# A NEW *LOPHOTURUS* SPECIES (DIPLOPODA, POLYXENIDA, LOPHOPROCTIDAE) FROM RODRIGUES ISLAND, THE REPUBLIC OF MAURITIUS: MORPHOLOGICAL AND MOLECULAR EVIDENCE

CUONG HUYNH<sup>1</sup> AND ANNEKE A. VEENSTRA<sup>1</sup>

<sup>1</sup>Centre for Cellular and Molecular Biology (CCMB), Deakin University, Burwood, Victoria 3125, Australia

Correspondence: Cuong Huynh, cuong.huynh@deakin.edu.au

**ABSTRACT**: A new penicillate millipede *Lophoturus porchi* sp. n. (Lophoproctidae) is described from Caverne de la Vierge, François Leguat Giant Tortoise and Cave Reserve, Rodrigues Island, Mauritius. A comparison of the body length, number of sensilla on the gnathochilarial palp, number of linguiform processes and structure of the labral surface as well as genetics based on the 18S and COI genes indicate that this is a new *Lophoturus* species.

Keywords: Penicillate millipede, Lophoturus, Rodrigues Island, Mauritius, phylogeny

## INTRODUCTION

The Mascarene Islands are a group of three islands in the Indian Ocean, east of Madagascar: Mauritius, Rodrigues and Reunion (Figure 1). The Mascarene Islands were the focus of many studies on penicillate millipede diversity in the 1960s (Condé & Jacquemin 1962; Nguyen Duy-Jacquemin & Condé 1967, 1969). Species found in this region include *Mauritixenus gracilicornis* Verhoeff 1939 (Nguyen Duy-Jacquemin & Condé 1967), *Mauritixenus betschi* Nguyen Duy-Jacquemin & Condé 1969, *M. borbonicus* (Condé & Jacquemin 1962), *M. pauliani* (Condé & Jacquemin 1962), *Silvestrus seminudus* Jones 1937, and *Saroxenus alluaudi* (Brolemann 1920) — all from the family Polyxenidae — as well as *Alloproctoides*  *dawydoffi* (Attems 1938), *A. remyi* Marquet and Condé 1950, and *Lophoturus madecassus* (Marquet & Condé 1950) from the family Lophoproctidae. Recent fieldwork in the cave 'Caverne de la Vierge', located in the François Leguat Giant Tortoise and Cave Reserve, Plaine Corail, in the southwest of Rodrigues Island, resulted in the discovery of an additional new lophoproctid species. In this paper, *Lophoturus porchi* sp. n. is described based on comparative morphology and a molecular study of the 18S and COI genes, all indicating that this is a new species.

## MATERIALS AND METHODS

Rodrigues Island is a small volcanic island about 108 km<sup>2</sup> in area located 560 km east of Mauritius Island. Penicillate



Figure 1: Locality map for Rodrigues Island, showing the location of Plain Corail containing the François Leguat Giant Tortoise and Cave Reserve.

millipedes from the genus *Lophoturus* (Lophoproctidae) were collected in November 2016 by the first author from dry leaf litter among boulders on the slopes, up to 15 m inside the entrance of the Caverne de la Vierge (Figure 2).

#### Morphological study

*Lophoturus* specimens were examined and measured using light microscopy and prepared for taxonomic illustration following the staining and slide mounting technique of Short and Huynh (2010). This technique was modified (see the paragraph below) to permit the extraction of DNA for genetic studies. The remaining cuticles of the specimens were mounted on slides for morphometric analysis as described in Huynh and Veenstra (2015). Scanning electron microscopy (SEM) followed the technique of Huynh and Veenstra (2018a). The holotype and paratypes are deposited in the Queensland Museum (QMS), Brisbane, Australia.

## Genetic study

The quantity of DNA extracted from three individuals of *Lophoturus* was determined using a NanoDrop 1000 Spectrophotometer (ND 1000V3.60 software)

following the manufacturer's instructions. Two genes were sequenced for this study: the 18S small subunit ribosomal RNA gene (primers 1F and 5R, White et al. 1990) and the mitochondrial cytochrome c oxidase subunit I gene, COI (primers dgLCO1490 and dgHCO2198, Meyer 2003). Both primer sets are conserved universal primers for these gene regions and are common molecular markers used for species-level identification. The 18S gene marker has been used to elucidate relationships among arthropod groups including crustaceans, insects and myriapods (Turbeville et al. 1991; Luan et al. 2005; Wesener et al. 2010, 2016). This region has also been used to help separate penicillate millipede species of the genera Lophoturus Brolemann 1931, Monographis Attems 1907 and Phryssonotus Scudder 1885 in combination with morphological characters (Huynh & Veenstra 2015, 2018a, 2018b, 2020). The COI region was included because it is commonly used in the Barcode of Life (2010-2020) for species identification. The polymerase chain reaction (PCR) protocol followed Huynh and Veenstra (2018a). Representative DNA sequences from Lophoturus porchi sp. n. have been deposited in GenBank with the following accession numbers for Lophoturus porchi sp. n.: MT664794



Figure 2: Entrance to 'Caverne de la Vierge'.

