Zootaxa 4462 (3): 426–434
http://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4462.3.8
http://zoobank.org/urn:lsid:zoobank.org:pub:7D1DC08A-90FA-4258-B03B-B015F93CCA7F

First record of the millipede genus *Nesorthomorpha* Jeekel, 1980 in Vietnam with description of a new species (Diplopoda, Polydesmida, Paradoxosomatidae)

ANH D. NGUYEN[1,2,5], BINH T.T. TRAN[3] & MINH D. LE[4]

[1]*Duy Tan University, 254, Nguyen Van Linh, Da Nang City, VIETNAM.*

[2]*Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, 18, Hoangquocviet Rd., Caugiay, Hanoi, VIETNAM.*

[3]*Department of Zoology, Faculty of Biology, Hanoi National University of Education, 136, Xuan Thuy, Cau Giay, Hanoi, VIETNAM.*

[4]*Faculty of Education, Ha Tinh University, 447, 26/3 Street, Ha Tinh City, VIETNAM.*

[5]*Corresponding author: Anh D. Nguyen. E-mail:* ducanh410@yahoo.com *or* ducanh.iebr@gmail.com

Abstract

The genus *Nesorthomorpha* Jeekel, 1980 is recorded in Vietnam for the first time based on the discovery of the new spe- cies *Nesorthomorpha montana* n. sp. from the Highlands of Vietnam. An identification key to the new and 8 previously known *Nesorthomorpha* species is also provided. The relationship between the new species and 9 other species of 5 genera of the tribe Orthomorphini was analyzed using a 500 base pair fragment of the mitochondrial 16S rRNA gene. The result indicates that the new species appears to be closely related to the genus *Orthomorpha*.

Key words: Millipede, *Nesorthomorpha*, new record, new species, Vietnam

Introduction

Nesorthomorpha was proposed for three species: *Orthomorpha coriacea* Carl, 1902; *Orthomorpha armata* Carl, 1902; and *Strongylosoma atroroseum* Pocock, 1894 (Jeekel, 1980). Several additional species were later described in the genus (Golovatch 1996; Golovatch & Wytwer 2001), and the genus currently consists of 8 species:

N. coriacea (Carl, 1902) from Java, Indonesia.
N. armata (Carl, 1902) from Java, Indonesia.
N. atrorosea (Pocock, 1894) from Java, Indonesia.
N. communis Golovatch & Wytwer, 2001 from Java, Indonesia.
N. phasmatis Golovatch, 1995 from Java, Indonesia.
N. picturata Golovatch, 1995 from Java, Indonesia.
N. similis Golovatch, 1995 from Java, Indonesia.
N. typica Golovatch, 1995 from Java, Indonesia.

The genus *Nesorthomorpha* is easily distinguished from closely related paradoxosomatid genera by the presence of well-developed paranota, gonopods with an additional spiniform or elongate triangular process near the base of the lamina medialis (lamina on medial side of solenophore), and by the tip of the gonopod that is deeply split into two long processes.

To date, the application of molecular data for understanding phylogenetic relationships between higher level millipede taxa has been widely used (Sierwald *et al.,* 2003; Sierwald & Bond 2007; Woo *et al.* 2007; Brewer & Bond 2013; Brewer *et al.* 2013; Miyazawa *et al.* 2014; Fernández *et al.* 2016), and the integration of molecular and morphological data has also been applied to lower level millipede taxa, for example, Pimvichai *et al.* (2014, 2018) for Harpagophoridae (Spirostreptida), Pachybolidae (Spirobolida); Wesener *et al.* (2014) for Sphaerotheriida; Marek & Bond (2006, 2007), Marek (2010), and Means & Marek (2017) for Xystodesmidae (Polydesmida).

 Accepted by P. Marek: 24 Jul. 2018; published: 28 Aug. 2018

Among millipedes, the Paradoxosomatidae is a large and species-rich family with more than 1,000 species in 200 genera, and 22 tribes (Nguyen & Sierwald, 2013). However, there are just a few molecular phylogenetic studies for paradoxosomatid taxa, e.g. Wojcieszek & Simmons (2012), Decker (2016a, b), Decker *et al.* (2017), Nguyen *et al.* (2017), and Nguyen (2017).

Continuing our work on the millipede fauna of Vietnam, this paper documents the genus *Nesorthomorpha* Jeekel, 1980 in Vietnam for the first time, and we describe a new species, *Nesorthomorpha montana* n. sp. This study also provides a molecular phylogenetic analysis of the relationships between the new species and other paradoxosomatid taxa.

Material and methods

Millipede specimens were collected during field expeditions organized by the Vietnam-Russian Tropical Center, Ministry of Defense in Ngoc Linh Mountains, Chu Mom Ray and Kon Ka Kinh National Parks in the Highlands of Vietnam. All specimens were preserved in 80% ethanol, and examined using an Olympus SZX11 microscope.

Left gonopods were dissected for morphological examination. Line drawings were made with the help of a camera lucida attached to an Olympus SZX11 microscope. Color images were taken using a DinoLite Eyepiece 2.0 and SEM images were taken using an ABT20 machine in Ibaraki University (Japan). Line drawings, color and SEM images were assembled using Adobe Photoshop CS6.

