


Taxonomic review of the Afrotropical millipede genus *Scaptodesmus* Cook, 1896 (Diplopoda, Polydesmida, Chelodesmidae), with integrative descriptions of three new species from Cameroon

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Abstract

The genus *Scaptodesmus* Cook, 1896, is revised based on recent material collected from Cameroon. Three new species are described and illustrated: *S. kala* **sp. nov.**, *S. manengouba* **sp. nov.**, and *S. vandenspiegeli* **sp. nov.** Additionally, the diagnoses of two old and well-defined species of the genus, *S. porati* Cook, 1896, and *S. granulosus* (Attems, 1931), are revised. The species *Scaptodesmus dentatus* Silvestri, 1909, previously regarded as *incertae sedis*, is here confirmed as such, since its taxonomic affiliation remains uncertain. An identification key to and a distribution map for all *Scaptodesmus* species known so far are provided. Barcoding base on COI sequencing was successfully performed for all three new species and compared with previously published sequences from the family Chelodesmidae. The results reveal that the three new species are all genetically distinct from one another. A maximum likelihood phylogenetic tree constructed using the dataset of available species resulted in a well-resolved and well-supported phylogeny. In all cases, barcoding data were consistent with traditional morphological taxonomic classifications. This work highlights the importance of integrated taxonomy in resolving relationships within millipede species groups below the family level.

Key words: taxonomy, COI, DNA barcoding, millipede, Pepodesminae, Afrotropical Region

Introduction

The basically tropical family Chelodesmidae Cook, 1895 is one of the largest, not only in the order Polydesmida Pocock, 1887, but also in the entire class Diplopoda, currently comprising approximately 800 species (Hoffman 1980; Shear 2011). Members of this family show a wide range of morphological diversity, including varied coloration, paraterga/paranota/keels of different shapes, and males possessing numerous and differentiated processes on their gonopods (Hoffman 1969; Bouzan *et al.* 2017). Hoffman (1980) divided the family into two subfamilies: the Chelodesminae Cook, 1895, which includes Neotropical species, and the Prepodesminae Cook, 1896, encompassing West African members and a few species occurring in Spain (Mauriès 1971). Chelodesminae presently contain almost 180 genera in 21 tribes, most genera still being unassigned to a tribe (Golovatch & Bouzan 2025), whereas the Prepodesminae has remained without division into tribes.

The genus *Scaptodesmus* Cook, 1896, was originally established to include a single, and type, species: *S. porati* Cook, 1896, from Cameroon (Cook 1896). This species had initially been misidentified and redescribed by Porat (1894) as *Paradesmus erythropus* (Lucas, 1858), from Gabon, presently known as *Anisodesmus erythropus* (Lucas, 1858). Porat's (1894) re-description and illustrations, although adequate for the time, depicted the gonopods too small and schematic, leading to subsequent taxonomic confusion.

Silvestri (1907) described two new species of *Scaptodesmus*: *S. roccatii* Silvestri, 1907, from Uganda, and *S. rugifer* Silvestri, 1907, from Uganda and Tanzania, but he failed then to illustrate them. Two years later, however, he redescribed and illustrated these species in detail and introduced a new variety, *S. rugifer* var. *dentatus* Silvestri, 1909, based on an immature female holotype (Silvestri 1909).

Carl (1909) compared *Scaptodesmus* to the closely related genus *Odontokrepis* Attems, 1899 (currently a junior subjective synonym of *Anisodesmus* Cook, 1895), noting similarities in habitus and the presence of a relatively large telson, features also observed in the Oxydesmidae, a closely related Afrotropical family. Carl (1909) also proposed the genus *Mesodesmus* Carl, 1909, to accommodate Silvestri's two species. Attems (1931) later established the monotypic genus *Kyphopyge* Attems, 1931 for the new species *K. granulosa* Attems, 1931, from Zaire (presently the Democratic Republic of the Congo), later recorded from Gabon as well (Demange 1971). Based on detailed descriptions alone, however, Hoffman (1980) regarded the genus *Kyphopyge* as a junior subjective synonym of *Scaptodesmus*. Originally described as *S. rugifer* var. *dentatus*, it was later elevated to species level by Attems (1912) as *Mesodesmus dentatus* (Silvestri, 1909) based on the first description of a male collected at "Rugege Forest", Rwanda. This species is characterized by its small size (width ≤ 2 mm) and unique gonopod structure, including a short, articulated pre-femoral process and a postfemoral process represented by a falcate seminal branch, or solenomere. Its classification had been contentious, with the species having been placed in several genera (e.g. *Scaptodesmus* Cook, 1896, *Mesodesmus* Silvestri, 1909, *Cordyloporus* Attems, 1898, *Paltophorus* Attems, 1937, and *Pimodesmus* Chamberlin, 1927) before Hoffman (1980) consolidated these genera. However, its gonopod morphology and paratergal structure as described by Attems (1912), preclude its inclusion in *Scaptodesmus*, and it was considered *incertae sedis* by Demange & Mauriès (1975).

Hoffman (1980) recognized four species in *Scaptodesmus*, distributed across Nigeria, Cameroon, Gabon, and the Democratic Republic of the Congo (formerly Zaire). According to the online Global Millipede Database by Petra Sierwald, Peter Decker, and Jörg Spelda ([MilliBase; <http://www.millibase.org>], consulted on 22.05.2025) and the important specialized literature survey, only two species are currently recognized as belonging to the genus *Scaptodesmus*: *Scaptodesmus porati* Cook, 1896, the type of the genus, and *S. granulatus* (Attems, 1931), with *S. dentatus* Silvestri, 1909, remaining *incertae sedis*.

In this study, we describe three new species of the millipede genus *Scaptodesmus* from Cameroon, using an integrative taxonomic approach that combines morphological characters and DNA barcoding of the cytochrome c oxidase subunit I (COI) gene. We also revise the genus, provide a distribution map, and an identification key to all currently recognized species.

Material and methods

Specimen Collection and Preservation: This study is based on material from Cameroon, collected between 2015 and 2024. Specimens were actively searched along transects at Manengouba Mountain (Littoral Region), Kala Mountain and Eloumden Mountain, as well as in a patch of forest near Obala in the Southern Plateau Forest of Cameroon. The specimens were collected by hand or with the help of forceps and preserved in 90% ethanol. All samples were deposited in the collections of the Natural History Museum in Neuchâtel, Switzerland, with only a few duplicates retained for Armand Richard Nzoko Fiemapong's private collection (ARNF).

Morphological Analysis: Specimens for scanning electron microscopy (SEM) were air-dried, mounted on aluminum stubs, and coated with gold. They were visualized using a JEOL 8500F thermal field emission gun electron probe microanalyzer at the SEM imaging platform of CSEM ("Centre Suisse d'Électronique et de Microtechnique") in Neuchâtel, Switzerland. All measurements are reported in millimeters unless otherwise stated. Photographs were taken with a Canon EOS 6D camera and processed using Adobe Photoshop Lightroom (<http://www.adobe.com>) and Helicon Focus v. 5.3 (<http://www.heliconsoft.com>). The terminology used to describe the gonopod structures follows that of VandenSpiegel *et al.* (2016).

DNA Extraction, Amplification, and Sequencing: DNA barcodes were primarily generated by the Canadian Centre for DNA Barcoding (CCDB) in Guelph, Canada, using one or two legs removed from specimens preserved in 96% ethanol following the standard methodology and protocol developed at CCDB (Ivanova *et al.* 2006, DeWaard *et al.* 2008).

Additional sequences were produced in the Laboratory of Soil Biodiversity at the University of Neuchâtel, Switzerland. DNA was extracted from two to three legs of recently collected millipede specimens using the Nucleospin Tissue Kit (Macherey-Nagel), following the manufacturer's protocol.

The cytochrome c oxidase subunit I (COI) gene was amplified using the primer pairs LepF (5'-ATT-CAA-CCA-ATC-ATA-AAG-ATA-TTG-G) and LepR (5'-TAA-ACT-TCT-GCA-TGT-CCA-AAA-AAT-CA) (Hebert *et al.*, 2004). Polymerase chain reactions (PCR) were performed using GoTaq Hot Start polymerase, with a blank sample as a negative control. The master mix for each sample contained 7.625 µL of distilled water, 3.0 µL Colorless Flexi Buffer, 0.75 µL of each forward and reverse primer, 0.3 µL dNTPs, 0.075 µL GoTaq G2 Hot Start and 3 µL of DNA template, resulting in a final reaction volume of 15 µL.

The PCR profile for the COI gene included an initial denaturation step at 94°C for 2 minutes, followed by 46 cycles of denaturation at 94°C for 1 minute, annealing at 51°C for 1 minute, and extension at 72°C for 1 minute, with a final extension at 72°C for 5 minutes. PCR products were run on a 1% agarose gel electrophoresis stained with GelRed (Biotium, Remont, CA, USA) to test for amplification, and purified using the Millipore plate purification method (https://www.merckmillipore.com/CH/fr/product/MultiScreen-PCR96-Filter-Plate,MM_NF-LSKMPCR50).

Purified products were sequenced bi-directionally by Macrogen Europe (Amsterdam, Netherlands) using the same primers as in the PCR.

Sequence Processing and Accessibility: Sequences were checked, assembled, and trimmed using the Barcode Toolkit program (https://github.com/lentendu/barcode_toolkit). All sequences are publicly accessible on the BOLD (Barcode of Life Data System) and NCBI (National Center for Biotechnology Information) websites, with accession numbers provided in Table 1.

TABLE 1. Taxon sampling and accession numbers of *Scaptodesmus* and outgroup species.