Family	Genus	Species	Collecting location	18S rRNA	COI
Lophoproctidae	Alloproctoides	Alloproctoides consonensis	Vietnam	MH729069	MH737737
		Alloproctoides dawydoffi	Vietnam	MH729070	MH737734
		Alloproctoides remyi	Mauritius	MH729071	MH737735
	Lophoturus	Lophoturus boondallus	Australia	MG210573	MG204536
		Lophoturus molloyensis	Australia	MG210574	MG204537
		Lophoturus porchi	Mauritius	MT664794	MT679994
		Lophoturus queenslandicus	Australia	MG210575	MG204535
Polyxenidae	Monographis	Monographis condorensis	Vietnam	MH729072	_
		Monographis dongnaiensis	Vietnam	KP255446	_
		Monographis phuquocensis	Vietnam	MG210571	_
		Monographis queenslandica	Australia	KF147166	_
	Polyxenus	Polyxenus fasciculatatus	Europe	AF173235	_
		Polyxenus lagurus	Europe	MF592763	_
	Unixenus	Unixenus corticolus	Australia	MG283313	_
		Unixenus intragramineus	Vietnam	MG210572	_
		Unixenus karajinensis	Australia	MF592754	_
		Unixenus mjobergi	Australia	MF592755	-
		Unixenus moniqueae	Vietnam	MH729073	_
Synxenidae	Phryssonotus	Phryssonotus australis	Australia	KY820871	_
		Phryssonotus novaehollandiae	Australia	KY820870	-
		Phryssonotus occidentalis	Australia	KY820872	_
Outgroups		Sphaeromimus musicus	Africa	FJ409961	-
		Procyliosoma leae	Australia	FJ409955	FJ409910
		Glomeridella minima	Europe	-	JN271878

Table 1: GenBank accession numbers of the partial sequences of 18S and COI of Lophoturus porchi, other penicillate millipedes and the outgroups that were used in the study of the genetic relationship.

(18S) and MT679994 (COI). BLAST search (http://www. ncbi.nlm.nih.gov) from the 18S and COI sequences of the new species was queried to find sequences of closely related species. All prior sequences from the BLAST search were aligned with new sequences from the studied species using BioEdit (Hall 1999). MEGA 7 (Kumar et al. 2016) was used to generate a maximum-likelihood tree with bootstrap values for determining the phylogenetic relationships. Numbers above branches represent bootstrap values. The GenBank accession numbers for the sequences from penicillate millipede species and outgroups are listed in Table 1.

### TAXONOMY

## Subclass Penicillata Latreille, 1831 Order Polyxenida Lucas, 1840 Family Lophoproctidae Silvestri, 1897 Genus Lophoturus Brolemann, 1931 Alloproctus Silvestri, 1948: 217. Alloproctinus Jeekel, 1963: 156. Type species: Lophoturus obscurus Brolemann, 1931

#### Generic diagnosis

The genus is recognised by the following characteristics: absence of eyes, antennal articles VII and VIII equal in length, four sensory cones reduced in size, gnathochilarium with medial palp only, coxal gland absent and claws simple. *Lophoturus* is characterised by 0 to 4 pairs of linguiform processes on each side of a median cleft of the labrum and antennal article VI with 3 thick sensilla (Ishii et al. 1999: 252, key).

The genus *Lophoturus* Brolemann, 1931 comprises 32 species (30 species and 2 subspecies); the species names and their distributions are shown in Table 2.

#### Lophoturus porchi sp. nov.

#### Material examined

Type specimens. Adult male holotype (QMS 113006) collected from the 'Caverne de la Vierge' (19.757683°S, 63.370097°E), elevation 30 m, in the François Leguat Giant Tortoise and Cave Reserve on Plaine Corail, located in the southwest of Rodrigues Island; collected by C. Huynh on 25 November 2016.

Paratypes: 3 adult females (QMS 113007–9), 1 adult male (QMS 113010) were collected from the same place and on the same date as the holotype.

#### Diagnosis

Adults 2.6–3.6 mm in length. Ommatidia absent. Antennal article VI with a conical sensillum and three long thick bacilliform sensilla. Labrum with three pairs of linguiform processes, labrum surface setose. Gnathochilarial palp with 40–44 sensilla (males), 18–20 sensilla (females).

#### Description

Body length: Holotype male body length 2.8 mm (Paratypes: male 2.6 mm, females 3.4–3.6 mm). Male caudal trichome bundle narrower in width, bundle slightly longer (0.6 mm) than in female (0.5 mm).

