

## The land snail genus *Opisthoporus* Benson in L. Pfeiffer, 1851 (Gastropoda: Caenogastropoda: Cyclophoridae) from Vietnam, with description of a new species

Do Duc Sang<sup>1\*</sup>, Bui Thi Chinh<sup>2</sup> & Do Van Nhuong<sup>3</sup>

**Abstract.** Species of the genus *Opisthoporus* Benson in L. Pfeiffer, 1851 (family Cyclophoridae) occurring in Vietnam are reviewed and presented. In total, three species are included: *Opisthoporus beddomei* Dautzenberg & Fischer, 1908; *O. lubricus* Dautzenberg & Fischer, 1908; and *O. thuathienhuensis*, new species. *Opisthoporus thuathienhuensis*, new species, differs most distinctly from related congeners by its small inverted U-shaped breathing tube that has its distal end touching the last whorl. The new species is known only from limestone hills of Thua Thien Hue Province, central Vietnam, where terrestrial gastropod fauna is diverse, but relatively poorly known. This discovery represents the first record of the genus *Opisthoporus* in central Vietnam. A checklist of *Opisthoporus* taxa (mainly literature data) is presented.

**Key words.** systematics, limestone hill, breathing tube, Thua Thien Hue, Vietnam

### INTRODUCTION

Land snails of the family Cyclophoridae are a characteristic and widespread component of the terrestrial fauna of the forested tropics of Asia, Africa and Australia, comprising more than 56 genera and subgenera (Nevill, 1878; Kobelt, 1902, 1908; Bartsch, 1932; Low & Tan, 2017). The Cyclophoridae is divided into four subfamilies, including Cyclophorinae Gray, 1847; Spirostomatinae Tielecke, 1940; Alycaeinae Blanford, 1864; and Pterocyclinae Kobelt & von Möllendorff, 1897 (Vaught, 1989). In Vietnam, all subfamilies except Spirostomatinae have been discovered (Kobelt, 1902, 1913; Dautzenberg & Fischer, 1905, 1908; Páll-Gergely et al., 2017). Around 150 species have been thus far reported (Vermeulen & Maassen, 2003; Nguyen, 2016, 2017, 2018; Páll-Gergely et al., 2017; D.S. Do & V.N. Do, 2019; Vermeulen et al., 2019).

*Opisthoporus* Benson in L. Pfeiffer, 1851, one of the more than 40 genera of Cyclophorinae, has a wide distribution range that covers the Southeast Asia and South China regions (von Möllendorff, 1894; Kobelt, 1902, 1908; Fischer &

Dautzenberg, 1904; Kobelt, 1913). Currently, *Opisthoporus* comprises 33 nominal species and subspecies, of which some 22 were described from Malaysia and Indonesia, and around 11 from other areas such as Thailand, Cambodia, Philippines, Laos, Vietnam, and southern China (Kobelt, 1913; Foon et al., 2017; Low & Tan, 2017; Inkhabilay et al., 2019; Sutcharit et al., 2019). The current species delimitation of *Opisthoporus* is reliant on the works of Kobelt (1902, 1908, 1913) and Egorov (2009), which are mainly based on the breathing tube structures, degree of apertural lip expansion, the calcareous operculum, and other shell characters.

Previously, only two *Opisthoporus* species were known from Vietnam, both described from Quang-Huyen (Dautzenberg & Fischer, 1908). It has been more than a century since they were described. The present paper aims to conduct a study of the *Opisthoporus* species found in Vietnam, including distribution range and sampling materials from different regions of northern and central Vietnam. Here, we describe a new species and report a new record from central Vietnam.

### MATERIAL AND METHODS

This study is based on material collected during surveys by the first and second authors in north and central Vietnam in 2015–2019. Description of the new species in this paper is based on shell morphology, colouration, and patterns. Identification of *Opisthoporus beddomei* and *Opisthoporus lubricus* is based on published descriptions and figures (see literature cited herein). Type material was not located in the Institut royal des Sciences naturelles de Belgique (Brussels, Belgium) and the Muséum National d’Histoire Naturelle (Paris, France), where they could have been deposited.

Accepted by: Tan Siong Kiat

<sup>1</sup>Department of Applied Zoology, Faculty of Biology, Hanoi University of Science (Vietnam National University, Hanoi), 334 Nguyen Trai, Thanh Xuan, Hanoi, Vietnam; Email: do.ducsang@hus.edu.vn (\*corresponding author)

<sup>2</sup>Faculty of Biology, Hue University of Education, Hue University, 34 Le Loi, Hue, Vietnam

<sup>3</sup>Faculty of Biology, Hanoi National University of Education, 136 Xuan Thuy, Dich Vong, Cau Giay, Ha Noi, Vietnam

Terminology used in the description of the shell characters, including features of the peristome, breathing tube structures, body whorl, umbilicus and apertural lip expansion, follow Stoliczka (1872), Vermeulen & Junau (2007), and Egorov (2009). Shell measurements were made for adult specimens (with a developed outer lip) using digital calipers. The counting of shell whorls (to the nearest  $\frac{1}{4}$  whorl) follows Kerney & Cameron (1979: 13).

These specimens were deposited in the following institutions: Vietnam National Museum of Nature (VNMN), Vietnam; Zoological Collection of Biological Museum (ZMHU), Hanoi University of Science, Vietnam; Zoological Reference Collection (ZRC) of the Lee Kong Chian Natural History Museum, National University of Singapore, Singapore; and the Laboratory of Zoology, Hue University of Education (LZ-HUE), Vietnam.

## SYSTEMATICS

### Superfamily Cyclophoroidea Gray, 1847

#### Family Cyclophoridae Gray, 1847

#### Subfamily Cyclophorinae Gray, 1847

#### *Opisthoporus* Benson in L. Pfeiffer, 1851

*Opisthoporus* Benson in L. Pfeiffer, 1851: 8; Benson, 1855: 14; von Martens, 1867: 110; Stoliczka, 1872: 265; Nevill, 1878: 263; von Möllendorff, 1900: 136; Kobelt, 1902: 188, 213; 1913: 834; Gude, 1921: 130; Bartsch, 1932: 323; Egorov, 2009: 16; Low & Tan, 2017: 15.