Species	Country	Locality	BOLD accession number	Genbank Accession Number	References
<i>Scaptodesmus kala</i> sp. nov	Cameroon	Kala mountain	-	PV666127	Present study
<i>Scaptodesmus kala</i> sp. nov	Cameroon	Kala mountain	-	PV666128	Present study
<i>Scaptodesmus kala</i> sp. nov	Cameroon	Kala mountain	-	PV666126	Present study
<i>Scaptodesmus manengouba</i> sp. nov	Cameroon	Manengouba mountain	DPCMR014-24	-	Present study
<i>Scaptodesmus manengouba</i> sp. nov	Cameroon	Manengouba mountain	DPCMR015-24	-	Present study
<i>Scaptodesmus manengouba</i> sp. nov	Cameroon	Manengouba mountain	DPCMR016-24	-	Present study
<i>Scaptodesmus vandenspigeli</i> sp. nov	Cameroon	Eloumden mountain	DPCMR013-24	-	Present study
<i>Scaptodesmus vandenspigeli</i> sp. nov	Cameroon	Eloumden mountain	DPCMR020-24	-	Present study
<i>Scaptodesmus</i> sp.	Cameroon	Ebo Forest	DPCMR022-24	-	Present study
<i>Diaphorodesmus dorsicornis</i> (Porat, 1894)	Cameroon	Ebo Forest	DPCMR028-24	-	Present study
<i>Diaphorodesmus dorsicornis</i> Porat (1894)	Cameroon	Ebo Forest	DPCMR0130-24	-	Present study
<i>Heptodesmus orator</i> Hoffman, 1982	Cameroon	Ebo Forest	DPCMR011-24	-	Present study
<i>Heptadesmus orator</i> Hoffman, 1982	Cameroon	Ebo Forest	DPCMR012-24	-	Present study
<i>Brachyurodesmus albus</i> Bouzan, Santos-Silva, Brescovit & Soares, 2024	Brazil	-	-	OQ940719-1	Santos-Silva <i>et al.</i> , 2024

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TABLE 1. (Continued)

Species	Country	Locality	BOLD accession number	Genbank Accession Number	References
<i>Brachyurodesmus albus</i> Bouzan, Santos-Silva, Brescovit & Soares, 2024	Brazil	-	-	OQ940720-1	Santos-Silva <i>et al.</i> , 2024
<i>Brachyurodesmus albus</i> Bouzan, Santos-Silva, Brescovit & Soares, 2024	Brazil	-	-	OQ940721-1	Santos-Silva <i>et al.</i> , 2024
<i>Brachyurodesmus albus</i> Bouzan, Santos-Silva, Brescovit & Soares, 2024	Brazil	-	-	OQ940722-1	Santos-Silva <i>et al.</i> , 2024
<i>Brachyurodesmus albus</i> Bouzan, Santos-Silva, Brescovit & Soares, 2024	Brazil	-	-	OQ940718-1	Santos-Silva <i>et al.</i> , 2024
<i>Chondrodesmus riparius</i> Carl, 1914	Poland	-	-	MW072789.1	Bienias <i>et al.</i> , 2021

Phylogenetic Analyses: For phylogenetic analyses, all Chelodesmidae sequences from GenBank (see Table 1) and the BOLD database were selected based on BLAST comparative results. Outgroups were selected primarily from the closely related family Oxydesmidae, along with some representative genera from the family Chelodesmidae. The species selected for this study were *Diaphorodesmus doricornis* (Porat, 1894), *Brachyurodesmus albus* Bouzan, Santos-Silva, Brescovit & Soares, 2024, *Chondrodesmus riparius* Carl, 1914, and *Heptadesmus orator* Hoffman, 1982. COI sequences were aligned using MAFFT (Katoh *et al.* 2002) and trimmed with Trimal (Capella-Gutiérrez *et al.* 2009). Phylogenetic trees were constructed using IQ-Tree version 2.3.6 (Minh *et al.* 2020). Genetic distances between Chelodesmidan samples were calculated using the Kimura 2-parameter model in MEGA version 10.0 (Kumar *et al.* 2018).

The Maximum Likelihood (ML) analyses were conducted using the COI dataset. Bootstrap analysis was performed with 1,000 replicates to assess node support. The final trees were visualized using FigTree version 1.4.4 (Rambaut 2021).

Museum collection acronyms and abbreviations:

ZMH:	Zoologisches Museum Hamburg, Leibniz-Institut für Analyse des Biodiversitätswandels, Hamburg, Germany (Curator, Danilo Hans)
NHMN:	Natural History Museum of Neuchâtel, Neuchâtel, Switzerland (Curator: Jessica Litman)
ARNF:	Personal collection of Armand Richard Nzoko Fiemapong
SEM:	Scanning Electron Microscope
slo:	solenomere
sph:	solenophore
pfp:	postfemoral process
AV:	anterior valve
PV:	posterior valve
OP:	operculum.

Results

Molecular analysis

COI dataset: The final aligned COI dataset comprised a 669 bp fragment from 19 chelodesmid specimens, including the outgroup *Heptadesmus orator* (Oxydesmidae), *Diaphorodesmus dorsicornis* (Prepodesminae), along with two species from the subfamily Chelodesminae: *Chondrodesmus riparius* and *Brachyurodesmus albus*. The nucleotide frequencies were: 19.3% for adenine (A), 41.3% for thymine (T), 24.8% for guanine (G), and 14.6% for cytosine (C). The dataset contained 220 parsimony-informative sites (32.88%) and 231 variable sites (34.53%).

Genetic distance: The average Kimura 2-parameter (K2P) genetic distance among the 19 chelodesmid specimens was $18.0 \pm 0.01\%$. Genetic distances between the outgroups and the newly described species are detailed in Table 2. Among the new species, genetic distances ranged from 10.9–11.7% between *S. kala* **sp. nov.** and *S. manengouba* **sp. nov.**, from 15.0–16.5% between *S. vandenspiegeli* **sp. nov.** and *S. kala* **sp. nov.**, and from 14.9–15.1% between *S. vandenspiegeli* **sp. nov.** and *S. manengouba* **sp. nov.**

Phylogenetic analysis: The COI fragment was sequenced from nine *Scaptodesmus* specimens and six outgroup samples (see Table 1). Following the trimming process, the final alignment of the COI marker comprised 669 bp for 19 sequences of seven taxa (including outgroups).

The phylogenetic trees were constructed using the maximum likelihood (ML) method based on the sequence alignments of the COI gene datasets (669 bp). The results demonstrate that all *Scaptodesmus* species analyzed were recovered as monophyletic within the same clade with high bootstrap value support (Fig. 1). The four *Scaptodesmus* species, including the three newly described ones, resulted in the formation of three distinct clades: clade 1 comprises *S. vandenspiegeli* **sp. nov.**; clade 2, *S. kala* **sp. nov.**, and *S. manengouba* **sp. nov.**; and clade 3 includes *Scaptodesmus* sp., another new species that has not been described in this study due to insufficient material.

Taxonomic part

Class Diplopoda Blainville in Gervais, 1844

Order Polydesmida Leach, 1815

Family Chelodesmidae Cook, 1895

Subfamily Prepodesminae Cook, 1896

Genus *Scaptodesmus* Cook, 1896

Scaptodesmus Cook, 1896: 16 (original description).

urn:lsid:zoobank.org:act:CE8D01B6-DC13-49B8-AF91-8A4BBFBB58AB

Type-species: *Scaptodesmus porati* Cook, 1896, Cameroons, by original designation.

Historical diagnosis. According to Cook (1896), the genus *Scaptodesmus* is easily recognized by the presence of ozopores located on distinct excavations at the lateral margins of the carinae, the dorsum very slightly convex, and the telson with the marginal processes very strongly developed.

Updated diagnosis. A genus of Chelodesmidae (subfamily: Prepodesminae), distinguished by the absence of a conspicuous paramedian or dorsomedian horn on the metaterga; subrectangular, elevated, horizontal paranota with dentate lateral, anterior, and posterior margins, combined with a slightly convex dorsum (Figs 2A, 3, 7, 10); the normal pore formula (5, 7, 9, 10, 12, 13, 15–19), with ozopores being located on distinct excavations along the lateral margins of the paranota (Figs 2A, 4A, 11A–B, 8B–D), gonopod telopodites suberect, *in situ* directed forward (Fig. 8F), held parallel to each other, not crossing mesally; femoral process subcylindrical, usually densely setose, elongated, partly erect, taking up ca. 2/3 total telopodite length, without femorite, with a complex dorsal postfemoral process (**pfp**) demarcated from acropodite by a distinct cingulum; acropodite twisted and divided into two lobes (Figs 2C, D, 5, 9, 12C–F). External branch forming a solenophore (**sph**), larger than internal branch, or solenomere (**slo**), supporting a seminal groove all along (Fig. 2C–D).

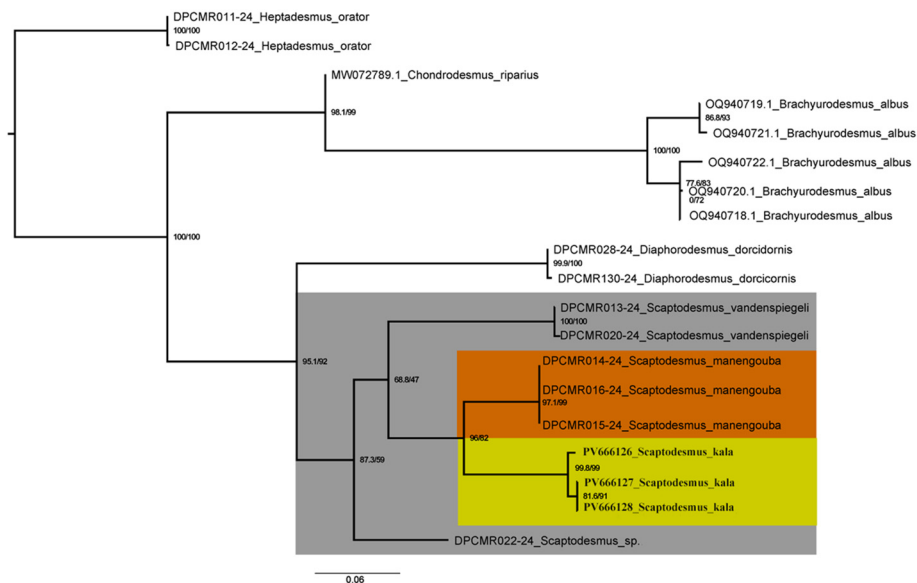


FIGURE 1. Maximum likelihood (ML) tree built from the COI dataset. The SH-aLRT support (%) and the ultrafast bootstrap support (%) are shown close to nodes.

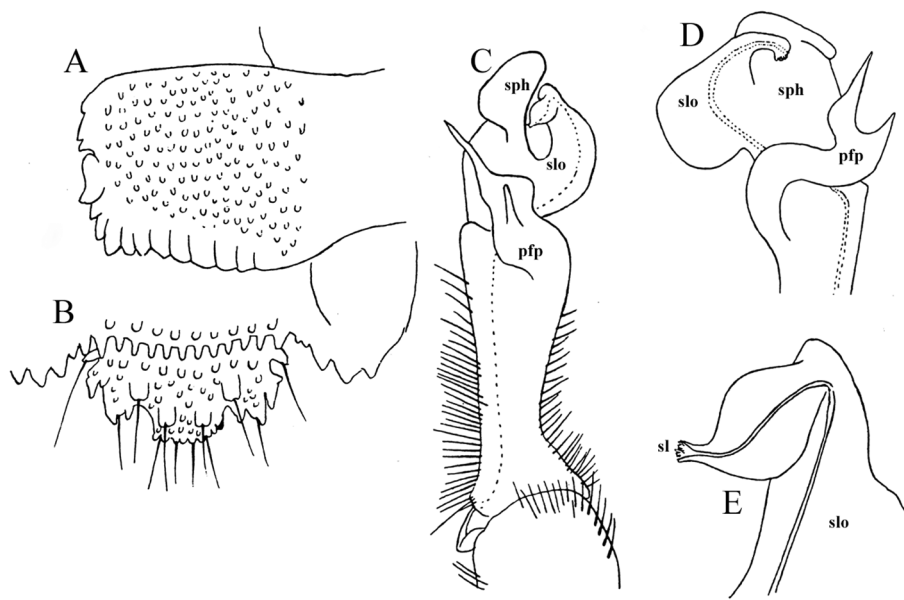


FIGURE 2. *Scaptodesmus granulosus* (Attems, 1931), **A.** Paranota. **B.** telson. **C, D & E.** Gonopods of a male (ZMH) from Buea in Cameroon. **C.** Right gonopod, mesal view, **D.** Tip of right gonopod, ventro-mesal view. **E.** solenomere branch showing the seminal groove. After Attems (1931), not to scale. Labels added by present authors. **Abbreviations:** slo, solenomere lobe; sl, solenomere proper; sph, solenophore; pfp, postfemoral process.