**Colouration:** Head with brown-red patches appeared laterally extending to vertex area of the head capsule; body light milky colour with contrasting white pleural trichomes, and lighter coloured caudal bundle (Figure 3).



Figure 3: A live specimen of Lophoturus porchi sp. n.

**Head:** Ommatidia absent. Vertex with two posterior trichome groups and a large medial gap. Each trichome group arranged in two rows: anterior row, curved slightly with the unevenly arranged trichomes of similar size; posterior row with 2–4 trichome sockets; a narrow medial space between these 2 rows. Holotype with vertex

posterior trichome groups with 16 sockets (left: L) and 18 sockets (right: R) in the anterior rows; four sockets (L) and two sockets (R) in the posterior rows (Figures 4A, I) (Paratypes with 16-22 sockets in the anterior rows and 2-4 in the posterior ones (Figure 5A)). Trichobothria: Trichobothrium sockets arranged unevenly; trichobothrium **b**, the largest socket located closest to head capsule edge in lateral position, trichobothrium a, a medium-sized socket located furthest from head capsule edge, trichobothrium c, the smallest socket located anterior to sockets a and b. Trichobothria a and b have typically thin sensory hairs with narrow cylindrical funicles compared with trichobothrium c, the latter with a claviform funicle. (Figures 4A, E; 5F). Antennae: Eight antennal articles, four reduced sensory cones, antennal articles VII and VIII equal in length (Figures 6A, 7A) typical of Lophoproctidae. Antennal article VI with 3 thick bacilliform sensilla (T) of different lengths: Ta short, located in anterior position; Ti the longest, located in the intermediate position; Tp medium-sized, located in posterior position; a conical sensillum (c) located next to Tp (Figures 6C, 7B). Antennal article VII with 2 long thick bacilliform sensilla with different lengths: Ta shorter than Tp; setiform sensillum (s) located distally and between Ta and Tp; a conical sensillum (c) located in posterior position next to Tp (Figures 6B, 7B). Clypeolabrum: With 12 setae (holotype), each seta 0.2 times as long as labrum width (paratypes with 11-15 setae). Labrum surface setose, with tiny, backward facing hairs; posterior margin of the labrum has a deep groove with a row of tiny setae located anteriorly; three pairs of linguiform processes with a median cleft between lobulated lamellae at anterior edge of labrum (Figures 4I, 5E). Gnathochilarium: medial palps only, 40 sensilla on each palp in holotype male (paratypes: males with 35 sensilla (an exception can be seen in the SEM of a male specimen showed 43 (Figure 5C)), females with 18–19 sensilla) (Figures 4F, G; 5D).

Trunk: Body with ten tergites, nine pleural projections, and telson excluding caudal bundle. 13 pairs of legs. Collum (Tergite 1): Trichome sockets forming two oval shapes laterally, a large medial gap. Lateral protuberances (the first pleural projections) with a small number of trichome sockets on each side (Figure 4B). Other tergites with a pair of pleural projections located anterolaterally (Figure 5A). Holotype with 61 (L) and 65 (R) trichome sockets on the collum. Lateral protuberances with eight (L) and nine (R) trichome sockets (Figure 4B) (Paratypes with 50-64 sockets, lateral protuberances with 6-9 sockets). Tergites 2-9 have two lateroposterior oval groups of trichome sockets separated by a small medial gap, and with a few sockets extending laterally. Tergite 10 with two lateroposterior oval groups of trichome sockets without extended sockets on both ends and with a large medial



Figure 4: Holotype male, Lophoturus porchi sp. n., **A**. Head capsule showing the vertex area (V), posterior vertex trichome sockets (pv) and sockets of trichobothria a, b and c; **B**. Collum (col) with lateral protuberances (Lp); **C**. Tergite 2 (T2) and **D**. Tergite 10 (T10), all show trichome socket patterns; **E**. Trichobothria a, b (thin, funicular, cylindrical structures) and c (claviform funicle); **F**. Left gnathochilarium ( $\mathcal{F}$ : 40 sensilla, showing 28 sensilla and 12 sockets of missing sensilla) and **G**. ( $\mathcal{Q}$ : 19 sensilla, showing 18 sensilla and 1 socket of missing sensillum); **H**. Posterior vertex trichome sockets (pv): left hand side (pv LHS) and right hand side (pv RHS); **I**. Clypeo-labrum: 12 setae, a deep groove with a row of tiny based setae located anteriorly, setose surface, 3 pairs of linguiform processes (lp) with a median cleft and lobulated margin anteriorly.

