



Notorhinus floresi sp. nov. gen. nov.: The first records of Siphonophorida in Chile and Siphonorhinidae in South America (Colobognatha)

Leif Moritz^{1,2}, Antonio Parra-Gómez³

¹ Leibniz Institute for the Analysis of Biodiversity Change, Zoological Research Museum Alexander Koenig, Adenauerallee 127, Bonn, Germany

² Institute of Evolutionary Biology and Animal Ecology, University of Bonn, An der Immenburg, Bonn, Germany

³ Facultad de Ciencias, Universidad Austral de Chile, Av. Rector Eduardo Morales Miranda 23, Valdivia, Chile

<https://zoobank.org/D1591625-B28B-4400-BA86-CBD3C480012A>

Corresponding author: Leif Moritz (moritz.leif@gmail.com)

Received 13 January 2023

Accepted 10 March 2023

Published 9 June 2023

Academic Editors Andy Sombke, Klaus-Dieter Klass

Citation: Moritz L, Parra-Gómez A (2023) *Notorhinus floresi* sp. nov. gen. nov.: The first records of Siphonophorida in Chile and Siphonorhinidae in South America (Colobognatha). Arthropod Systematics & Phylogeny 81: 565–579. <https://doi.org/10.3897/asp.81.e100520>

Abstract

The millipede family Siphonorhinidae (order Siphonophorida) shows a scattered distribution in South Africa, Madagascar, India, Southeast Asia, and North America. So far, the family is unknown from South America, while species of Siphonophoridae, the second family of the order, are relatively abundant on the continent. However, not a single Siphonophorida is known from Chile. Here we describe the monotypic genus *Notorhinus* gen. nov. with *N. floresi* sp. nov. and record a second *Notorhinus* (undescribed) species, as first records of the order Siphonophorida in Chile and of the family Siphonorhinidae in South America. *Notorhinus* gen. nov. is distinct from the remaining Siphonorhinidae by the arrangement of the sensilla basiconica on the antennae and other somatic and sexual characters. However, it shows close morphological affinities to the North American genus *Illacme* Cook and Loomis 1928. In the Americas Siphonorhinidae were previously only known from California (USA), where they inhabit subterranean micro-habitats. The Chilean species was found under a piece of decaying wood in a small patch of fragmented native forest. Thus, the group shows a disjunct antitropical distribution in America at ca. 37° North and 38° South. They might be the relict of a once greater distribution, which persisted in these areas due to similar climatic conditions.

Keywords

antitropical, Biobio, endemic, millipede, new genus, new species

1. Introduction

Among millipedes (Diplopoda) the Colobognatha, with the four orders Platydesmida, Polyzoniida, Siphonocryptida and Siphonophorida, are extraordinary in many aspects. Colobognathan taxa show strongly modified heads and mouthparts for suctorial feeding (Moritz et al. 2021,

2022), some display maternal or paternal brood-care (Wong et al. 2020; Moritz et al. 2023), and they exhibit a fragmented and relictual distribution in widely separated areas (Cook and Loomis 1928; Shelley and Golovatch 2011). The interesting biogeography of the group

is probably the relict of a once wider distribution (Marek et al. 2016) and might be related to their adaptation towards certain vegetation and climate, as the Colobognatha show greater ecological limitations than other Diplopoda (Cook and Loomis 1928) and are often restricted to very humid habitats (Golovatch et al. 2015). Prime examples of this scattered distribution can be found in the order Siphonophorida and especially in the family Siphonorhinidae (Fig. 1A). The Siphonophorida are characterized by separate tergites, pleurites and sternites, modification of male leg-pair 9 and 10 to leg-like gonopods, absence of ommatidia, a head, which is conical/pyriform or drawn out into a beak, and strongly modified mouthparts (Read and Enghoff 2009). The order comprises a total of 118 described species to date (Enghoff et al. 2015; Marek et al. 2016; Wesener 2023), which are classified in two families: Siphonophoridae Newport, 1844 and Siphonorhinidae Cook, 1895. The group has previously been referred to as a “taxonomist’s nightmare” (Read and Enghoff 2009: 543) and got the “taxonomists’ award for the least popular group among Diplopoda” (Jeekel 2001: 44). This is mainly due to the weakly modified gonopods, compared to those of other helminthomorph taxa, in which the gonopods are highly species specific (Jeekel 2001). In the Siphonophoridae the head extends into a long beak and the antennae are straight, while in the Siphonorhinidae the pyriform head lacks such a beak and carries elbowed antennae (Enghoff et al. 2015). Both groups are already known from the Cretaceous of Myanmar ca. 99 million years ago (Wesener and Moritz 2018). The Siphonorhinidae include five genera, the monotypic *Kleruchus* Attems, 1938 and *Nematozonium* Verhoeff 1939, *Illacme* Cook and Loomis, 1928 with two species, *Siphonorhinus* Pocock, 1894 with eight species (Jeekel 2001; Marek et al. 2016), and *Madagascarhinus* Wesener, 2023 with two species (Wesener 2023). Detailed catalogues of the group have been provided by Jeekel (2001) and Marek et al. (2016). The family Siphonorhinidae is distributed in South Africa, Madagascar, India, Southeast Asia, and North America (Fig. 1A). Not a single species of the family has been recorded from South America (Jeekel 2001; Enghoff et al. 2015; Marek et al. 2016), where the family Siphonophoridae appears to be quite diverse and widespread (Shelley 1996; Read and Enghoff 2009, 2018, 2019). However, from Chile not a single representative of the order Siphonophorida, neither the families Siphonophoridae nor Siphonorhinidae, has been reported so far (Parra-Gómez 2022).

With a north-south extension of more than 4,000 km, the narrow country of Chile spans a wide array of climatic conditions and biomes (Veblen et al. 2007) and contains one of the world’s major biodiversity hotspots: The Chilean Winter Rainfall–Valdivian Forest hotspot (ChV) in south-central Chile, that mainly includes the Chilean matorral and Valdivian temperate forests (Arroyo et al. 2004; Mittermeier et al. 2011; Fuentes-Castillo et al. 2020). Chile, and especially this hotspot, harbor a rich biodiversity with many endemic plants and animals (Arroyo et al. 2004), including several endemic millipede species distributed in five orders (Parra-Gómez 2022). However, these areas are already threatened by habitat

loss (Arroyo et al. 2004). 65 of the 75 known Diplopoda species from Chile are considered to be endemic and most of these millipedes can be found in the south-central zone (Parra-Gómez 2022), including a relatively high diversity of the colobognathan order Polyzoniida (Mauriès and Silva 1971; Golovatch 2014; Parra-Gómez 2022). This area is characterized by evergreen broadleaved trees, evergreen coniferous vegetation and a humid temperate to Mediterranean climate (Veblen et al. 2007).

Here we describe the genus *Notorhinus* **gen. nov.** and the species *Notorhinus floresi* **sp. nov.** which is the first record of the order Siphonophorida in Chile and of the family Siphonorhinidae in South America. Furthermore, we record another representative of the genus *Notorhinus* **gen. nov.** from Chile.

2. Material and Methods

2.1. Abbreviations

br – body-ring(s); **MNHNC** – Museo Nacional de Historia Natural de Chile, Casilla 787, Santiago, Chile; **SEM** – Scanning electron microscopy; **ZFMK** – Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 127, Bonn, Germany; **T** – telson (further abbreviations in figure legends).

2.2. Specimen collecting

Specimens were collected by hand during trips throughout 2019 and 2020 to El Natri and near Caramavida in the Biobio region, Chile. Specimens were preserved in 70% ethanol and are stored at the MNHNC and ZFMK.

2.3. Distribution map

Worldwide distribution of the Siphonorhinidae (Fig. 1A) and the records of Siphonorhinidae from Chile (Fig. 1B, C) were mapped in QGIS 3.28.1 based on literature records (Pocock 1894; Silvestri 1895; Attems 1930, 1936, 1938; Turk 1947; Shelley and Hoffman 2004; Shelley and Golovatch 2011; Marek et al. 2012, 2016; Wesener 2014, 2023) and the data presented here. Where no coordinates were given, approximate coordinates were taken based on the locality descriptions. A distributional map of the species from Chile was made based on the ecoregions provided by Olson et al. (2001) and satellite data from Maptiler and OpenStreetMap contributors.

2.4. Examination and photographs

Specimens were examined with a Zeiss Discovery V12 stereo microscope. Photographs were taken at different focus planes and stacked with MicroPublisher 5.0 RTV

