same branch, but on different branches (interspersed with species that do build nests) reinforces the



idea that the absence of nest reports for these species is due to a lack of field observation.

We also call attention to the fact that 44 years elapsed between the description of *Q. albomarginis* (Chamberlin, 1925) and the publication of the first article describing open mud nests (Rodríguez & Guerrero, 1976). In the case of *Q. limbata*, 71 years separate the species description (Roewer, 1943) from the first published description of its nest (Rojas & Solano, 2014). The other three species with known nests were reported by Pinto-da-Rocha and Bragagnolo (2017). At this point, it is difficult to know if the pendular disc nest is an autapomorphy of *Q. pendula* sp. nov. or if it arose earlier, since we have no available data for either *Q. marginata* or the other nomoclastid genera. More knowledge of parental care in *Q. marginata* would help us clarify the origin of the nests in the genus *Quindina*, as this is the sister group for the remaining species of the genus. In the event that it builds a pendular disc nest, hypotheses about its origin in the most recent common ancestor of the genus or even in an ancestor external to the genus would be more plausible. On the other hand, if *Q. marginata* builds open mud nests, it would be more likely that the pendular disc nest is an autapomorphy of *Q. pendula* sp. nov. Finally, in the case that *Q. marginata* does not build nests, it would be more probable that the origin of the nests is in one of the internal groups of the genus *Quindina*.

This study enriches our knowledge on parental care behavior and nest construction in the genus *Quindina*. Until recently, only one type of nest had been reported for this genus in the scientific literature (Pinto-da-Rocha & Bragagnolo, 2017; Quesada-Hidalgo et al., 2019; Rojas et al., 2019) and now we know that there are variations in the shape and structure of the nests. Likewise, we can observe that our knowledge about the species within this genus, as well as for the whole Nomoclastidae family, has increased steadily in the last ten years (Kury et al., 2024; Kury & Villarreal, 2015; Pinto-da-Rocha & Bragagnolo, 2017; Pinzón-Morales & Pinto-da-Rocha, 2020; Quesada-Hidalgo et al.,

2019; Requena et al., 2014; Rojas et al., 2019; Rojas & Solano, 2014; Villarreal & Kury, 2023). Beyond the genus *Quindina* and order Opiliones as a whole, the results obtained in this study are of great importance in our understanding of egg care and nest construction in arthropods. The construction of hanging nests with fragments of plant material has not been previously reported in other groups of arachnids or in any of the classes within Arthropoda, so our findings are relevant for any further studies about the evolution of parental care in this phylum.

Ethical statement: the authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgments section. A signed document has been filed in the journal archives.

See supplementary material
a53v72n1-MS1

ACKNOWLEDGMENTS

We express our gratitude to all the people who supported the development of this work: Nicolás Briceño, who assisted us with the collection of specimens; Manuel David Cortés who identified the bryophyte species; Osvaldo Villarreal, who provided us with the setk script and recorded the species and nests in the municipality of Tena (department of Cundinamarca); Christian Franco García, who recorded the pendular disc nest in the municipality of Saboyá (department of Boyacá); Daniela Ahumada, who helped us with the extraction and observation of the male genitalia; Conchita Pinzón, who offered initial feedback on the phylogenetic analysis and species description; Paula Nuñez, who aided in the elaboration of the illustrations; Víctor Rodríguez Saavedra, who registered the specimens in the collection of the Museo de Ciencias de la Universidad El Bosque MCUB; Cristina Rheims, who kindly

reviewed the language of an early version of the manuscript; David Hernández, who kindly checked and reviewed the language for the final manuscript; and the anonymous reviewers, who provided their valuable feedback. We also give thanks to the Willi Hennig Society for providing us with the TNT v.1.5 software. The participation of Héctor Lancheros in this study was done within the framework of the “Ecological Interactions of Plants in Colombian Ecosystems: Phase I” project, from the Biology Research Group GRIB of Universidad El Bosque. This study was funded by CAPES, CNPq (306722/2018-6), FAPESP (BIOTA, 2013/50297-0), NSF (DOB 1343578), and NASA to Ricardo Pinto-da-Rocha.