69



Figure 5: SEM images of *Lophoturus porchi* sp. n., **A**. Dorsal view of the head capsule, showing the vertex area (V), posterior vertex trichomes group (pv), trichobothria (tr), collum (col) with lateral protuberance (Lp); T2: tergite 2 and the associated pleural projections (pp); **B**. Ventral view, frons (f), labrum (l), gnathochilaria (g) and leg 1; **C**. Gnathochilarium in male showing 43 sensilla on the medial palp (some sockets of missing sensilla); **D**. Female with 18 sensilla; **E**. Clypeo-labrum (l) showing the deep groove (gr), a posterior row of setae (se), setose surface, 2 of the 3 pairs of the linguiform process (lp) visible and lobulated margin; **F**. Trichobothria a, b and c: Trichobothrium b, largest socket located closest to the edge of the head capsule in the lateral position, trichobothrium a, medium size socket located furthest from the edge of head capsule, trichobothrium c, smallest socket located anterior to sockets a and b.



Figure 6: Holotype male, *Lophoturus porchi* sp. n., A. Antennal articles VI, VII and VIII with 4 reduced sensory cones (sc), show the arrangement of sensilla on antennal articles VI and VII; **B**. Sensilla on antennal article VII: Two thick bacilliform sensilla (T), Ta - short (anterior) and Tp – longer length (posterior), setiform sensillum (s) between them and a conical sensillum (c) located in posterior position; **C**. Sensilla on antennal article VI: Three long thick bacilliform sensilla (Ta: shortest, Ti: longest and Tp: medium length), a conical sensillum (c) located in the posterior position. (Arrows indicate sensilla from B (article VII) and C (article VI).)

gap with few existing intermediate trichome sockets. Tergite 2 with 68 (L) and 69 (R) trichome sockets (Figure 4C), tergite 10 with 47 (L) and 46 (R) trichome sockets (Figure 4D) (Paratypes: tergite 2 with 51–67 sockets, tergite 10 with 30–51). Legs: Leg segmentation following Manton (1956). Each of Legs 1 and 2 without trochanter; leg 1 without tarsus 1. Chaetotaxy (setae on leg articles): Holotype male, coxa 1: three pubescent oval setae (Figures 8C, 9C), coxa 2: three, coxae 3–13: 4–6; pre-femur and femur: 1–2 pubescent oval setae and one smaller located in ventromedial position of femur; post-femur: a smaller pubescent oval setae (Figures 8A, 9A) (Paratypes with the

same chaetotaxy); last sternite: seven pubescent oval setae (Paratypes with 0-8 sockets). Tarsus 2 with a spine (Figure 8B). Male sex organs: two penes on coxa 2 (Figures 8A, 9A), coxal glands absent. Telotarsus-Claw: A simple robust structure, claw (c) with two laterodorsal denticles (ldd) equal in length and a small spine located on claw in the ventral position, called the basal denticle (bd) (Figures 8D, 9B). Telson: Dorsal ornamental trichome sockets arranged symmetrically on both sides of telson. Holotype with seven sockets of trichome a (Paratypes with 6–8) trichome *a*); a single trichome *b*, two large protruding basal sockets of trichome c: c1 and c3 (c2 absent) (Figures 8E, 9D). Caudal bundles: Type I as described by Condé and Nguyen Duy-Jacquemin (2008), male with a single caudal bundle, uniformly sized sockets carrying caudal trichomes; female, two caudal bundles: main dorsal structure, similar to that of male, and two laterosternal structures with finer nest trichome sockets (nest trichomes are a type of trichome used for building a nest to protect eggs (Huynh & Veenstra 2014)).

## Phylogenetic analysis

Sequences from *Lophoturus porchi* sp. n. were compared to other penicillate millipede sequences available from GenBank (Table 1). The maximum likelihood trees of 18S and COI generated by 1000 bootstrap replications from MEGA 7 (Kumar et al. 2016) yielded the phylogenetic trees with bootstrap values shown on the nodes of the clade. *Lophoturus porchi* sp. n. joined the same clades of *Lophoturus* species on both 18S (Figure 10A) and COI trees (Figure 10B). Our phylogenetic analysis indicates that these species are all well separated from one another.

## Remarks

Lophoturus porchi sp. n. is the second record of a Lophoturus species after L. madecassus (Marquet & Condé 1950) found on the Mascarene Islands, where intensive studies on penicillate millipedes were carried out in the 1960s. L. porchi sp. n. has so far only been found on Rodrigues Island. This new species differs from L. madecassus in the number of pairs of legs in adult — Lophoturus porchi sp. n. has 13 pairs of legs compared with L. madecassus with 11 pairs of legs. Despite Lophoturus porchi sp. n. being found in a cave, it lacks the features that characterise a troglomorphic species. Lophoturus porchi sp. n. is pigmented, and the antennae, legs and claw structures are not typical of those seen in the troglomorphic species such as L. speophilus Nguyen Duy-Jacquemin 2014. L. speophilus has elongate antennae, legs, and a telotarsus indicative of a cave-dwelling species (Nguyen Duy-Jacquemin 2014). Lophoturus porchi sp. n. and L. speophilus differ from other Lophoturus species in each



Figure 7: SEM images of *Lophoturus porchi* sp. n., **A**. Right antenna showing eight articles and the arrangement of sensilla on the articles VI and VII; **B**. Antennal article VII with two thick bacilliform sensilla, Ta (short) and Tp (long), setiform sensillum (s) between them and a conical sensillum (c) located in the posterior position; antennal article VII with three thick bacilliform sensilla (Ta, Ti and Tp) and a conical sensillum (c).