*Tubicyclotus* – Habe, 1965: 119.

*Siphonocyclus* von Möllendorff, 1900: 136; Egorov, 2009: 17.

**Type species.** *Cyclostoma taylorianum* L. Pfeiffer, 1851.

**Diagnosis.** Shell discoidal in shape, with spire that varies from rather high conical to nearly flat, and a wide umbilicus, unicoloured or adorned with irregular axial brownish stripes, usually covered by thin hairy periostracum. Terminal part of the last whorl is separated from the penultimate whorl, or completely attached to the penultimate whorl. Body whorl with breathing tube behind apertural margin. Aperture circular, peristome double or single, with an expanded outer lip. Operculum calcareous, circular, multi-lamellar, nucleus central, with external fringe deeply grooved (H. Adams & A. Adams, 1855; Benson, 1855; Egorov, 2009).

**Remarks.** The *Opisthoporus* is superficially similar to the *Cyclotus* Swainson, 1840, in general shell form, colouration and pattern, and in the structure of the operculum. However, it can be distinguished from *Cyclotus* by the presence of a breathing tube, which is a curved hollow horn-like projection that opens into the last whorl behind the operculum (Kobelt, 1913; Bartsch, 1932; Egorov, 2009; Páll-Gergely et al., 2016). The genera *Opisthoporus*, *Pterocyclus* Benson, 1832, *Rhiostoma* Benson, 1860, and *Pearsonia* Kobelt, 1902, have many similar features (see Sutcharit et al., 2019). However,



Fig. 1. Approximate localities of *Opisthoporus* spp. in Vietnam. (1): *Opisthoporus beddomei*; (2): *Opisthoporus lubricus*; (3): *Opisthoporus thuathienhuensis*, new species. The numbered locality names are detailed in Table 1.

the structure of the breathing tube varies from notch-like to completely tubular in *Pterocyclus* (see Sutcharit et al., 2014), whereas it always forms a complete tube in *Opisthoporus*. *Rhiostoma* differs from *Opisthoporus* by its calcareous cup-shaped operculum, the peculiar detached and extended terminal part of last whorl. The operculum of *Opisthoporus* is calcareous, rather thin, and concave on both sides. *Pearsonia* has the breathing tube situated far away from the peristome and the outer lip forms a peristomal projection near the suture (see Tumpeeswan & Tumpeeswan, 2015).

Currently, the genus *Opisthoporus* is considered a genus (e.g., Stoliczka, 1872; von Möllendorff, 1900; Bartsch, 1932; van Benthem Jutting, 1960; Bragado et al., 2000; Low & Tan, 2017) or subgenus of *Cyclotus* (e.g., Nevill, 1878; Kobelt, 1912; Gude, 1921; Egorov, 2009; Inkhavilay et al., 2019; Sutcharit et al., 2019). In this paper, we treat *Opisthoporus* as a full genus. For other details on the systematics and nomenclature of the *Opisthoporus* and related genera, see Egorov (2009). Nevertheless, the reliability of currently accepted conchology-based systematics has not been thoroughly examined along other lines of evidence, and further research based on anatomical and radula characteristics or molecular analyses will no doubt be needed to answer questions regarding the systematic positions and affinities of the above genera.

#### *Opisthoporus beddomei* Dautzenberg & Fischer, 1908 (Figs. 1, 2A–D, 3A, D, G; Table 1, 2)

*Opisthoporus beddomei* Dautzenberg & Fischer, 1908: 200, pl. 7 figs. 1–4 (type locality: Quang-Huyen, Vietnam).

*Cyclotus (Opisthoporus) beddomei* – Kobelt, 1913: 836, pl. 124 figs. 1–4.

Table 1. Shell size variation in *Opisthoporus* spp. specimen collections.

Species and locality	No. of specimens	Range, mean ± S.D. (mm) of shell			
		Shell height (SH)	Shell width (SW)	SH/SW ratio	Aperture diameter
<i>Opisthoporus beddomei</i>					
1. Nam Dong, Thua Thien Hue, Vietnam	15	8.1–10.3 8.9 ± 0.65	15.3–20.0 16.8 ± 1.02	0.49–0.57 0.52 ± 0.03	6.1–7.0 6.3 ± 1.8
<i>Opisthoporus lubricus</i>					
2. Trang Dinh, Lang Son, Vietnam	9	9.2–16.3 12.6 ± 0.66	16.1–25.8 20.5 ± 0.92	0.58–0.63 0.61 ± 0.02	7.5–8.9 8.4 ± 0.37
3. Bac Son, Lang Son, Vietnam	27	11.2–14.9 12.9 ± 0.74	17.8–24.5 21.7 ± 1.12	0.55–0.62 0.59 ± 0.03	7.4–8.8 8.2 ± 0.26
4. Huu Lung, Lang Son, Vietnam	6	11.2–13.8 12.3 ± 0.66	15.4–18.6 19.1 ± 0.95	0.57–0.62 0.60 ± 0.02	7.3–8.6 8.0 ± 0.23
5. Vo Nhai, Thai Nguyen, Vietnam	5	9.8–11.3 10.4 ± 0.58	15.7–18.0 17.4 ± 0.83	0.58–0.62 0.60 ± 0.02	7.3–8.6 8.1 ± 0.29
<i>Opisthoporus thuathienhuensis</i> , new species					
6. Nam Dong, Thua Thien Hue, Vietnam	9	8.7–12.3 10.0 ± 0.91	14.0–19.5 15.7 ± 1.10	0.60–0.65 0.63 ± 0.03	5.9–6.8 6.5 ± 0.22

Table 2. Comparison of shell morphology between *Opisthoporus thuathienhuensis*, new species, and its Vietnamese congeners based on Dautzenberg & Fischer (1908) and this study.