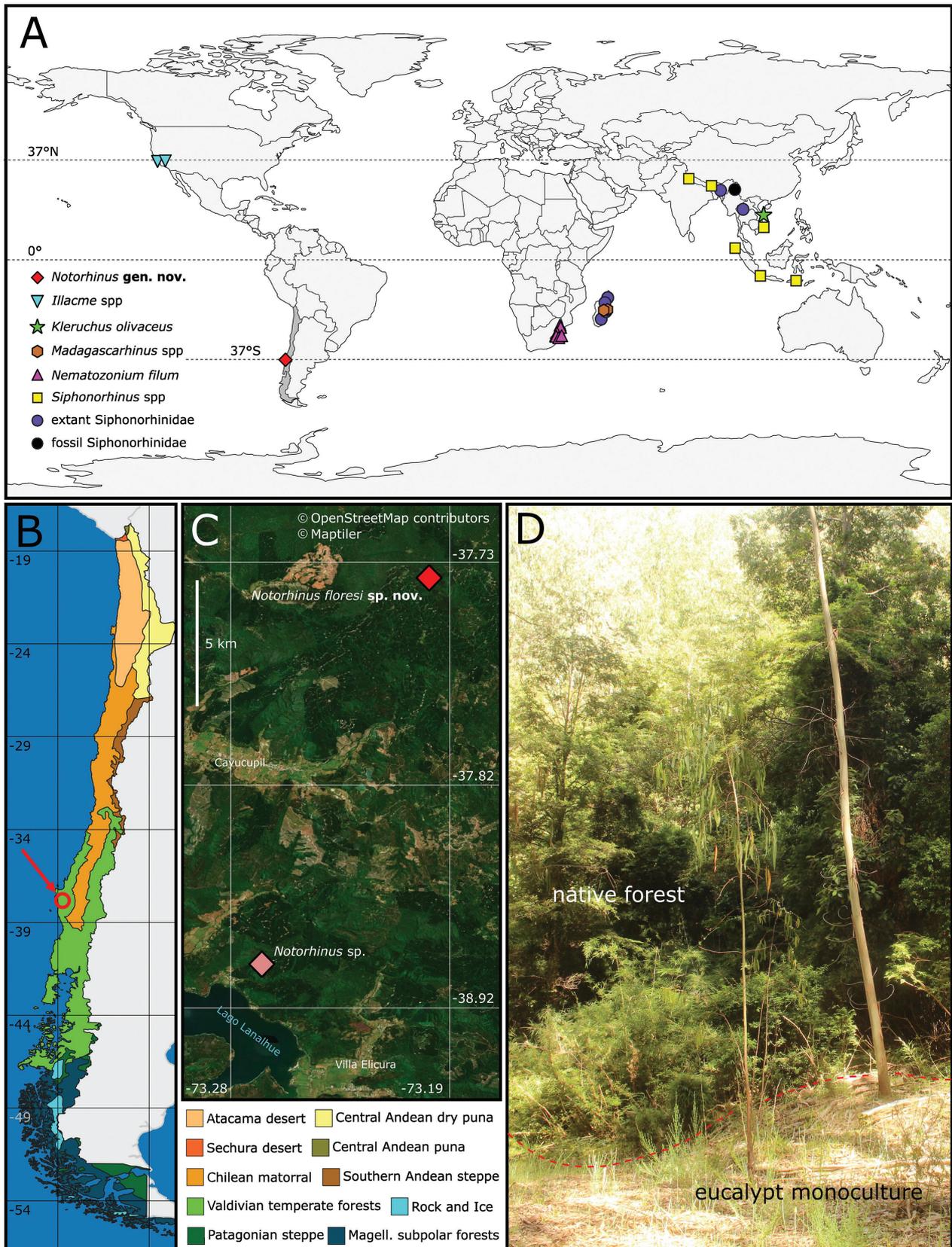


Figure 1. Distribution and habitat of the Siphonorhinidae and *Notorhinus floresi* sp. nov. **A** Distribution of Siphonorhinidae in the world. Records from: Pocock (1894); Silvestri (1895); Attems (1930, 1936, 1938); Turk (1947); Shelley and Hoffman (2004); Shelley and Golovatch (2011); Marek et al. (2012, 2016); Wesener (2014, 2023). Where no coordinates were available, approximate coordinates were taken based on the locality description. Map data from NaturalEarth. **B** Distribution of *Notorhinus* sp. nov. in Chile. Map data from Olson et al. (2001). **C** Localities of *Notorhinus floresi* sp. nov. (e23) and *Notorhinus* sp. (e27) in the region Biobío. Map data from Maptiler and OpenStreetMap contributors. **D** Habitat of *Notorhinus floresi* sp. nov., a native forest surrounded by eucalypt monoculture. Photograph by Edgardo Flores.

camera (Q Imaging) mounted to a Leica Z6 imaging system with AUTO-MONTAGE PRO version 5.03.0061 (Synoptics Ltd). The number of body-rings was counted (including the collum, excluding the telson), and the length of the animals were measured from the photographs, and body-width was measured based on SEM images (see below) in IMAGEJ 1.53c (Schneider et al. 2012). Additional images are deposited on Zenodo (<https://doi.org/10.5281/zenodo.7515111>).

2.5. Scanning electron microscopy (SEM)

For SEM the head, body-rings, telson and gonopods of the male holotype of *N. floresi* **sp. nov.** (MNHNC 8387), and the head, body-rings and telson of the single female *Notorhinus* sp. (MNHNC 8390) were dissected under a Zeiss Discovery V12 stereo microscope. The body parts were transferred via an ascending ethanol series from 70% ethanol to 100% ethanol, air dried and placed with conductive tape on SEM stubs. Due to the small size of the dissected specimens and the mesh size of the available sample container critical point drying was not possible. The samples were sputtered with gold (35 nm) with a Cressington Sputter Coater 108auto and examined with a Zeiss Sigma 300 VP scanning electron microscope. Brightness and contrast of the images were adjusted in GIMP 2.10.20.

3. Results

3.1. Taxonomy

Class Diplopoda de Blainville in Gervais, 1844

Subclass Chilognatha Latreille, 1802/1803

Infraclass Helminthomorpha Pocock, 1887

Subterclass Colobognatha Brandt, 1834

Order Siphonophorida Newport, 1844

3.1.1. Family Siphonorhinidae Cook, 1895

Remarks. The specimens (*Notorhinus floresi* **sp. nov.** and *Notorhinus* sp. (MNHNC 8390)) can be placed in the family Siphonorhinidae based on the following characters: Head pyriform, not extended into beak (rostrum) (Figs 3A, 8A); antennae elbowed; antennomere 2 longer than wide (Figs 3B, 8C); gnathochilarium consisting of separate plates (Figs 3G, 8B); anterior margin of collum straight (compare Enghoff et al. 2015; Marek et al. 2016).

According to a key provided by Shelley (1996: 23) members of the family Siphonorhinidae lack sensory pits on antennomeres 5 and 6 (see also Marek et al. 2012), as is the case in the specimens studied here (Figs 3E, 8C). However, lack of these sensory pits seems to apply only to the North American genus *Illacme* (Marek et al. 2012, 2016), the Malagasy genus *Madagascarhinus* (Wesener 2023) and the South African genus *Nematozonium* (Shelley and Hoffman 2004), as these sensory pits have been reported for *Siphonorhinus* (Attems 1930, 1938) and *Kleruchus* (Attems, 1938).

3.1.2. Genus *Notorhinus* gen. nov.

<http://zoobank.org/5CF0E1D3-B711-450A-80FD-012AF-96FA691>

Type species. *Notorhinus floresi* **sp. nov.**

Diagnosis. Pale, thin and elongated Siphonorhinidae with pyriform heads. In *Notorhinus* **gen. nov.** (Figs 2, 7) two backwards projecting spines are situated behind the elevated ozopores (Figs 4E, 8G), and the posterior margin of the metazonite (limbus) carries sculptures in shape of a fluke (tail-fin) (Figs 4D, 8H). *Notorhinus* **gen. nov.** differs from all other Siphonorhinidae genera by the absence of sensilla basiconica on antennomere 5 and the arrangement of numerous sensilla basiconica on antennomere 6 in a field not sunken into a sensory pit (Figs 3E, 8C). In *Siphonorhinus* and *Kleruchus* (see Attems 1930 for *S. pellita*; Attems 1938 for *Teratognathus* (syn. of *Siphonorhinus*) and *Kleruchus*) numerous sensilla basiconica are located in sensory pits (Sinnesgruben sensu Attems 1930) on antennomeres 5 and 6. In *Illacme* few sensilla basiconica are arranged in rows along the apical margin of antennomeres 5 and 6 (Marek et al. 2012, 2016) and in *Madagascarhinus* sensilla basiconica are arranged in 2–3 rows on antennomeres 5 and 6 (Wesener 2023). In *Nematozonium* no sensory structures are evident on the antennae according to Shelley and Hoffman (2004). *Notorhinus* **gen. nov.** differs from *Illacme* by the fusion of the first legs' coxae to the sternite (Fig. 3G), forming a coxosternite (see Marek et al. 2012, 2016 for *Illacme*), as is the case in *Siphonorhinus* (see Enghoff et al. 2015). Furthermore, the specimens differ from *Kleruchus* by the presence of an anal scale/hypoproct (Figs 4F, 8I) (Anal-schuppe sensu Attems 1938).

Remarks. Several characters are shared with the genus *Illacme* Cook and Loomis, 1928 (see Marek et al. 2012, 2016 for detailed documentation): antennomeres 5 and 6 longer and wider; antennae elbowed between antennomeres 3 and 4 (Fig. 3B); presence of cluster of spiniform sensilla basiconica (spiniform basiconic sensilla sensu Marek et al. 2016) next to apical sensory cones (Fig. 3F); labrum with incision, lined by teeth; pores of salivary glands arranged in a single circular field above the labrum (Fig. 3C); gonopods with 7 podomeres (Fig. 5E); posterior gonopods apical podomere with three branches: two