REFERENCES

- Acosta, L. E., Pérez-Gonzalez, A., & Tourinho, A. L. (2007). Methods and techniques of study: Methods for taxonomic study. In G. Machado, R. Pinto-da-Rocha, & G. Giribet (Eds.), *Harvestment: the biology of Opiliones* (pp. 494–505). Harvard University Press.
- Battaglia, E., Foobarian, A., Zeimetz, B., Bonnefille, G., Jaubert, J., Coulter, M., Albinet, M., Tonthat, Q., & Norris, R. (2021). *Viking: Analyzer, Explorer and Manager of topological data and GPS* (Version 1.8) [Computer software]. <https://sourceforge.net/projects/viking/>
- Chamberlin, R. V. (1925). Diagnoses of new American Arachnida. *Bulletin of the Museum of Comparative Zoölogy at Harvard College*, 67(4), 211–248.
- Dhooria, M. S. (2016). *Fundamentals of applied acarology*. Springer. <https://doi.org/10.1007/978-981-10-1594-6>
- Farris, J. S. (1969). A successive approximations approach to character weighting. *Systematic Zoology*, 18(4), 374–385. <https://doi.org/10.2307/2412182>
- Farris, J. S. (1989). The retention index and the rescaled consistency index. *Cladistics*, 5, 417–419. <https://doi.org/10.1111/j.1096-0031.1989.tb00573.x>
- Giribet, G. (2003). Stability in phylogenetic formulations and its relationship to nodal support. *Systematic Biology*, 52(4), 554–564. <https://doi.org/10.1080/10635150390223730>
- Goloboff, P. A. (1993). Estimating character weights during tree search. *Cladistics*, 9(1), 83–91. <https://doi.org/10.1111/j.1096-0031.1993.tb00209.x>
- Goloboff, P. A. (2022). *From observations to optimal phylogenetic trees: phylogenetic analysis of morphological data* (Vol. 1, p. 298). CRC Press. <https://doi.org/10.1201/9781003220084>
- Goloboff, P. A., & Catalano S. A. (2016). TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics*, 32(3), 221–238. <https://doi.org/10.1111/cla.12160>
- Goloboff, P. A., & Farris, J. S. (2001). Methods for quick consensus estimation. *Cladistics*, 17, S26–S34. <https://doi.org/10.1006/clad.2000.0156>
- Goloboff, P. A., Carpenter, J. M., Arias, J. S., & Miranda-Esquivel, D. R. (2008). Weighting against homoplasy improves phylogenetic analysis of morphological data sets. *Cladistics*, 24(5), 758–773. <https://doi.org/10.1111/j.1096-0031.2008.00209.x>
- Hara, M. R., Gnaspini, P., & Machado, G. (2003). Male egg guarding behavior in the neotropical harvestman *Ampheres leucopheus* (Mello-Leitão 1922) (Opiliones, Gonyleptidae). *The Journal of Arachnology*, 31(3), 441–444. <https://doi.org/10.1636/S02-32>
- Kimball, S., Mattis, P., & GIMP development team. (2022). *GIMP: GNU Image Manipulation Program* (Version 2.10.32) [Computer software]. <https://www.gimp.org/>
- Kury, A. B. (2016). A classification of the penial microsetae of Gonyleptoidea (Opiliones: Laniatores). *Zootaxa*, 4179(1), 144–150. <https://doi.org/10.11646/zootaxa.4179.1.13>
- Kury, A. B., & Villarreal, O. (2015). The prickly blade mapped: establishing homologies and a chaetotaxy for macrosetae of penis ventral plate in Gonyleptoidea (Arachnida, Opiliones, Laniatores). *Zoological Journal of the Linnean Society*, 174, 1–46. <https://doi.org/10.1111/zoj.12225>
- Kury, A. B., Villarreal, O., & Medrano, M. (2024). On the systematic allocation of *Liomma* Roewer, 1959 (Arachnida: Opiliones: Nomoclastidae) and discovery of a putative synapomorphy for Nomoclastinae. *Journal of Natural History*, 58(1–4), 1–13. <https://doi.org/10.1080/00222933.2023.2287765>
- Machado, G., & Warfel, J. (2006). First case of maternal care in the family Cranidae (Opiliones, Laniatores). *The Journal of Arachnology*, 34, 269–272. <https://doi.org/10.1636/S04-63.1>
- Machado, G., Requena, G. S., Buzatto, B. A., Osses, F., & Rosseto, L. M. (2004). Five new cases of paternal care in harvestmen (Arachnida: Opiliones): implications for the evolution of male guarding in the neotropical family Gonyleptidae. *Sociobiology*, 44(2), 1–22.
- Mora, G. (1990). Paternal care in a Neotropical harvestman, *Zygopachylus albomarginis* (Arachnida, Opiliones: Gonyleptidae). *Animal Behaviour*, 39, 582–593. [https://doi.org/10.1016/S0003-3472\(05\)80425-7](https://doi.org/10.1016/S0003-3472(05)80425-7)