Species	Breathing tube	Shell colour	Zig-zag pattern	Peristome	Number of whorls
<i>O. beddomei</i>	Oblique	Pale yellow	Dorsal side	Double	4–4½
<i>O. lubricus</i>	Forward or upright	Yellowish brown	Dorsal side	Double	4½–5
<i>O. thuathienhuensis</i>	Backward	Brown	Absent	Single	3¾–4

**Material examined.** 7 shells (LZ-HUE 1021), 5 shells (ZMHU), 2 figured shells (figs. 2A, B, 3A, D, G), Vietnam, Thua Thien Hue Province, Nam Dong District, Thuong Quang Commune, Limestone hill, 215 m a.s.l., 16°06'51"N, 107°38'27"E, coll. T.C. Bui, 16 September 2017; 3 shells (LZ-HUE 1022), Vietnam, Thua Thien Hue Province, Nam Dong District, Thuong Quang Commune, Limestone hill, 111 m a.s.l., 16°07'08"N, 107°37'20"E, coll. T.C. Bui, 10 July 2018.

**Diagnosis.** Shell brownish grey with numerous, rather regularly spaced growth lines that form distinct axial lines. Breathing tube curved towards the antepenultimate whorl.

**Distribution.** *Opisthoporus beddomei* is known from northern and central Vietnam (Cao Bang and Thua Thien Hue Provinces) (Dautzenberg & Fischer, 1908; this study).

**Remarks.** *Opisthoporus beddomei* is characterised by a medium-sized thin shell, with corneous and translucent periostracum, and a surface that has a brownish grey colour pattern. Like its congeners, the last part of its last whorl is usually slightly detached from the penultimate whorl. This species is most similar to *O. lubricus*, although they differ

slightly in terms of shell colouration. Both species have similar aperture morphology with the double peristome and white lip, although *O. beddomei* has a less prominent expansion on the upper part of its lip. The most distinctive difference between the two is the breathing tube, which is curved towards the antepenultimate whorl in *O. beddomei* and upright or curved forward towards the aperture in *O. lubricus*.

Its type locality Quang-Huyen most probably refers to Quang Uyen District in Cao Bang Province, although this species was not present in samples collected from surveys conducted in north Vietnam. Our discovery of this species from Thua Thien Hue, shell width of up to 20.0 mm, represents a range extension and the first record of *Opisthoporus beddomei* in central Vietnam.

***Opisthoporus lubricus* Dautzenberg & Fischer, 1908**  
(Figs. 1, 2E–G, 3B, E, H; Table 1, 2)

*Opisthoporus lubricus* Dautzenberg & Fischer, 1908: 201, pl. 7 figs. 5–8 (type locality: Quang-Huyen, Vietnam).  
*Cyclotus (Opisthoporus) lubricus* – Kobelt, 1913: 836, pl. 124 figs. 5–8.