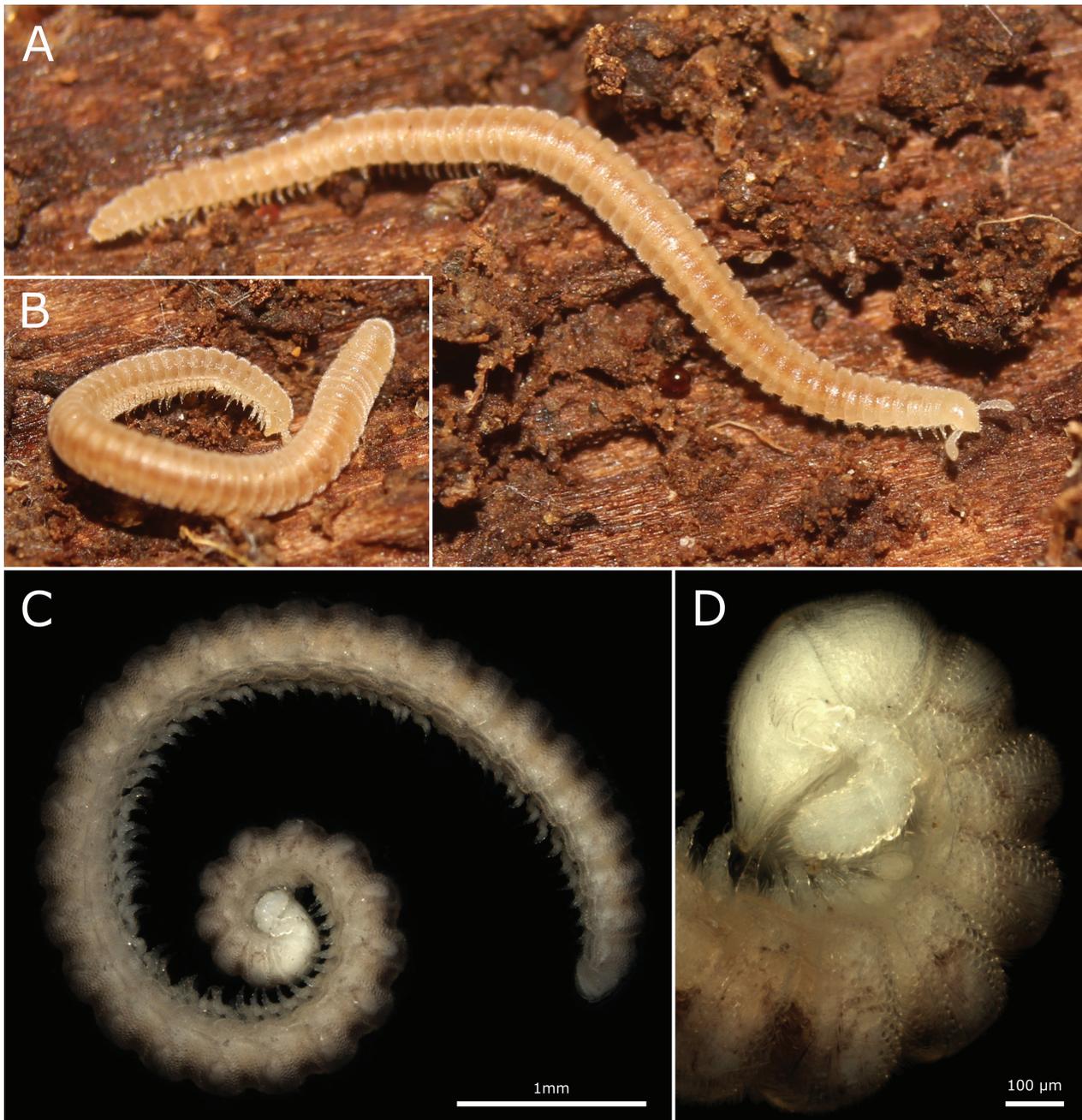


Figure 2. *Notorhinus floresi* sp. nov., photographs. **A, B** Living specimen in its natural habitat. Photographs by Edgardo Flores. **C** Male paratype (ZFMK-MYR 12267), habitus, lateral view. **D** Female paratype (ZFMK-MYR 12269), head, lateral view.

apically laminate/flattened branches and a single posterior spine-like branch (Fig. 5F). However, some of these characters are not well studied in the remaining genera of the Siphonorhinidae.

Etymology. Noto is derived from the ancient greek νότος (nótos) meaning south and refers to the distribution of the genus in South America and the fact that it is the most southern record of the family Siphonorhinidae. Rhinus is derived from the ancient Greek ῥίς (rhís; genitive: ῥινός (rhīnós)), meaning nose, and refers to the acuminate head shape. Rhinus is often part of taxonomic names in the group (e.g. Siphonorhinidae Cook, 1895, *Siphonorhinus* Pocock, 1894, *Madagascarhinus* Wesener, 2023).

3.1.3. *Notorhinus floresi* sp. nov.

<http://zoobank.org/B5E4AFC7-4DF3-407A-B4B2-A0574A98B372>

Figs 2–5

Diagnosis. Small (< 13 mm) elongated Siphonorhinidae with arched metazonites. Body pale, covered by setae, creating a velvety appearance (Fig. 2A). Anterior and posterior gonopods with 7 podomeres (Fig. 5E). Posterior gonopod apically with 3 branches, 2 laminate and 1 spinous (Fig. 5F). Pseudopenis prominent, cone-shaped (Fig. 5B). Posterior margin of metazonite (limbus) with small fluke-shaped sculpture (Fig. 4D). Antennomere 7

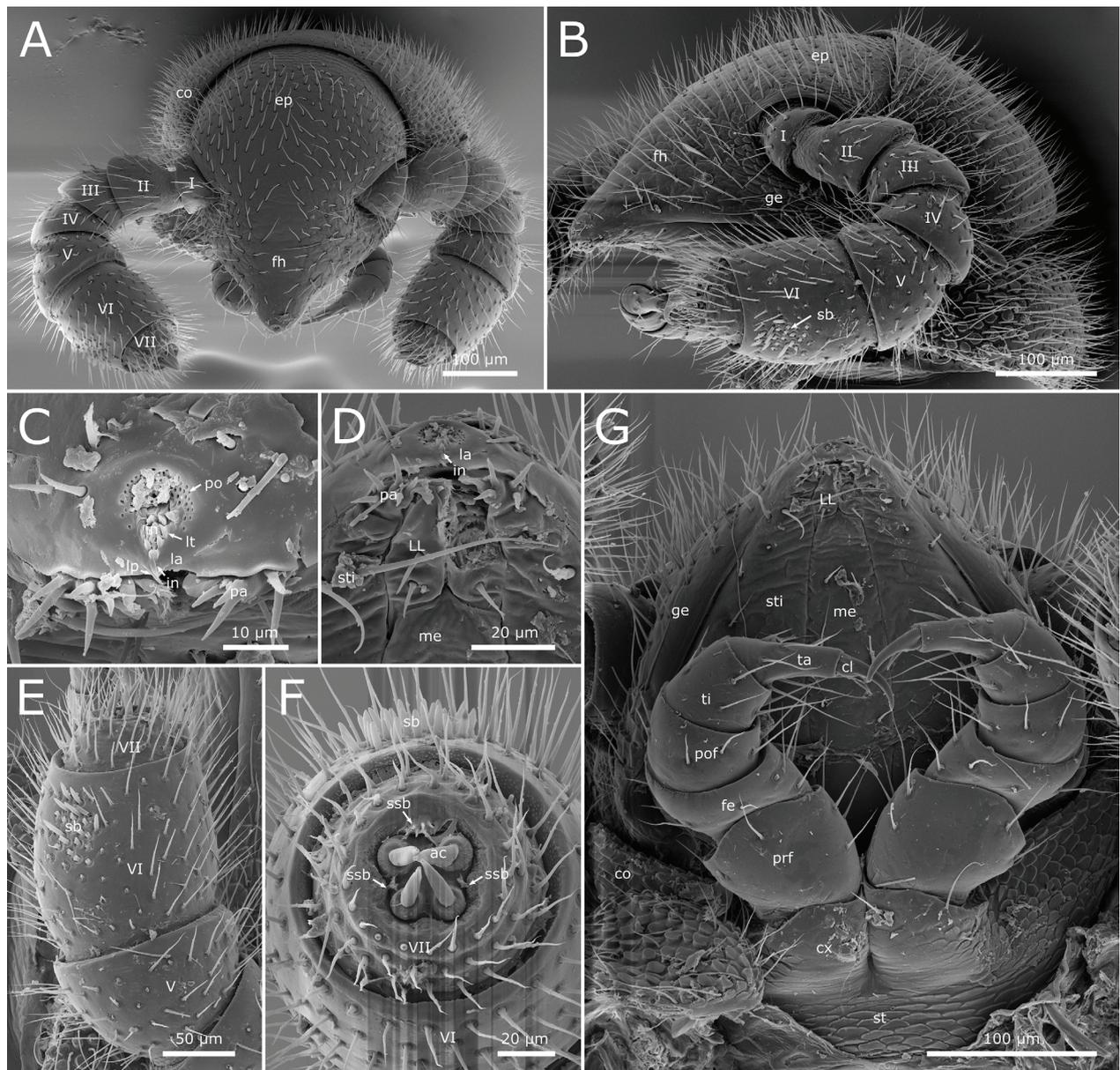


Figure 3. *Notorhinus floresi* sp. nov., male holotype (MNHNC 8387), head, SEM. **A** Head, frontal view. **B** Head, lateral view. **C** Labrum, frontal view. **D** Labrum and gnathochilarium, ventral view. **E** Apical antennomeres, lateral view. **F** Apical antennomere, apical view. **G** Gnathochilarium and leg-pair 1, ventral view. Abbreviations: I–VII = antennomeres, ac = apical cones, cl = claw, co = collum, cx = coxa, ep = epicranium, fe = femur, fh = forehead, ge = genae, in = incision of the labrum, la = labrum, LL = lamella lingualis, lp = spinous protuberances of labrum, lt = teeth lining labral incision, me = mentum, pa = palp-like structure, po = pores of the salivary glands, pof = postfemur, prf = prefemur, sb = sensilla basiconica, ssb = spiniform sensilla basiconica, sti = gnathochilarial stipes, ta = tarsus, ti = tibia.

with spiniform sensilla basiconica in 2 rows (Fig. 3F) (1 row in *Notorhinus* sp.). Metazonite posterior margin straight (Fig. 4A) (sinuate in *Notorhinus* sp.). Differs from *Notorhinus* sp. (MNHNC 8390) in coloration, number of body-rings and its length relative to the number of body-rings (Fig. 2A): *Notorhinus* sp. has 80 body-rings but is only 11.5 mm long, while *Notorhinus floresi* sp. nov. has up to 54 body-rings, but a length of up to 13.8 mm.

Etymology. The species epithet *floresi* refers to Edgardo Flores, who collected the examined specimens, and honors his continuous engagement in nature conservation

and his persistence on the protection of Nahuelbuta National Park and adjacent areas. Noun in genitive.

Material examined. **Holotype:** ♂ (MNHNC 8387); CHILE: Biobío, near Caramavida; 37.72698°S 73.19339°W; 21.iix.2019; Edgardo Flores leg. (e23); hand collected under a decaying piece of wood, in a relictual forest surrounded by eucalypt plantations (Fig. 1C, D). — **Paratypes:** 2 ♂ (ZFMK-MYR 12267, ZFMK-MYR 12268); 3 ♀ (MNHNC 8388, MNHNC 8389, ZFMK-MYR 12269); same data as holotype.