- Pinto-da-Rocha, R., & Bragagnolo, C. (2017). Cladistic analysis of the family Nomoclastidae with descriptions of a new genus and eight new species (Opiliones, Laniatores). *Invertebrate Systematics*, 31, 91–123. <https://doi.org/10.1071/IS15050>
- Pinzón-Morales, C. A., & Pinto-da-Rocha, R. (2020). Two new Colombian harvestmen of the genus *Quindina* Roewer, 1914 (Opiliones: Nomoclastidae). *Zootaxa*, 4748(3), 531–547. <https://doi.org/10.11646/zootaxa.4748.3.7>
- QGIS.org. (2021). *QGIS Geographic Information System* (Version 3.16.4) [Computer software]. Open Source Geospatial Foundation Project. <https://www.qgis.org/>
- Quesada-Hidalgo, R., Solano-Brenes, D., Requena, G. S., & Machado, G. (2019). The good fathers: efficiency of male care and the protective role of foster parents in a Neotropical arachnid. *Animal Behaviour*, 150, 147–155. <https://doi.org/10.1016/j.anbehav.2019.02.007>
- Requena, G. S., Munguía-Steyer, R., & Machado, G. (2014). Paternal care and sexual selection in arthropods. In R. H. Macedo & G. Machado (Eds.), *Sexual Selection: Perspectives and Models from the Neotropics* (pp. 201–233). Academic Press. <https://doi.org/10.1016/B978-0-12-416028-6.00008-6>
- Rodríguez, C. A., & Guerrero, S. (1976). La historia natural y el comportamiento de *Zygopachylus albomarginis* (Chamberlin) (Arachnida, Opiliones: Gonyleptidae). *Biotropica*, 8(4), 242–247. <https://doi.org/10.2307/2989716>
- Roewer, C. F. (1943). Über gonyleptiden. Weitere weberknechte (Arachn., Opil.) XI. *Senckenbergiana*, 26, 12–68.
- Rojas, A., & Solano, D. (2014). Efecto del sitio de construcción en la duración del nido y el fitness de los machos de *Poassa limbata* (Opiliones, Manaosbiidae). In J. Ponce-Saavedra & O. F. Francke (Eds.), *IV Congreso Latinoamericano de Aracnología. Morelia (México)*. Universidad Michoacana de San Nicolás de Hidalgo.
- Rojas, A., Solano-Brenes, D., Muniz, D. G., & Machado, G. (2019). Gone with the rain: negative effects of rainfall on male reproductive success in a nest-building arachnid. *Behavioral Ecology*, 30(4), 1145–1156. <https://doi.org/10.1093/beheco/arz063>
- Rueden, C. T., Schindelin, J., Hiner, M. C., DeZonia, B. E., Walter, A. E., Arena, E. T., & Eliceiri, K. W. (2017). ImageJ2: ImageJ for the next generation of scientific image data. *BMC Bioinformatics*, 18(1), 529. <https://doi.org/10.1186/s12859-017-1934-z>
- The Document Foundation. (2022). *LibreOffice Draw* (Version 7.4.5.1) [Computer software]. <https://www.libreoffice.org/>
- Villarreal, O., & García, A. F. (2021). On the phylogenetic relationships of *Muscopilio*, a new Andean genus of basibiont harvestmen (Opiliones: Agoristenidae). *Zoologischer Anzeiger*, 292, 150–162.
- Villarreal, O., & Kury, A. B. (2023). A family affair: diagnosing and delimiting Prostygndidae (Opiliones: Gonyleptoidea). *Arthropoda*, 1(4), 460–472.