

Taxonomic revision of the Elephant Pupinid snail genus *Pollicaria* Gould, 1856 (Prosobranchia, Pupinidae)

Bangon Kongim¹, Chirasak Sutcharit², Fred Naggs³, Somsak Panha²

1 Department of Biology, Faculty of Science, Mahasarakham University, Kantharawichai, Maha Sarakham 44150, Thailand **2** Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok 10330, Thailand **3** Department of Life Sciences, The Natural History Museum, London SW7 5BD, United Kingdom

Corresponding author: Somsak Panha (somsak.Pan@chula.ac.th)

Academic editor: E. Neubert | Received 2 January 2012 | Accepted 4 March 2013 | Published 11 April 2013

Citation: Kongim B, Sutcharit C, Naggs F, Panha S (2013) Taxonomic revision of the Elephant Pupinid snail genus *Pollicaria* Gould, 1856 (Prosobranchia, Pupinidae). ZooKeys 287: 19–40. doi: 10.3897/zookeys.287.4617

Abstract

The status of species currently assigned to the Southeast Asian Elephant Pupinid snail genus *Pollicaria* Gould, 1856 is reassessed. Shell, radular and reproductive morphology are investigated and analysed with reference to karyotype patterns previously reported and to distribution patterns among the species. Six previously described species are recognised: *P. gravida* (Benson, 1856), *P. myersii* (Haines, 1855), *P. mouhoti* (Pfeiffer, 1862), *P. elephas* (Morgan, 1885), *P. crossei* (Dautzenberg & d'Hamonville, 1887) and *P. rochebruni* (Mabille, 1887). A new subspecies, *P. mouhoti monochroma* **ssp. n.**, is proposed and a dichotomous key to species is provided.

Keywords

Systematics, Indochina, Gastropoda, land snail, Southeast Asia, anatomy

Introduction

Land operculate snails of the family Pupinidae generally possess a pupoid shell shape and exhibit a wide range of shell height from 5–50 mm. Apart from size, their often distinctive shells can also be distinguished from other members of the Cyclophoroidea

by unique features of the genitalia, notably the long bursa copulatrix (Wenz 1938, Tielecke 1940). About 20 extant genera range from South Asia, East Asia to Southeast Asia, Melanesia, Micronesia and part of Australia (Solem 1959, Vaught 1989, Stanisic 1998, Stanisic et al. 2010). Fossil representatives are known from the European Cretaceous (Naggs and Raheem 2005) and British Eocene (Sandberger 1873). They generally occur in tropical forest and most commonly and abundantly in limestone areas. Fourteen pupinid genera have been recorded from Indochina (Kobelt 1902), including the very distinctive Elephant Pupinid genus *Pollicaria* Gould, 1856 which is endemic to the region.

Hitherto, nine nominal species of the *Pollicaria* have been described (Crosse 1885, Kobelt 1902, Gude 1921, Pain 1974). *Pollicaria*, as “*Hybocystis*”, was first revised by Crosse (1885) and by Fischer (1885) who detailed the anatomy. Crosse (1885) recognized four species of *Pollicaria* and separated those species into two species groups, which are now unrecognized. Subsequently, two additional species were described from Vietnam (Dautzenberg and d’Hammonville 1887, Mabille 1887a). These six nominal species were revised by Kobelt (1902) and more recently Pain (1974). Relying solely on shell morphology, Kobelt (1902) placed *P. crossei* into synonymy with *P. rochebruni*. Pain (1974), partly followed Kobelt’s classification but recognized only three species: *P. gravida* (Benson, 1856), *P. myersii* (Haines, 1855) and *P. elephas* (Morgan, 1885), placing *P. mouhoti* into synonymy with *P. myersii*. However, Pain’s study was of limited value because it was based on an examination of few specimens and populations and did not examine the type specimens. Hence the true status of species still remains unresolved. Apart from the studies of Crosse (1885) and Fischer (1885) none of the subsequent studies on *Pollicaria* have used anatomical data or studied type material.

The large shell size (up to 50 mm in height) and distinctive yellow to orange body colour render *Pollicaria* very distinctive and easily recognizable, although some confusion might arise from the helicoid shape exhibited by juveniles. The fact that populations are often widely scattered and highly localized may account for their having been little studied and consequently poorly known (Crosse 1885, Kobelt 1902). Recently, karyotypic studies and preliminary allozyme analysis (Kongim et al. 2009, 2010, Panha unpub. data) have indicated that the species placed in synonymy by Kobelt (1902) and Pain (1974) should be recognized as distinct species.

Herein, we provide the first critical and comprehensive revision of *Pollicaria* based on a detailed morphological study of newly collected specimens and their comparison with type material.

Materials and methods

Snails were collected and distributions recorded, mostly from limestone areas throughout Thailand, Laos, Vietnam and Peninsular Malaysia. Species identifications were made by comparison with type material, primarily at The Natural History Museum

(London), Muséum National d'Histoire Naturelle (Paris), and University Museum of Zoology Cambridge (Cambridge). Living snails were photographed before examining the external and internal morphological characters. Adult shells were measured for height, diameter and whorl number. Features of the genitalia were examined for between 5 to 10 individuals of each species. Radulae were extracted and examined using a Scanning Electron Microscope (JEOL, JSM-5410 LV), and radular teeth shape and formulae were described.

Anatomical abbreviation: The following anatomical terminology used in this study was modified from Fischer (1885), Wenz (1938), Tielecke (1940) and Cox (1964): an, anus; at, atrium; bc, bursa copulatrix; cm, columellar muscle; ct, cephalic tentacles; dg, digestive gland; e, eye spots; ft, foot; h, head-portion of spermatophore; k, kidney; lc, lung cavity; me, mantle edge; op, operculum; ov, oviduct; p, penis; pcd, pericardium; pg, prostate gland; rt, rectum; sg, seminal groove; sr, seminal receptacle; st, stomach; t, tail-portion of spermatophore; ts, testis; ut, uterus; ven, ventricle.

Institutional abbreviation: **NHMUK**, The Natural History Museum, London; **CUMZ**, Chulalongkorn University, Museum of Zoology, Bangkok, Thailand; **MNHN**, Muséum National d'Histoire Naturelle, Paris; **RBINS**, Royal Belgian Institute of Natural Sciences, Brussels, Belgium; **SMF**, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt, a.m.; **UMZC**, University Museum of Zoology Cambridge, Cambridge; **ZMA**, Zoologische Museum of Amsterdam, Amsterdam; **ZMB**, Zoologisches Museum of Berlin, Berlin; **ZMMSU**, Zoological Museum of Mahasarakham University, Thailand.

Results of morphological studies

Shell characters: *Pollicaria* Gould, 1856 is distinguished from other closely related genera such as *Pupina* Vignard, 1829, *Pupinella* Gray, 1850 and *Raphaulus* Pfeiffer, 1856 by having greater shell size, a breathing device in the form of a shallow posterior angled groove, and with or without a parietal declining shoulder inside the peristome (Fig. 1D). *Pupina* and *Pupinella* have anterior (columellar) and posterior (sutural) canals, with the columellar canal slightly twisted in *Pupinella* (Fig. 1A, B); *Raphaulus* has a complete posterior tube (Fig. 1C). *Pollicaria* differs from *Tortulosa* Gray, 1847 (Fig. 1E) and *Schistoloma* Kobelt, 1902 (Fig. 1F) by having a pupoid shell shape, larger shell size that lacks either an anterior (peristomal) groove (Fig. 1E) or posterior groove (Fig. 1F) respectively.