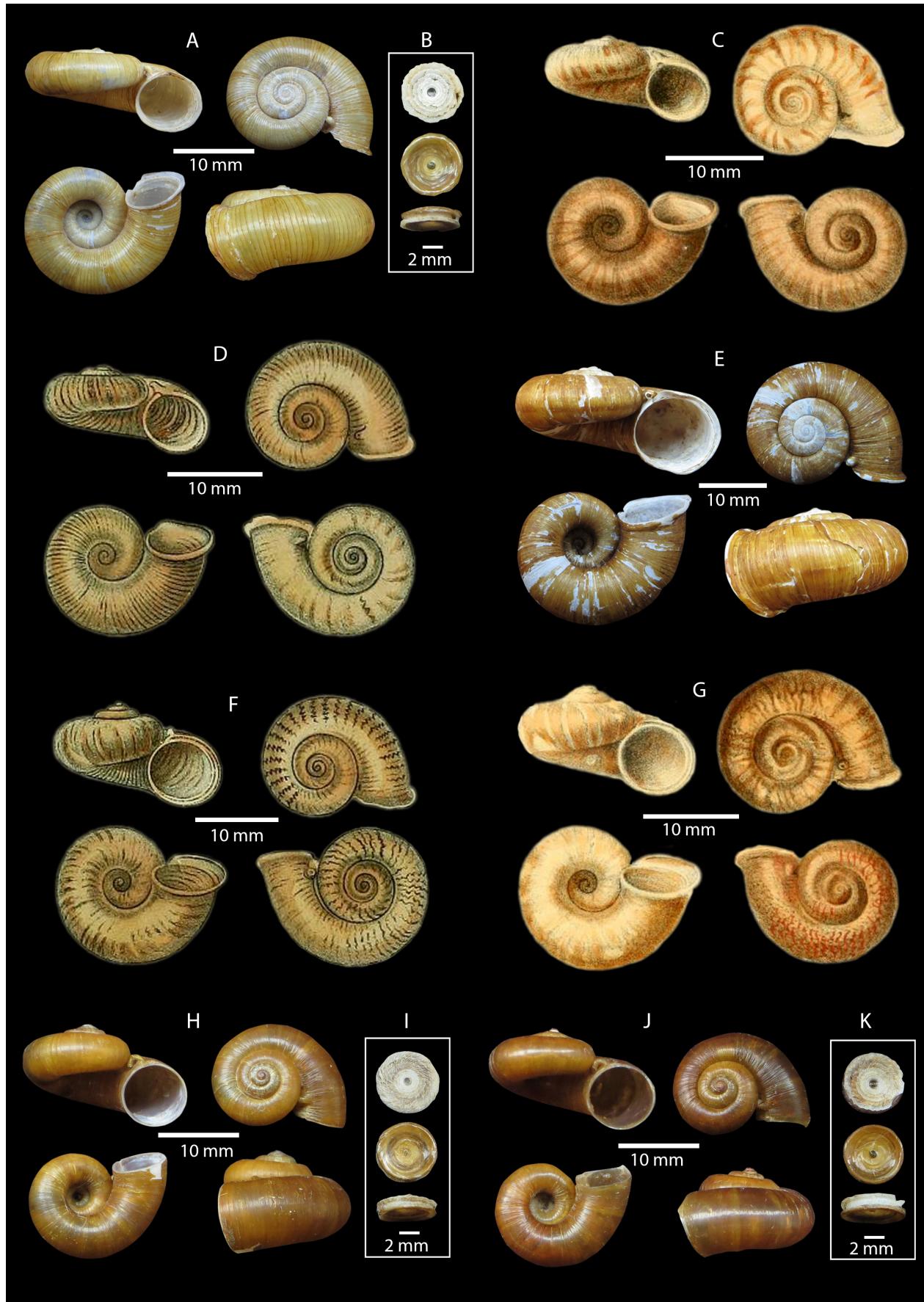


Fig. 2. Shell (apertural view, dorsal view, ventral view, and side view) and operculum (outer surface, inner surface, and side view) of *Opisthoporus* spp. in Vietnam. A–D, *Opisthoporus beddomei* Dautzenberg & Fischer, 1908; A, B, ZMHU/5; C, from Dautzenberg & Fischer, 1908; D, from Kobelt, 1913. E–G, *Opisthoporus lubricus* Dautzenberg & Fischer, 1908; E, ZMHU/4; F, from Kobelt, 1913; G, from Dautzenberg & Fischer, 1908. H–K, *Opisthoporus thuathienhuensis*, new species; H, I, holotype VNMN\_IZ 000.000.176; J, K, paratypes ZRC.MOL. 15631. Photographs by D.S. Do and T.S. Nguyen.

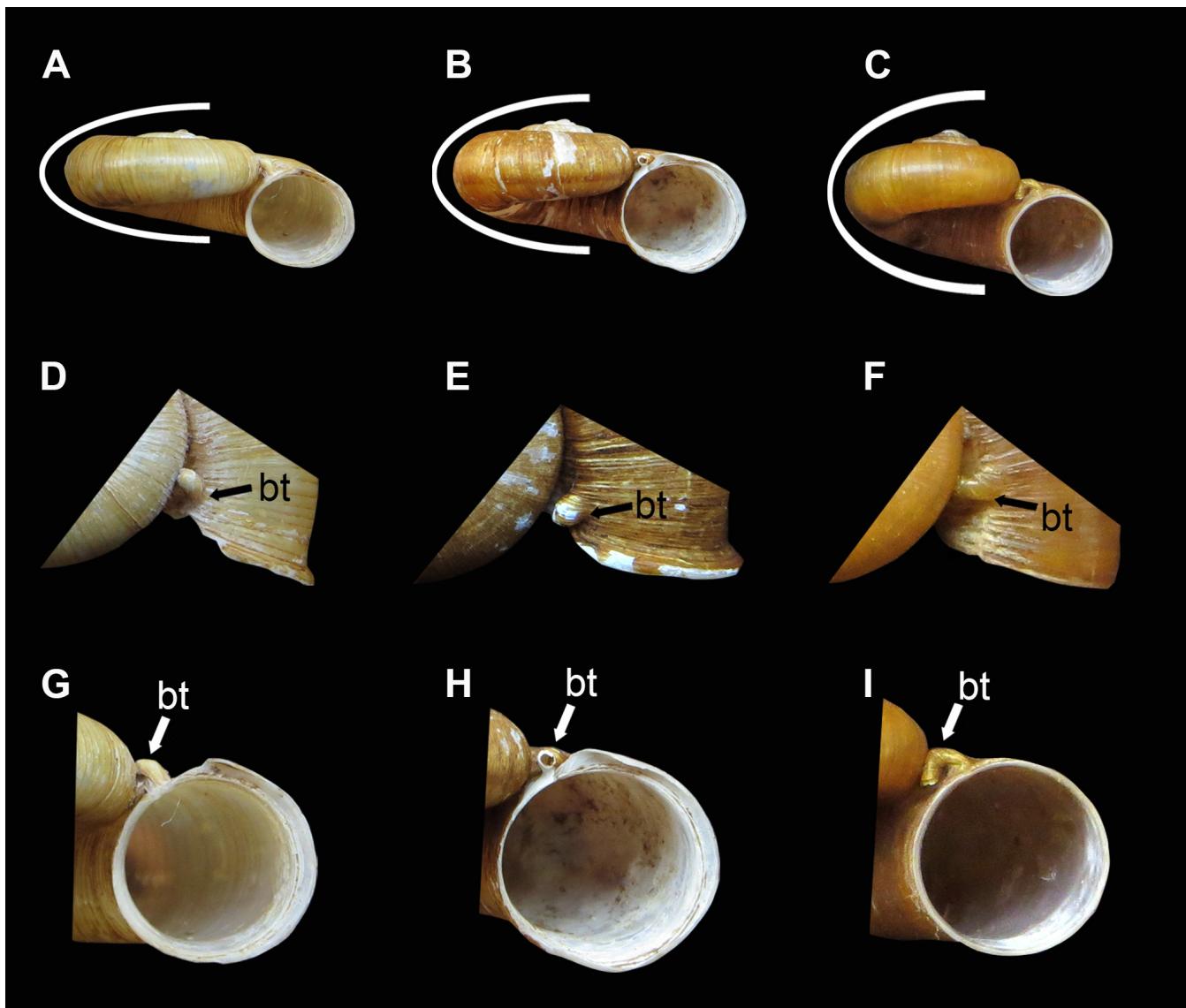


Fig. 3. Comparison of shell profile, breathing tube, and peristome of *Opisthoporus* spp. in Vietnam. A, D, G, *Opisthoporus beddomei* (ZMHU/5), with oblique breathing tube and double peristome; B, E, H, *Opisthoporus lubricus* (ZMHU/4), with forward pointing breathing tube and double peristome; C, F, I, *Opisthoporus thuathienhuensis*, new species (holotype VNMN\_IZ 000.000.176), with inverted U-shaped breathing tube and single peristome. Photographs by D.S. Do and T.S. Nguyen.