Description. Measurements: Male holotype (MNHNC 8387): br47+T, 12 mm long; male paratype (ZFMK-MYR

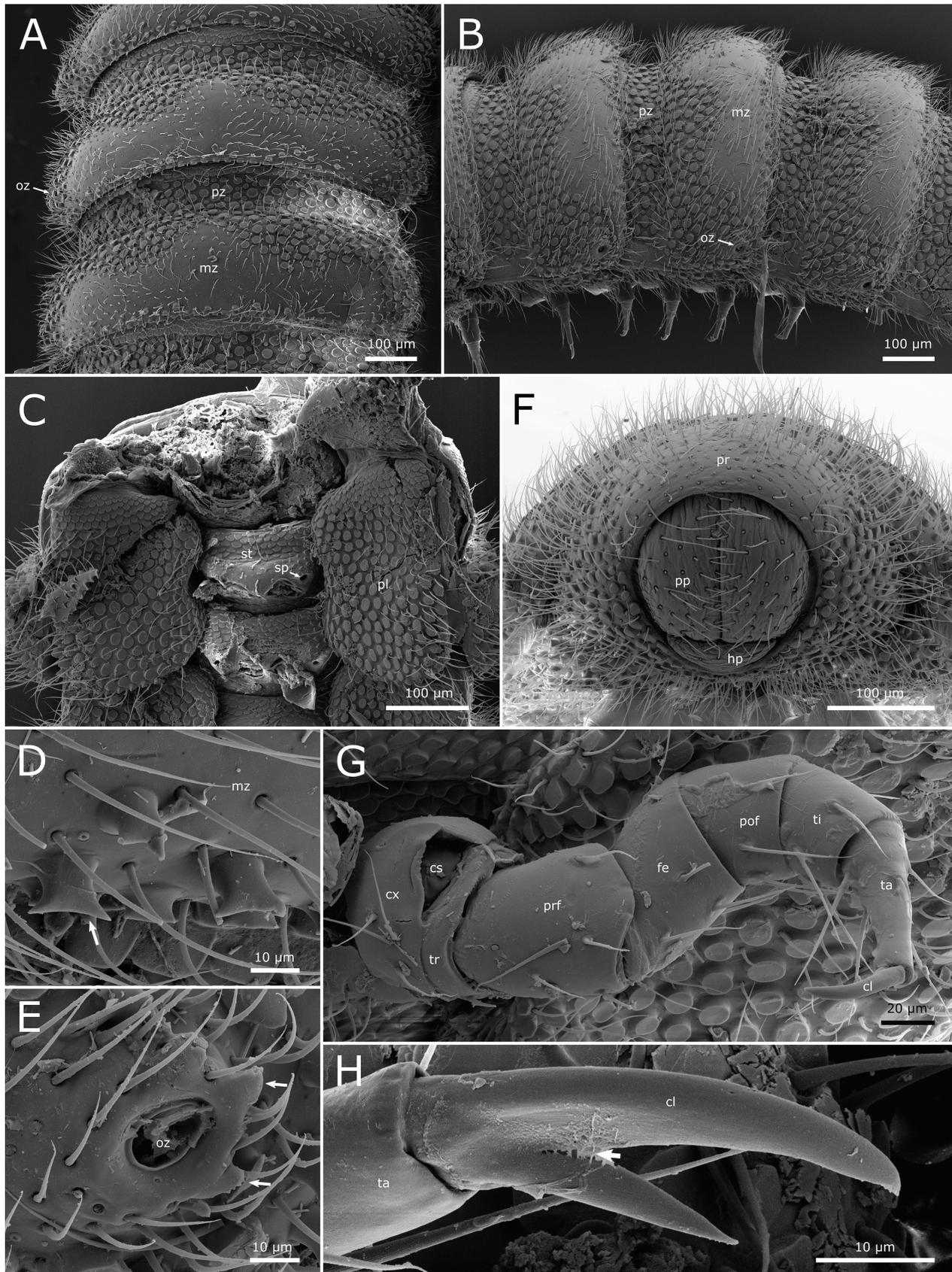


Figure 4. *Notorhinus floresi* sp. nov., male holotype (MNHNC 8387), body-rings and legs, SEM. **A** Mid-body-rings, dorsal view. **B** Mid-body-rings, lateral view. **C** Mid-body-rings, ventral view, legs removed. **D** Metazonite posterior margin (limbus), arrow indicates fluke-shaped sculpture. **E** Ozopore, lateral view, arrows indicate spines behind ozopore. **F** Telson, posterior view. **G** Mid-body leg, anterior view. **H** Leg 2, tarsal claw, arrow indicates division of tarsal claw. Abbreviations: cl = claw, cs = coxal sac, cx = coxa, fe = femur, hp = hypoproct (subanal scale), mz = metazonite, oz = ozopore, pl = pleurite, pof = postfemur, pp = paraproct (anal valve), pr = preanal ring, prf = prefemur, pz = prozonite, sp = spiracle, st = sternite, ta = tarsus, ti = tibia, tr = trochanter.

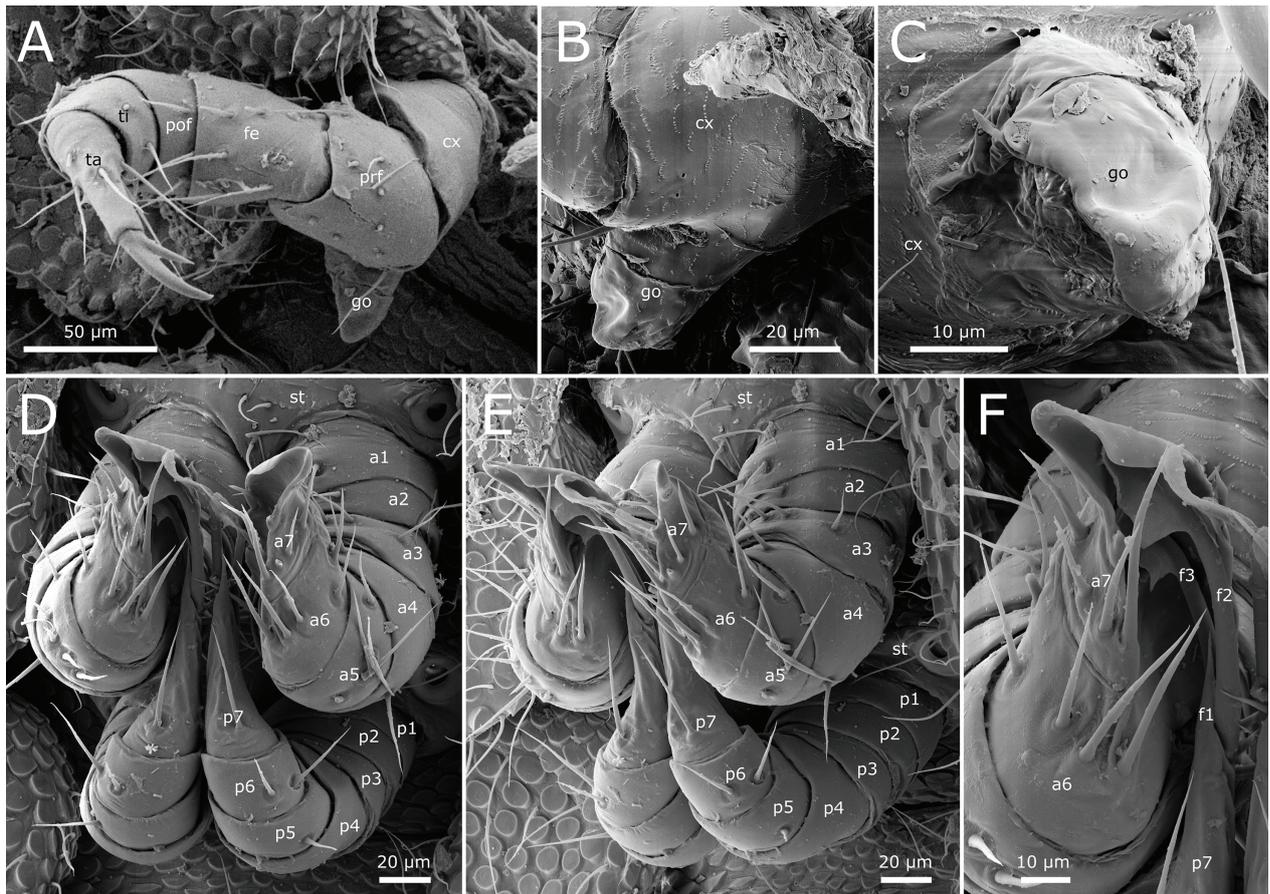


Figure 5. *Notorhinus floresi* sp. nov., male holotype (MNHNC 8387), sexual characters, SEM. **A** Leg 2, ventral view. **B** Male pseudopenis bearing the gonopore, ventral view. **C** Male pseudopenis bearing the gonopore, posterior view. **D** Anterior and posterior gonopods, ventral view. **E** Anterior and posterior gonopods, ventro-lateral view. **F** Right anterior and posterior gonopod, detail of the apical podomeres. Abbreviations: a1–a7 = podomeres of the anterior gonopod, cx = coxa, f1 = pointed/spinous branch of the posterior gonopod's apical podomere, f2 and f3 = laminate branches of the posterior gonopod's apical podomere, go = pseudopenis carrying the gonopore, p1–p7 = podomeres of the posterior gonopod, st = sternite associated with anterior gonopods.

12267): br37+T, 8.9 mm; male paratype (ZFMK-MYR 12268): br54+T, 13.8 mm; female paratype (MNHNC 8389): br42+T, 10.7 mm; female paratype (MNHNC 8388): br49+T, 12.8 mm; female paratype (ZFMK-MYR 12269): br47+T, 10.9 mm. Body thread-like, elongate thin, pale white (Fig. 2A–C), in ethanol head lighter in coloration than body (Fig. 2C, D). — **Head:** Head pyriform, anteriorly tapering, widest behind antennae, covered by long setae (Fig. 3A), posterior and lateral of antennae covered by scale-like sculpture (Fig. 3B). Labrum incised, two lateral spinous protuberances on each side of incision, incision lined by up to 5 teeth on each side. Salivary glands opening via > 50 small pores, arranged in a circular field above labrum (Fig. 3C, D). Lateral margin (genae) and anterior margin (labrum) of head capsule straight, tightly appressed to gnathochilarium (Fig. 3B). Antennae inserting laterally in posterior half of head capsule (Fig. 3A), with 7 antennomeres + apical disc, elbowed between antennomeres 3 and 4. Antennomere 6 longest ($6 > 2 > 5 > 1 = 3 = 4 > 7$), 2 and 6 longer than wide, 1, 3–5 and 7 wider than long, 5 and 6 widest. Each antennomere with several rows of setae (Fig. 3B). Antennomere 5 without sensilla basiconica. Antennomere 6 with ca. 25 sensilla basiconica arranged in a circular field