External features: As recorded in the literature, *Pollicaria* was found to possess a yellow-orange to pale orange body, usually with dark orange cephalic tentacles (Fig. 2). Body colour variation within species appeared to be largely confined to patches of dark-brown or blackish spots spread across areas of the head and dorsal foot. Such variation may be present between different populations or can occur on different growth stages within populations.

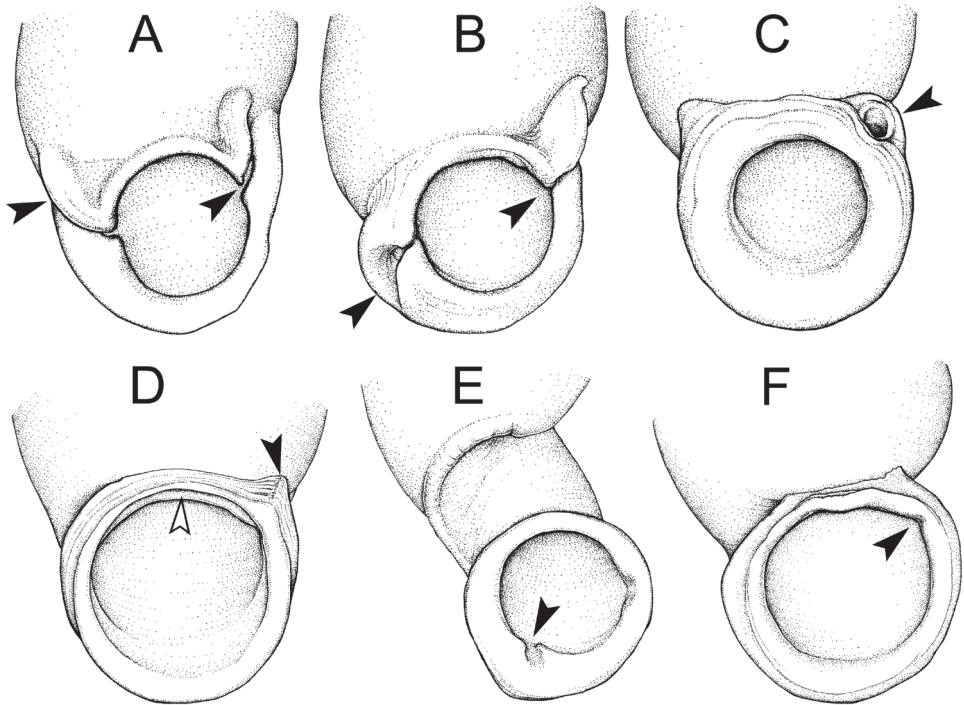


Figure 1. Breathing devices of six genera within the Pupinidae; black arrow indicates the position of breathing devices. **A** Anterior and posterior canals of *Pupina* **B** Anterior canal and twisted posterior canal of *Pupinella* **C** Complete posterior tube in *Raphaulus* **D** Shallow posterior angled groove of *Pollicaria*, white arrow indicates the parietal declining shoulder inside peristome **E** Anterior (peristomal) groove inside aperture of *Tortulosa* **F** Thin posterior groove inside aperture of *Schistoloma*.

The foot (ft) is broad and short; cephalic tentacles (ct) long with dark eye spots (e) located at outer base; snout broad. Animal dioecious; genital groove present at right side running downwards from pallial gonoduct. Male with conical external penis (p) on the right side (penis usually broad and enlarged in breeding season) located below cephalic tentacles, and with seminal groove (sg) on penis (Fig. 3A); female with only genital groove on the right side disappear external penis. Operculum (op) attached to opercular lobe or disk posterior-dorsally on foot (Fig. 3B).

No external anatomical features were found to exhibit useful taxonomic characters.

Internal anatomy: The internal anatomical description of *P. mouhoti mouhoti* collected from Tam Wungdang, Nern Maprang, Phitsanulok, Thailand serves as being representative of the genus. Kidney (k) a brownish lobule, constricted-triangular in shape. Heart located on the left side of kidney; pericardium (pcd) thin, atrium (at) slightly larger than ventricle (vn). Lung cavity (lc) with reticulated vessels. Stomach (st) embedded in dark brown lobulated digestive gland (dg). Rectum (rt) large, attached to genital apparatus (prostate gland or uterus), and tapering anteriorly to anus

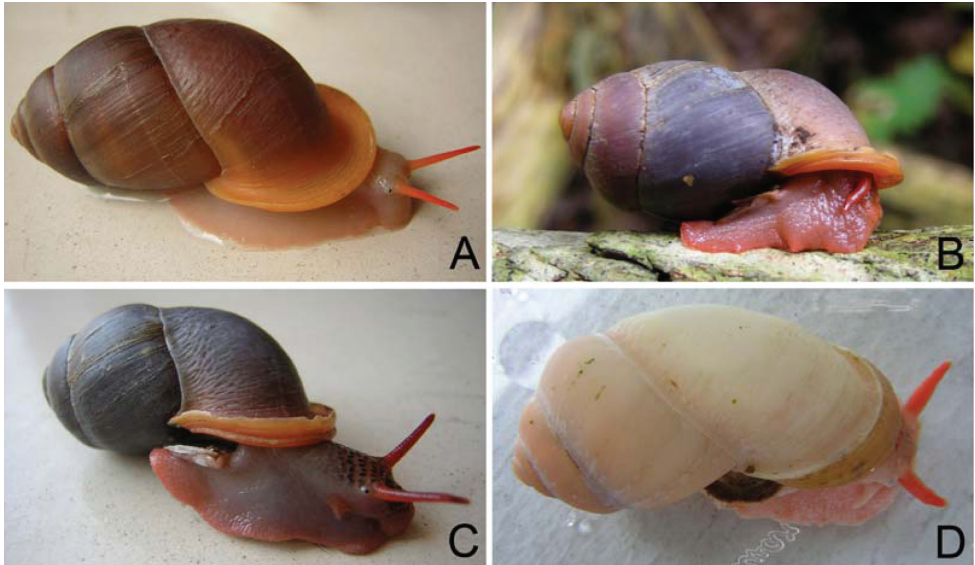


Figure 2. Living snails. **A** *Pollicaria myersii* from Pahom, Vang Vieng, Laos (CUMZ 1572; shell height about 40 mm) **B** *Pollicaria mouhoti mouhoti* from Tam Wungdang, Phitsanulok (CUMZ 1533; shell height about 35 mm) **C** *Pollicaria mouhoti monochroma* ssp. n. from the type locality (paratype CUMZ 1548; shell height about 30 mm) **D** *Pollicaria elephas* from Ipoh, Perak, Malaysia (CUMZ 1536; shell height about 45 mm).

(an), which opens close to mantle collar edge. Mantle edge (me) smooth and slightly thickened. Columellar muscle (cm) large, broad, thickened and whitish (Fig. 3A–D).