List of species

Scaptodesmus porati Cook, 1896

urn:lsid:zoobank.org:act:835743F8-DDE3-4456-AC97-54164492DA2F

Diagnosis. This species differs from congeners by the coloration being mostly red or reddish-brown; lateral margin of paranota usually yellowish; top of head rugulose, forehead wrinkled and densely setose; telson with a very strongly developed marginal process.

Distribution. Only known from the type locality: Mapanja, Cameroon.

TABLE 2. Pairwise nucleotide differences (Kimura 2-parameter model) over sequence pairs between *Scaptodesmus* and outgroups species.

Specimens	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)	(16)	(17)	(18)	(19)
(1)DPCMR011-24_ <i>Heptadesmus orator</i>	-																		
(2)DPCMR012-24_ <i>Heptadesmus orator</i>	0.002																		
(3)MW072789.1_ <i>Chondrodesmus riparius</i>	0.192	0.195																	
(4)OQ940719.1_ <i>Brachyurodesmus albus</i>	0.222	0.224	0.148																
(5)OQ940721.1_ <i>Brachyurodesmus albus</i>	0.222	0.224	0.148	0.005															
(6)OQ940722.1_ <i>Brachyurodesmus albus</i>	0.237	0.239	0.157	0.065	0.074														
(7)OQ940720.1_ <i>Brachyurodesmus albus</i>	0.222	0.224	0.140	0.052	0.054	0.018													
(8)OQ940718.1_ <i>Brachyurodesmus albus</i>	0.218	0.220	0.143	0.049	0.058	0.015	0.002												
(9)DPCMR028-24_ <i>Diaphorodesmus dorcicornis</i>	0.227	0.227	0.187	0.221	0.221	0.234	0.229	0.224											
(10)DPCMR130-24_ <i>Diaphorodesmus dorcicornis</i>	0.227	0.227	0.187	0.221	0.221	0.234	0.229	0.224	0.003										
(11)DPCMR013-24_ <i>Scaptodesmus vandenspiegeli</i> sp. nov	0.224	0.224	0.210	0.277	0.280	0.263	0.263	0.255	0.197	0.193									
(12)DPCMR020-24_ <i>Scaptodesmus vandenspiegeli</i> sp. nov	0.222	0.222	0.207	0.274	0.277	0.256	0.256	0.248	0.191	0.187	0.005								
(13)DPCMR022-24_ <i>Scaptodesmus</i> sp.	0.215	0.215	0.175	0.247	0.241	0.248	0.248	0.243	0.185	0.187	0.149	0.151							
(14)DPCMR014-24_ <i>Scaptodesmus manengouba</i> sp. nov	0.193	0.193	0.188	0.218	0.220	0.237	0.232	0.225	0.167	0.167	0.148	0.150	0.143						

TABLE 2. (Continued)

Specimens	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)	(16)	(17)	(18)	(19)
(15)DPCMR015-24_ <i>Scaptodesmus manengouba</i> sp. nov	0.193	0.193	0.188	0.218	0.220	0.237	0.232	0.225	0.167	0.167	0.148	0.150	0.143	0.000					
(16)DPCMR016-24_ <i>Scaptodesmus manengouba</i> sp. nov	0.193	0.193	0.188	0.218	0.220	0.237	0.232	0.225	0.167	0.167	0.148	0.150	0.143	0.000	0.000				
(17)DC604_ <i>Scaptodesmus</i> <i>Kala sp. nov</i>	0.222	0.222	0.200	0.236	0.236	0.240	0.240	0.235	0.196	0.196	0.165	0.167	0.152	0.109	0.109	0.109			
(18)DC526_ <i>Scaptodesmus</i> <i>kala sp. nov</i>	0.217	0.217	0.197	0.238	0.238	0.238	0.234	0.230	0.200	0.200	0.162	0.164	0.152	0.111	0.111	0.111	0.013		
(19)DC603_ <i>Scaptodesmus</i> <i>kala sp. nov</i>	0.217	0.217	0.197	0.234	0.234	0.238	0.234	0.230	0.200	0.200	0.162	0.164	0.152	0.111	0.111	0.111	0.012	0.000-	-

***Scaptodesmus granulosus* (Attems, 1931)**

Kyphopyge granulosa Attems, 1931, by original designation

urn:lsid:zoobank.org:act:DD216F03-2061-4E39-91D7-A896EBDB1FBA

Figs 2 & 14

Diagnosis. This species differs from congeners by a greyish black coloration; paranota subrectangular with lateral, anterior and posterior edges denticulate (Fig. 2A). Lateral edges usually forming three lobes: two tridentate, corresponding to anterior and posterior edges. Poreless rings usually with three tridentate lobes. Telson short and broad, densely granulated all over (Fig. 2B). Gonopods (Fig. 2C–E) featuring a postfemoral process (**pfp**) located on caudal surface, curved at a right angle anteriorly and straight distally, divided distally into two unequal spiniform branches. Solenomere lobe (**slo**) broad and falcate, extending from outer to inner edge, accompanied by a broad, elongated, racket-shaped lamellar solenophore (**sph**), curved inwards, opposite solenomere branch.

Distribution. Buea, Cameroon; Gabon; Democratic Republic of the Congo; ?Nigeria.

Remark. The type of this species, originally claimed as having been housed in the ZMH, is lost (Dr. Danilo Hans, personal communication).



FIGURE 3. *Scaptodesmus kala* sp. nov., female paratype (NHMN-62-4). A, B & C. Habitus, dorsolateral, ventrolateral and lateral views, respectively. Scale bars: 1.0 mm.

***Scaptodesmus kala* sp. nov.**

urn:lsid:zoobank.org:act:047F0B3C-C242-4BA1-B9FD-950523127F62

Figs 3–6 & 14

Material examined. Holotype male (NHMN-62-2), Cameroon, Center Region, Kala Mountain, 3.829667N, 11.339264E, 1050 m a.s.l., secondary forest, 25.V.2024, leg. A.R. Nzoko Fiemapong.

Paratypes: 1 male, 2 females (NHMN-62-3); 2 females (NHMN-62-4), same data, together with holotype; 1 male (SEM, ARNF), same locality, but 22.V.2024; 1 fragmented female (NHMN-62-5), 1 female (NHMN-62-6), 1 female (ARNF), same locality, but 21.V.2024; 2 fragmented males, 1 female (NHMN-62-7), same locality, but 24.V.2024; 1 female, (ARNF), 1 male (ARNF), same locality, but 17.V.2024, all leg. A. R. Nzoko Fiemapong. 1 male, 2 females (ARNF), 1 male (NHMN-62-8), 1 female (NHMN-62-9), secondary forest, Kala Mountain, 3.831365N, 11.342354E 1010 m a.s.l., secondary forest, 25.V.2024, leg. A.R. Nzoko Fiemapong.

Etymology. To emphasize the type locality; noun in apposition.

Diagnosis. This species differs from congeners by the gonopod aperture being transversely ovoid, the anterior margin forming a small, apical, conical projection (Fig. 4D). Gonopod postfemoral process (**pfp**) markedly enlarged, rake-shaped, tip bearing 3 or 4 minute denticles (Fig. 5). The medial branch constituting a solenophore (**sph**) and a lateral branch, or solenomere (**slo**), the latter bearing a small solenomere proper (**sl**) at its tip.

Description. Length of holotype, 38 mm (male), width of midbody pro- and metazona, 4 and 10 mm (male), respectively. Length of paratypes, 48 mm, width of midbody pro- and metazona, 4.5–5 and 11–11.5 mm (male, female), respectively. Coloration (preserved in 70% alcohol) brown to light brown-yellowish on paratergal callus, legs yellow-brown (Fig. 3B–C). Venter and clypeolabral region brownish; antennae light brown.

Head densely setose in clypeolabral region and shagreened behind antennae, interantennal isthmus almost as wide as diameter of antennal socket. Antennae long and only slightly clavate, reaching *in situ* the anterior margin of body ring 4 when stretched dorsally; antennomeres 5 and 6 each bearing a dorso-apical group of tiny bacilliform sensilla; in length, antennomere 2>6>3=4–5>1>7; apical segment densely pilose, with usual four sensory cones.

Body with 20 segments (male, female). In width, collum < ring 2<3<4<5<6–17, body tapering towards telson thereafter. Collum transversely ellipsoid, subflabellate, covering the head from above. Dorsal surface regularly granulate (Figs 3A, 4A). Dorsum slightly convex (Fig. 3A). Prozona smooth and slightly shining; metazona dull, densely granulate. Metazona with transverse sulci dividing them dorsally into two halves. Paranota inclined somewhat downwards, lateral edges forming irregular teeth, especially so on poriferous rings. A particularly pronounced axial line dividing metaterga 2–16 into two equal parts, less pronounced on following rings. Caudal corner of paranota increasingly high and drawn behind, near tergal margin on rings 17–19. Sharp spines, tubercles or cones observed at pleurosternal margins near coxae. Dorsum slightly declined, paratergal margins increasingly well inclined caudad starting with ring 16, thereafter mostly lying at about body midheight; only paraterga 17–19 increasingly clearly drawn past rear tergal margin, 19th sharp. Sides below paraterga densely granulate, grains in caudal row being longer, spiniform and sharp. Ozopores visible, open flush on surface near midlength slightly above lateral edge of paraterga (Fig. 3C).

Epiproct short, small, spade-shaped, flattened dorsoventrally, subtruncate, and dorsally granulate-tuberculate (Figs 3B, 4B). Hypoproct densely granulate-tuberculate, roundly subtrapeziform, with 1+1 caudal setae very distinctly separated and borne on minute knobs (Fig. 2B). Paraprocts likewise densely granulate (Fig. 3B).