Figure 8: Holotype male, *Lophoturus porchi* sp. n., A. 2nd leg showing seven leg articles (co: coxa (1), pf: pre-femur (2), f: femur (3), pof: post-femur (4), tib: tibia (5), T1: tarsus 1 (6), T2: tarsus 2 (7), c: claw) and sex organ – penis (P); B. Spine on tarsus 2; C. A pubescent oval seta present on the coxa, pre-femur, the distal edge of femur and the posterior edge of the last sternite; a similar, smaller version of this seta present on the distal edge of the post-femur; D. Telotarsus–claw structures (lateral view), laterodorsal denticles (ldd), basal denticle (bd), small denticle (smd) and claw (c). E. The ornamental trichome sockets, located dorsally above the caudal bundle, with 7 trichomes a, one b and 2 trichomes c (c1 and c3).



Figure 9: SEM images of *Lophoturus porchi* sp. n., **A**. 3rd leg showing eight leg articles (co: coxa (1), tro: trochanter (2), pf: prefemur (3), f: femur (4), pof: post-femur (5), tib: tibia (6), T1: tarsus 1 (7), T2: tarsus 2 (8), c: claw), sex organ – penis (P) on leg 2 (Leg 2 lacks trochanter); **B**. Telotarsus–claw (lateral view): laterodorsal denticles (ldd), basal denticle (bd), small denticle (smd) and claw (c); **C**. A pubescent oval seta present on the coxa, pre-femur, the distal edge of femur and the posterior edge of the last sternite; **D**. Female caudal bundle structure showed the ornamental trichome sockets of trichomes a, trichome b and trichomes c; and two main parts of the caudal bundle: The caudal bundle trichome sockets (cbts) located dorsally and two nest trichome sockets (nts) ventrally.

having 3 pairs of linguiform processes; however, these two species can be distinguished by the body length, number of sensilla on gnathochilarial palps, and the presence of setae over the surface of the labrum in *L. porchi* but not in *L. speophilus*. These features, as well as the genetic makeup, make this species distinctly different from other *Lophoturus* species in the family Lophoproctidae.

## Etymology

*Lophoturus porchi* sp. n. is named after Dr Nicholas Porch for his extensive contribution to the knowledge of fossil invertebrates, primarily insects, found on Mauritius and Rodrigues Islands.

## DISCUSSION

The discovery of *Lophoturus porchi* sp. n. extends our knowledge of the fauna of penicillate millipedes in the Mascarene Islands. This is the fourth record of a *Lophoturus* species in the Indian Ocean. Most of studies of this group

of millipedes have been focussed on the Australo-Pacific Ocean, where similar lophoproctid species in the genera Alloproctoides and Lophoturus have been found on a number of islands in that region (Nguyen Duy-Jacquemin, 1982). Lophoturus madecassus (Marquet & Condé 1950), Lophoturus obscurus (Brolemann 1931) Lophoturus catalai Condé & Nguyen Duy-Jacquemin 1977, L. tongae Nguyen Duy-Jacquemin & Condé 1982 and L. o. kurtchevae Nguyen Duy-Jacquemin & Condé 1982, have been recorded from some archipelagos in the southern Pacific. Lophoturus okinawa Nguyen Duy-Jacquemin & Condé 1982 was reported from southern Japan and Taiwan, while two cave species — Lophoturus humphreysi Nguyen Duy-Jacquemin 2014 and L. speophilus Nguyen Duy-Jacquemin 2014 — were described from Christmas Island, Australia. The tropical and subtropical distribution of Lophoturus species (Lophoproctidae) worldwide is shown in Table 2.

73



Figure 10: Genetic analysis of *Lophoturus porchi* with other penicillate millipedes from the GenBank showed on the molecular phylogenetic tree. Analysis by maximum likelihood method based on **A**. 18S and **B**. COI gene. Numbers above branches represent bootstrap values (>50).

Because individual species of Lophoproctidae may be so morphologically similar, genetic sequencing will continue to play a valuable role in the identification of new species such as *Lophoturus porchi*.

#### Acknowledgements

Special thanks to the management of the François Leguat Giant Tortoise and Cave Reserve on Rodrigues Island, for giving us full access to the cave reserve; to Dr Nicholas Porch for permission to join his fieldwork in Mauritius and Rodrigues Island; to the Vurmally family, who provided a homestay through the time when C.H. stayed in Anse Quito, Rodrigues; and to Dr Duc Anh Nguyen, Professor Sergei Golovatch and Megan Short for reviewing this article.