Total genomic DNA was extracted from head and leg tissues using a DNeasy Blood & Tissue Kit (Qiagen Inc.). We first used the primer set COI-1F20 (5’-ACT CTA CTA ATC ATA AGG AT-3’) and COI-1R19 (5’-TAA ACC TCCGGG TGA CCAA-3’), but did not successfully amplify the fragment of the cytochrome c oxidase subunit I (COI) from the new species. Therefore, the primer set, 16S-1F19 (5'- CCG GTT TGA ACT CAG ATCA-3') and 16S-1R20 (5'-TGA CTG TTT AGC AAA GAC AT-3'), was used to amplify a 520 bp fragment of the mitochondrial 16S rRNA gene. Polymerase chain reaction (PCR) protocols for amplification follow Nguyen *et al.* (2017). PCR products were screened for successful amplifications of a fragment of 16S rRNA through electrophoresis in 1% agarose gel in 1X TBE buffer. PCR products were purified using ExosapIT or an QIAquick PCR Purification Kit (Qiagen Inc.), then were sequenced by Solgen, Inc. (Korea) on an Applied Biosystems automatic sequencer (ABI3130 XL) using the same primer sets as in the initial PCR.

Fragments of the 16S rRNA sequence were manually checked using BioEdit ver. 7.1. (Hall, 1999), and BLAST searches (Altschul *et al.*, 1990) to rule out contamination, and confirm whether or not they are millipede sequences. All confirmed sequences were aligned with the multiple sequence alignment program MUSCLE ver. 3.8.31 (Edgar, 2004).

The relationships between the new species and 13 species belonging to 7 genera, including two outgroups of the genera *Tylopus* and *Oxidus* (tribe Sulciferini) were analyzed. K2P (Kimura 2 parameter) distances were estimated using MEGA ver. 7.0 (Kumar *et al.*, 2016). Two tribes, Orthomorphini and Sulciferini, both belonging to the family Paradoxosomatidae, are widely distributed in the Oriental region, and well known in Vietnam (Nguyen & Sierwald, 2013). Therefore, we used two representatives of the tribe Sulciferini (*Tylopus* and *Oxidus*) as outgroups when analyzing the phylogenetic relationship of five orthomorphinine genera.

ModelFinder was performed in MEGA 7.0 to identify the best fit maximum likelihood substitution model (Kumar *et al.*, 2016). The selected model was Hasegawa-Kishino-Yano (HKY) + Gamma Distribution (G) with the lowest Bayesian Information Criterion (BIC) score of 5574.00 and lnL of -2639.57.

Phylogenetic trees were reconstructed using maximum likelihood (ML) and Bayesian inference (BI). Maximum likelihood bootstrap analysis was carried out using MEGA 6.0 with 1000 replicates (Kumar *et al.*, 2016). A tree was inferred using MrBayes ver. 3.1.2 with 10 million generations, a chain heating parameter of 0.06, and sampling every 1000 generations (Huelsenbeck & Bollback 2001). Nucleotide sequences were deposited at GenBank. Collection localities, specimen vouchers, and GenBank accession numbers are summarized in Table 1.

Holotype, paratypes and total genomic DNA are deposited in the Department of Soil Ecology, Institute of Ecology and Biological Resources (IEBR), Vietnam Academy of Science and Technology, Hanoi, Vietnam.

TABLE 1. Species vouchers and accession numbers deposited in Genbank

No.	Species	Locality	Voucher	Accession number
1	*Antheromorpha festiva* (Broelemann, 1916)	Yok Don N.P., Dak Lak Prov.	IEBR-519	KX755577
2	*Oxidus gigas* (Attems, 1953)	Sapa, Lao Cai Prov.	IEBR-133	KX755581
3	*Oxidus riukiaria* (Verhoeff, 1940)	Okinawa Isls., Japan	IEBR-500	KX755583
4	*Tylopus hilaroides* Golovatch, 1984	Cuc Phuong N.P., Ninh Binh Prov.	IEBR-198	KX755588
5	*Tylopus roseiparaterga* Nguyen, 2012	Tam Dao N.P., Vinh Phuc Prov.	IEBR-185A	KX755590
6	*Orthomorpha scabra* Jeekel, 1964	Bi Doup—Nui Ba N.P., Lam Dong Prov.	IEBR-Myr 432	MG564334
7	*Orthomorpha glandulosa* (Attems, 1937)	Quang Nam, Phuoc My	IEBR-Myr 237	MG564333
8	*Orthomorpha arboricola* (Attems, 1937)	Ngoc Linh Mts., Kon Tum Prov.	IEBR-Myr 455	MG564332
9	*Orthomorphoides setosus* (Attems, 1937)	Bi Doup—Nui Ba N.P., Lam Dong Prov.	IEBR-Myr 523	MG564335
10	*Nesorthomorpha montana* n. sp.	Ngoc Linh Mts., Kon Tum Prov.	IEBR-Myr 453	MG564338
11	*Nesorthomorpha montana* n. sp.	Chu Mom Ray N.P., Dak Lak Prov.	IEBR-Myr 561	MG564337
12	*Nesorthomorpha montana* n. sp.	Chu Mom Ray N.P., Dak Lak Prov.	IEBR-Myr 596	MG564339
13	*Desmoxytes cervaria* (Attems, 1953)	Sa Pa, Lao Cai Prov.	IEBR-Myr 32	MG564329
14	*Desmoxytes proxima* Nguyen *et al*., 2005	Sa Pa, Lao Cai Prov.	IEBR-Myr 243	MG564331
15	*Desmoxytes enghoffi* Nguyen *et al*., 2005	Phong Nha—Ke Bang N.P., Quang Binh Prov.	IEBR-IPE 5	MG564330
16	*Piccola odontopyga* (Attems, 1953)	Bi Doup—Nui Ba N.P., Lam Dong Prov.	IEBR-Myr 463	MG564336

Taxonomy

Class Diplopoda de Blainville in Gervais,

1844 Order Polydesmida Pocock, 1887

Family Paradoxosomatidae Daday, 1889

Tribe Orthomorphini Brölemann, 1916

Genus *Nesorthomorpha* Jeekel, 1980

Type species: *Orthomorpha coriacea* Carl, 1902.