Testis (ts) with branched tubules, bright orange, occupying around 2–3 whorls from apex. Vas deferens thin and slender-straight tube attached to prostate gland at around two-third of its length proximal to external penis. Prostate gland (pg) large, long and slender, pale yellowish; proximally with genital opening. Seminal groove (sg) small, distinct and connected from genital opening on the right side of snail to external penis. External penis (pen) digitiform, short, located posteriorly, below cephalic tentacles (Fig. 3A, C).

Ovary bright orange multi-lobulated gland embedded in digestive gland. Pale yellow oviduct (ov) extends from ovary to uterus (ut) near the base of seminal receptacle. Bursa copulatrix (bc) cream to whitish long pouch that receives and digests the spermatophore case. Uterus (ut) large, curved pea-pod shape, posterior end rounded and anterior end tapering with genital opening (Fig. 3D).

Spermatophore tadpole shaped, about 20 mm long. Anterior portion or head of spermatophore (h) is a swollen pouch with thickened wall that is packed with sperm. Posterior portion or tail (t) tapering to slender tube is about half of the total length (Fig. 3E).

Both male and female genital organs of all species except *P. gravida* were examined and no distinguishing species-level taxonomic characters were found.

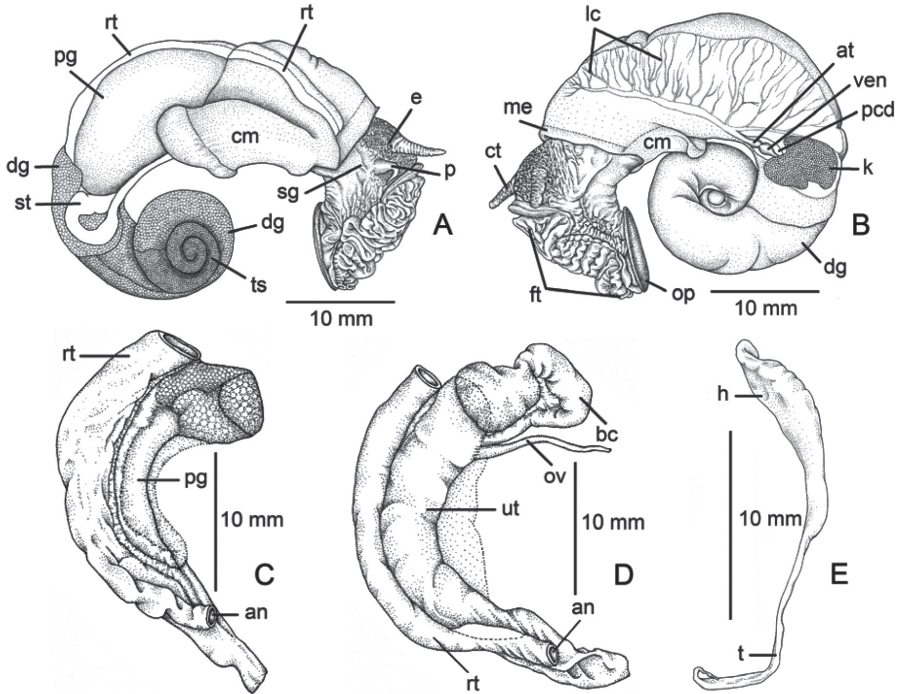


Figure 3. General anatomy, genitalia and spermatophore of *Pollicaria mouboti mouboti*. **A** Right side of snail showing male genital organ **B** Left side of snail showing pallial cavity and circulatory system **C** Male genital organ **D** Female genital organ **E** Spermatophore from uterus.

Systematic account

Family Pupinidae Pfeiffer, 1853

Genus *Pollicaria* Gould, 1856

<http://species-id.net/wiki/Pollicaria>

Pollicaria Gould, 1856: 14. Gould 1862: 221. von Martens 1867: 67. Stoliczka 1871: 150. Kobelt 1902: 288. Wenz 1938: 475.

Hainesia Pfeiffer, 1856b: 120 (part.).

Hybocystis Benson, 1859: 90. Blanford 1864: 460. Crosse 1885: 180. Fischer 1885: 174.

Type species: *Cyclostoma pollex* Gould, 1856: 14; by monotypy (see ICZN, 1999, Art. 68.3). The type species '*Cyclostoma pollex* Gould, 1856 [October]' is currently recognized as a junior subjective synonym of *Megalomastoma gravidum* Benson, 1856 [March].

Note. When describing his new species as *Cyclostoma pollex*, Gould (1856) simultaneously proposed the new generic name *Pollicaria* for this new nominal species. Gould also doubtfully included *Cyclostoma myersii* Haines, 1855 and *Cyclostoma chrysalis* Pfeiffer, 1852 in the *Pollicaria* Gould, 1856. Benson (1859) published a new generic name *Hybocystis* containing a single species from Burma *Megalomastoma gravi-*

dum Benson, 1856. Although Benson (1860) noted that *Hybocystis* was a junior subjective synonym of *Pollicaria* Gould, 1856, the name *Pollicaria* was widely overlooked prior to Kobelt's (1902) review of cyclophoroideans and both Wenz (1938) and Pain (1974) continued to mistakenly cite *Megalomastoma gravidum* Benson, 1856 as the type species. With only the doubtful inclusion of *Cyclostoma myersii* Haines, 1855 and *Cyclostoma chrysalis* Pfeiffer, 1852 in the original description of *Pollicaria*, the type species of *Pollicaria* was unequivocally fixed in the original publication by monotypy.

Diagnosis. Shell pupoid, small to large (shell height 35–50 mm), thickened and solid. Shell smooth or malleated sculpture from almost white to pale yellow, reddish brown and nearly black; periostracum generally thick. Whorls 5–7, last whorl expanded, body whorl distorted when adult; sutures weakly impressed. Aperture rounded, shallow to absent posterior angled groove; peristome continuous and thickened; lip duplicated and reflexed; umbilicus narrow. Operculum multi-lamellar calcareous plate. Radula taenioglossate with seven teeth in each transverse row.

Keys to species and subspecies of the genus *Pollicaria* recognized in this study

- | | | |
|---|---|--------------------------------------|
| 1 | Peristome with declining shoulder inside peristome (Fig. 1A) | 2 |
| – | Peristome without declining shoulder inside peristome (Fig. 1B) | 4 |
| 2 | Shell small (height < 35 mm) | 3 |
| – | Shell large (height > 40 mm), shell ground colour brown to black, periostracum corneous | <i>P. rochebruni</i> |
| 3 | Shell pale yellow | <i>P. grvida</i> |
| – | Shell bright orange | <i>P. crossei</i> |
| 4 | Shell usually large (height > 40 mm) | 5 |
| – | Shell small (height < 35 mm) to medium (35 < height < 40 mm), with bright orange, purple to black | 6 |
| 5 | Shell dark orange to pale orange, lip duplicated, dorsal part of last whorl pitted | <i>P. elephas</i> |
| – | Shell elongate pupoid, brown to red, periostracum thick corneous, lip expanded, dorsal part of last whorl malleated | <i>P. myersii</i> |
| 6 | Spire and apex bright yellow to orange, shell medium (35 < height < 40 mm) | <i>P. mouboti mouboti</i> |
| – | Spire monochrome purple to black, shell small (height < 35 mm) | <i>P. mouboti monochroma</i> ssp. n. |

Pollicaria grvida (Benson, 1856)

http://species-id.net/wiki/Pollicaria_grvida

Fig. 4A–E; Tables 1, 2

Megalostoma gravidum Benson, 1856 [March]: 229. Type locality: Moulmein. Hanley and Theobald 1870: pl. 7, fig. 1.