## **Conflict of interest**

The authors declare no conflicts of interest.

#### References

- Attems, C., 1907. Javanische myriopoden, gesammelt von Direktor K. Kraepelin im Jahre 1903. *Mitteilungen aus dem Naturhistorischen Museum Hamburg* 24: 77–138.
- Attems, C., 1938. Die von Dr. C. Dawydoff in französisch Indochina gesammelten Myriopoden. Mémoires du Muséum national d'Histoire naturelle, Nouvelle Série 6(2): 187–353.
- Barcode of Life (2010–2020). Available from URL:http:// www.barcodeoflife.org (Accessed 30 June 2020).
- Brolemann, H.W., 1920. Diplopoda in: Voyage de Ch.
  Alluaud et R. Jeannel en Afrique orientale (1911–1912). *Resultals scientifiques. Myriapodes* 3: 49–298.
  L. Lhomme, Paris.
- Brolemann, H.W., 1926. Myriapodes recueillis en Afrique occidentale française par M. l'administrateur en chef L. Duboscq. Archives de zoologie expérimentale et générale 65(1): 1–159.
- Brolemann, H.W., 1931. Myriapodes recueillis en Nouvelle-Calédonie et aux Loyality. Archives de Zoologie expérimentale et générale 72(2): 275–316.
- Chamberlin, R.V., 1955. New millipedes from Peru and adjacent parts. *University of Utah, Biological Series* 11(5): 1–47.

Spec	ies name	Country found	
1.	Lophoturus adisi Ishii, Nguyen Duy-Jacquemin & Condé, 1999	Brazil	
2.	Lophoturus aequatus (Loomis, 1936)	US Florida - Haiti	
3.	Lophoturus anisorhabdus (Condé & Terver, 1964)	Guatemala	
4.	Lophoturus boondallus Huynh & Veenstra, 2018	Australia	
5.	Lophoturus catalai Condé & Nguyen Duy-Jacquemin, 1977	New Caledonia	
6.	Lophoturus crassipes Condé & Terver, 1979	St. Martin Island, Dominica	
7.	Lophoturus danhomenou (Brolemann, 1926)	Ivory Coast	
8.	Lophoturus difficilis Condé & Jacquemin, 1963	India	
9.	Lophoturus drifti (Condé & Terver, 1964)	Guatemala	
10.	Lophoturus fluctuans (Condé & Terver, 1964)	Guatemala	
11.	Lophoturus guineensis (Silvestri, 1948)	Europe	
12.	Lophoturus hesperius (Condé & Terver, 1963)	Ivory Coast	
13.	Lophoturus humphreysi Nguyen Duy-Jacquemin, 2014	Christmas Island, Australia	
14.	Lophoturus jianshuiensis Ishii & Yin, 2000	China	
15.	Lophoturus judsoni Nguyen Duy-Jacquemin, 2002	Trinidad - Tobago	
16.	Lophoturus longisetis (Pocock, 1894)	Caribbean Islands	
17.	Lophoturus longisetis scopiger Condé & Terver, 1979	Caribbean Islands	
18.	Lophoturus madecassus (Marquet &Condé, 1950)	Australia, Madagascar, Tonga, Vietnam	
19.	Lophoturus molloyensis Huynh & Veenstra, 2018	Australia	
20.	Lophoturus monserratensis Nguyen Duy-Jacquemin, 2002	Columbia	
21.	Lophoturus niveus (Loomis, 1934)	Caribbean Islands	
22.	Lophoturus obscurus (Brolemann, 1931)	New Caledonia	
23.	Lophoturus obscurus kurtchevae Nguyen Duy-Jacquemin & Condé, 1982	Papua New Guinea	
24.	Lophoturus okinawai (Nguyen Duy-Jacquemin & Condé, 1982)	Japan, Taiwan	
25.	Lophoturus peruanus (Silvestri, 1949)	Peru	
26.	Lophoturus porchi sp. n.	Mauritius (Rodrigues Island)	
27.	Lophoturus quebradanus (Chamberlin, 1955)	Peru	
28.	Lophoturus queenslandicus (Verhoeff, 1924)	Australia	
29.	Lophoturus speophilus Nguyen Duy-Jacquemin, 2014	Christmas Island, Australia	
30.	Lophoturus sturmi Nguyen Duy-Jacquemin, 2002	Columbia	
31.	Lophoturus tongae Nguyen Duy-Jacquemin & Condé, 1982	Tonga	
32.	Lophoturus vicarius Condé & Terver, 1979	Caribbean Islands	

Table 2: A list of species and subspecies in the genus Lophoturus (Lophoproctidae) found worldwide.