**Material examined.** 5 shells (ZMHU), 2 figured shells (figs. 2E, 3B, E, H), Vietnam, Lang Son Province, Trang Dinh District, Tri Phuong Commune, Bo Village, Limestone karst forest, 429 m a.s.l., 22°19'28"N, 106°29'15"E, coll. D.S. Do, 10 July 2018; 4 shells (ZMHU), Vietnam, Lang Son Province, Trang Dinh District, Chi Minh Commune, Lung Phay Village, Limestone karst forest, 482 m a.s.l., 22°20'09"N, 106°27'02"E, coll. D.S. Do, 10 July 2018; 27 shells (ZMHU), Vietnam, Lang Son Province, Bac Son District, Nga Hai Village, Limestone mountain with depleted primary forest, 397 m a.s.l., 21°47'41"N, 106°09'13"E, coll. D.S. Do, 9 July 2018; 6 shells (ZMHU), Vietnam, Lang Son Province, Huu Lung District, Quyet Thang Commune, Bong Village, Limestone karst forest, 627 m a.s.l., 21°38'40"N, 106°14'06"E, coll. C.N. Duong, 20 December 2018; 5 shells (ZMHU), Vietnam, Thai Nguyen Province, Vo Nhai District, Than Sa-Phuong Hoang Nature Reserve, Densely vegetated limestone hill, 260 m a.s.l., 21°50'51"N, 105°53'19"E, coll. D.S. Do & T.B. Nguyen, 14 May 2017.

**Diagnosis.** Shell yellow to yellowish brown with a short and stout breathing tube directed toward aperture.

**Distribution.** *Opisthoporus lubricus* is known from its type locality in northeastern Vietnam (Cao Bang, Lang Son and Thai Nguyen Provinces) (Dautzenberg & Fischer, 1908; this study).

**Remarks.** *Opisthoporus lubricus* has a thick shell, with thin corneous periostracum. The shell colour is usually rather uniform yellow to yellowish brown, with a darker brown spiral band below the periphery. This species differs mainly from *Opisthoporus beddomei* by its larger shell with darker colouration, somewhat higher spire, slightly different aperture morphology, and breathing tube structure (see also Remarks for that species).

Table 3. Known species and subspecies of *Opisthoporus* and their respective type localities.

S/N	Species	Type locality
1.	<i>O. beddomei</i> Dautzenberg & Fischer, 1908	Quang-Huyen (Quang Uyen, Cao Bang) Vietnam
2.	<i>O. bernardii</i> (Pfeiffer, 1862)	Siam (Thailand)
3.	<i>O. bialatus</i> von Möllendorff, 1902	Kelantan, Malaysia
4.	<i>O. biciliatus</i> (Mousson, 1849)	Borneo
5.	<i>O. birostris</i> (Pfeiffer, 1854)	Sarawak, Borneo
6.	<i>O. cavernae</i> (Godwin-Austen, 1889)	“Sarawak proper”
7.	<i>O. celebicus</i> (P. Sarasin & S. Sarasin, 1899)	“Dongala an der Palos-Bai”, Celebes
8.	<i>O. corniculus</i> (Mousson, 1849)	“Aus den Kaffeepflanzen von Pardana”, Java, Indonesia
9.	<i>O. dautzenbergi</i> Sykes, 1902	Kelantan, Malaysia
10.	<i>O. deflexus</i> von Möllendorff, 1897	“in regione Badung”, Hubei, China
11.	<i>O. euryomphalus</i> (Pfeiffer, 1856)	Borneo
12.	<i>O. gwendolae</i> (Godwin-Austen, 1889)	Niah Hills, Sarawak, Malaysia
13.	<i>O. hungerfordi</i> (Godwin-Austen, 1889)	Molu Hills, Borneo, Malaysia
14.	<i>O. iris</i> (Godwin-Austen, 1889)	Borneo
15.	<i>O. latistriatus</i> (de Morgan, 1885)	Gunung Lano, Perak, Peninsular Malaysia
16.	<i>O. latistrigus</i> von Martens, 1865	Borneo, Malaysia
17.	<i>O. lubricus</i> Dautzenberg & Fischer, 1908	Quang-Huyen (Quang Uyen, Cao Bang), Vietnam
18.	<i>O. penangensis</i> (Stoliczka, 1872)	Penang, Malaysia
19.	<i>O. pertusus</i> (Morelet, 1861)	Borneo, Malaysia
20.	<i>O. pterocyloides</i> (Pfeiffer, 1855)	Borneo, Malaysia
21.	<i>O. quadrasi busuangensis</i> Bartsch, 1932	Busuanga, Philippines
22.	<i>O. quadrasi palawanensis</i> Bartsch, 1932	Iwahig, Palawan, Philippines
23.	<i>O. quadrasi quadrasi</i> Hidalgo, 1888	Ille de Balabae, Philippines
24.	<i>O. quadrasi turturinganus</i> Bartsch, 1932	Turturingan, Palawan, Philippines
25.	<i>O. rhoistoma</i> Gredler, 1902	Borneo, Malaysia
26.	<i>O. serenae</i> Vermeulen & Junau, 2007	Sarawak, Malaysia
27.	<i>O. setosus</i> von Möllendorff, 1894	Samui, Thailand
28.	<i>O. siamensis</i> von Martens, 1860	Siam (Thailand)
29.	<i>O. singaporeanus</i> Low & Tan, 2017	Singapore
30.	<i>O. solutus</i> (Stoliczka, 1872)	Penang, Malaysia
31.	<i>O. spiniferus</i> (Morelet, 1861)	Borneo, Malaysia
32.	<i>O. sumatrana</i> von Martens, 1864	Sumatra, Indonesia
33.	<i>O. thuathienhuensis</i> , new species	Thua Thien Hue, Vietnam
34.	<i>O. tubuliferus</i> (Pfeiffer, 1854)	Unknown

***Opisthoporus thuathienhuensis* D. S. Do, T. C. Bui & V. N. Do, new species**

(Figs. 1, 2H–K, 3C, F, I; Table 1, 2)

**Material examined.** Holotype (1 shell, shell height 10.1 mm, shell width 16.0 mm; Figs. 2H, I, 3C, F, I) (VNMM\_IZ 000.000.176), Vietnam, Thua Thien Hue Province, Nam Dong District, Thuong Quang Commune, Limestone mountain, 217 m a.s.l., 16°06'56"N, 107°38'32"E, coll. T.C. Bui, 16 September 2017; Paratypes: 6 paratypes (ZMHU.MOL 001), 2 paratypes (ZRC.MOL. 15631), same data as holotype.

**Etymology.** The specific epithet “thuathienhuensis” is derived from its type locality Thua Thien Hue Province in central Vietnam, with the Latin suffix “-ensis” added to form an adjective.