Sterna broad, about 2.5–3 times as wide as coxa length, almost flat, microgranulate and slightly setose on metazona, prozona being smooth and devoid of setae (Fig. 3B). Gonapophyses on male coxae 2 vestigial. Legs long, about 1.5 times as long as midbody height (male, female); in length, femur > tarsus > prefemur = tibia > postfemur > coxa; claw very small, slightly curved; tarsi densely setose, but forming no brushes on ventral surface (Fig. 4C).

Gonopod aperture transversely ovoid in shape and fully concealing the gonocoxae and the bases of telopodites, with slightly elevated lateral and anterior edges, the latter forming a small cone at tip (Fig. 4D).

Gonopod (Figs 5A–C): coxites of medium size and subcylindrical; fused at base to a small membranous sternal remnant and, distodorsally, bearing a dense field of setae, including a pair of particularly long, closely placed distalmost ones (Fig. 5B, C).

Cannulae slender, without peculiarities (Fig. 5B). Telopodites *in situ* directed forward, held subparallel to each other and suberect. Prefemoral region densely setose, as usual, subcylindrical, taking up ca. 2/3 total length of telopodite. Femorite absent, but a large and complex postfemoral process (**pfp**) present, markedly enlarged, bent at a right angle, rake-shaped, bearing 3–4 minute denticles at tip (Fig. 5). Acropodite twisted and divided into two prominent lobes: a medial solenophore lobe (**sph**) and a lateral, small and falcate branch, or solenomere lobe (**slo**), this bearing a small solenomere proper (**sl**) at its apex.

Female. Cyphopods cordiform in anterior and posterior views (Fig. 6), located directly behind second pair of legs on body ring 3; composed of two densely setose vulvae (Fig. 6). Anterior and posterior valves joined distally, with a separation line barely distinguishable. Operculum (**OP**) relatively large and only lightly covered with small setae (Fig. 6A–C).

Distribution. *Scaptodesmus kala* **sp. nov.** is only known from its type locality (see Fig. 14). This species inhabits degraded secondary forests, where it has been found in leaf litter and decaying dead wood. It co-occurs with *S. vandenspiegeli* **sp. nov.** on Kala Mountain in the Central Region of Cameroon. Notably, it has mainly been observed during the rainy season.

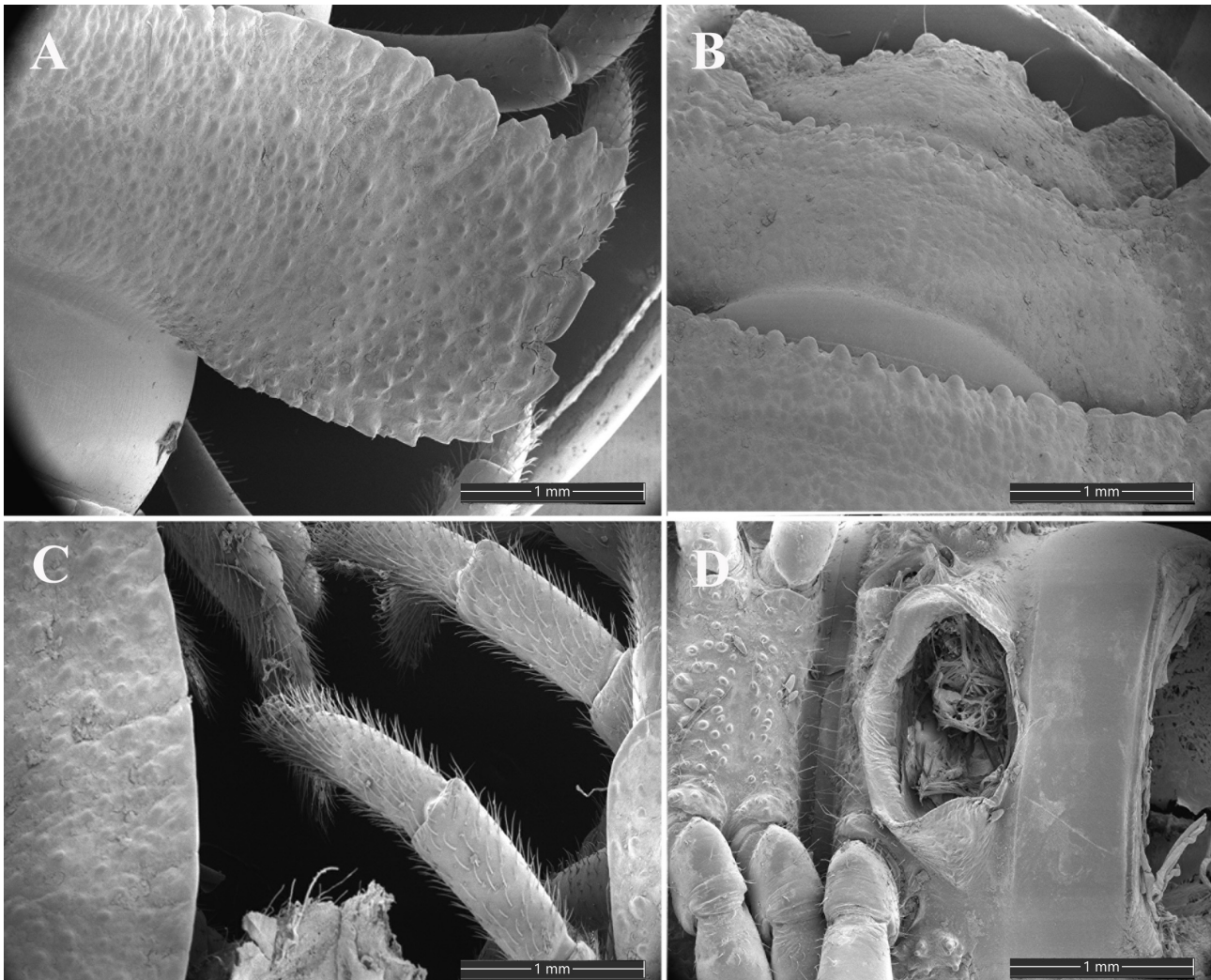


FIGURE 4. SEM micrographs of *Scaptodesmus kala* sp. nov., male paratype, (ARNF). **A.** Poriferous paraterga of midbody segments dorsal views, **B.** posterior part of body dorsal views, **C & D.** anterior legs and ventral views showing sternal region and gonopod aperture, respectively. **Scale bars:** 1.0 mm. (**A, B, C, D**).

***Scaptodesmus manengouba* sp. nov.**

urn:lsid:zoobank.org:act:AF96C472-A182-48B8-AD26-AD4E42ABB721

Figs 7–9 & 14

Material examined: Holotype male (NHMN-62-10), Cameroon, Littoral Region, Manengouba Mountain, 4.98536N, 9.82125E, 2175 m a.s.l., forest, 16.VIII.2020, leg. A.R. Nzoko Fiemapong and M. Kameni Ngalieu. Paratypes: 1 male (NHMN-62-11), 1 fragmented male (NHMN-62-12), 1 male (SEM, ARNF), same data, together with holotype.

Etymology. To emphasize the type locality; noun in apposition.

Diagnosis. Adult males of *S. manengouba* sp. nov. are distinguished from other congeners by the small body size (25 mm length); gonopod postfemoral process (**pfp**) complex, folded into a lateral groove (9A–B); acropodite external branch forming a small, elongate and falcate solenomere (**slo**), adjacent to a larger, subrounded, mesal solenophore (**sph**).

Description. Length of holotype, ca. 25 mm (male), width of midbody pro- and metazona, 3 and 4 mm (male), respectively. Length of paratypes, 25 mm, width of midbody pro- and metazona, 2.7–3 and 3–4 mm (male), respectively. Coloration (preserved in 70% ethanol) brown with yellow-orange-brown paraterga; legs and clypeolabral region light yellowish (Fig. 7A); antennae brown, venter yellowish brown (Fig. 7C).

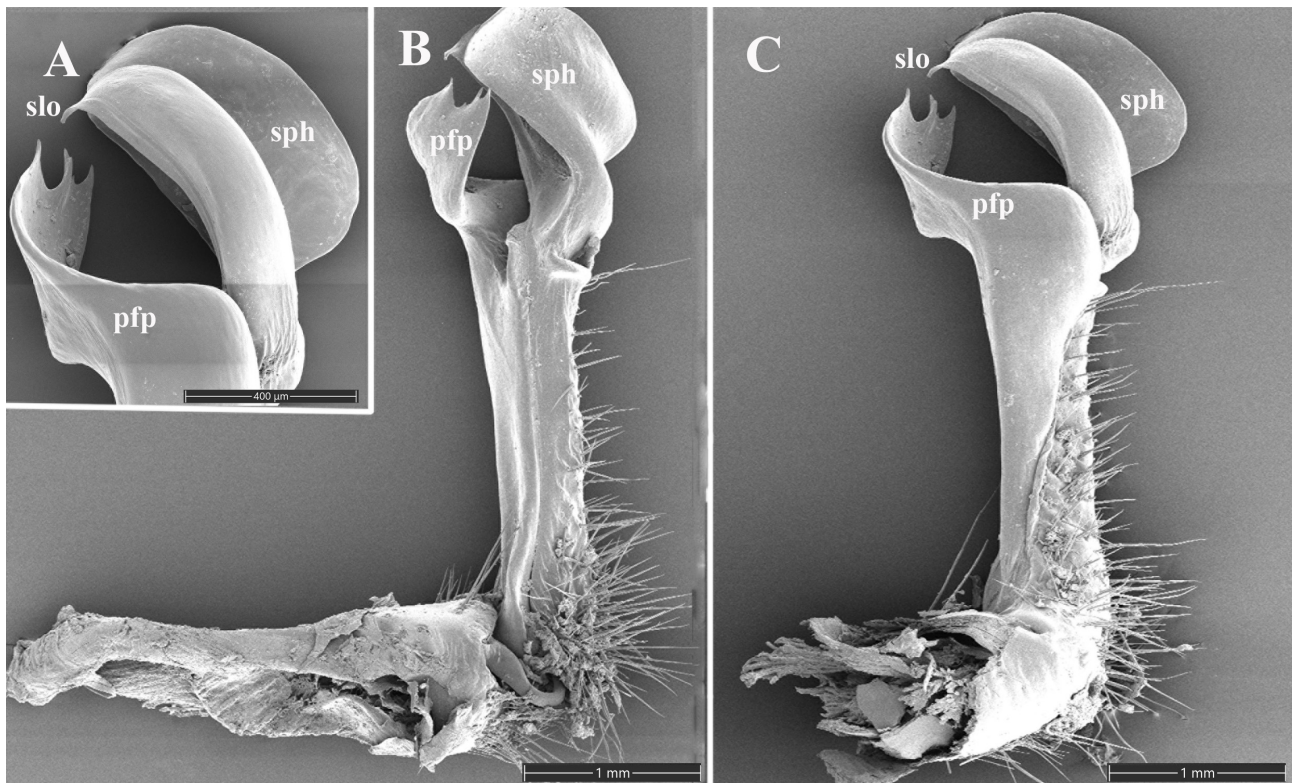


FIGURE 5. SEM micrographs of *Scaptodesmus kala* **sp. nov.**, male paratype, **A**) Tip of left gonopod, lateral view; **B**. left gonopod, mesal view; **C**. right gonopod lateral view. **Abbreviations:** slo, solenomere lobe; sph, solenophore; pfp, postfemoral process. **Scale bars:** 400 µm (**A**), 1.0 mm (**B**, **C**)