- Condé, B. & Jacquemin, M., 1962. Dipolopodes Pénicillates de Madagascar et des Mascareignes. *Revue française d'Entomologie* 29(4): 254–285.
- Condé, B. & Nguyen Duy-Jacquemin, M., 1963. Diplopodes Pénicillates récoltés à Bombay par P.A. Remy. *Revue française d'Entomologie* 30: 68–78.
- Condé, B. & Terver, D., 1963. Diplopodes Pénicillates de Côte d'Ivoire (Récoltes de M. Vuillaume). *Bulletin de l'Institut français d'Afrique noire* pp. 669–684.
- Condé, B. & Terver, D., 1964. Pénicillates du Surinam et du Guatemala (Diplopodes, Lophoproctidae). *Studies on the Fauna of Surinam and Other Guyanas* 7(22): 1–21.
- Condé, B. & Nguyen Duy-Jacquemin, M., 1977. De

l'utilisation nouvelle du nom de genre Lophoturus Brölemann (Diplopodes, Pénicillates). *Bulletin du Muséum national d'Histoire naturelle*, 3e Série, (477), *Zoologie* 334: 909–915.

- Condé, B. & Terver, D., 1979. Missions Muséum Antilles: Diplopodes Pénicillates. *Revue d'Écologie et de Biologie du Sol* 16(1): 137–149.
- Condé, B. & Nguyen Duy-Jacquemin, M., 2008. Classification actuelle des Diplopodes Pénicillates (Myriapodes) avec nouvelles définition des taxa. *Bulletin de la Société Zoologique de France* 13(4): 291–302.
- GenBank website: http://www.ncbi.nlm.nih.gov (Accessed 25 June 2020).

- Hall, T.A., 1999. BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acid Symposium*, *Series* 41: 95–98.
- Huynh, C. & Veenstra, A., 2014, Reproduction, egg morphology and development observed in *Monographis queenslandicus* (Diplopoda: Polyxenidae), *Invertebrate zoology* 11(2): 335–345.
- Huynh, C. & Veenstra, A., 2015. Description of a new species of penicillate millipede from the genus *Monographis* (Diplopoda: Polyxenidae) found in Vietnam. *Zootaxa* 3964(4): 460–474.
- Huynh, C. & Veenstra, A., 2018a. Two new species of *Phryssonotus* (Diplopoda: Synxenidae) from southern and western Australia. *Australian Journal of Zoology* 65(4): 248–256.
- Huynh, C. & Veenstra, A., 2018b. Two new *Lophoturus* species (Diplopoda, Polyxenida, Lophoproctidae) from Queensland, Australia. *ZooKeys* (741): 133–154.
- Huynh, C. & Veenstra, A., 2020. Three new species of penicillate millipedes from the Con Dao Islands of southeast Vietnam (Diplopoda, Lophoproctidae and Polyxenidae). *Zootaxa* 4759 (1): 1–30.
- Ishii, K., Nguyen Duy-Jacquemin M. & Condé, B., 1999. The first penicillate millipedes from the vicinity of Manaus, Central Amazonia, Brazil (Diplopoda: Polyxenida). *Amazoniana* 15(3–4): 239–267.
- Ishii, K. & Yin, W.-Y., 2000. New species of Penicillata (Diplopoda) from Yunnan, Southwest China. In *Taxonomical studies on the soil fauna of Yunnan Province in Southwest China*, J. Aoki, W.Y. Yin & G. Imadate, eds. *Tokai University Press*, Tokyo, pp. 91– 116.
- Jeekel, C.A.W., 1963. *Alloproctinus* nom. nov. (Diplopoda, Pollyxenida). *Entomologische Berichten* (Amsterdam) 23(8): 156.
- Jones, S., 1937. On two new south Indian pselaphognathous diplopods. *Zoologischer Anzeiger* 119(5–6): 138–146.
- Kumar, S., Stecher, G. & Tamura, K., 2016. MEGA7: Molecular Evolutionary Genetics Analysis Version 7.0 for bigger datasets. *Molecular Biology and Evolution* 33: 1870–1874.
- Latreille, P.A., 1831. Cours d'Entomologie et d'histoire naturelle des Crustacés des Arachnides, des Myriapodes et des Insectes à l'usage des élèves de l'école du Muséum d'Histoire Naturelle. Paris: Muséum d'Histoire Naturelle, Roret, P., 1–568.
- Loomis, H.F., 1934. Three new Cuban millipeds, with notes on two little-known species. *Bulletin of the Museum of Comparative Zoology* 75(9): 357–363.
- Loomis, H.F. 1936. The millipeds of Hispaniola, with descriptions of a new family, new genera, and new species. *Bulletin of the Museum of Comparative Zoology* 80(1): 1–191.