Nesorthomorpha montana n. sp.

(Figs 1–3)

Material examined. *Holotype*: male (IEBR-453H) Kon Tum Province, Ngoc Linh Mts. (15°00'–15°18'N, 107°41'–08°01'E), primary forest, 1,900 m a.s.l, 31 March 2004, coll. Anh D. Nguyen. *Paratypes*: 1 female (IEBR-453P) same date as holotype; 1 male (IEBR-458) same locality, secondary forest, 1,700 m a.s.l., 21 March–9 April 2006, coll. Anh D. Nguyen. *Non-types*: 3 females (IEBR-Myr 561) Gia Lai Province, Chu Mon Ray National Park, natural forests, 500–750 m a.s.l., 5 Oct. 2005, coll. Mai Phu Quy; 1 male, 1 female (IEBR-Myr
596) Gia Lai Province, Chu Mom Ray National Park (14°18′–14°38′N, 107°29′–107°47′ E), natural forests, 1,200 m a.s.l., 31 March 2015, leg. Le Xuan Son; 1 male, 1 female (IEBR-Myr 633) Gia Lai Province, Kon Ka Kinh National Park (14°09′– 14°30′N, 108°16′–108°28′E), near head office, natural forests, 890 m a.s.l., 21–24 May 2017, coll. Anh D. Nguyen.

Diagnosis. The species differs from its congeners in the following combination of characters. Sternum 5 with two elevated, small, and rounded processes between coxae 4. Both lamina medialis and lamina lateralis of gonopod solenophore unfolded. Lamina medialis with a long spiniform process d in the middle. Tip of gonopod trifid: terminal and subterminal prongs lobed (tp and stp, respectively), middle prong (mp) a tiny denticle.

Description. Based on Holotype (male) IEBR-453H.

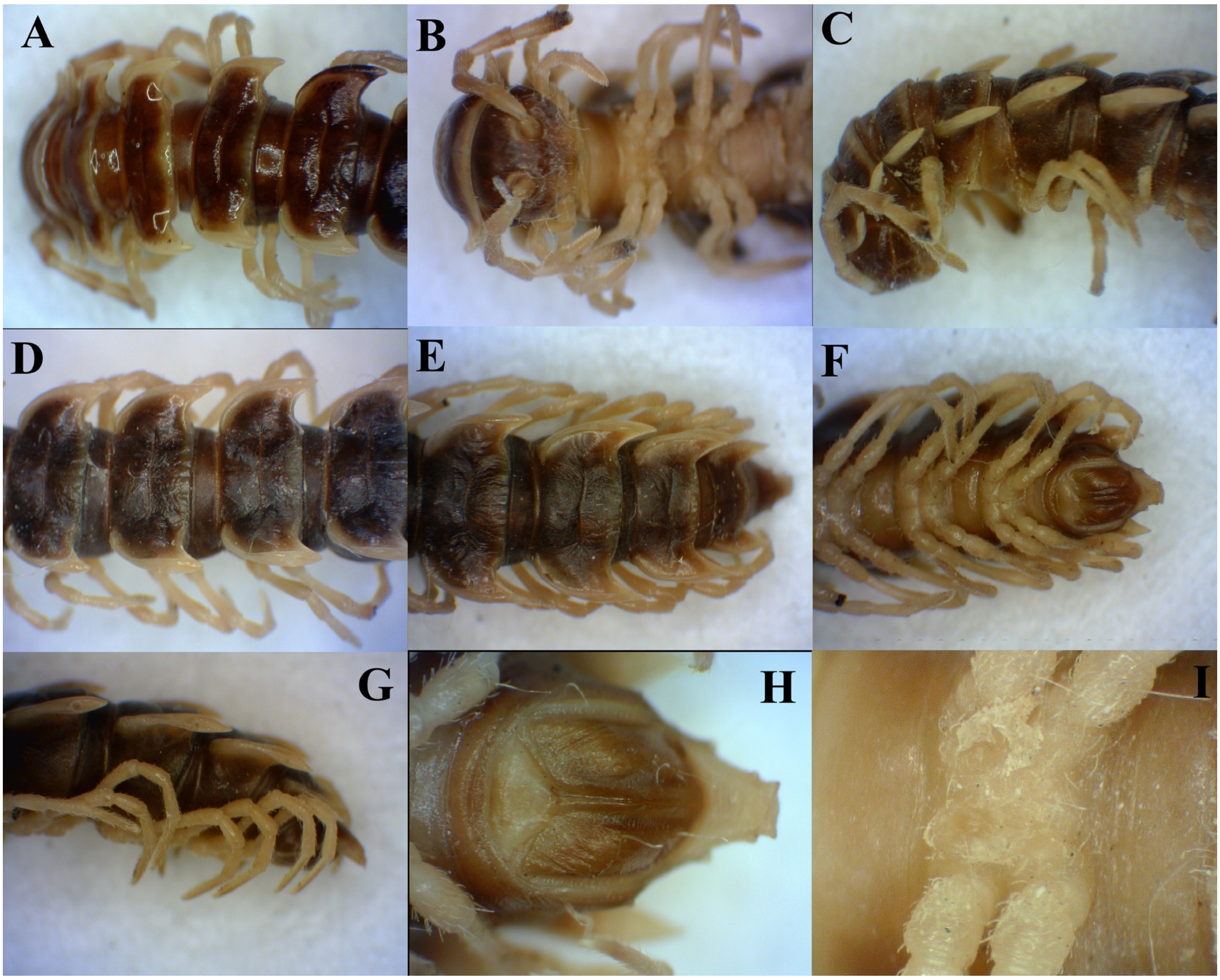

FIGURE 1. *Nesorthomorpha montana* n. sp. from holotype (IEBR-453H). Anterior body section, dorsal (A), ventral (B) and lateral view (C); midbody section, dorsal view (D); posterior body section, dorsal (E), ventral (F) and lateral view (G); hypoproct and epiproct, ventral view (H); sternum 5th, ventral view (I). Images not to scale.