(not sunken into a sensory pit) located laterally in some distance from antennomere's apical margin (Fig. 3E). Antennomere 7 on apical margin with a lateral group of 8 spiniform sensilla basiconica arranged in two rows, and a single spiniform sensilla basiconica each at anterior and posterior margin, projecting above apical disc between apical cones. Apical disc sunken into antennomere 7 with 4 apical sensory cones, base of apical cones elevated (Fig. 3F). Gnathochilarium triangular, tightly appressed to head capsule consisting of stipites, mentum and lamellae linguales (proximal part not visible). Stipites each with 5 marginal setae, apically with palp-like extension, each with 5 sensilla (Fig. 3D). Mentum with 6 (3+3) setae arranged in 2 longitudinal rows. Lamellae linguales each with 2 short setae, mesal margins apically with hair-like structures (Fig. 3D, G). Mandibles internalized, not visible externally (Fig. 3A, B). — **Body-rings:** Collum longer than following tergite, covering posterior part of head, anterior margin almost straight. Collum covered by long setae and laterally with scale-like sculpturing (Fig. 3A, B). Each body-ring consisting of free tergite (1), pleurites (2) and sternites (2) (Fig. 4A–C). Body-rings 2–4 shorter than following body-rings. Tergites clearly divided into prozonite and metazonite (Fig. 4A, B). Prozonite

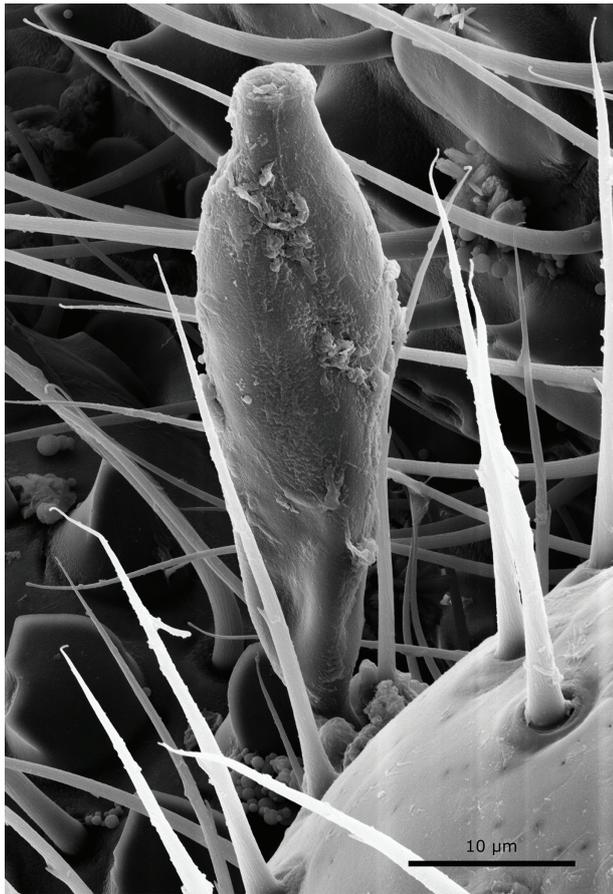


Figure 6. Fungus in amphomorph stage on antennomere 4 of the male holotype (MNHNC 8387) of *Notorhinus floresi* sp. nov.

narrower than metazonite, covered by circular cylinder/pillar-shaped sculpturing, lateral sculpturing becoming more acuminate, anterior margin with scale-like sculpturing, with few setae along anterior and posterior margin (Fig. 4A, B). Metazonite arched, circular/cylindrical sculpture restricted to anterior and lateral areas, resulting in a crown-shaped smooth dorsal area. Metazonite covered by setae (Fig. 4A, B). Posterior margin of metazonite (limbus) with 2 irregular rows of fluke-shaped sculptures (Fig. 4D). Ozopores from body-ring 5 onwards, positioned laterally in posterior half of metazonite, slightly elevated, surrounded by a ring of setae, with 2 posterior spines and 3 setae between spines (Fig. 4E). Pleurites almost rectangular, anteriorly and posteriorly rounded, laterally slightly curved towards legs. Pleurites anteriorly covered by setae and circular/cylindrical sculptures, posterior lateral sculpturing acuminate, anterior part of pleurite covered by flat scale-like sculptures (Fig. 4C). Sternites rectangular with a transverse elevation projecting between the legs' coxae. Margins of this elevation with scale-like sculpturing, spiracles located laterally of legs (Fig. 4C). — **Telson:** Preanal ring ca. as long as preceding body-ring, posteriorly rounded in dorsal view, covered by setae. Cylindrical sculpture restricted to lateral and ventral part and the anterior margin, dorsal surface without sculpture (Fig. 4F). Anal valves (paraprocts) covered by setae, proximally with scale-like sculpturing. Subanal

scale (hypoproct) present, with few setae and flat scale-like sculpture (Fig. 4F). — **Legs:** Leg pairs 1 and 2 with 6 podomeres: coxa, prefemur, femur, postfemur, tibia and tarsus. Coxae of leg-pair 1 fused to sternite (coxosternite) (Fig. 3G). From leg-pair 3 onwards with coxal sacs and short additional podomere (trochanter) between coxa and prefemur: Prefemur = tarsus > femur = coxa > postfemur = tibia > trochanter (Fig. 4G). Coxae almost touching mesally. Podomeres with few long setae (Fig. 4G). Tarsal claw bifurcated, ventral branch ca. 2/3 of length of dorsal branch on anterior legs (Fig. 4H), ventral branch decreasing in size on posterior legs. Last body-ring anterior of telson apodous. — **Male sexual characters:** Male gonopores on pseudopenes situated posteriorly on coxae of leg-pair 2 (Fig. 5A), pseudopenis knob-like/cone-shaped in ventral view (Fig. 5B), latero-posterior surface excavated with membranous surfaces (Fig. 5C). Leg-pair 9 and 10 modified to leg-like gonopods (Fig. 5D). Anterior gonopods with 7 podomeres, tapering distally. Each podomere with few setae arranged in a row. Podomere 1 with 2 anterior setae, podomere 2 with 1 anterior seta, podomere 3 with 3 anterior setae, podomere 4 with 1 anterior and 1 posterior setae, podomere 5 with 1 lateral and 4 posterior setae, podomere 6 with 2 lateral and 3 posterior setae, podomere 7 with 4 posterior setae (Fig. 5D, E). Apical podomere (7) flap-like, forming a sheath engulfing the tip of the posterior gonopod (Fig. 5F). Posterior gonopod with 7 podomeres, tapering distally. Podomeres 1–4 without setae, podomere 5 with 1 lateral seta, podomere 6 with 2 lateral setae, podomere 7 proximally with 1 posterior seta (Fig. 5D, E). Apical podomere (7) elongated, forming 3 branches, 1 short and pointed (spinous) posterior branch, and 2 long anterior branches, both proximally thin cylindrical, distally flattened (laminar) and paddle-shaped, almost triangular with sinuate margin. The 2 long branches rest in the sheath formed by anterior gonopod (Fig. 5F). — **Female sexual characters:** Female gonopores inconspicuous, behind 2nd coxa.

Remarks. A fungus in amphomorph state was located on the 4th antennomere (left) of the male holotype (Fig. 6).

3.1.4. *Notorhinus* sp.

Figs 7, 8

Material examined. 1♀ (MNHNC 8390); CHILE: Biobío, El Natri, Lanalhue, Contulmo; 37.9°S 73.27°W; 23.iv.2020; Edgardo Flores leg. (e27).

Remarks. Body elongate and thread-like, pale white (Fig. 7), 11.5 mm long, 0.37 mm wide, br80+T. Head pyriform (Fig. 8A) with incised labrum (Fig. 8B) and antennae elbowed between antennomere 4 and 5 (Fig. 8C). Sensilla basiconica on antennomere 5 absent, sensilla basiconica on antennomere 6 arranged in oval field (Fig. 8C), 6 spiniform sensilla basiconica on antennomere 7 arranged in single row (Fig. 8D) (2 rows in *N. floresi* sp. nov.). Lateral metazonal sculpturing present (Fig. 8F).



Figure 7. *Notorhinus* sp., female (MNHNC 8390). **A** Habitus, lateral view. **B** Head and anterior body, lateral view.

Two backwards projecting spines behind the ozopores and 3 setae between spines (Fig. 8G) as present in *N. floresi* sp. nov. Fluke-shaped projections on the posterior margin of metazonites (limbus) (Fig. 8H) as in *N. floresi* sp. nov. Because only a single female specimen of *Notorhinus* sp. (MNHNC 8390) is known, we refrain from describing it as a new species until male specimens are available.

4. Discussion

4.1. Affinities of *Notorhinus* gen. nov. to *Illacme* Cook and Loomis, 1928

Notorhinus gen. nov. is distinct from the remaining Siphonorhinidae genera in its morphology as pointed out in the genus diagnosis. However, it shows morphological similarities to the North American genus *Illacme* Cook and Loomis, 1928 or at least one of its members (Table 1). *Notorhinus* gen. nov. shares with *Illacme* the structure of the gonopods with 7 podomeres in both pairs, the absence of sensory pits on the antennae and the presence of a lateral group of spiniform sensilla basiconica on antennomere 7, reaching between the apical cones. Furthermore, the single isolated spiniform sensilla basiconica on the anterior and posterior margin of antennomere 7 might also be present in *Illacme plenipes* Cook and Loomis, 1928 (compare Marek et al. 2012, fig. 13).

Notorhinus gen. nov. shares with *Illacme plenipes* the two backwards projecting spines behind the ozopores with three setae in between, but the spines are shorter and stouter than in *I. plenipes*. *Notorhinus* gen. nov. also shares with *I. plenipes* the projections on the posterior margin of the metazonites (limbus), but in *Notorhinus* gen. nov. these projections are rather fluke-shaped and not as well developed as in *I. plenipes*, in which these have been described as anchor-shaped (Marek et al. 2012, 2016). Moreover, *Notorhinus floresi* sp. nov. shares with *I. plenipes* the presence of 3 branches (articles) on the posterior gonopod's apical podomeres, two laminate flattened ones and one spinous. *N. floresi* sp. nov. also shares with *I. plenipes* the straight posterior margin of the metazonite, while the margin is sinuate in *Illacme tobini* Marek, Shear and Krejca, 2016 and *Notorhinus* sp. (MNHNC 8390). Therefore, we suggest that the South American *Notorhinus* gen. nov. is more closely related to the North American *Illacme*, than to the Asian and African genera. However, most of these characters are not well studied in Siphonorhinidae, except for *Illacme* thanks to Marek et al. (2012, 2016).