Otopoma blennus Benson, 1856: 231. Type locality: Moulmein.

Cyclostoma pollex Gould, 1856 [October]: 14. Type locality: Tavoy, British Burma. Gould 1862: 221.

Hybocystis gravida—Benson, 1859: 91. Pfeiffer 1860: 123, 124, pl. 35, figs 1–4. Blanford 1864: 460. Crosse 1885: 187–190, pl. 11, fig. 2. Fischer 1885: 174.

Pollicaria gravida—Stoliczka, 1871: 150. Sowerby 1878: Pupinidae, pl. 8, species 68. Kobelt 1902: 289, 290, fig. 65. Gude 1921: 191, fig. 29. Wenz 1938: 475, fig. 1213. Pain 1974: 174, pl. 6 fig. 7.

Cyclostoma (Pollicaria) pollex—Johnson, 1964: 129.

Material examined. Five shells in the type series of W.H. Benson, the specimen with similar shape, size and colour to the original description is designated here as the lectotype of *Megalomastoma gravidum* Benson, 1856 UMZC I.102935.A (height 32 mm, width 18 mm; Fig. 4A) and paralectotypes UMZC I.102935.B-E (4 shells, Fig. 4B); syntype of *Otopoma blennus* Benson, 1856 UMZC I.102930.A-B (2 shells, Fig. 4C).

Burma: NHMUK 79.9.1.5-6 (2 shells), Theobald colln. Acc. no. 1592 (2 shells), B.R. Lucas colln. Acc. no. 2351 (2 shells), Trechmann colln. Acc. no. 2176 (2 shells), 2 lots of E.R. Sykes collns. Acc. no. 1825 (1 shell and 2 shells); ZMA: R.v. Lennep colln. Acc. no. 1876 (1 shell); ZMB: Paetel colln. (1 shell), 2 lots of Dunker collns. (1 shell, 2 shells), Nevill colln. ZMB 20723 (2 shells). Farm Cave, Moulmein: NHMUK 88.124.863.4-5 (3 shells, Fig. 4D, E). Moulmein, Burma: NHMUK 71.9.23.193 (1 shell), 24.06.4.4 (2 shells), 1954.6.2.1231-1 (2 shells), H. Cuming colln. (4 shells), 2 lots of H.F./W.T. Blanford collns. Acc. no. 1944 (5 shells, 2 shells), T. Oldham colln. Acc. no. 1733 (2 shells); ZMA: Schepman colln. (1 shell). Unknown locality: NHMUK V.W. MacAndrew coll. (4 shells), H.E.J. Biggs colln. Acc. no. 2258 (2 shells), H. Cuming colln. (1 shell).

Description. Shell. Shell small for *Pollicaria*, pupoid, pale orange, yellow to white. Periostracum thin and transparent; shell surface smooth. Whorls 5–6; sutures moderately impressed; apex slightly inclined to right; spire short. Last whorl large about two-thirds of shell height, distorted and flattened in front. Aperture rounded with a shallow posterior angled groove. Peristome continuous, with distinct parietal declining shoulder internally. Lip thickened, little expanded, and margin moderately duplicated; umbilicus narrow. Operculum thick, calcareous, multispiral.

Distribution. Accepted records are confined to Burma: Moulmein, Damontha, Tavoy and Tenasserim (Benson 1856, 1859, Stoliczka 1871, Crosse 1885, Kobelt 1902, Gude 1921, Pain 1974). Records from Northern Vietnam of *P. crossei* and *P. rochebruni* are considered to be distinct species.

Remarks. *Otopoma blennus* Benson, 1856 and *Cyclostoma pollex* Gould, 1856 have long been considered as junior synonyms of *P. gravida* and this classification has been followed by a number of authors (Hanley and Theobald 1870, Sowerby 1878, Crosse 1885, Kobelt 1902, Pain 1974). Subsequently, *P. crossei* and *P. rochebruni* from Vietnam were also placed into synonymy with this species (see Pain 1974). However, examination of the type specimens of these three species (Figs 4A, B; 5D, F) dem-



Figure 4. Shell morphology of *Pollicaria* spp. **A–E** *Pollicaria gravida* **A** lectotype UMZC I.102935. **A B** paralectotype UMZC I.102935. **B–E** **C** syntype of *Otopoma blennus* Benson, 1856 UMZC I.102930. **A** and **D**, **E** specimens from Farm Caves, Moulmein, Burma (NHMUK 88.124.863.4–5; specimen with ‘x’ was figured in Gude (1921), fig. 29) **F**, **G** *Pollicaria myersii* **F** form Siam (NHMUK 20090242; specimen figured in Pfeiffer, 1856a, pl. 19, figs 1, 2), and **G** specimen from Pahom, Vang Vieng, Laos (CUMZ 1572) **H**, **I** *Pollicaria mouhoti mouhoti* **H** lectotype (NHMUK 20130071/1), and **I** specimen from Tam Wungdang, Phitsanulok (CUMZ 1533) **J**, **K** *Pollicaria mouhoti monochroma* ssp. n. from the type locality, **J** holotype CUMZ 1577, and **K** paratype CUMZ 1548.

onstrated that *P. gravida* could be distinguished from *P. crossi* and *P. rochebruni* by having a whitish to yellowish shell colour with swollen whorls, impressed sutures and with the last whorl flattened ventrally (Table 1). Furthermore, *P. gravida* is mainly

Table 1. Comparative morphological characters and karyotype among *Pollicaria* species recognized in this study.

Characters	<i>P. gravida</i>	<i>P. myersii</i>	<i>P. mouhoti</i>	<i>P. elephas</i>	<i>P. rochebruni</i>	<i>P. crossei</i>
Shell size (shell height)	small (height <35 mm)	large (height > 40 mm)	small to medium	large (height > 40 mm)	medium (35 < height > 40 mm)	small (height <35 mm)
Umbilicus	perforate	narrow	subumbilicate	narrow	narrow	narrow
Periostracum; shell colour	transparent; whitish to yellow	transparent; monochrome pale orange	transparent; monochrome black or with orange apex	transparent; yellow to orange	thicken corneous; reddish to orange	transparent; pale to deep orange
Sculpture on last whorl	absent	with thin wrinkle sculpture	with prominent wrinkle sculpture	with prominent wrinkle sculpture	absent	absent
Peristome shape; colour	rounded; as hell colour	slightly distorted; orange	slightly distorted; bright orange to reddish	rounded; as shell colour	rounded; as shell colour	rounded; as shell colour
Apertural groove	present	absent	absent	absent	present	present
Karyotype*	not available	4m+6sm+2st+ 1t	6m+4sm+2st+ 1t 7m+3sm+ 2st+ 1t	2m+6sm+2st+ 3t	3m+7sm+2st+ 1t	2m+8sm+2st+ 1t

* Data from Kongim et al. (2009, 2010); the chromosome morphology abbreviations: m, metacentric; sm, submetacentric; st, subtelocentric; t, telocentric.

Table 2. Shell size variation among *Pollicaria* species recognized in this study.