Measurements: Holotype ca. 31.2 mm in length; width of midbody pro- and metazonites 2.0 mm and 3.2 mm, respectively. Coloration (Fig. 1): Whole body reddish brown except lateral area of paranota. Calluses, marginal posterior area of metaterga, waist between pro- and metazonite whitish yellow. Sterna, legs, antennae yellowish brown. Distal part of antennomere 6 and whole antennomere 7 blackish brown. Head: (Figs 1B–C) Slightly smaller than collum. Clypeolabral region modestly setose. Frons weakly convex, divided in 2 parts by distinct, thin epicranial suture. Antennae (Figs 1B–C) long, claviform, reaching body ring 4 laterally. Most antennomeres subequal in length except for the shortest antennomeres, 7 and 1. Tergites: Collum slightly narrower than body ring 2; surface shining and almost smooth, only faintly rugulose on medioposterior area. Collum with 3 rows of setae: 3+3 in anterior, 1+1 in middle, 1+1 in posterior. Body rings 4<3<2=5−17 in width, posteriorly gradually tapering towards telson. Prozonites shining and smooth. Metatergites shining; anterior half faintly rugulose, and posterior half considerably rugose. Metatergites with a row of 2+2 setae on anterior half and another row of 3+3 setiferous knobs near posterior margin. Transverse sulcus present on metaterga 5−19, reaching base of paranota. Waist between pro- and metaterga narrow, posterior margin beaded. Pleura with dense covering of microgranules. Pleurosternal carinae present as a full crest with a small caudal tooth on body rings 2−4, thereafter (moving posteriorly) reduced to a small caudal tooth on body rings 5–9, to a minute denticle on body rings 10–16, and missing on subsequent body rings. Paranota (Figs 1A, C, D, E, G) well developed, subhorizontal: lying about equal to metatergal surface. Caudal corner beak-like and pointed, more protuberant on posterior-most paranota, surpassing posterior contour of metaterga. Calluses thin on poreless paranota, but thicker on pore-bearing paranota. Epiproct (Figs 1F, H) long, broadly truncated, dorsoventrally flattened, with two tiny apicolateral tubercles. Epiproct apex with four spinnerets. Hypoproct (Fig. 1H) triangular with two distolateral, well-separated, setiferous knobs. Sterna sparsely setose, without modifications except for fifth sternum with two small, broadly rounded, highly elevated ventrad processes between coxae 4 (Fig. 1I). Legs: Long and slender, about 1.6X (male), 1.4X (female) longer than midbody height. Tarsal brushes present on leg pairs 1–27, absent on other legs. Prefemora not swollen. Femora without modifications. Gonopod (Figs 2–3): Coxae cylindrical, half as long as the telopodite; distoventral part sparsely setose. Prefemur densely setose, set off from acropodite by an oblique sulcus laterally. Acropodite long, slender, slightly curved posteroventrad, with an oblique sulcus laterally. Prostatic groove ending in a flagelliform solenomere apically. Both lamina medialis and lamina lateralis unfolded. Lamina medialis with a spiniform process d in the middle. Tip of gonopod trifid: terminal and subterminal prongs lobate (tp and stp, respectively), middle prong (mp) a tiny denticle.