**Diagnosis.** Shell devoid of patterns on both dorsal and ventral sides of shell. Small breathing tube in the form of

an inverted U-shape, distal end touching the last whorl. Peristome single, slightly thickened, not expanded.

**Description.** Shell slightly thick, medium sized (shell height 8.7–12.3 mm, shell width 14.0–19.5 mm), sub-discoidal with wide umbilicus. Spire low, obtuse. Whorls 3½–4, well-rounded. The last whorl is partially detached from the penultimate whorl. Sutures deeply impressed. Umbilicus wide, about ¼ of shell diameter. Periostracum brown, translucent, shiny, without spiral sculpture. Protoconch smooth and glossy, two whorls. Teleoconch sculptured with irregularly spaced, inconspicuous growth lines, spiral sculpture virtually absent. Breathing tube present near the suture, situated a little distance (ca. 1.4–2.2 mm) from the peristome. Breathing tube curved, forming a reversed U-shape, the distal end pointing back towards the last whorl. Aperture circular, with pale yellow, slightly thickened, and non-expanded peristome.

Opercum solid, round, bi-layered, the outer calcified layer thicker than the inner corneous layer. Outer surface slightly concave, covered with fine growth lines, nucleus usually deeply sunken. Inner surface smooth, glossy, and concave.

**Distribution.** The new species is thus far known only from the limestone mountain in Thuong Quang Commune, Nam Dong District, Thua Thien Hue Province, central Vietnam.

**Remarks.** The new species differs distinctly from *O. beddomei* and *O. lubricus* by its single peristome without an expanded lip and small breathing tube, which forms an inverted U-shape with distal end touching the last whorl.

## DISCUSSION

The discovery of *Opisthoporus* from central Vietnam shows an expanded distribution range for the genus, especially to the mainland of Southeast Asia. In Vietnam, the distribution of the known *Opisthoporus* is discontinuous. Present knowledge remains patchy. Three species are now known from northern and central Vietnam (this study), but no *Opisthoporus* are known from large areas of Vietnam including the northwest, northeastern coast, highlands and southern areas. Recent surveys have concentrated on the rich terrestrial operculate snail fauna of limestone karst forests, small isolated limestone hills and rocks, natural forest, and coastal island, where many new species have been found and doubtless many remain to be discovered (Nguyen, 2016, 2017, 2018; Páll-Gergely et al., 2017; Vermeulen et al., 2019). Against this background, we suggest that additional *Opisthoporus* species may be found in the abovementioned areas of Vietnam upon further surveys.

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## LITERATURE CITED

- Adams H & Adams A (1854–1858) The Genera of Recent Mollusca; Arranged According to Their Organization. Volume 2. John van Voorst, Paternoster Row, London, 661 pp. [1855: Pp. 93–284, pls. 73–96].
- Bartsch P (1932) The Philippine land molluscs of the genus *Opisthoporus*. Contributions to the biology of the Philippine Archipelago and adjacent regions. United States National Museum, Bulletin, 100: 323–327.
- Benson WH (1832) Account of new genus of land snails, allies to the genus *Cyclostoma*, of Lamarck; with a description of species found on the outlying rock of the Rajmahal range of hills. Journal of the Asiatic Society of Bengal, 1: 11–14.
- Benson WH (1855) Characters of the genus *Opisthoporus*, an Eastern form of the Cyclostomacea, with remarks on its affinities and notes on several opercula. The Annals and Magazine of Natural History, Including Zoology, Botany, and Geology, Series 2, 15: 13–17.
- Benson WH (1860) On *Clostophis* and *Rhiostoma*, new Burmese genera of land-shells. The Annals and Magazine of Natural History, Including Zoology, Botany, and Geology, Series 3, 5: 95–97.
- Blanford WT (1864) On the classification of the Cyclostomacea of Eastern Asia. The Annals and Magazine of Natural History, Including Zoology, Botany, and Geology, Series 3, 13: 441–465.
- Bragado D, Rey I, Villena M & Soriano O (2000) Catálogo de las colecciones Zoológicas de Asia del Museo Nacional de Ciencias Naturales. II. Moluscos terrestres y dulceacuícolas. Museo Nacional de Ciencias Naturales, Madrid, 529 pp.
- Dautzenberg P & Fischer H (1905) Liste des Mollusques récoltés par M. H. Mansuy en Indo-Chine et au Yunnan et description d'espèces nouvelles. Journal de Conchyliologie, 53: 343–471.
- Dautzenberg P & Fischer H (1908) Liste des Mollusques récoltés par M. Mansuy en Indo-Chine et description d'espèces Nouvelles. II. Journal de Conchyliologie, 56: 169–217.
- de Morgan J (1885a) Mollusques terrestres et fluviatiles du royaume de Pékar et des pays voisins (Presquile Malaise). Bulletin de la Société Zoologique de France, 10: 353–428.
- de Morgan J (1885b) Note sur quelques espèces nouvelles de Mollusques terrestres recueillis dans la Péninsule Malaise. Le Naturaliste, 9: 68–70.
- Do DS & Do VN (2019) Family Cyclophoridae in Vietnam (Gastropoda: Cyclophoroidea): The genus *Cyclophorus* Montfort, 1810. Ruthenica, 29: 1–53.
- Egorov R (2005) Preliminary classification of the recent terrestrial pectinibranch mollusks. Club Conchylia Informationen, 37: 21–32.
- Egorov RV (2009) The genus *Cyclotus* Guilding in Swainson, 1840: Systematics and nomenclature. Conchylia, 40: 16–22.
- Fischer H & Dautzenberg P (1904) Catalogue des mollusques terrestres et fluviatiles de l'Indo-Chine orientale cités jusqu'à ce jour. In: Pavie A (ed.) Mission Pavie, Indo-Chine 1879–1895. Études Diverses. III. Ernest Leroux, Paris, pp. 390–450.
- Fischer P (1880–1887) Manuel de Conchyliologie et de Paléontologie Conchyliologique, ou Histoire Naturelle des Mollusques Vivants et Fossiles. Librairie F. Savy, Paris, xxiv + 1369 pp., 23 pls. [1885: Pp. 689–896].
- Fischer P (1891) Catalogue et distribution géographique des Mollusques terrestres, fluviatiles & marins d'une partie de l'Indo-Chine (Siam, Laos, Cambodia, Cochinchine, Annam, Tonkin). Imprimerie Dejussieu père et fils, Autun, 193 pp.
- Foon KJ, Clements RG & Liew ST (2017) Diversity and biogeography of land snails (Mollusca, Gastropoda) in the limestone hills of Perak, Peninsular Malaysia. Zookeys, 682: 1–94.
- Godwin-Austen HH (1889) On a collection of land-shells made in Borneo by Mr. A. Everett, with descriptions of supposed new species. Part I. Cyclostomacea. Proceedings of the Zoological Society of London, 57: 332–355.
- Gray JE (1847) A list of the genera of recent Mollusca, their synonyma and types. Proceedings of the Zoological Society of London, 15: 129–219.
- Gredler V (1902) Zur conchylien-fauna von Borneo und Celebes. Nachrichtenblatt der Deutschen Malakozoologischen Gesellschaft, 34: 53–62.
- Gude GK (1921) The Fauna of British India, Including Ceylon and Burma. Mollusca.—III. Land Operculates (Cyclophoridae, Truncatellidae, Assimineidae, Helicinidae). Today and Tomorrow's Printers and Publishers, New Delhi, 386 pp.