Species, Locality and CUMZ nos.	Number of adult shell examined	Ranges, Mean \pm SD in mm of:			Whorl ranges
		Shell Height	Shell Width	h/d Ratio	
<i>Pollicaria gravida</i>					
UMZC and NHMUK collections	14	24.7–34.3 29.8 \pm 2.54	14.6–19.0 17.4 \pm 1.58	1.65–1.82 1.71 \pm 0.12	5 $\frac{3}{4}$ –6 $\frac{1}{4}$
<i>Pollicaria myersii</i>					
Pahom, Vang Vieng, Laos: 1520, 1572	10	37.8–50.6 43.4 \pm 3.94	18.6–23.9 21.1 \pm 1.68	1.97–2.16 2.06 \pm 0.05	6 $\frac{3}{4}$ –7
<i>Pollicaria mouboti mouboti</i>					
Namnao N. P., Phetchabun: 1538, 1574	7	36.2–41.5 37.6 \pm 1.74	18.4–21.6 19.6 \pm 0.96	1.85–1.99 1.92 \pm 0.05	6 $\frac{1}{2}$
Phu Kiew Wildlife Sanctuary, Chaiyaphum: 1551, 1528, 1529, 1571	65	33.6–44.1 37.7 \pm 2.26	17.8–23.3 19.5 \pm 1.20	1.86–2.14 1.94 \pm 0.06	6–6 $\frac{3}{4}$
Tam Wungdang, Phitsanulok: 1533, 1537	40	33.4–40.8 36.7 \pm 1.81	17.6–21.2 19.0 \pm 0.83	1.86–2.05 1.93 \pm 0.05	6–6 $\frac{1}{2}$
Wat Pa-Mamuang, Phitsanulok: 1541	13	33.9–40.4 37.7 \pm 2.12	18.4–20.2 19.6 \pm 0.78	1.82–2.04 1.92 \pm 0.06	6–6 $\frac{1}{2}$
<i>Pollicaria mouboti monochroma</i> ssp. n.					
Phu Phalom, Loei: 1547	23	31.1–42.6 38.2 \pm 2.52	17.9–21.4 19.4 \pm 0.97	1.55–2.15 1.98 \pm 0.11	6–6 $\frac{1}{2}$
Tam Pha Bing, Loei: 1561, 1562	134	30.5–39.1 34.5 \pm 2.09	16.4–20.6 18.4 \pm 1.03	1.78–2.13 1.88 \pm 0.05	5 $\frac{3}{4}$ –6 $\frac{1}{2}$
Tam Pha Singh, Loei: 1543	33	29.6–37.9 33.8 \pm 2.41	15.8–19.5 17.6 \pm 1.03	1.71–2.00 1.92 \pm 0.06	5 $\frac{3}{4}$ –6 $\frac{1}{4}$
Wat Tam Pha Poo, Loei: 1545	56	30.2–36.7 32.5 \pm 1.37	16.1–19.3 17.2 \pm 0.64	1.76–2.00 1.89 \pm 0.05	5 $\frac{3}{4}$ –6
<i>Pollicaria elephas</i>					
Ampang Baru, Ipoh, Perak, Malaysia: 1535	51	36.4–51.1 43.9 \pm 3.12	19.4–24.5 21.9 \pm 1.31	1.85–2.12 2.01 \pm 0.06	6–6 $\frac{3}{4}$
Gunung Kenting, Ipoh, Perak, Malaysia: 1534, 1536, 1596	182	36.4–49.9, 42.3 \pm 2.34	11.1–25.6 21.9 \pm 1.64	1.78–3.79 1.4 \pm 0.15	6–6 $\frac{3}{4}$
<i>Pollicaria rochebruni</i>					
Cuc Phuong N. P., Vietnam: 1521, 1532	8	32.6–42.3 40.1 \pm 2.26	18.1–22.9 20.6 \pm 1.66	1.80–2.09 1.95 \pm 0.11	6 $\frac{1}{4}$
Phuong Nga N. P., Vietnam: 1523, 1539, 1552	5	37.8–45.0 40.8 \pm 2.74	20.0–21.8 20.7 \pm 0.71	1.89–2.07 1.97 \pm 0.07	6 $\frac{1}{4}$ –6 $\frac{3}{4}$
<i>Pollicaria crossei</i>					
Cuc Phuong N. P., Vietnam: 1521, 1522, 1588	10	32.6–38.0 35.3 \pm 1.74	17.6–18.9 18.9 \pm 1.01	1.82–1.93 1.87 \pm 0.06	6 $\frac{1}{4}$
Hulien, Vietnam: 1590	5	32.7–36.2 34.9 \pm 1.43	18.0–19.8 18.7 \pm 0.07	1.82–1.93 1.87 \pm 0.05	6 $\frac{1}{4}$

restricted to the western edge of the *Pollicaria* distribution in Tavoy and Tenasserim of Burma, and does not overlap with the two Vietnamese species in the east (Pain 1974). Unfortunately, none of the live specimens of *P. gravida* were examined cytogenetically for additional discrimination of these three species.

***Pollicaria myersii* (Haines, 1855)**

http://species-id.net/wiki/Pollicaria_myersii

Figs 2A; 4F, G; 6A; Tables 1, 2

Cyclostoma (*Megalostoma*) *myersii* Haines, 1855: 157, pl. 5, fig. 9–11. Type locality: Siam.

Megalostoma myersi—Pfeiffer, 1856a: 67, pl. 19, figs 1, 2.

Megalostoma (*Hainesia*) *myersi*—Pfeiffer, 1856b: 120.

Megalostoma myersii—von Martens, 1860: 11.

Pollicaria myersi—von Martens, 1867: 67. Sowerby 1878: Pupinidae, pl. 8, species 69. Kobelt 1902: 290.

Hybocystis myersi—Crosse, 1885: 191–193, pl. 11, fig. 4.

Pollicaria myersii—Habe, 1964: 114, pl. 2, fig. 13. Pain 1974: 175, 176, pl. 6, figs 2, 5.

Material examined. Siam: NHMUK 20090242 (Fig. 4F). Pahom, Vang Vieng, Laos: CUMZ 1531, 1572 (Fig. 4G), 1591; ZMMSU 0009.

Description. Shell: Shell large, reddish brown to light orange. Periostracum thin, corneous; shell surface usually with fine malleations on upper half of last whorl. Aperture almost circular with a shallow posterior angled groove. Peristome yellow, parietal declining shoulder absent. Lip thickened, broadly expanded, re-flexed, with concentric margin.

Radula: Radular teeth arranged in v-shaped rows, each transverse row with 7 teeth (2-1-1-1-2). Central tooth with well developed central cusp and one smaller lateral cusp on each side; central cusp large, elongate with pointed tip. Lateral teeth with 2 cusps, outer cusp largest and elongate shape with pointed tip, and with relatively small pointed tip of inner lateral cusps. Inner and outer marginal teeth with 2 cusps; central cusp large, flanked by small inner lateral cusps.

Distribution: The type locality of this species was given as the broad location of “Siam” (see Haines 1855). Subsequently, *P. mouhoti* was synonymised with *P. myersii* (von Martens 1867, Pain 1974) thus expanding the distribution of *P. myersii* beyond its historical range. However, in this study the distribution of the species is restricted to limestone areas of Vientiane to Luang Prabang, Laos, and probably the northern part of Thailand.