4.2. Biogeography and habitat preferences of Siphonorhinidae in the Americas

Notorhinus floresi sp. nov. and the undescribed *Notorhinus* species (MNHNC 8390) occur in Chile at ca. 38° South, while *Illacme plenipes* and *Illacme tobini* occur

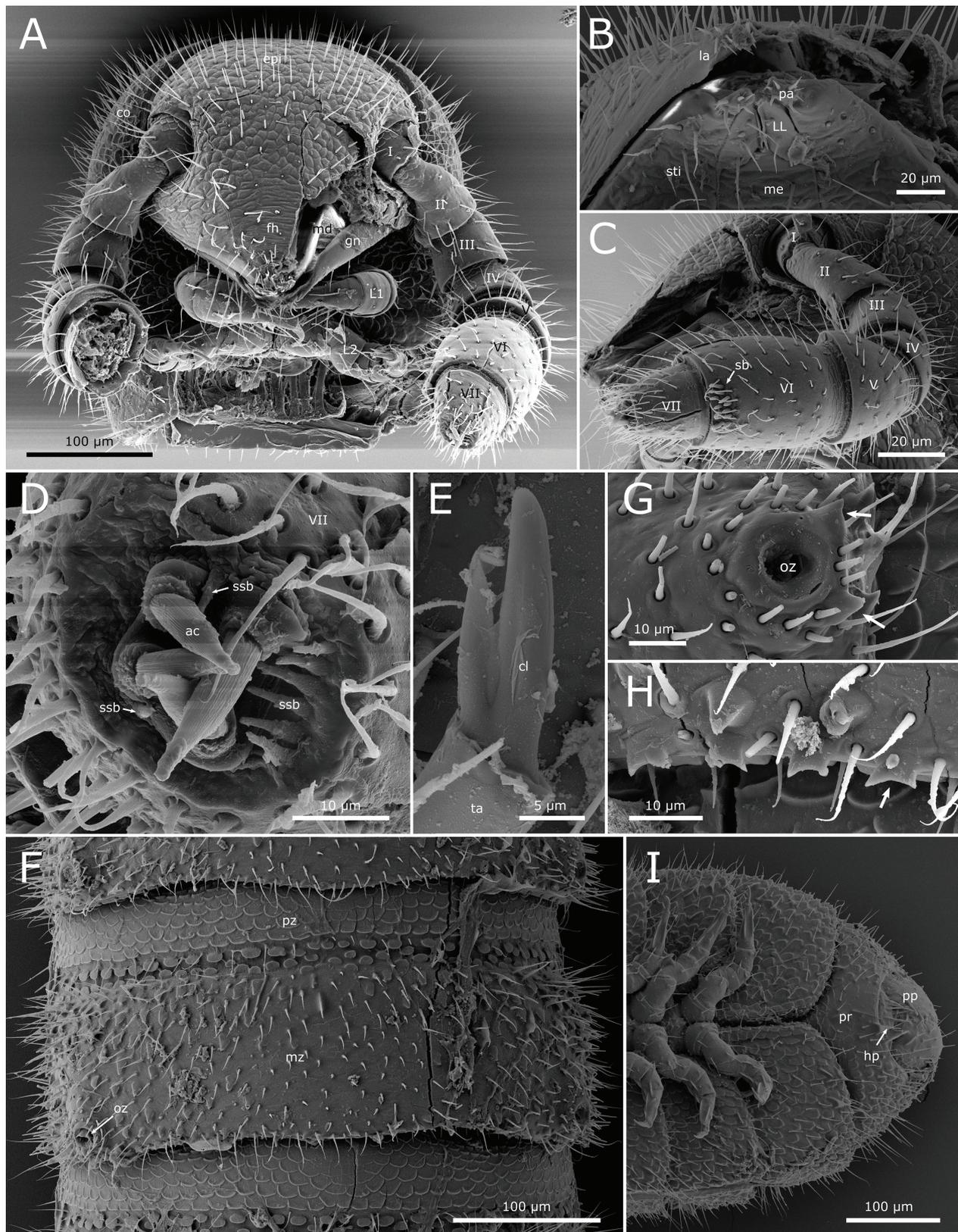


Figure 8. *Notorhinus* sp., female (MNHNC 8390), SEM. **A** Head and anterior body-rings, frontal view. **B** Apical parts of gnathochilarium and labrum, ventral view. **C** Left antenna, lateral view. **D** Antennomere 7 with apical sensory structures. **E** Tarsal claw of mid-body leg. **F** Mid-body tergite, dorsal view. **G** Ozopore, lateral view, arrows indicate spines behind ozopore. **H** Posterior tergal margin (limbus), dorsal view, arrow indicates fluke-shaped sculpture. **I** Posterior body-rings and telson, ventral view. Abbreviations: I–VII = antennomeres, ac = apical cone, cl = tarsal claw, co = collum, ep = epicranium, fh = forehead, gn = gnathochilarium, hp = hypoproct, L1 = leg-pair 1, L2 = leg-pair 2, la = labrum, LL = lamella lingualis, md = mandible gnathal lobe, me = mentum, mz = metazonite, oz = ozopore, pp = paraproct, pr = preanal ring, pz = prozonite, sb = sensilla basiconica, ssb = spiniform sensilla basiconica, sti = gnathochilarial stipes, ta = tarsus.

Table 1. Comparison of morphological characters in *Notorhinus* **gen. nov.** and *Illacme* Cook and Loomis, 1928 based on Marek et al. (2016: table 1). n indicates the number of specimens measured. Asterisk (*) indicates characters not included in Marek et al. (2016: table 1).

	<i>Notorhinus floresi</i> sp. nov.	<i>Notorhinus</i> sp. (e27)	<i>Illacme plenipes</i> Cook and Loomis, 1928	<i>Illacme tobini</i> Marek, Shear and Krejca, 2016
Number of body-rings* (T = telson)	37–54 + T [n = 6]	80 + T [n = 1]	84–192 + T (Marek et al. 2012: table 1) [n = 8]	108 + T (Marek et al. 2016: table 2) [n = 1]
Length*	8.9–13.8 mm [n = 6]	11.5 mm [n = 1]	13.4–40.4 mm (Marek et al. 2016: table 3) [n = 8]	19.7 mm (Marek et al. 2016: table 2) [n = 1]
Antennae, Antennomere 5 sensilla basiconica*	Absent	Absent	Present, row along apical margin (Marek et al. 2012: fig. 14; Marek et al. 2016: fig. 3B)	Present, row along apical margin (Marek et al. 2016: fig. 3A)
Antennae, Antennomere 6 sensilla basiconica*	Present, in field in some distance from apical margin (Fig. 3E)	Present, in two rows close to apical margin (Fig. 8C)	Present, row along apical margin (Marek et al. 2012: fig. 14; Marek et al. 2016: fig. 3B)	Present, row along apical margin (Marek et al. 2016: fig. 3A)
Antennae, Antennomere 7, spiniform sensilla*	In cluster of 8 (Fig. 3F)	In row of 6 (Fig. 8D)	In cluster of 5 (Marek et al. 2012: fig. 13)	In cluster of 4 (Marek et al. 2016: 18)
Metazonite/prozonite	Metazonite wider than prozonite (Fig. 4A)	Almost equal in width (Fig. 8F)	Almost equal in width (Marek et al. 2016: fig. 10B)	Metazonite wider than prozonite (Marek et al. 2016: fig. 10A)
Metazonite sculpture (except margin)*	Extending laterally and dorsally (Fig. 4A, B)	Restricted to lateral portion (Fig. 8F)	Absent (Marek et al. 2016: fig. 10B)	Absent (Marek et al. 2016: fig. 10A)
Spines behind ozopore (on paraproct)	2 short backwards projecting spines (Fig. 4E)	2 short backwards projecting spines (Fig. 8G)	2 large backwards projecting spines (Marek et al. 2016: fig. 10D)	Absent (Marek et al. 2016: fig. 10C)
Sculpture on metazonite posterior margin (limbus)	Fluke-shaped spines (Fig. 4D)	Fluke-shaped spines (Fig. 8H)	Anchor-shaped spines (Marek et al. 2016: fig. 10F)	Quadrate spines (Marek et al. 2016: fig. 10E)
Metazonite posterior margin shape	Straight (Fig. 4A)	Sinuate (Fig. 8F)	Straight (Marek et al. 2016: fig. 10B)	Sinuate (Marek et al. 2016: fig. 10A)
Telson sculpture/spines	Lateral and ventral surfaces (Fig. 4F)	Lateral surface only (Fig. 8I)	All surfaces (Marek et al. 2016: fig. 11B)	Lateral surface only (Marek et al. 2016: fig. 11A)
Hypoproct setation	> 2 setae (Fig. 4F)	> 2 setae (Fig. 8I)	> 2 setae (Marek et al. 2016: fig. 11B)	2 setae (Marek et al. 2016: fig. 11A)
Tarsal claw bifurcation, length of smaller claw*	Long (2/3 of length of claw) (Fig. 4H)	Long (2/3 of length of claw) (Fig. 8E)	Long (2/3 of length of claw) (Marek et al. 2012: fig. 27)	Long (2/3 of length of claw) (Marek et al. 2016: fig. 17C)
Anterior gonopod, podomere 3, setation	3 setae (Fig. 5E)	?	6 setae (Marek et al. 2016: fig. 9B, D, F)	2 setae (Marek et al. 2016: fig. 9A, C, E)
Anterior gonopod apex, setae/spines	5 setae (Fig. 5F)	?	3 setae (Marek et al. 2016: fig. 9D, F)	9 setae (Marek et al. 2016: fig. 9C, E)
Posterior gonopod apex, branches (articles)	Bundle of 3 styliiform branches (Fig. 5F)	?	Bundle of 3 styliiform branches (Marek et al. 2016: fig. 11D)	Bundle of 4 styliiform branches (Marek et al. 2016: fig. 11C)
Posterior gonopod apex, margin of apically flattened branches*	Sinuate (Fig. 5F)	?	Serrated (Marek et al. 2012: fig. 12)	Serrated (Marek et al. 2016: fig. 11C)

in California (USA) at ca. 37° North (Marek et al. 2012, 2016). All three species occur close to the Pacific coast mostly in wet subterranean/poorly lighted microhabitats within temperate to Mediterranean humid native woodlands (Veblen et al. 2007; Marek et al. 2012). Thus, the known distribution of Siphonorhinidae in America is antitropical (amphitropical), meaning that the taxon shows a disjunct distribution with representatives occurring at similar latitudes in the northern and southern hemisphere, but not in the tropical region in between (Hubbs 1952). Examples of antitropical distributions include many marine taxa, like fishes (Randall 1981), whales (Barnes 1985), echinoderms (Naughton et al. 2014), mollusks