- Habe T (1965) Operculated land molluscs from Southeast Asia. *Nature and Life in Southeast Asia*, 4: 111–128.
- Hidalgo JG (1888) Recherches conchyliologiques de M. Quadras aux îles Philippines (suite). *Journal de Conchyliologie*, 36: 30–97.
- Inkhavilay K, Sutcharit C, Bantaowong U, Chanabun R, Siriwit W, Srisonchai R, Pholyotha A, Jirapatrasilp P & Panha S (2019) Annotated checklist of the terrestrial molluscs from Laos (Mollusca, Gastropoda). *ZooKeys*, 834: 1–166.
- Kerney MP & Cameron RAD (1979) *A Field Guide to the Land Snails of Britain and Northwest Europe*. Collins, London, 288 pp.
- Kobelt W (1902) Das Tierreich: Cyclophoridae. R. Friedländer und Sohn, Berlin, Germany, 662 pp.
- Kobelt W (1907–1908) Die gedeckelten Lungenschnecken (Cyclostomacea). In: *Abbildungen nach der Natur mit Beschreibungen. Cyclophoridae I. Systematisches Conchylien-Cabinet von Martini und Chemnitz*. Band 1. Abteilung 19. Tome 2. Verlag von Bauer und Raspe (Emil Küster), Nürnberg, pp. 401–711. [1907: Pp. 401–608, pls. 51–79; 1908: Pp. 609–711, pls. 80–103].
- Kobelt W (1912) Diagnosen neuer Cyclotiden. *Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft*, 44: 8–10.
- Kobelt W (1913) Die gedeckelten Lungenschnecken (Cyclostomacea). In: *Abbildungen nach der Natur mit Beschreibungen. Cyclophoridae II. Systematisches Conchylien-Cabinet von Martini und Chemnitz*. Band 1. Abteilung 19. Tome 3. Verlag von Bauer und Raspe (Emil Küster), Nürnberg, pp. 713–1048.
- Kobelt W & von Möllendorff OF (1897) Catalog der gegenwärtig lebend bekannten Pneumonopomen. *Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft*, 29: 105–120.
- Low MEY & Tan SK (2017) Nomenclature of the genus *Opisthoporus* Benson in L. Pfeiffer, 1851: The type species of the genus and *Opisthoporus singaporeanus* nom. nov. for *Cyclostoma rostellatum* L. Pfeiffer, 1851, a junior primary homonym of *Cyclostoma rostellatum* Partiot, 1848 (Gastropoda: Cyclophoroidea: Cyclophoridae). *Occasional Molluscan Papers*, 6: 15–17.
- Morelet A (1861) Diagnoses de trois Cyclostomes nouveaux. *Journal de Conchyliologie*, 9: 176–177.
- Morlet L (1889) Catalogue des coquilles recueillies par M. Pavie dans le Cambodge et le Royaume de Siam, et description d'espèces nouvelles (1). *Journal de Conchyliologie*, 37: 121–200.
- Mousson A (1849) Die Land-und Süßwasser-Mollusken von Java. Nach den Sendungen des Herrn Seminardirektors Zollinger. Friedrich Schulthes, Zürich, vi + 126 pp., 22 pls.
- Nevill G (1878) Hand List of Mollusca in the Indian Museum, Calcutta. Part 1. Gastropoda. The Trustees of the Indian Museum, Calcutta, 338 pp.
- Nguyen NT (2016) Vietnamese New Mollusks. 48HrBooks, Akron, Ohio, 205 pp.
- Nguyen NT (2017) New Shells of Southeast Asia. 48HrBooks, Akron, Ohio, 128 pp.
- Nguyen NT (2018) New Shells of South Asia. 48HrBooks, Akron, Ohio, 173 pp.
- Páll-Gergely B, Naggs F & Asami T (2016) Novel shell device for gas exchange in an operculated land snail. *Biology Letters*, 12: 20160151.
- Páll-Gergely B, Hunyadi A, Đỗ DS, Naggs F & Asami T (2017) Revision of the Alycaeidae of China, Laos and Vietnam (Gastropoda: Cyclophoroidea) I: The genera *Dicharax* and *Metalycaeus*. *Zootaxa*, 4331: 1–124.
- Pfeiffer L (1851) Uebersicht der Gattung *Pterocyclos* Bens. *Zeitschrift für Malakozoologie*, 8: 1–10.
- Pfeiffer L (1854) Descriptions of twenty-three new species of land shells, from the Collection of H. Cuming Esq. *Proceedings of the Zoological Society of London*, 21: 48–53.
- Pfeiffer L (1855) Descriptions of eighteen new species of Cyclostomacea, from Mr. Cuming's Collection. *Proceedings of the Zoological Society of London*, 22: 299–303.
- Pfeiffer L (1856) Descriptions of sixteen new species of Pneumonopoma, from the Collection of H. Cuming Esq. *Proceedings of the Zoological Society of London*, 24: 336–339.
- Pfeiffer L (1858) *Monographia Pneumonoporum Viventium*. Volume 2. Cassellis, Sumptibus Theodori Fischer, London, 249 pp.
- Pfeiffer L (1862) Diagnoses de neuf espèces nouvelles provenant de Siam. *Journal de Conchyliologie*, 10: 39–46.
- Pfeiffer L (1865) *Monographia Pneumonoporum Viventium*. Volume 3. Cassellis, Sumptibus Theodori Fischer, London, 284 pp.
- Sarasin P & Sarasin F (1899) Materialien zur Naturgeschichte der Insel Celebes. Band 2. Die Land-Mollusken von Celebes. Kreidel Verlag, Wiesbaden, viii + 248 pp.
- Stoliczka F (1872) On the land shells of Penang Island, with descriptions of the animals and anatomical notes; part first, Cyclostomacea. *Journal of the Asiatic Society of Bengal*, 41: 261–271.
- Sutcharit C, Ablett JD & Panha S (2019) An annotated type catalogue of seven genera of operculate land snails (Caenogastropoda, Cyclophoridae) in the Natural History Museum, London. *ZooKeys*, 842: 1–65.
- Sutcharit C, Tongkerd P & Panha S (2014) The land snail genus *Pterocyclos* Benson, 1832 (Caenogastropoda: Cyclophoridae) from Thailand and Peninsular Malaysia, with description of two new species. *Raffles Bulletin of Zoology*, 62: 330–338.
- Swainson W (1840) *A Treatise on Malacology or Shells and Shell-Fish*. Longman, London, viii + 419 pp.
- Sykes ER (1902) On a collection of land and fresh water shells from Kelantan, Malay Peninsula. *Journal of Malacology*, 9: 60–63.
- Tan SK & Woo HPM (2010) A Preliminary Checklist of the Molluscs of Singapore. Raffles Museum of Biodiversity Research, National University of Singapore, Singapore, 78 pp.
- Tenison-Woods JE (1888) Malaysian land and freshwater Mollusca. *Proceedings of the Linnean Society of New South Wales*, 2: 1003–1100.
- Tielecke H (1940) Anatomie, phylogenie und tiergeographie der Cyclophoridae. *Archiv für Naturgeschichte: Zeitschrift für Systematische Zoologie*, 9: 317–371.
- Tumpeeswan S & Tumpeeswan C (2015) First record and description of a new species of the land snail genus *Pearsonia* Kobelt, 1902 (Cyclophoridae: Pterocylinae) from Thailand, with a note on radula morphology. *Raffles Bulletin of Zoology*, 63: 287–292.
- van Benthem Jutting WSS (1949) On a collection of non-marine Mollusca from Malaya in the Raffles Museum, Singapore, with an appendix on cave shells. *Bulletin of the Raffles Museum*, 19: 50–77.
- van Benthem Jutting WSS (1959) Catalogue of the non-marine Mollusca of Sumatra and of its satellite islands. *Beaufortia*, 7: 41–191.
- van Benthem Jutting WSS (1960) Some notes on land and freshwater Mollusca of Malaya. *Basteria*, 24: 10–20.
- Vaught KC (1989) *A Classification of the Living Mollusca*. American Malacologist, Inc., Melbourne, Florida, 189 pp.
- Vermeulen JJ & Junau DJ (2007) Bukit Sarang (Sarawak, Malaysia), an isolated limestone hill with an extraordinary snail fauna. *Basteria*, 71: 209–220.
- Vermeulen JJ, Luu HT, Theary K & Anker K (2019) New species of land snails (Mollusca: Gastropoda: Caenogastropoda and Pulmonata) of the Mekong delta limestone hills (Cambodia, Vietnam). *Folia Malacologica*, 27: 7–41.
- Vermeulen JJ & Maassen WJM (2003) The Non-Marine Mollusk Fauna of the Pu Luong, Cuc Phuong, Phu Ly and Ha Long