Remarks: The syntype AMNH 43629 could not be traced (Siddal and Watson, personal communication). Due to the proximity of the geographic distributions and similarity in shell morphology of the two species, *P. mouhoti* have long been considered a junior synonym of *P. myersii* (see Pain 1974). However, *P. myersii* can be distinguished from *P. mouhoti* by an elongated purple to pale orange shell with thin periostracum, rounded aperture and very fine wrinkles on the dorsal part of the last whorl (Table 1, Fig. 4F, K). *P. myersii* differs from *P. gravida*, *P. rochebrunii* and *P. crossei* by having a larger shell, no apertural groove and noticeable wrinkles on last whorl (Tables 1, 2).

***Pollicaria mouhoti* (Pfeiffer, 1862)**

http://species-id.net/wiki/Pollicaria_mouhoti

Hybocystis mouhoti Pfeiffer, 1862: 276, pl. 36, fig. 13. Type locality: Laos Mountain, Cambodia. Pfeiffer 1863: 227, 228, pl. 59, figs 5–8. Crosse 1885: 190, 191, pl. 11, fig. 3.

Megalostoma (Hybocystis) mouhoti—von Martens, 1867: 67.

Pollicaria mouhoti—Sowerby, 1878: Pupinidae, pl. 8, species 67. Kobelt 1902: 290.

Diagnosis. Shell small to large, pupoid, solid; monochrome purple to black, sometimes with yellowish to bright orange spire. Periostracum thin; shell surface with distinct malaeations on upper half of last whorl. Whorls 5–6; sutures moderately impressed; apex obtuse. Last whorl large about two-thirds of shell height, distorted and flattened in front. Aperture almost circular, shallow posterior angled groove present. Peristome and inside aperture orange to red; parietal declining shoulder absent. Lip thickened, expanded, reflexed, margin slightly duplicated; umbilicus narrow. Operculum calcareous concentric.

Distribution. The type locality of *P. mouhoti* was given as Laos Mountain, Cambodia. However, subsequent records of this species were from Thailand, Laos and Cambodia (Pfeiffer 1862, Crosse 1885, Kobelt 1902, Solem 1966).

Remarks. von Martens (1867) and Pain (1974) synonymised this species with *P. myersii* and stated that all *Pollicaria* specimens collected from Thailand should be regarded as this species. However, examination of the type specimens of *P. mouhoti* (Fig. 4H) showed that it was clearly distinct from *P. myersii* in shell shape, sculpture and colour pattern. The major distinguishing shell characters of *P. mouhoti* are the smaller shell size, purplish shell colour, bright orange spire, expanded bright orange to red apertural lip and bold wrinkles on the dorsal side of last whorl (Tables 1, 2). In addition, the chromosome analysis shows a clear difference in karyotype patterns between these two species (Kongim et al. 2009, 2010). Hence, *P. mouhoti* is removed from the synonymy of *P. myersii* and reinstated as a distinct species.

***Pollicaria mouhoti mouhoti* (Pfeiffer, 1862)**

http://species-id.net/wiki/Pollicaria_mouhoti_mouhoti

Figs 2B; 3A_E; 4H, I; 6B; Tables 1, 2

Material examined. Three syntype shells in H. Cuming collection, the figures and labels with type specimen are designated here as the lectotype of *Hybocystis mouhoti* Pfeiffer, 1862 NHMUK 20130071/1 (height 34.2 mm, width 18.1 mm; Fig. 4H) and paralectotype NHMUK 20130071/2–3 (2 shells). Cambodia: ZMA Wright colln. (2 shells), R.v. Lennep colln. (1 shell). Laos Mountain: ZMB Paetel colln. (1 shell). Phu Kradung, Loei: CUMZ 1586. Namnao National Park, Phetchabun: CUMZ 1574, 1538; ZMMSU 0002. Tam Yai Namnao, Phetchabun: CUMZ 1559. Phu Phaman, Khon Kaen: ZMMSU

0012. Phu Kiew Wildlife Sanctuary, Nongbuadang, Chaiyaphum: CUMZ 1528, 1529, 1551, 1571, 1576, 1582, 1585; ZMMSU 0003, 0020-4, 0027, 0029. Phu Phachit, Chaiyaphum: ZMMSU 0013. Tam Tao, Nernmaprang, Phitsanulok: CUMZ 1558. Tam Wungdang, Nernmaprang, Phitsanulok: CUMZ 1533 (Fig. 4I), 1537, 1544, 1554, 1575. Wat Pa Mamuang, Nernmaprang, Phitsanulok: CUMZ 1541; ZMMSU 0015. Wat Thepitakpunnaram, Pakchong, Nakhon Ratchasima: CUMZ 1583. Tam Pu Loop, Phuphaman, Khon Kaen: CUMZ 1526. Namprom Dam, Khon Kaen: CUMZ 1584.

Description. Shell: This nominotypical subspecies is characterized by the large shell size (Table 2). Shell with last whorl and penultimate whorl purple to black; first to third whorls distinct yellow to bright orange. Lip expanded, red to orange.

Radula: Taenioglossate radula, teeth arrangement with central, lateral and marginal teeth shape similar to *P. myersii*. Differences include a central tooth with well developed central cusp and lateral cusp on each side; lateral teeth triangular in shape with a pointed tip; inner marginal teeth composed of 3 cusps; central cusp flanked with small inner and outer lateral cusps.

Distribution. This subspecies occupies the southern limit of the species' range in Cambodia and several localities in Loei, Phitsanulok, Chaiyaphum, Khon Kaen, Phetchabun Nakhon Ratchasima and Saraburi Provinces in Thailand.

Remarks. The characters distinguishing this nominotypical subspecies from *P. myersii* are the smaller shell size and mainly purple coloured shell with whorls 2-3 pale to bright orange and bright orange to red lip (Tables 1, 2), and a distinct karyotype pattern (Kongim et al. 2009, 2010).

***Pollicaria mouhoti monochroma* Kongim & Panha ssp. n.**

http://species-id.net/wiki/Pollicaria_mouhoti_monochroma

Figs 2C, 4J, K; 6C; Tables 1, 2

Type material. Holotype: CUMZ 1577 (Fig. 4J; height 34.5 mm, width 18.4 mm, 6½ whorls) from the type locality, paratypes CUMZ 1548 (Fig. 4K; 9 shells), 1561 (82 shells), 1562 (85 shells); NHMUK 20130073 (5 shells); MNHN IM-2012-2103; SMF341492 (5 shells).

Type locality. Limestone outcrop with dry forest at Wat Tam Pha Bing, Wungsapoong District, Loei Province, Thailand (17°14'1.3"N, 101°44'3.5"E).