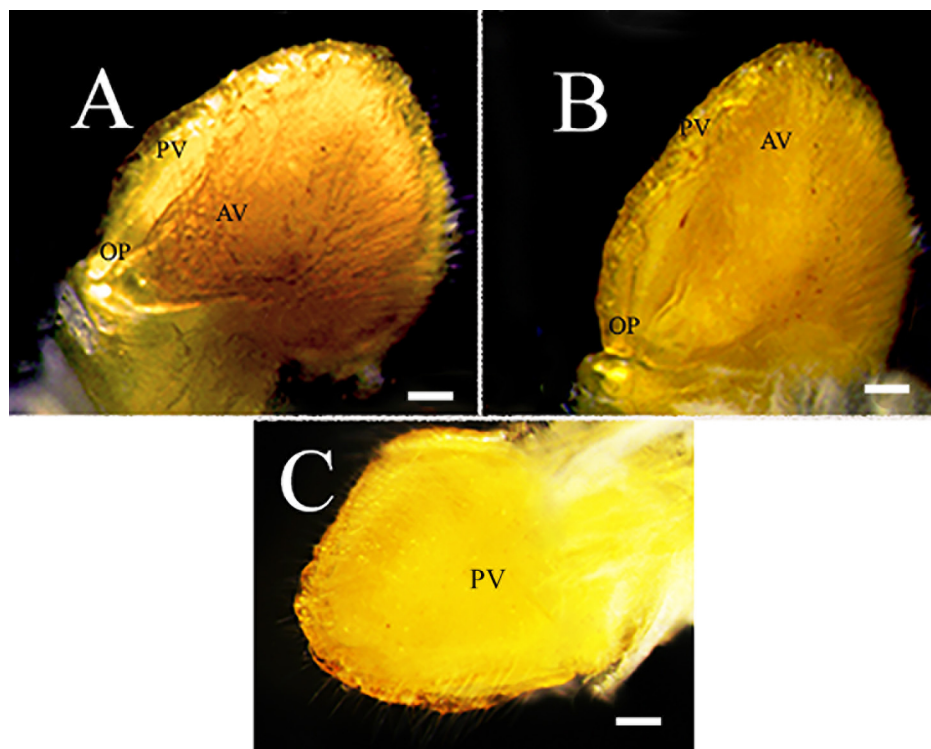


FIGURE 6. *Scaptodesmus kala* **sp. nov.**, female paratype (NHMN-62-7). detail of right cyphopod: **A–B**. lateroventral view; **C**. posterior view. **Scale bars:** 275 µm. **Abbreviations:** AV, anterior valve; PV, posterior valve; OP, operculum. **Scale bars:** 250 µm (**A**, **B**, **C**).

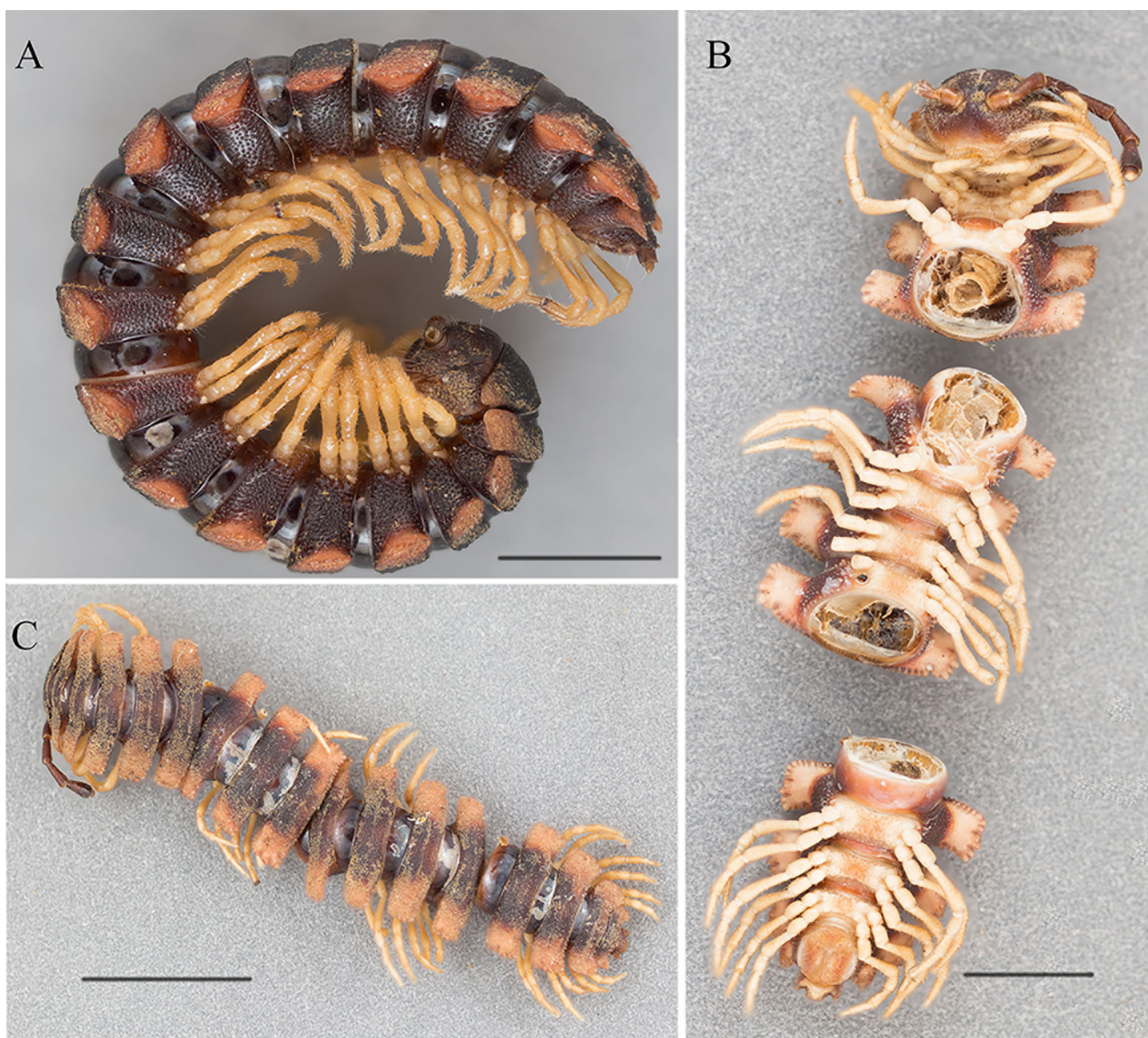


FIGURE 7. A, B & C. *Scaptodesmus manengouba* sp. nov, male paratype (NHMN-62-11). **A.** habitus, lateral view; **B.** ventral view, **C.** dorsal view. **Scale bars:** 1.0 mm (**A, B, C**)

Head densely microtuberculate; moderately setose in dorsal view (Figs 7C, 8A). Interantennal isthmus about half as broad as diameter of antennal sockets. Antennae long and clavate (Fig. 7B), reaching *in situ* the anterior margin of body ring 4 when stretched dorsally; antennomeres 5 and 6 each bearing a dorso-apical group of tiny bacilliform sensilla; in length, antennomere $6 > 2 = 3 - 5 > 1 > 7$; apical segment densely pilose with usual four sensory cones.

Body with 20 segments (male). In width, head = collum < ring 2 < 3 < 4 < 5 < 6 = 7–16; body then tapering towards telson. Collum (Fig. 8A) transversely ellipsoid, not covering the head from above; sides narrowly rounded; dorsal surface microgranulate (Figs 7A–C, 8A–F). Dorsum slightly declined (Figs 7C, 8A, C, E). Prozona smooth and shining; metazona dull, densely granulate; dorsal surface of metaterga uniformly microgranulate. Paraterga broad, set at about the upper 1/3 of body, tips undulated to slightly sawtooth-like, with the pores opening into a bulge (=peritremata) featuring two denticles behind and three in front of the pore (Fig. 8B, D). Pleurosternal margins with a field of tubercles, near the coxae. The dorsum exhibits a slight downward inclination, while the paraterga margin displays an increasingly posterior orientation towards the caudal margin, from segment 16 onwards, mostly lying at about half of body height and slightly bent down; only paraterga 16–19 increasingly clearly drawn behind the rear tergal margin. Sides below paraterga densely granulate, featuring spiniform in caudal margin. Ozopores visible, open flush on surface near midlength, slightly above the lateral edge of paraterga (Fig. 8D).