(Koufopanou 1999; Hilbish et al. 2000), and terrestrial plants from North and South America (Raven 1963; Simpson et al. 2017), but also terrestrial insects like some wingless darkling beetles from Africa and Europe (Kamiński et al. 2021) and bees from North and South America (Wilson et al. 2014; Freitas et al. 2022). Observing such a distribution in millipedes is remarkable as these soil-organisms show a very limited dispersal ability and are often adapted to certain micro-habitats (Sierwald and Bond 2007; Golovatch and Kime 2009). The exchange between the North and South American flora and fauna, referred to as Great American Biotic Interchange (GABI), is often associated with the rise of the Isthmus of Pana-

ma in the late Pliocene about 3 million years ago (Leigh et al. 2014). However, for some taxa it has been shown that this exchange probably already started earlier in the Miocene (Cody 2010; Pinto-Sánchez et al. 2011; Wilson et al. 2014). The antitropical distribution of the American Siphonophoridae might be explained by a once wider distribution in North and South America followed by extinction events in the tropics due to changes in climate and environmental conditions. However, the observed pattern might also be due to incomplete sampling, as these enigmatic animals, typically restricted to small soil habitats, are often overlooked, with *I. plenipes* collected for the first time since its description (Cook and Loomis 1928) in 2006 (Marek and Bond 2006), a second *Illacme* species only described recently (Marek et al. 2016), and the specimens described here only discovered in 2019 and 2020. Due to their restriction to very small habitats, Shelley (1996: 22) concluded that to find Siphonophorida “one must not only investigate the right habitat but also fortuitously dislodge the one or few rocks or logs that shelter them”. Thus, “the probability of discovering siphonophorids is low and apparently chiefly a matter of chance” (Shelley 1996: 22). Furthermore, the group received only little attention by taxonomists (Jeckel 2001). Antitropical distributions have been assumed for other taxa, which had to be corrected later, when species were discovered in the tropics (e.g. Harris and Armitage 1997; Holzenthal and Harris 2002). Currently, we exclude an anthropogenic introduction of the species to Chile, as there is no species of the order known to have been expanded through human activities. This is further supported by the rarity of these millipedes across the globe (Marek et al. 2012), and the habitat in a small relict of native forest in which they were found.

Specimens of *N. floresi* **sp. nov.** were encountered in a small, fragmented patch of native forest between eucalypt plantations near Camaravida, which lays within the Chilean Winter Rainfall–Valdivian Forest hotspot. The temperature and precipitation in this biodiversity hotspot is affected by anthropogenic climate change, and especially smaller protected areas appear to be vulnerable in this region (Fuentes-Castillo et al. 2020). The siphonophorid millipedes might have evolved in mild consistent habitats and climate for hundred millions of years and thus they are dependent on certain microhabitats and climatic conditions (Marek et al. 2012). Therefore, climate change and habitat loss pose a serious risk to them, thus protection and preservation of these habitats is essential.

4.3. The Diplopoda fauna of Chile

The Chilean Diplopoda fauna shows predominantly Gondwanan affinities, with closely related taxa occurring in South Africa, Australia, and other Gondwanan landmasses, rather than in other South American regions (Shelley and Golovatch 2011; Golovatch 2014). With the addition of Siphonophorida a total of six native orders can be found in Chile (Chordeumatida, Polydesmida, Polyxenida, Polyzoniida, Siphonophorida and Spirost-

reptida) (Parra-Gómez 2022). This is the first record of a new millipede order for the country in 65 years, the last addition was the order Polyzoniida in 1957 (Chamberlin 1957). Furthermore, the order Julida has been introduced to Chile, with 5 species native to Europe, and can even be found in natural habitats inside national parks (Golovatch 2014; Parra-Gómez 2022). The native millipede species usually have a narrow distribution, and are often endemic, with the highest diversity in the temperate regions at mid-latitudes (Parra-Gómez and Fernández 2022). However, the knowledge on their distribution remains obscure, with several latitudinal gaps without any records and fragmentary distributions for various taxa (Parra-Gómez 2022).

5. Conclusion

The discovery and description of *Notorhinus* **gen. nov.** is a significant contribution to our knowledge of the Colobognatha, as this is the first record of the order Siphonophorida in Chile and of the family Siphonophoridae in South America. *Notorhinus* **gen. nov.** represents the most southern occurrence of the family Siphonophoridae. While *Notorhinus* **gen. nov.** is morphologically distinct from the remaining Siphonophoridae genera it shares several somatic and sexual characters with the North American genus *Illacme* Cook and Loomis, 1928.

6. Acknowledgements

We would like to express our deepest gratitude to Edgardo Flores for his collection efforts and for providing the specimens studied here, as well as photographs of the specimens and their habitat. Furthermore, we would like to thank Pooja Avinipully Anilkumar (ZFMK) for taking some additional SEM images of *Notorhinus floresi* **sp. nov.**, and Jorge Pérez Schultheiss (MNHN, Chile) for logistic support. LM thanks Thomas Wesener (ZFMK) for discussions and encouragement. We thank Paul Marek for discussions. We are grateful to Andy Sombke and Klaus-Dieter Klass, and the two reviewers Henrik Enghoff and Zoltan Korsós for valuable comments on the manuscript.

7. References

- Arroyo MTK, Marquet PA, Marticorena C, Simonetti JA, Cavieres L, Squeo F, Rozzi R (2004) Chilean winter Rainfall–Valdivian forests. In: Mittermeier RA, Gil PR, Hoffmann M, Pilgrim J, Brooks T, Mittermeier CG, Lamoreux J, da Fonseca GAB (Eds) Hotspots revisited: Earth’s biologically wealthiest and most threatened ecosystems. CEMEX, Mexico D.F.: 99–103.
- Attems CMT (1930) Myriopoden der Kleinen Sunda-Inseln, gesammelt von der Expedition Dr. Rensch. Mitteilungen aus dem Zoologischen Museum in Berlin 16(1): 117–184.
- Attems CMT (1936) Diplopoda of India. Memoirs of the Indian Museum 11(4): 133–323.

- Attems CMT (1938) Die von Dr. C. Dawydoff in französisch Indochina gesammelten Myriopoden. Mémoires du Muséum National d'Histoire Naturelle 6(2): 187–353.
- Barnes LG (1985) Evolution, taxonomy and antitropical distributions of the porpoises (Phocoenidae, Mammalia). Marine Mammal Science 1(2): 149–165.
- Brandt JF (1837) Note sur un ordre nouveau de la classe des myriapodes et sur l'établissement des sections de cette classe d'animaux en général. Bulletin Scientifique de L'Académie Impériale des Sciences de Saint-Petersbourg 1: 178–179.
- Chamberlin RV (1957) The Diplopoda of the Lund University and California Academy of Sciences expeditions. Lunds Universitets Arsskrift, Ny Följd, Avd. 2: 1–44.
- Cody S, Richardson JE, Rull V, Ellis C, Pennington RT (2010) The great American biotic interchange revisited. Ecography 33(2): 326–332. <https://doi.org/10.1111/j.1600-0587.2010.06327.x>
- Cook OF, Collins GN (1895) The Craspedosomatidae of North America. Annals of the New York Academy of Sciences 9: 1–100.
- Cook OF, Loomis HF (1928) Millipedes of the order Colobognatha, with descriptions of six new genera and type species, from Arizona and California. Proceedings of the United States National Museum 72(18): 1–26.
- Enghoff H, Golovatch SI, Short M, Stoev P, Wesener T (2015) Diplopoda – taxonomic overview. In: Minelli A (Ed.) Treatise on Zoology – Anatomy, Taxonomy, Biology. The Myriapoda, Volume 2. Brill, Leiden, pp. 363–453. https://doi.org/10.1163/9789004188273_017
- Freitas FV, Branstetter MG, Casali DM, Aguiar AJ, Griswold T, Almeida EA (2022) Phylogenomic dating and Bayesian biogeography illuminate an antitropical pattern for eucerine bees. Journal of Biogeography 49(6): 1034–1047. <https://doi.org/10.1111/jbi.14359>
- Fuentes-Castillo T, Hernández HJ, Plissock P (2020) Hotspots and ecoregion vulnerability driven by climate change velocity in Southern South America. Regional Environmental Change 20(1): 1–15. <https://doi.org/10.1007/s10113-020-01595-9>
- Gervais P (1844) Études sur les Myriapodes. Annales des Sciences Naturelles, Série 3(2): 51–80.
- Golovatch SI (2009) Millipedes (Diplopoda) in extreme environments. In: Golovatch SI, Makarova OL, Babenko AB, Penev LD (Eds) Species and Communities in Extreme Environments: Festschrift towards the 75th Anniversary and a Laudatio in Honour of Academician Yuri Ivanovich Chernov. Pensoft & KMK Scientific Press, Moscow, pp. 87–112.
- Golovatch SI (2014) On some new or poorly-known millipedes from Chile and Argentina (Diplopoda). Russian Entomological Journal 23: 249–281. <https://doi.org/10.15298/RUSENTJ.23.4.02>
- Golovatch SI, Kime RD (2009) Millipede (Diplopoda) distributions: A review. Soil Organisms 81(3): 565–597.
- Golovatch SI, Evsyukov A, Reip HS (2015) Colobognatha millipedes in the Caucasus (Diplopoda: Polyzoniida, Platydesmida, Siphonocryptida). Zootaxa 3972(2): 250–266. <https://doi.org/10.11646/zootaxa.3972.2.6>
- Harris SC, Armitage BJ (1997) New member of the Chilean genus *Nothotrichia* from North America (Trichoptera: Hydroptilidae). Proceedings of the 8th International Symposium on Trichoptera: 123–128.
- Hilbish TJ, Mullinax A, Dolven SI, Meyer A, Koehn RK, Rawson PD (2000) Origin of the antitropical distribution pattern in marine mussels (*Mytilus* spp.): routes and timing of transequatorial migration. Marine Biology 136(1): 69–77. <https://doi.org/10.1007/s002270050010>
- Hoffman RL (1980) Classification of the Diplopoda. Muséum d'Histoire Naturelle, Geneve, 237 pp.
- Holzenthal RW, Harris SC (2002) New species of *Nothotrichia* Flint (Trichoptera: Hydroptilidae) from Brazil and Costa Rica. Proceedings of the Entomological Society of Washington 104(1): 106–110.
- Hubbs CL (1952) Antitropical distribution of fishes and other organisms. Symposium on problems of bipolarity and of pantemperate faunas. Proceedings of the Seventh Pacific Science Congress 3: 324–329.
- Jeckel CAW (2001) A bibliographic catalogue of the Siphonophorida (Diplopoda). Myriapod Memoranda 3: 44–71.
- Kamiński MJ, Smith AD, Kanda K, Iwan D, Kergoat GJ (2022) Old origin for an European-African amphitropical disjunction pattern: New insights from a case study on wingless darkling beetles. Journal of Biogeography 49(1): 130–141. <https://doi.org/10.1111/jbi.14288>
- Koufopanou V, Reid DG, Ridgway SA, Thomas RH (1999) A molecular phylogeny of the patellid limpets (Gastropoda: Patellidae) and its implications for the origins of their antitropical distribution. Molecular Phylogenetics and Evolution 11(1): 138–156. <https://doi.org/10.1006/mpev.1998.0557>
- Latreille PA (1802) Histoire Naturelle, Générale et Particulière des Crustacés et des Insectes. Ouvrage Faisant suite à l'Histoire Naturelle Générale et Particulière, Composée par LeClerc de Buffon, et Rédigée par C.S. Sonnini, Membre de Plusieurs Sociétés Savantes. Dufart, Paris. Vol. 3, 468 pp.
- Leigh EG, O'Dea A, Vermeij GJ (2014) Historical biogeography of the Isthmus of Panama. Biological Reviews of the Cambridge Philosophical Society 89(1): 148–172. <https://doi.org/10.1111/brv.12048>
- Marek PE, Bond JE (2006) The rediscovery of *Illacme plenipes*, the leggiest animal on the planet. Nature 441: 707.
- Marek PE, Krejca JK, Shear WA (2016) A new species of *Illacme* Cook & Loomis, 1928 from Sequoia National Park, California, with a world catalog of the Siphonorhinidae (Diplopoda, Siphonophorida). ZooKeys 626: 1–43. <https://doi.org/10.3897/zookeys.626.9681>
- Marek PE, Shear WA, Bond JE (2012) A redescription of the leggiest animal, the millipede *Illacme plenipes*, with notes on its natural history and biogeography (Diplopoda, Siphonophorida, Siphonorhinidae). ZooKeys 241: 77–112. <https://doi.org/10.3897/zookeys.241.3831>
- Mauriès JP, Silva F (1971) Colobognathes du chili. I. Espèces nouvelles du genre *Siphonotus* Brandt (Diplopoda). Bulletin du Muséum National d'Histoire Naturelle, 2e Série, Tome 42(5): 887–902.
- Mittermeier RA, Turner WR, Larsen FW, Brooks TM, Gascon C (2011) Global biodiversity conservation: The critical role of hotspots. In: Zachos FE, Habel JC (Eds) Biodiversity Hotspots – Distribution and Protection of Conservation Priority Areas. Springer, Heidelberg, pp. 3–22. <https://doi.org/10.1007/978-3-642-20992-5>
- Moritz L, Blanke A, Hammel JU, Wesener T (2021) First steps toward suctorial feeding in millipedes: Comparative morphology of the head of the Platydesmida (Diplopoda: Colobognatha). Invertebrate Biology 140(2): e12312. <https://doi.org/10.1111/ivb.12312>
- Moritz L, Borisova E, Hammel JU, Blanke A, Wesener T (2022) A previously unknown feeding mode in millipedes and the convergence of fluid feeding across arthropods. Science Advances 8(7): eabm0577. <https://doi.org/10.1126/sciadv.abm0577>
- Moritz L, Wesener T, Wipfler B (2023) Habitat, aggregations and postembryonic development of the siphonocryptid millipede *Hirudicryptus canariensis* (Loksa, 1967) in the laurel forest of Tenerife (Diplopoda: Siphonocryptida). Graellsia 79(1): e180. <https://doi.org/10.3989/graellsia.2023.v79.347>