Other material examined. Phakeng-Phanang, Loei: ZMMSU 0025, 0026. Phu Luang Wildlife Sanctuary, Loei: CUMZ 1524. Phu Phalom, Muang, Loei: CUMZ 1547, 1560, 1565, 1567, 1580. Phu Phasamyod, Loei: ZMMSU 0011. Tam Erawan, Wungsapoong, Loei: CUMZ 1555, 1579. Tam Pha Bing, Wungsapoong, Loei: CUMZ 1548, 1561, 1562, 1577, ZMMSU 0001, 0004, 0006, 0017, 0028. Tam Pha Singh, Wungsapoong, Loei: CUMZ 1543, 1546. Wat Po Thi-sat, Nonghin, Loei: CUMZ 1557. Wat Tam Kuhawari, Nonghin, Loei: CUMZ 1540, 1549. Wat Tam Pha Mak-ho, Wungsapoong, Loei: CUMZ 1530, 1542. Wat Tam Pha Poo, Loei: CUMZ 1545, 1550. Wat Tam Piya, Loei: CUMZ 1527. Khao Wungpha, Nawung,

Nongbua Lumphoo: CUMZ 1563, 1564. Nawung, Nongbua Lumphoo: CUMZ 1581. Tam Suwankuha, Nongbua Lumphoo: ZMMSU 0007.

Etymology. From the Greek *monos* = one or single, and *chroma* = color of the skin; referring to the characteristic uniform dark brown to blackish spire color of the shell.

Description. Shell: Shell relatively small, pupoid, monochrome purple to black. Periostracum thin and transparent. Whorls 5-6; sutures moderately impressed; apex obtuse; spire short. Last whorl large about two-thirds of shell height, flattened in front. Shell surface rough with malleations on upper half of last whorl. Aperture almost circular, shallow posterior angled groove present; peristome continuous, yellow to pale orange. Lip thickened, broadly expanded; umbilicus narrow. Operculum thick, calcareous, concentric, exterior little concave.

Radula: Taenioglossate radula, teeth arrangement with central, lateral and marginal teeth shape similar to the nominotypical subspecies.

Distribution. *Pollicaria mouhoti monochroma* ssp. n. is restricted to the northern limit of the species' distribution in Loei, Phetchabun, Chaiyaphum and Nongbua Lumphoo Provinces.

Remark. *Pollicaria mouhoti monochroma* ssp. n. can be distinguished from the nominotypical subspecies by having a much smaller, entirely black to purple shell (Tables 1, 2) and a distinct karyotype pattern (see Kongim et al. 2009, 2010). The shell size and shape of this subspecies are similar to that of *P. gravida* and *P. crossei*, but the purple shell is a distinguishing characteristic.

Shell character variations can be observed in the Phu Pha Lom, Loei Province population. These individuals exhibit a relatively larger shell than the typical populations (Table 2), however, the monochrome black shell and similar karyotype pattern indicate that they belong to this subspecies (Kongim et al. 2009).

***Pollicaria elephas* (Morgan, 1885)**

http://species-id.net/wiki/Pollicaria_elephas

Figs 2D; 5A–C; 6D; Tables 1, 2

Hybocystis elephas Morgan, 1885b: 70. Type locality: Perak. Morgan 1885a: 404, 405, pl. 7, fig. 1. Crosse 1885: 183–186, pl. 11, fig. 1. Fischer 1885: 174. Möllendorff 1886: 314. Möllendorff 1891: 346. Kobelt and Möllendorff 1899: 137.

Hybocystis jousseaumei Morgan, 1885b: 70. Type locality: Kinta, Perak. Morgan 1885a: 405, 406, pl. 7, fig. 2. Crosse 1885: 184.

Pollicaria elephas—Kobelt, 1902: 289. Laidlaw 1928: 33. van Benthem Jutting 1960: 12. Pain 1974: 176, pl. 6, fig. 1, 3. Abbott 1989: 46, 1 figure. Chan 1997: 11, fig. 1–2.

Material examined. Five lots with 13 specimens of syntype deposited in MNHN, the specimen figured in the original publication is designated as the lectotype of *Hybocystis elephas* Morgan, 1885 MNHN 21309 (Fig. 5A), paralectotype MNHN 21310 (5 shells), 21311 (2 shells), 21312 (3 shells), 21313 (2 shells), RBINS 525391 (1 shell).

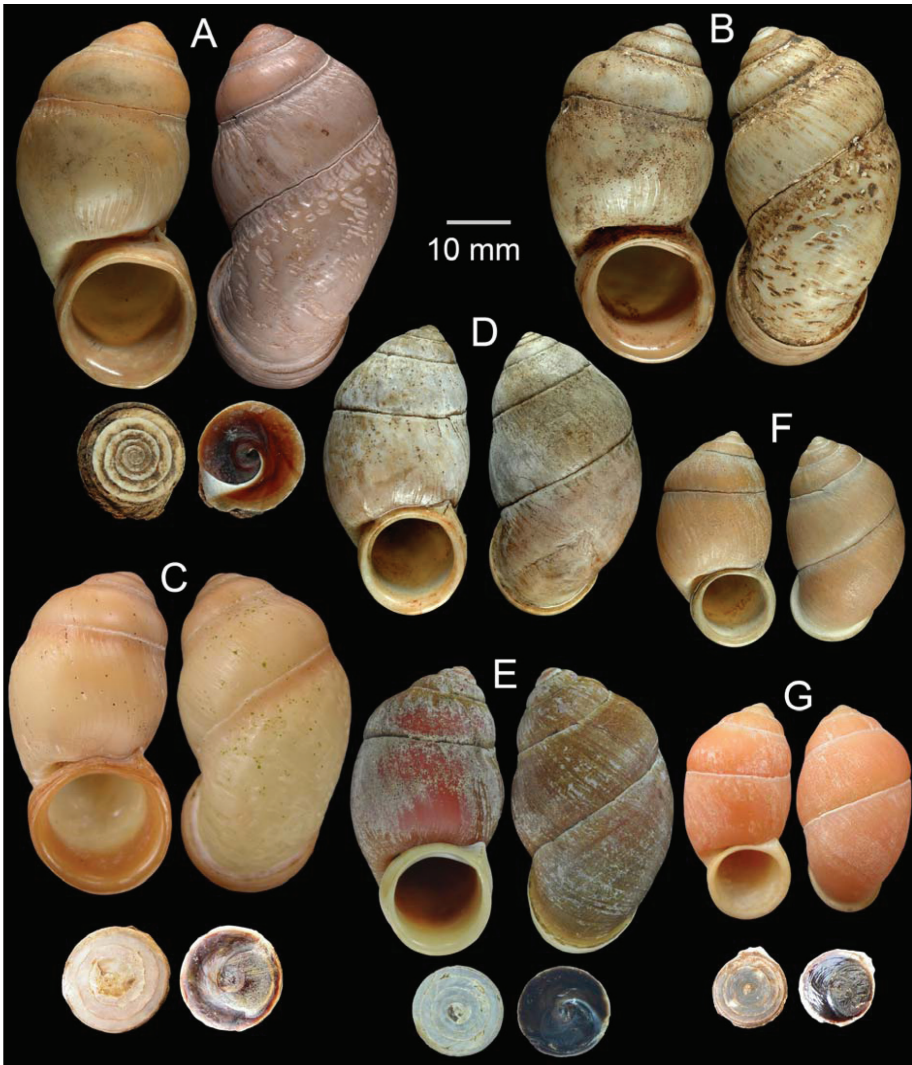


Figure 5. Shell morphology of *Pollicaria* spp. **A–C** *Pollicaria elephas* **A** lectotype of *Pollicaria elephas* (MNHN 21309) **B** lectotype of *Hybocystis jousseaumei* Morgan, 1885 (MNHN 21308), and **C** specimen from Gunung Kenting, Ipoh, Perak, Malaysia (CUMZ 1536) **D, E** *Pollicaria rochebruni* **D** lectotype (MNHN 21305), and **E** specimen from Phuong Nga National Park, Vietnam (CUMZ 1568) **F, G** *Pollicaria crosssei*, **F** lectotype (MNHN 21304), and **G** specimen from Cuc Phuong National Park, Vietnam (CUMZ 1588).