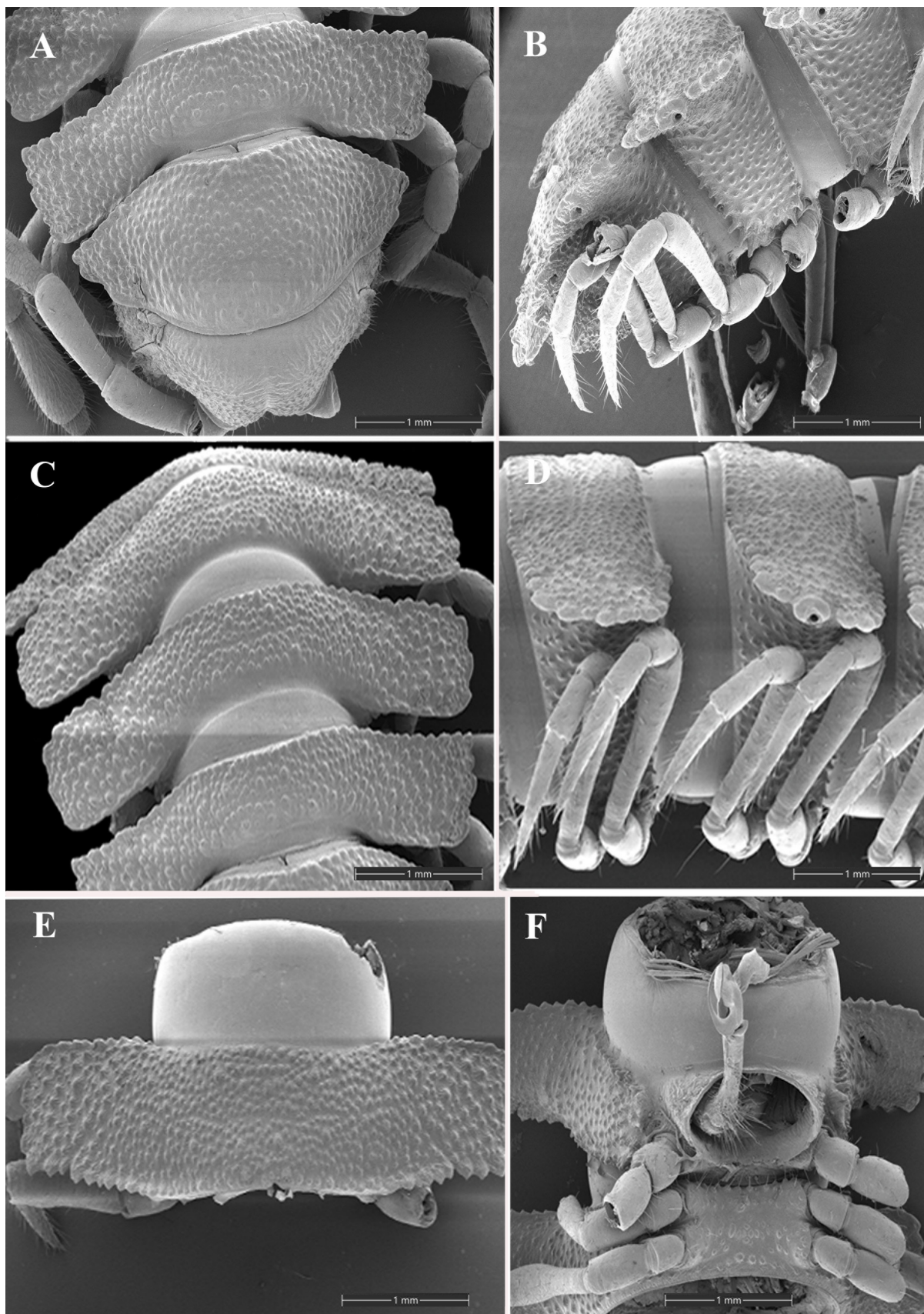


FIGURE 8. SEM micrographs of *Scaptodesmus manengouba* **sp. nov.**, male paratype (ARNF). **A.** head collum and first segment, dorsal view; **B.** caudal margin, latero-pleural view; **C.** four first anterior body segment anterior view; **D.** mid-body segment, lateral view; **E.** mid-body segment showing pro and metazonae; **F.** sternal region, gonopod aperture and left gonopod *in situ*, ventral view. **Scale bars:** 1.0 mm (**A, B, C, D, E & F**).



FIGURE 9. SEM micrographs of *Scaptodesmus manengouba* **sp. nov.**, male paratype (ARNF). **A & B.** right gonopod, mesal view; **C.** left gonopod, dorsal view. **Abbreviations:** **slo**, solenomere lobe; **sph**, solenophore; **pfp**, postfemoral process. **Scale bars:** 500 μ m (**A**); 200 μ m (**B**); 300 μ m (**C**).

Epiproct short, broad, spade-shaped, strongly flattened, subtruncate, and densely granulated (Fig. 7B–C). Hypoproct densely granulate, roundly subtrapeziform, with 1+1 caudal setae distinctly separated and borne on minute knobs (Fig. 6B). Paraprocts likewise densely granulate (Fig. 8B).

Sterna broad, about twice as wide as the coxa length, almost flat, microgranulate and slightly setose (Figs 7B, 8F). Gonapophyses on male coxae 2 vestigial. Spiracles (Fig. 7A) large, remarkably tubiform. Legs long, about 2.0 times as long as the midbody height (male); in length, femur > tarsus > tibia > prefemur > postfemur > coxa; claw very small, slightly curved; tarsi densely setose, but forming no brushes on ventral surface.

Gonopod aperture ovoid and relatively large; its lateral and posterior edges slightly elevated (Fig. 8F). This structure fully conceals the gonocoxae and the bases of the telopodites.

Gonopods (Fig. 8F): coxites of medium size and subcylindrical in shape. Telopodites *in situ* directed forward, held subparallel to each other and suberect. Prefemoral region densely setose and erect, taking up ca. 2/3 of total length of telopodite (Figs 8F, 9A). Femorite absent, but a large and complex postfemoral process (**pfp**) present, folded into a lateral groove (Fig. 9). Acropodite clearly twisted and divided parabasally into two branches. The small, elongate and falcate lateral branch forming the solenomere (**slo**), next to a larger, sub-rounded medial branch, the solenophore (**sph**).

Female. Unknown

Distribution. This species is only known from the type locality (Fig. 14). It was found in a relatively well-preserved forest, on Mount Manengouba, in decomposing leaf litter.

***Scaptodesmus vandenspiegeli* sp. nov**

urn:lsid:zoobank.org:act:2F2B336E-F414-49BD-A1F5-4C65CC3E0304

Figs 10–13 & 14

Material examined: Holotype male (NHMN-62-13), Cameroon, Center Region, Zamakoe secondary Forest, 3.5563N, 11.5218E, 706 m a.s.l., 21.III.2015, leg. A. R. Nzoko Fiemapong.

Paratypes: male (NHMN-62-14), Cameroon, Center Region, Lékié Division, Obala, Cacao based agroforest, 4.168376 N, 10.213165 E, 641 m a.s.l., 26.IV.2023, leg. Guibai Jean and A. R. Nzoko Fiemapong; 1 female (NHMN-62-15), Cameroon Littoral Region, Ebo Forest, 4.346097 N, 10.213165 E; 18.IV.2022, 1 male (SEM, ARNF), Cameroon, Center Region, Kala Mountain 03.83544N, 11.35148E, 1050 m a.s.l., mature natural secondary forest, 22.V.2024; 1 female (ARNF), same locality and date; 1 female (NHMN-62-16) Ongot, 3.85N, 11.483334E, degraded secondary forest, ca 810 m a.s.l., 08.VII.2022, all leg. A.R. Nzoko Fiemapong.

Etymology. To honor Dr. Didier Vandenspiegel, a taxonomist who has greatly contributed to the knowledge of Afrotropical and other Diplopoda.

Diagnosis. This species differs from congeners by the marbled olivaceous-brown coloration without special yellow spots at lateral margins of paraterga (Fig. 10). Gonopod postfemoral process (**pfp**) complex, presenting a small, rounded lamella just after the curvature and bifid distally (Fig. 12D); external branch of acropodite forming a large solenomere (**slo**), which has only an indistinct, small solenomere proper at its tip, next to a larger internal axe-shaped branch forming a solenophore (**sph**).



FIGURE 10. *Scaptodesmus vandenspiegeli* sp. nov, male paratype (NHMN-62-14), habitus, dorsal view. **Scale bar:** 5 mm.

Description. Length of holotype, ca. 43 mm, width of midbody pro- and metazona, 3.3 and 8 mm, respectively. Length of paratypes, 44 mm, width of midbody pro- and metazona, 3.5–4.5 and 9–10.5 mm (male, female), respectively. Dorsum granulate (Figs 10, 11C). Coloration (preserved in 70% ethanol) olivaceous-marbled-brown; antennae, venter and legs brown to light brown.

Head densely microgranulate; interantennal isthmus about half as broad as diameter of antennal socket. Antennae long and only slightly clavate, *in situ* reaching past body ring 4 when stretched dorsally; in length, antennomere $4 > 3 > 2 > 6 > 1 > 7$; apical segment with usual four sensory cones.

Body with 20 segments (male, female). In width, head < collum < ring 2 < 3 < 4 < 5 < 6–16, body tapering towards telson starting with ring 17. Collum transversely ellipsoid, not covering the head from above; sides narrowly rounded; dorsal surface densely and irregularly microgranulate (Figs 10, 11C). Dorsum slightly convex (Fig. 10). Prozona smooth and shining; metazona dull, densely microgranulate; pleurosternal region with transverse rows of small, tubercles/short spines. Metaterga 2–5 each with a small, evident impression at bases of paraterga, following paraterga (nearly) regularly convex, continuing the convex outline of mid-dorsal region. Paraterga broad, mostly

lying at about half body height, and slightly declined, paraterga 17–19 increasingly clearly drawn past rear tergal margin, 19th sharp. Sides below paraterga densely granulate, grains in the caudal row being longer, spiniform, and sharp. A thin and dark axial line sometimes traceable dorsally, particularly well visible on collum and prozona.