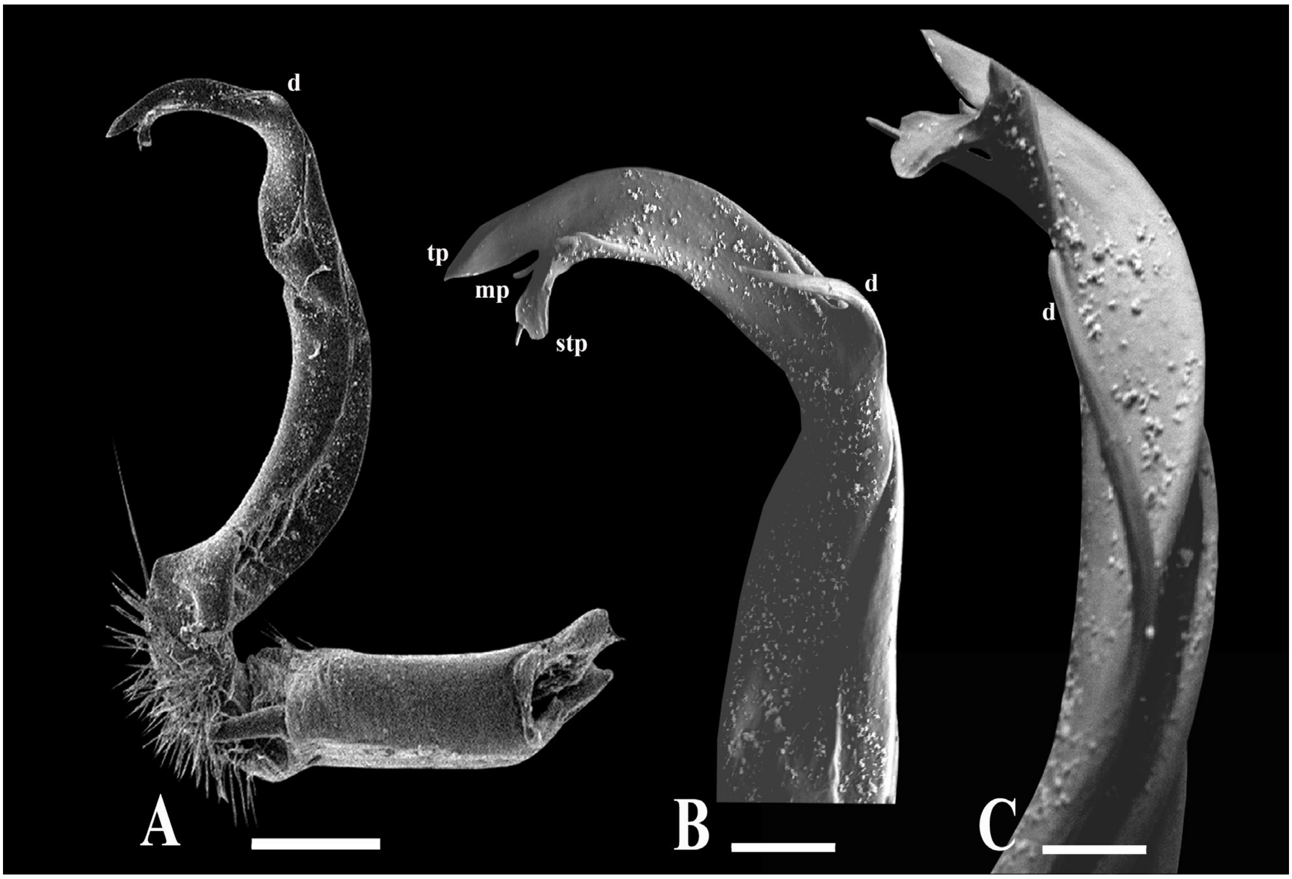

FIGURE 2. *Nesorthomorpha montana* n. sp. from holotype (IEBR-453H). Left gonopod, mesal view (A); distal part of gonopod, mesal view (B), mesodorsal view (C). Scale bar = 0.5 mm (A), = 0.1 mm (B and C). Notes: tp = terminal prong; stp = subterminal prong; mp = middle prong; d= spiniform process on lamina medialis.

Variation. Measurements. Body length 29.2–31.2 mm (males), 33.1 mm (female); width of midbody pro- and metazona 2.0 mm (male), 2.5 mm (female) and 2.8–3.2 mm (male), 3.8 mm (female), respectively. Coloration: Specimens from Kon Ka Kinh National Park are slightly different from others in coloration: they are almost black except the paranotal calluses and legs are castaneous brown.

Etymology. a Latin word "*montana*", which means "mountain", is an adjective to emphasize the mountainous habitats where the types were found.

Genetic distance and phylogenetic relationship. K2P distance between the new species and *Orthomorpha* species range from 0.143 to 0.163; between the new species and *Antheromorpha festiva* is 0.261. The distance between *Nesorthomorpha montana* n. sp. and other species varies from 0.148 to 0.317. Both ML and BI trees recover a clade that consisted of *Orthomorpha* species and *Nesorthomorpha montana* n. sp. with strong ML and BI values (100% bootstrap value and 0.98 posterior probability) (Fig. 4). The genus *Antheromorpha* is a weakly supported sister species (ML 54%; BI 0.89) to these two genera. *Desmoxytes* species formed a well-supported clade, and the genera *Piccola* and *Orthomorphoides* are sister to the ingroup taxa.