- Naughton KM, O'Hara TD, Appleton B, Cisternas PA (2014) Antitropical distributions and species delimitation in a group of ophiocomid brittle stars (Echinodermata: Ophiuroidea: Ophiocomidae). *Molecular Phylogenetics and Evolution* 78: 232–244. <https://doi.org/10.1016/j.ympev.2014.05.020>
- Newport G (1844) [Untitled]. *Proceedings of the Linnean Society of London* 1: 191–196.
- Olson D, Dinerstein E, Wikramanayake E, Burgess N, Powell G, Underwood E, d'Amico J, Itoua I, Strand H, Morrison J, Loucks C, Allnutt T, Ricketts T, Kura Y, Lamoreux J, Wettengel W, Hedao P, Kassem K (2001) Terrestrial ecoregions of the world: A new map of life on earth. *BioScience* 51: 933–938. [https://doi.org/10.1641/0006-3568\(2001\)051\[0933:TEOTWA\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2)
- Parra-Gómez A (2022) Catálogo de los milpiés (Myriapoda: Diplopoda) de Chile. *Revista Chilena de Entomología* 48(3): 451–504. <https://doi.org/10.35249/rche.48.3.22.02>
- Parra-Gómez A, Fernández LD (2022) Filling gaps in the diversity and biogeography of Chilean millipedes (Myriapoda: Diplopoda). *Arthropod Systematics & Phylogeny* 80: 561–573. <https://doi.org/10.3897/asp.80.e86810>
- Pinto-Sánchez NR, Ibáñez R, Madriñán S, Sanjur OI, Bermingham E, Crawford AJ (2012) The great American biotic interchange in frogs: multiple and early colonization of Central America by the South American genus *Pristimantis* (Anura: Craugastoridae). *Molecular Phylogenetics and Evolution* 62(3): 954–972. <https://doi.org/10.1016/j.ympev.2011.11.022>
- Pocock RI (1887) On the classification of the Diplopoda. *Annals and Magazine of Natural History* 5(20): 283–295.
- Pocock RI (1894) Chilopoda, Symphyla and Diplopoda from the Malay Archipelago. In: Weber M (Ed.) *Zoologische Ergebnisse einer Reise in Niederländisch Ost-Indien* Band 3, Leiden, pp. 307–404.
- Randall JE (1981) Examples of antitropical and antiequatorial distribution of Indo-West-Pacific fishes. *Pacific Science* 35(3): 197–209.
- Raven PH (1963) Amphitropical relationships in the floras of North and South America. *The Quarterly Review of Biology* 38(2): 151–177. <https://doi.org/10.1086/403797>
- Read HJ, Enghoff H (2009) The order Siphonophorida – A taxonomist's nightmare? Lessons from a Brazilian collection. *Soil Organisms* 81(3): 543–556
- Read HJ, Enghoff H (2018) Siphonophoridae from Brazilian Amazonia Part 1 – The genus *Columbianum* Verhoeff, 1941 (Diplopoda, Siphonophorida). *European Journal of Taxonomy* 477: 1–23. <https://doi.org/10.5852/ejt.2018.477>
- Read HJ, Enghoff H (2019) Siphonophoridae from Brazilian Amazonia. Part 2 – Two new tree-climbing species of the genus *Siphonophora*, including one showing pilosity polymorphism (Diplopoda, Siphonophorida). *European Journal of Taxonomy* 496: 1–26. <https://doi.org/10.5852/ejt.2019.496>
- Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9(7): 671–675. <https://doi.org/10.1038/nmeth.2089>
- Shelley RM (1996) The milliped order Siphonophorida in the United States and northern Mexico. *Myriapodologica* 4(4): 22–33.
- Shelley RM, Hoffman RL (2004) A contribution on the South African millipede genus, *Nematozonium* Verhoeff, 1939 (Siphonophorida: Siphonorhinidae). *African Entomology* 12(2): 217–222.
- Shelley RM, Golovatch SI (2011) Atlas of myriapod biogeography. I. Indigenous ordinal and supra-ordinal distributions in the Diplopoda: Perspectives on taxon origins and ages, and a hypothesis on the origin and early evolution of the class. *Insecta Mundi* 0158: 1–134.
- Sierwald P, Bond JE (2007). Current status of the myriapod class Diplopoda (millipedes): taxonomic diversity and phylogeny. *Annual Review of Entomology* 52(1): 401–420. <https://doi.org/10.1146/annurev.ento.52.111805.090210>
- Silvestri F (1895) I Chilopodi ed i Diplopodi di Sumatra e delle isole Nias, Engano e Mentavei. *Annali del Museo Civico di Storia Naturale di Genova, Serie 2* 14: 707–760.
- Simpson MG, Johnson LA, Villaverde T, Guilliams CM (2017) American amphitropical disjuncts: Perspectives from vascular plant analyses and prospects for future research. *American Journal of Botany* 104(11): 1600–1650. <http://dx.doi.org/10.3732/ajb.1700308>
- Turk FA (1947) On a collection of diplopods from North India, both cavernicolous and epigeal. *Proceedings of the Zoological Society of London* 117: 65–78. <https://doi.org/10.1111/j.1096-3642.1947.tb00498.x>
- Veblen TT, Young KR, Orme AR (2007) *The physical geography of South America*. Oxford University Press, New York, 361 pp.
- Verhoeff KW (1939) Polydesmoideen, Colobognathen und Geophilomorphen aus Südafrika, besonders Drakensbergen, Natal. *Annals of the Natal Museum* 9(2): 203–224.
- Wesener T (2014) First records of the order Siphonophorida from Madagascar and Mauritius (Diplopoda). *Revue Suisse de Zoologie* 121(3): 415–423.
- Wesener T (2023) *Madagascarhinus*, a new genus of the family Siphonorhinidae with two new species from Madagascar (Diplopoda, Siphonophorida). *Zootaxa* 5278(1): 163–175. <https://doi.org/10.11646/zootaxa.5278.1.9>
- Wesener T, Moritz L (2018) Checklist of the Myriapoda in Cretaceous Burmese amber and a correction of the Myriapoda identified by Zhang (2017). *Check List* 14(6): 1131–1140. <https://doi.org/10.15560/14.6.1131>
- Wilson JS, Carril OM, Sipes SD (2014) Revisiting the Great American Biotic Interchange through analyses of amphitropical bees. *Ecography* 37(8): 791–796. <https://doi.org/10.1111/ecog.00663>
- Wong VL, Hennen DA, Macias AM, Brewer MS, Kasson MT, Marek P (2020) Natural history of the social millipede *Brachycybe lecontei* Wood, 1864. *Biodiversity Data Journal* 8: e50770. <https://doi.org/10.3897/BDJ.8.e50770>