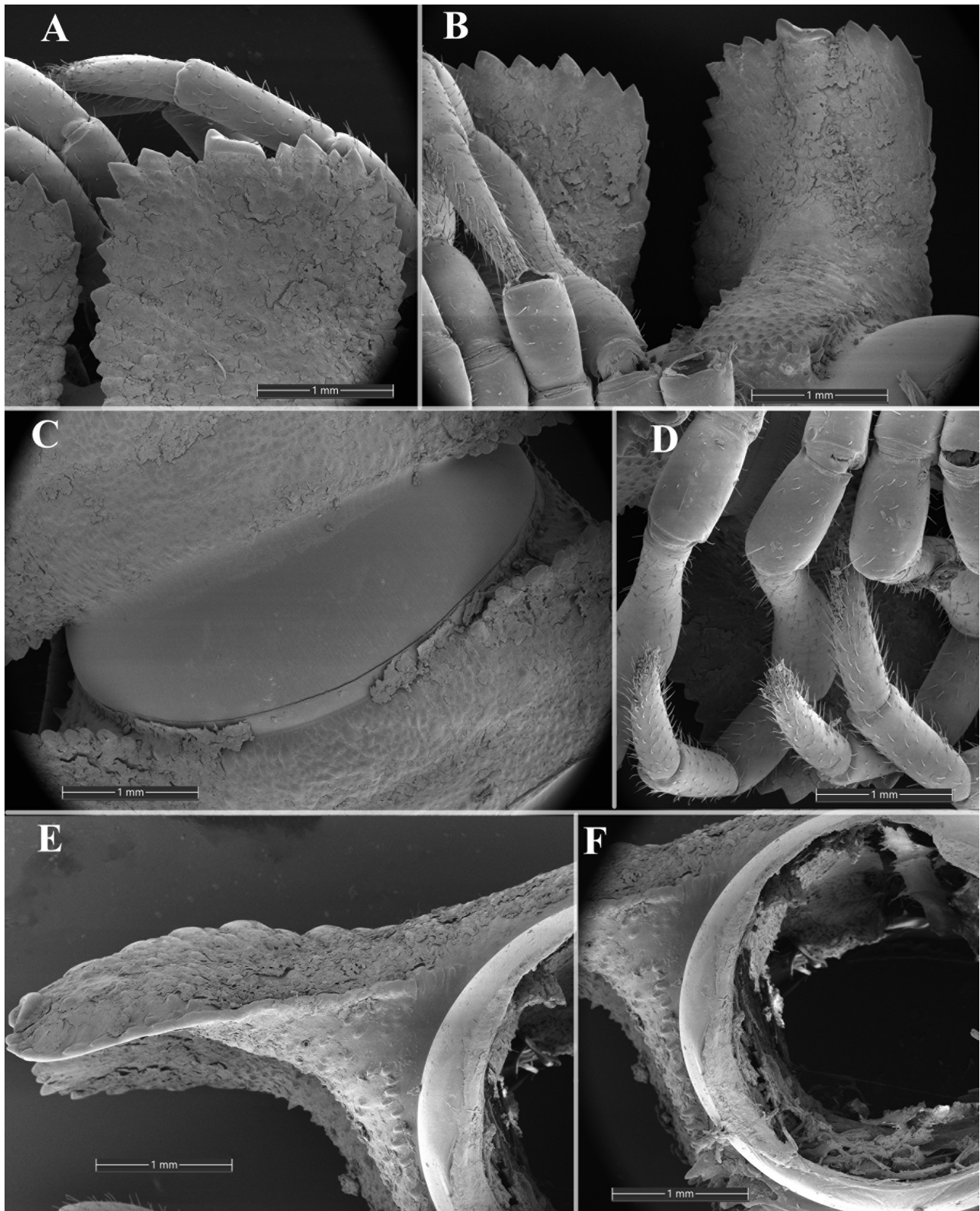


FIGURE 11. SEM micrographs of *Scaptodesmus vandenspiegeli* **sp. nov.**, male paratype (ARNF). **A & B.** mid body paraterga, dorsal and ventral view, respectively; **C.** dorsum presenting pro and metazonae margin; **D.** legs of mid-body segment, ventral view; **E & F.** cross-section of a midbody segment, caudal view. **Scale bars:** 1.0 mm (**A, B, C, D, E, F**)

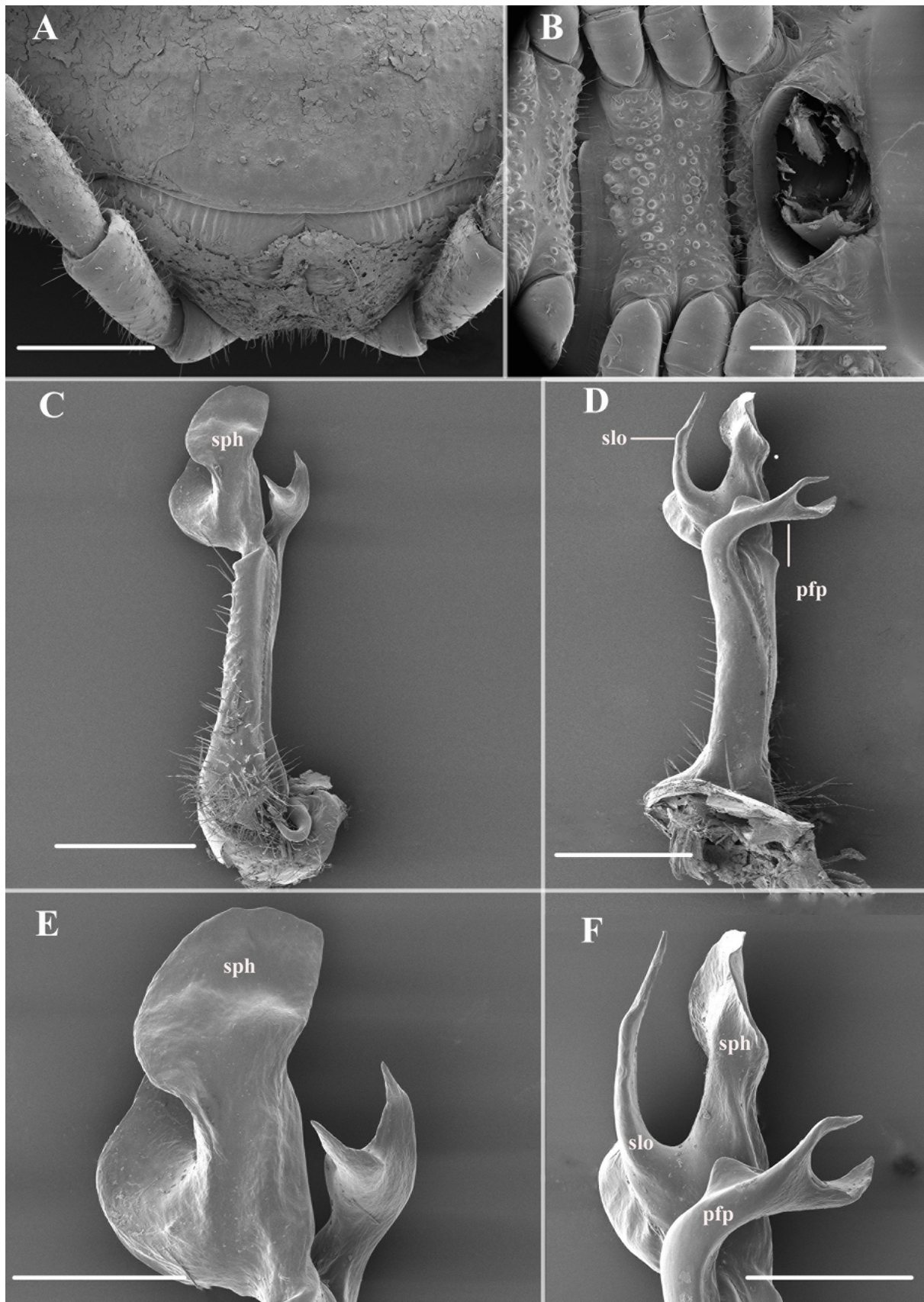


FIGURE 12. SEM micrographs of *Scaptodesmus vandenspiegeli* **sp. nov.**, male paratype, (ARNF). **A.** head and anterior margin of the collum, dorsal view; **B.** sternal region and gonopod aperture, ventral view; **C-E.** right gonopod, mesal view; **D-F.** left gonopod, dorsal view. **Abbreviations:** **slo**, solenomere lobe; **sph**, solenophore; **pfp**, postfemoral process. **Scale bars:** 1.0 mm (**A, B, C, D**); 400 μ m (**E, F**)

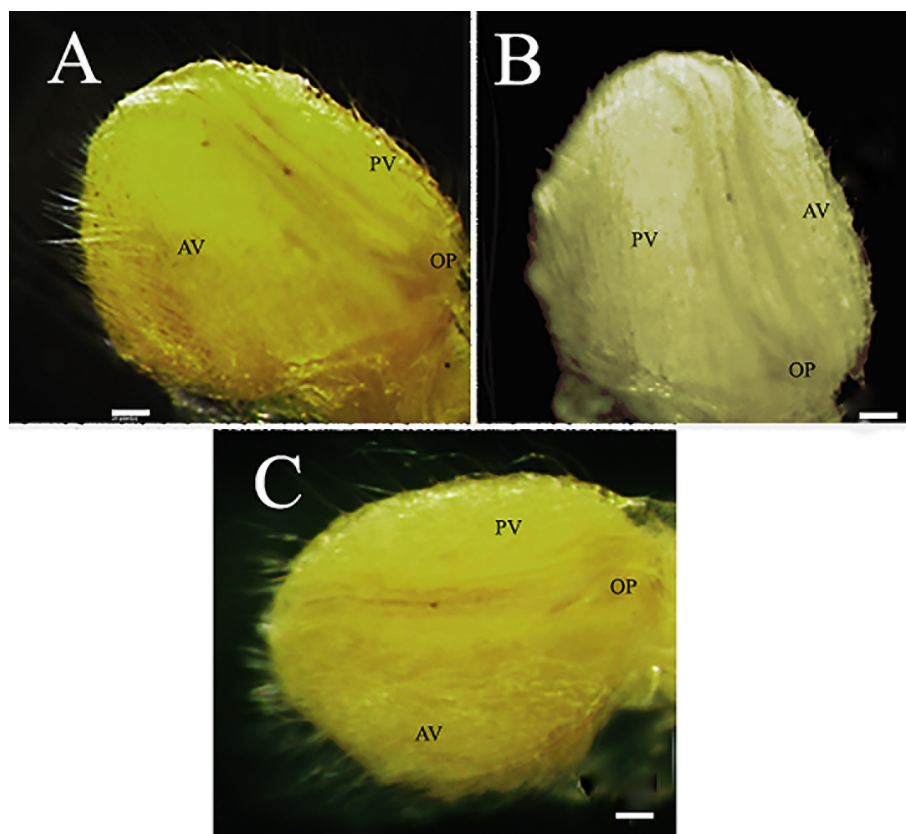


FIGURE 13. *Scaptodesmus vandenspiegeli* sp. nov, female paratype (NHMN-62-16). detail of left cyphopod: **A & B.** lateroventral view; **C.** ventral view. **Abbreviations:** AV, anterior valve; PV, posterior valve; OP, operculum. **Scale bars:** 250 μ m (**A, B, C**).

Epiproct short, spade-shaped, strongly flattened dorsoventrally, subtruncate, tuberculate dorsally (Fig. 10). Hypoproct microgranulate, subtrapeziform, with 1+1 caudal setae distinctly separated and borne on minute knobs. Paraprocts likewise densely microgranulate.

Sterna broad, almost flattened, densely granulate on metazona (Fig. 12B). Gonapophyses on male coxae 2 vestigial. Legs, very long and slender, about 1.5 times as long as the height at midbody (male), in length, femur > tarsus > tibia > prefemur = postfemur > coxa; claw very small, slightly curved; ventral surface of legs densely setose except for both postfemur and coxa. No brushes on ventral surface of tarsi (Fig. 11D).

Gonopod aperture (Fig. 12B) transversely ovoid, large, lateral and posterior edges slightly elevated, fully concealing both gonocoxae and bases of telopodites.

Gonopods (Fig. 12C-F): coxite medium-sized, subcylindrical, fused at base to a small membranous sternal remnant, poorly setose distodorsally, including a pair of very closely placed, distalmost and particularly long setae.

Cannulae slender, without peculiarities. Telopodites *in situ* directed forward, held subparallel to each other, suberect, not crossing each other mesally. Prefemoral part erect, taking up ca. 2/3 total length of telopodite. Femorite absent, but a relatively complex postfemoral process (**pfp**) present, recurved at a right-angle, bifid, bearing a small, rounded lamella/plate just after the curvature. Acropodite twisted, divided parabasally into two lobes: a medial, large and axe-shaped solenophore (**sph**) and a large lateral solenomere (**slo**) branch, this bearing an indistinct, small solenomere proper at its tip.