- Luan, Y.X., Mallatt, J.M., Xie, R.D., Yang, Y.M. & Yin, W.Y., 2005. The phylogenetic positions of three basalhexapod groups (Protura, Diplura, and Collembola) based on ribosomal RNA gene sequences. *Molecular Biology and Evolution* 22: 1579–1592.
- Lucas, H., 1840. Histoire Naturelle des Crustacés, des Arachnides et des Myriapodes. *P. Duménil, Paris.* pp. 600.
- Manton, S.M., 1956. The evolution of arthropodan locomotory mechanisms – Part 5: the structure, habits and evolution of the Pselaphognatha (Diplopoda). *Journal of the Linnean Society London* 43: 153–187.
- Marquet, M.L. & Condé, B., 1950. Contribution à la connaissance des Diplopodes Pénicillates d'Afrique et de la région madécasse. Mémoires de l'Institut Scientifique de Madagascar série A 4: 113–134.
- Meyer, C.P., 2003. Molecular systematics of cowries (Gastropoda: Cypraeidae) and diversification patterns in the tropics. *Biological Journal of the Linnean Society* 79: 401–459.
- Nguyen Duy-Jacquemin, M. & Condé, B., 1982. Lophoproctidés insulaires de l'océan Pacifique (Diplopodes Pénicillates). *Bulletin du Muséum national* d'Histoire naturelle, 4e série, Section A, Zoologie 4(1– 2): 95–118.
- Nguyen Duy-Jacquemin, M. & Condé, B., 1967. Mauritixenus, genre méconnu de Diplopode Pénicillate. Bulletin du Muséum national d'Histoire naturelle, 2e (39): 313–319.
- Nguyen Duy-Jacquemin, M. & Condé, B., 1969. Nouveaux représentants malgaches du genre *Mauritixenus* (Diplopodes pénicillates). Cahiers O.R.S.T.O.M. *Série Biologie* 7(4): 59–68.
- Nguyen Duy-Jacquemin, M., 2002. New species and distribution of the genera *Lophoturus* and *Ancistroxenus* (Myriapoda, Diplopoda, Penicillata) in the Caribbean and northern South America. *Zoosystema* 24(2): 451–470.
- Nguyen Duy-Jacquemin, M., 2014. Two new species of *Lophoturus* (Diplopoda, Penicillata, Lophoproctidae) from caves in Christmas Island, Australia, including the second troglomorph in Penicillata. *Zoosystema* 36(1): 29–39.
- Pocock, R.I., 1894. Contributions to our knowledge of the arthropod fauna of the West Indies. Part III. Diplopoda and Malacopoda, with a Supplement on the Arachnida of the Class Pedipalpi. *Journal of the Linnean Society of London* 24(157): 473–519, pl. 37–40.
- Scudder, S.H., 1885. Classe Myriopoda. Tausendfüssler. In *Handbuch der Palaeontologie. 1. Paleozoologie* 2, K.A. von Zittel, ed. Druck und Verlag von R. Oldenbourg, Munich & Leipzig, pp. 721–731.
- Short, M. & Huynh, C., 2010. A technique for examination of diagnostic characters of penicillate millipedes.

Memoirs of Queensland Museum, Nature 55(1): 231–234.

- Silvestri, F., 1948. Tavola sinottica dei generi dei Diplopoda Penicillata. *Bollettino del Laboratorio di Entomologia Agraria*, Portici (8): 214–220.
- Silvestri, F., 1949. Descrizioni di nuovi Diplopodi Penicellati. *Bollettino del Laboratorio di entomologia agraria "Filippo Silvestri"* 9: 1–7.
- Turbeville, J.M., Pfeifer, D M., Field, K.G. & Raff, R.A., 1991. The phylogenetic status of arthropods, as inferred from 18S rRNA sequences. *Molecular Biology and Evolution* (8): 669–686.
- Verhoeff, K.W., 1924. Results of Dr. E. Mjöberg's Swedish scientific expeditions to Australia 1910–1913. 34. Myriapoda: Diplopoda. Arkif för Zoologi 16(5): 1–142.
- Verhoeff, K.W., 1939. Diplopoden der Insel Mauritius und ihre zoogeographische Bedeutung. *Jenaische Zeitschrift für Naturwissenschaft* 73: 37–96.

Wesener, T., Raupach, M.J. & Sierwald, P., 2010. The origins of the giant pill-millipedes from Madagascar (Diplopoda: Sphaerotheriida: Arthroshaeridae). *Molecular Phylogenetics and Evolution* 57: 1184–1193.

77

- Wesener, T., Voigtländer, K., Decker, P., Oeyen, J.P. & Spelda, J., 2016. Barcoding of Central European *Cryptops* centipedes reveals large interspecific distances with ghost lineages and new species records from Germany and Austria (Chilopoda, Scolopendromorpha). *ZooKeys* 564: 21–46.
- White, T.J., Bruns, T., Lee, S. & Taylor, J.W., 1990.
  Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In *PCR Protocols: A Guide to Methods and Applications*, M.A. Innis, D.H. Gelfand, J.J. Sninsky, J.J. & T.J. White, eds. Academic Press, Inc., New York, pp. 315–322.