- Regions in Northern Vietnam. A Survey for the Vietnam Programme of FFI (Flora and Fauna International). Unpublished Report, 35 pp.
- von Martens E (1860) On the Mollusca of Siam. Proceedings of the Zoological Society of London, 28: 6–18.
- von Martens E (1865) Über neue Cyclostomaceen und Helicinen aus dem indischen Archipel vor. Monatsberichte der Königlichen Preussische Akademie des Wissenschaften zu Berlin, 1864: 116–121.
- von Martens E (1867) Die preussische expedition nach Ost-Asien, Nach amtlichen Quellen. Zoologischer Theil. Band 2. Die Landschnecken. Königlichen geheimen ober-hofbuchdruckerei (R. V. Decker), Berlin, xii + 447 pp, 22 pls.
- von Möllendorff OF (1885) Materialien zur Fauna von China. Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 12: 349–398.
- von Möllendorff OF (1891) On the land and freshwater shells of Perak. Proceedings of the Zoological Society of London, 59: 330–348.
- von Möllendorff OF (1893) Ueber den werth des deckels für die systematik. Nachrichtenblatt der Deutschen Malakozoologischen Gesellschaft, 25: 137–147.
- von Möllendorff OF (1894) On a collection of land-shells from the Samui Islands, Gulf of Siam. Proceedings of the Zoological Society of London, 1894: 146–156.
- von Möllendorff OF (1897) Diagnosen neuer und kritischer Landdeckelschnecken. Nachrichtsblatt der Deutschen Malakozoologischen, 29: 31–45.
- von Möllendorff OF (1898) Die Binnenmollusken Annams. Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft, 30: 65–85.
- von Möllendorff OF (1900) Zur Binnenmollusken-Fauna Annams III. Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft, 32: 129–139.
- von Möllendorff OF (1902) Binnenmollusken aus Hinterindien. Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft, 34: 135–162.
- Woodward SP (1868) A Manual of the Mollusca. A Treatise on Recent and Fossil Shells. Second Edition. Virtue & Co., London, xiv + 542 pp.