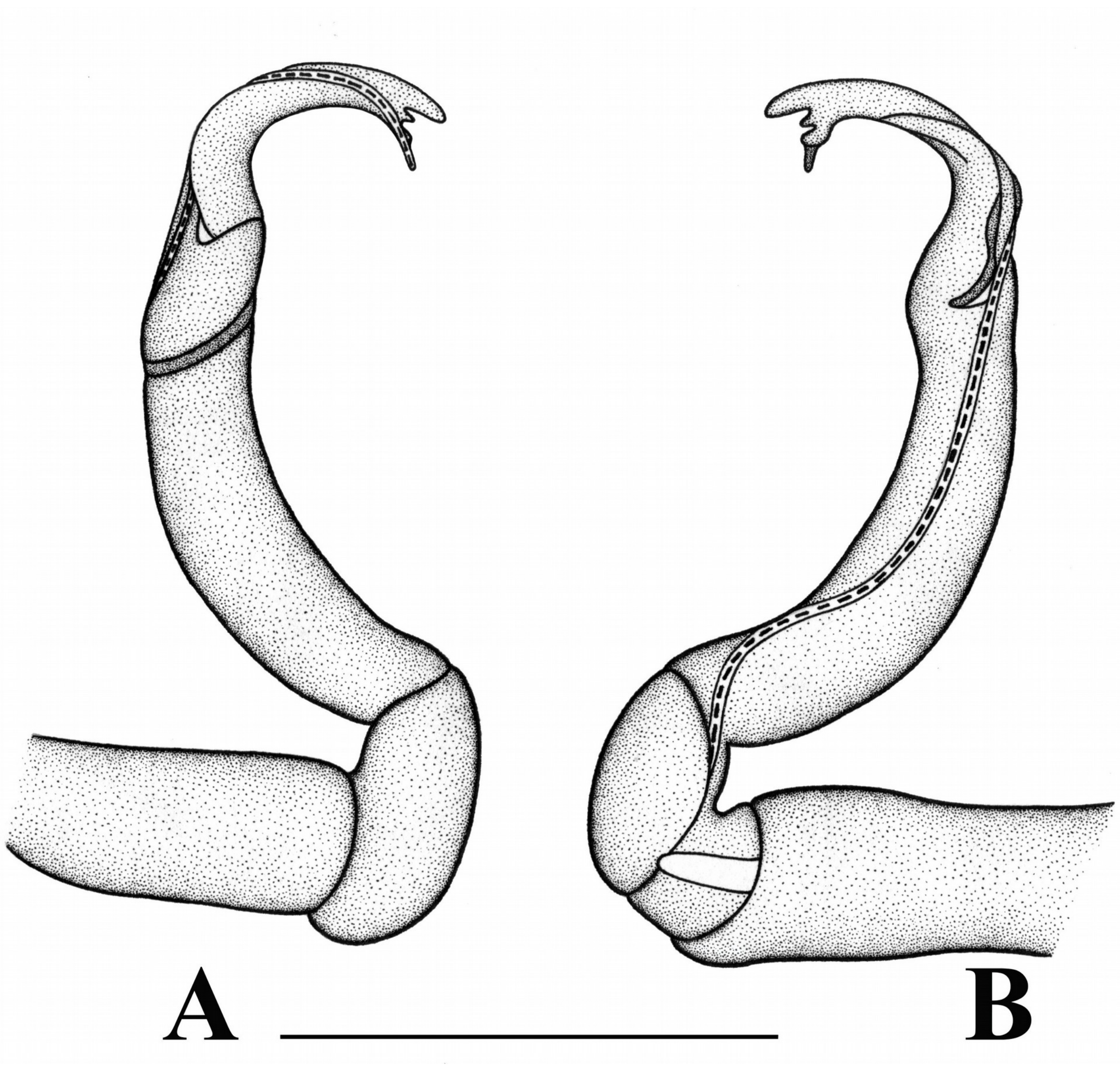

FIGURE 3. *Nesorthomorpha montana* n. sp. from holotype (IEBR-453H). Left gonopod, lateral view (A), mesal view (B). Scale bar = 1 mm.

A key to species of the genus *Nesorthomorpha* Jeekel, 1980
(Based on Golovatch & Wytwer, 2001)

1 Sternum 5 with two processes between coxae 4 (Fig.1I). Tip of gonopod trifid (Vietnam) . . . . *N. montana* n. sp.
- Sternum 5 with a single process between coxae 4. Tip of gonopod deeply split into two long processes (Java)........................2
2 Metaterga rugulose to rugose, or coarsely coriaceous to subgranulose...3
- Metaterga smooth...4
3 Metaterga coarsely coriaceous to subgranulose with two rows of setae. Sterna without modifications except for sternum 5 with a rectangular process between coxae 4. Lamina lateralis distally with a short rectangular lobe. . . . . *N. coriacea*
- Metaterga rugulose to rugose, with one row of setae. Sterna 8−19 with two pairs of spines near coxae, and sternum 5 with a

subquadrate, emarginate, setiferous process between coxae 4. Lamina lateralis with two carinae . . . . *N. typica*

4 Except sternum 5, other sterna with strongly pointed cones near leg coxae..5

- Except sternum 5, other sterna without modifications...6

5 Process of lamina medialis tuberculiform, short. Lamina lateralis without additional processes . . . . *N. armata*

- Process of lamina medialis short, spiniform. Lamina lateralis with two parabasal ridges . . . . *N. communis*

6 Lamina lateralis not folded and without carinate structures...7

- Lamina lateralis strongly folded, or with two carinae..8

7 Process of lamina medialis shorter than length of entire lamina. . . . . *N. phasmatis*

- Process of lamina medialis as long as length of entire lamina . . . . *N. atrorosea*

8 Lamina lateralis strongly folded . . . . *N. picturata*

- Lamina lateralis with two carinae . . . . *N. similis*

Discussion

The new species is atypical for the genus *Nesorthomorpha*, following the generic concept defined by Jeekel (1980) and Golovatch & Wytwer (2001). The gonopod tip of the new species is not deeply split as in other *Nesorthomorpha* species. In addition, the new species has a sternum 5 with 2 processes between coxae 4 which is another major difference to previously known species placed in the genus *Nesorthomorpha*. In contrast, the new species is closely similar to *Orthomorpha* species in terms of gonopod tip, well-developed paranota and the presence of sternal processes between coxae 4. Phylogenetically, the new species appears to be also closely related to *Orthomorpha* species (Fig. 4). However, despite the similarity, the presence of a spiniform process of the lamina medialis indicates that the species cannot be placed in the genus *Orthomorpha*. This character indicates that the species is a member of the genus *Nesorthomorpha*. While waiting more clear evidence and additional taxa to include in the phylogenetic analysis, it seems better to place this new species into the genus *Nesorthomorpha*. The new species, thus, appears to be intermediate between the two genera *Orthomorpha* and *Nesorthomorpha*, but a broader taxon sampling, especially with typical *Nesorthormorpha* species from Indonesia (Java), is needed to definitively confirm this relationship.