Female. Cyphopods located directly behind of leg-pair 2 on body ring 3; broadly ovoid in ventral view (Fig. 13). Anterior and posterior valves densely setose, ventral margins elevated, forming distinct carinae. Contact line between the two valves forming a median groove (Fig. 13B). Operculum small and relatively proximal (Fig. 13 C).

Distribution. This species is currently known from three localities in Cameroon's southern forest region, where it has been usually found under leaf litter and in decaying material. It has been recorded in syntopy with *S. kala* **sp. nov.** in the Central region of the country (Fig. 14). The species inhabits both degraded secondary forests and mature, undisturbed forest.

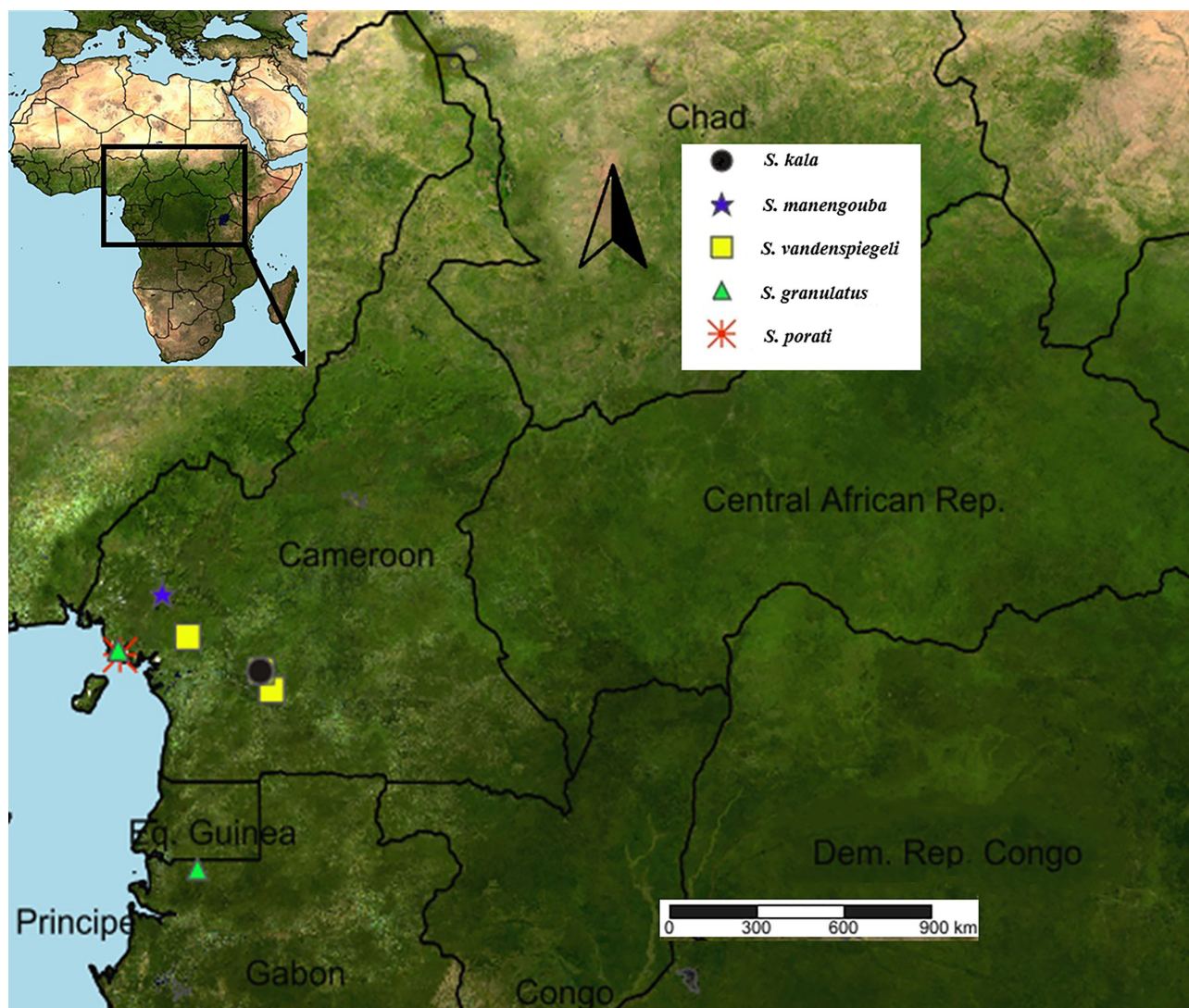


FIGURE 14. Known distribution of *Scaptodesmus* species in Afrotropical rainforests.

Key to species of *Scaptodesmus*

The key below is based on male characters and therefore, *Scaptodesmus porati* Cook, 1896 is excluded as the gonopods have never been illustrated.

1. Gonopod postfemoral process undivided, complex in structure, folded into a lateral groove, or rake-shaped and bearing 3–4-minute denticles distally. 2
- Gonopod postfemoral process bifurcate and mostly simple in structure. 3
2. Solenophore broad, opposite a relatively thin and falcate solenomere branch, lacking a solenomere proper at apex (Fig. 8). *S. manengouba* **sp. nov.**
- Solenomere branch about half as wide as solenophore, with a distinct, small solenomere proper at apex (Figs 4E, 4G) *S. kala* **sp. nov.**
3. Curvature of postfemoral process showing a small inner blade at mid-length (Figs 11D, 11F), tips of the two bifurcate branches of postfemoral process subequal in size *S. vandenspiegeli* **sp. nov.**
- Postfemoral process without small inner blade at mid-length of curvature, tips of the two bifurcate branches unequal in size (Fig. 2C) *S. granulatus*.

Discussion

Although some efforts have been made to generate DNA barcode data for African millipedes (Mwabvu *et al.* 2015; Wesener *et al.* 2020), no molecular studies have focused yet on those from Cameroon. This study presents the first DNA barcode data for *Scaptodesmus* species identified by morphology. However, some species of this understudied Afrotropical genus could not be included in our analyses. For instance, *S. granulatus* could not be included due to the loss of specimens from the Hamburg Museum's collection. Additionally, one new species was included in our study, but it remains undescribed due to insufficient material for a complete taxonomic description.

Our results revealed that all *Scaptodesmus* species analyzed are monophyletic, and the combined data support the validity of the newly discovered taxa as distinct species. This highlights the potential of classical DNA barcoding for species delimitation (Spelda *et al.* 2011). DNA sequence data can therefore play a vital role in confirming species validity, identifying undescribed taxa and supplementing the taxonomy based on male genitalia.

Due to their limited dispersal abilities and habitat specificity, millipedes are often local endemics (Hopkin & Read 1992). Consequently, significant interspecific genetic differentiation can be expected (Mwabvu *et al.* 2015).

This review of the genus *Scaptodesmus* reveals that it comprises five recognized species, of which three are newly described here. Previously, this millipede genus of the family Chelodesmidae was considered to comprise three species, including *S. dentatus* (Silvestri, 1909), whose status was uncertain (Demange & Mauriès 1975). The diagnosis of the genus, based primarily on gonopod configuration, confirms that *S. dentatus* does not belong to *Scaptodesmus*. Based on gonopod morphology, this species appears to be closely related to the genera *Paltoforus* Attems, 1937 and *Basacantha* Chamberlin, 1952, which feature a short prefemoral process, a long solenomere branch, a short and densely setose femoral part, and a tibiotarsus composed of a wide and twisted lamella (Attems 1931).

Based on gonopod structure and general morphological similarities, the genus *Scaptodesmus* appears to be closely related to the genera *Diaphorodesmus* Silvestri, 1896, *Diaphorodesmoides* Vandenspiegel, Golovatch & Mauriès, 2016 and *Cryptoporatia* Hoffman, 1980. Future phylogenetic studies may recover these genera as a new tribe within the Prepodesminae. Notably, species in these genera share several characteristics, including gonopods with a long prefemorate covered in numerous setae, and an acropodite that is typically subdivided into two branches: the solenomerite and the solenophore. The solenophore is positioned posteriorly.

Previously reported in Central and East Africa, this review restricts the distribution of *Scaptodesmus* to Central Africa, particularly Cameroon, where all species of the genus have been recorded. The genus is also present in Gabon, Nigeria and the Democratic Republic of the Congo (Hoffman 1980). *Scaptodesmus* appears to be quite diverse and largely endemic to Central Africa.

We are confident that future surveys will reveal additional species of this genus, providing a more comprehensive understanding of its distribution. Recent studies have highlighted that some species within this genus are syntopic, meaning that two to three species have the potential to coexist in the same habitat (Golovatch *et al.* 2018; Nzoko-Fiemapong *et al.* 2018). This is evident in *S. vandenspiegeli* **sp. nov.** and *S. kala* **sp. nov.**, which inhabit the same sites and biotopes. Although many new taxa and records remain to be discovered, this study establishes a robust basis for future research into the genus and millipede fauna of Cameroon.

Conclusion

The findings of this study indicate that *Scaptodesmus* is geographically restricted to Central Africa, where it primarily inhabits forest ecosystems. The genus is notable for its diversity, and it is likely that further species will be identified through additional surveys. Some species are sympatric or even syntopic. The *incertae sedis* status of *S. dentatus* was confirmed. Its morphology is more closely aligned with the genera *Pimodesmus* Chamberlin, 1927 and *Basacantha* Loksa, 1967, particularly in terms of the gonopods configuration. This study highlights the potential of integrated taxonomy to resolve relationships among millipede species groups below the family level, providing valuable insights into the diversity and evolutionary history of the genus *Scaptodesmus*.

Acknowledgements

We would like to thank the Ministry of Scientific Research and Innovation of Cameroon (permits 0000071/ MINRESI/ B00/ C00/ C10/ C13 and 000009/ MINRESI/ B00/ C00/ C10/ C13) and the Ministry of Forestry and Wildlife (permit 1835/ PRBS/ MINFOF/ SETAT/ DAFP/ SDVEF/ SC/ ALGG) for granting us research permits to conduct fieldwork in Cameroon. We would also like to thank Dr Danilo Harms, Curator of Arachnida and Myriapoda at the Museum of Nature Hamburg, for providing valuable information on *Scaptodesmus granulatus*, as well as Dr Guillaume Lentendu and Dr Christophe Praz for their advice and support. The first author acknowledges support from the Swiss Government Excellence Scholarships and financial support for lab work provided by the Leading House Africa Research Partnership Grant II (2023) and the Basler Stiftung für biologische Forschung (2023). Additional funding for millipede DNA sequencing was provided by the University of Guelph through Prof. Paul Hebert. We would also like to thank Marion Podolak of the 'Muséum cantonal des sciences naturelles' in Lausanne, Switzerland, for her assistance in taking some specimen images. An anonymous reviewer and Sergei Golovatch provided numerous comments and corrections which greatly enhanced the here presented work.

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