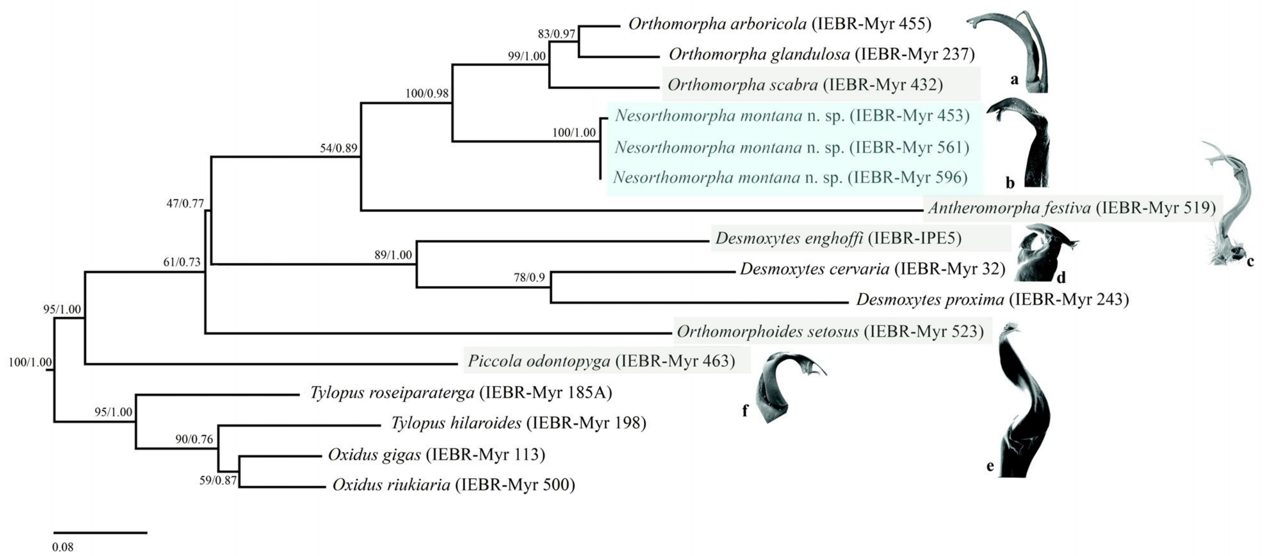

FIGURE 4. Phylogeny based on maximum likelihood and Bayesian inference from a 500 base pair fragment of the 16S rRNA. Scale bar = expected substitutions per site. Bootstrap and BI values are shown at nodes. Distal part of gonopods of select taxa: *Orthomorpha scabra* (a); *Nesorthomorpha montana* n. sp. (b); *Antheromorpha festiva* (c); *Desmoxytes enghoffi* (d); *Orthomorphoides setosus* (e); *Piccola odontopyga* (f).

The genus *Nesorthomorpha* Jeekel, 1980 was previously known from Java (Indonesia). The new species, found in Vietnam, has expanded its distribution northwards. Surprisingly, the record gap is nearly a 1000 km between Java and Vietnam. Whether this distributional gap between Java and Vietnam is an artifact of a lack of sampling in the intervening regions or an actual gap without other *Nesorthomorpha* taxa still remains an unanswered question regarding their distributional pattern.

The remarkable discovery of the genus *Nesorthomorpha* in Vietnam highlights that the millipede fauna of Vietnam is still poorly known. It also suggests that more intensive surveys, especially in remote areas, will reveal more unknown taxa.

Acknowledgements

The authors thank the Vietnamese-Russian Tropical Center, Ministry of Defense for kindly organizing the fieldwork in Ngoc Linh Mountains, Kon Ka Kinh and Chu Mom Ray National Parks. Mr. Jackson Means (Virginia Tech, U.S.A.) is kindly acknowledged for checking English. We also sincerely thank Drs Nesrine Akkari (Austria), Peter Decker (Germany) and Paul Marek (USA) for their invaluable comments which materially improve the paper. This research is funded by Vietnam National Foundation for Science and Technology Development (NAFOSTED) under grant number 106-NN.05-2015.22.

References

Brewer, M.S. & Bond, J.E. (2013) Ordinal-Level Phylogenomics of the Arthropod Class Diplopoda (Millipedes) Based on an Analysis of 221 Nuclear Protein-Coding Loci Generated Using Next-Generation Sequence Analyses. *PLoS ONE*, 8 (11), e79935.
https://doi.org/10.1371/journal.pone.0079935

Brewer, M.S., Swafford, L., Spruill, C.L. & Bond, J.E. (2013) Arthropod Phylogenetics in light of three novel millipedes (Myriapoda: Diplopoda) mitochondrial genomes with comments on the appropriateness of mitochondrial genome sequence data for inferring deep level relationships. *Plos ONE*, 8 (7), e68005.
https://doi.org/10.1371/journal.pone.0068005

Carl, J. (1902) Exotische Polydesmiden. *Revue Suisse de Zoologie*, 10, 563–679.
https://doi.org/10.5962/bhl.part.13794

Decker, P., Mesibov, R., Voigtlander, K. & Xylander, W.E.R. (2017) Revision of the Australian millipede genus *Pogonosternum* Jeekel, 1965, with descriptions of two new species (Diplopoda, Polydesmida, Paradoxosomatidae). *European Journal of Taxonomy*, 259, 1–34.
https://doi.org/10.5852/ejt.2017.259

Decker, P. (2016a) Integrative taxonomic revision of the polymorphic flat-millipede genera *Oncocladosoma* and *Somethus* in South Australia (Diplopoda: Polydesmida: Paradoxosomatidae). *Invertebrate Systematics*, 30 (3), 201–218.

Decker, P. (2016b) Phylogenetic analysis of the Australian trans-Bass Strait millipede genus *Pogonosternum* (Carl, 1912) (Diplopoda, Polydesmida, Paradoxosomatidae) indicates multiple glacial refugia in southeastern Australia. *ZooKeys*, 578, 15–31.

Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32 (5), 1792–1797.
https://doi.org/10.1093/nar/gkh340

Fernández, R., Edgecombe, G.D. & Giribet, G. (2016) Exploring phylogenetic relationships within Myriapoda and the effects of matrix composition and occupancy on phylogenomic reconstruction. *Systematic Biology*, 65 (5), syw041.
https://doi.org/10.1093/sysbio/syw041

Golovatch, S.I. & Wytwer, J. (2001) On two new species of the millipede family Paradoxosomatidae from Java, Indonesia, with reviews of the genera *Opisthodolichopus* Verhoeff, 1941 and *Nesorthomorpha* Jeekel, 1980 (Diplopoda: Polydesmida). *Annales Zoologici PAN*, 51 (4), 403–408.

Golovatch, S.I. (1994) On several new or poorly-known Oriental Parasoxosomatidae (Diplopoda Polydesmida), V. *Arthropoda Selecta*, 3 (3/4), 127–137.

Huelsenbeck, J.P. & Ronquist, F. (2001) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, 17, 754–755.
https://doi.org/10.1093/bioinformatics/17.8.754

Jeekel, C.A.W. (1980) On the classification of some little-known Parasoxosomatidae from Java and Sumatra (Diplopoda, Polydesmida). *Revue Suisse de Zoologie*, 87 (2), 323–340.
https://doi.org/10.5962/bhl.part.85521

Kumar, S., Stecher, G. & Tamura, K. (2016) MEGA 7: Molecular Evolution Genetics Analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution*, 33, 1870–1874.
https://doi.org/10.1093/molbev/msw054

Marek, P.E. & Bond, J.E. (2006) Phylogenetic systematics of the colorful, cyanide-producing millipedes of Appalachia (Polydesmida, Xystodesmidae, Apheloriini) using a total evidence Bayesian approach. *Molecular Phylogenetics and Evolution*, 41, 704–729. https://doi.org/10.1016/j.ympev.2006.05.043

Marek, P.E. & Bond, J.E. (2007) A reassessment of apheloriine millipede phylogeny: additional taxa, Bayesian inference, and direct optimization (Polydesmida: Xystodesmidae). *Zootaxa*, 1610, 27–39.

Marek, P.E. (2010) A revision of the Appalachian millipede genus *Brachoria* Chamberlin, 1939 (Polydesmida: Xystodesmidae: Apheloriini). *Zoological Journal of the Linnean Society*, 159, 817–889. https://doi.org/10.1111/j.1096-3642.2010.00633.x

Means, J.C. & Marek, P.E. (2017) Is geography an accurate predictor of evolutionary history in the millipede family Xystodesmidae? *PeerJ*, 5, e3854. https://doi.org/10.7717/peerj.3854

Miyazawa, H., Ueda, C., Yahata, K. & Su, Z.-H. (2014) Molecular phylogeny of Myriapoda provides insights into evolutionary patterns of the mode in post-embryonic development. *Scientific Reports*, 4, 4127. https://doi.org/10.1038/srep04127

Nguyen, A.D. (2017) A second species of the genus *Vietnamorpha* Golovatch, 1984 (Polydesmida, Paradoxosomatidae) and notes on the generic relationship. *Journal of Natural History*, 51 (39–40), 2331–2343. http://www.tandfonline.com/doi/full/10.1080/00222933.2017.1355491

Nguyen, A.D., Korsós, Z., Jang, K.H. & Hwang, U.W. (2017) A revision and phylogenetic analysis of the millipede genus *Oxidus* Cook, 1911 (Polydesmida: Paradoxosomatidae). *European Journal of Taxonomy*, 293, 1–22. https://doi.org/10.5852/ejt.2017.293

Pimvichai, P., Enghoff, H. & Panha, S. (2014) Molecular phylogeny of the Thyropygus allevatus group of giant millipedes and some closely related groups. *Molecular Phylogenetics and Evolution*, 71, 170–183. https://doi.org/10.1016/j.ympev.2013.11.006

Pimvichai, P., Enghoff, H., Panha, S. & Backeljau, T. (2018) Morphological and mitochondrial DNA data reshuffle the taxonomy of the genera *Atopochetus* Attems, *Litostrophus Chamberlin* and *Tonkinbolus* Verhoeff (Diplopoda: Spirobolida: Pachybolidae), with descriptions of nine new species. *Invertebrate Systematics*, 32, 159–195. https://doi.org/10.1071/IS17052

Pocock, R.I. (1894) Chilopoda, Symphyla, and Diplopoda from the Malay Archipelago. *Zoologische Ergebnisse einer Reise in Niederlandisch Ost-Indien, herausgegeben von Dr. Max Weber*, 3, 307–400.

Sierwald, P. & Bond, J.E. (2007) Current status of the myriapod class diplopoda (Millipedes): Taxonomic diversity and phylogeny. *Annual Review of Entomology*, 52, 401–420. https://doi.org/10.1146/annurev.ento.52.111805.090210

Sierwald, P., Shear, W.A., Shelley, R.M. & Bond, J.E. (2003) Millipede phylogeny revisited in the light of the enigmatic order Siphoniulida. *Journal of Zoological Systematics and Evolutionary Research*, 41, 87–99. https://doi.org/10.1046/j.1439-0469.2003.00202.x

Wesener, T., Michael J. Raupach, M.J. & Sierwald, P. (2010) The origins of the giant pill-millipedes from Madagascar (Diplopoda: Sphaerotheriida: Arthrosphaeridae). *Molecular Phylogenetics and Evolution*, 57, 1184–1193. https://doi.org/10.1016/j.ympev.2010.08.023

Wojcieszek, J.M. & Simmons, L.M. (2012) Evidence for stabilizing selection and slow divergent evolution of male genitalia in a millipede (*Antichiropus variabilis*). *Evolution*, 66, 1138–1153. https://doi.org/10.1111/j.1558-5646.2011.01509.x

Woo, H.J., Lee, Y.S., Park, S.J., Lim, J.T., Jang, K.H., Choi, E.H., Choi, Y.G. & Hwang, U.W. (2007) Complete mitochondrial genome of a troglobite millipede *Antrokoreana gracilipes* (Diplopoda, Juliformia, Julida), and juliformian phylogeny. *Molecules and Cells*, 23 (2), 182–191.