Single syntype specimen is designated as the lectotype of *Hybocystis jousseaumei* Morgan, 1885 MNHN 21308 (Fig. 5B). Ipoh, Perak, Malaysia: ZMA E.A. Meene colln. Acc. no. 1982 (1 shell). Near bridge over river, road Ipoh to Tanjong Rambutan, Perak, Malaysia: ZMA J. Drijver colln. (5 shells). Perak, Malaysia: ZMB 75821 (2 shells), 38044 (1 shell), M. Schulz colln. 1216 (3 shells, smallest shell excluded). Bukit Chintamani, Selangor, Malaysia: CUMZ 1534. Gunung Kenting, Ampang Baru, Ipoh, Perak, Malaysia: CUMZ 1535, 1536 (Fig. 5C), 1566, 1570.

Description. Shell: Shell large, elongate pupoid uniform yellow to orange. Periostracum thin, corneous; shell surface with fine growth lines and last whorl with distinctly strong pitting dorsally. Whorls 6-7 whorls; sutures impressed; apex obtuse. Last whorl large about two-third of shell height, flattened in front. Aperture rounded, with shallow to deep posterior angle groove. Peristome continuous, little elevated, yellow to orange, internal parietal declining shoulder absent. Lip thickened, duplicated, and with distinct growth ridges; umbilicus narrow. Operculum thick, calcareous, concentric.

Radula: Taenioglossate radula, teeth arrangement with central, lateral and marginal teeth shape similar to *P. myersii*. Minor differences are the well-developed central cusp with one to three small lateral cusps of the central tooth, and the slightly elongate and slender central cusp of the inner marginal teeth.

Distribution. This species has a restricted distribution and is known only from limestone outcrops in Perak, Peninsular Malaysia (Morgan 1885a, b). Material collected for this study was from Kinta valley, Perak, and the southern part of the species' historical range in Bukit Chintamani, Selangor, Peninsular Malaysia is considered to be this locally endemic species.

Remarks. The locally endemic *Pollicaria elephas* is confined to a few limestone outcrops in Peninsular Malaysia and shows several unique shell characters that separate it from its congeners. The major distinguishing characters of this species are the very large, monochrome yellowish to pale orange shell with the last whorl distorted ventrally and sculptured with scattered, deep pits dorsally; and rounded and thickened aperture. (Table 2, Fig. 5A–C).

Morgan (1885a, b) proposed two nominal species of *Pollicaria* from Perak, which differed mainly by the shell size (larger shell *Hybocystis elephas* and smaller shell *Hybocystis jousseaumei*). In the first revision of this genus, Crosse (1885) assumed that they were the same species and recognized only *P. elephas*. Thereafter *P. jousseaumei* was recognized as a synonym of *P. elephas* (Kobelt 1902, Pain 1974). Examination of the type specimens (Fig. 5A, B) confirmed *P. jousseaumei* as junior synonym of *P. elephas*. Moreover, the recent land snail survey in Perak, Peninsular Malaysia recorded both large and small shell forms of the species from the same localities.

***Pollicaria rochebruni* (Mabille, 1887)**

http://species-id.net/wiki/Pollicaria_rochebruni

Figs 5D, E; 6E; Tables 1, 2

Hybocystis rochebruni Mabille, 1887a: 12. Type locality: Tonkin. Mabille 1887b: 138, 139, pl. 2, figs 12, 13.

Pollicaria rochebruni—Kobelt, 1902: 290.

Material examined. Four specimens of the syntype deposited in MNHN, the figured specimen in original publication is designated here as the lectotype of *Hybocystis rochebruni* Mabille, 1887 MNHN 21305 (Fig. 5D) and other specimens as paralecto-

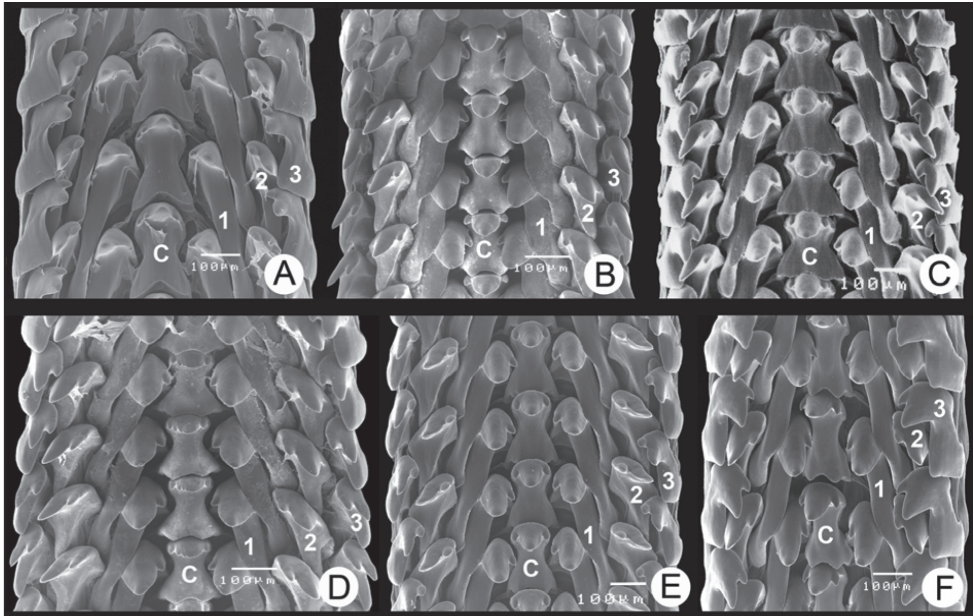


Figure 6. Radular morphology of *Pollicaria* spp. **A** *Pollicaria myersii* from Pahom, Vang Vieng, Laos (CUMZ 1572) **B** *Pollicaria mouhoti mouhoti* from Tam Wungdang, Phitsanulok (CUMZ 1533) **C** *Pollicaria mouhoti monochroma* ssp. n. from the type locality (paratype CUMZ 1548) **D** *Pollicaria elephas* from Gunung Kenting, Ipoh, Perak, Malaysia (CUMZ 1536) **E** *Pollicaria rochebruni* from Phuong Nga National Park, Vietnam (CUMZ 1568) **F** *Pollicaria crossei* from Cuc Phuong National Park, Ninh Binh Province, Vietnam (CUMZ 1588). Numbers indicated order of lateral and marginal teeth. Central tooth indicated by 'C'.

type MNHN 25855. Bac Ma National Park, Vietnam: CUMZ 1556. Hulien Nature reserve, Vietnam: CUMZ 1594. Khe Sen, Danang, Vietnam: CUMZ 1589. Phuong Nga National Park, Quang Binh, Vietnam: CUMZ 1523, 1539, 1552, 1568 (Fig. 5E). Cuc Phuong National Park, Ninh Binh, Vietnam: CUMZ 1532, 1568, 1573, 1587.

Description. Shell: Shell medium-sized, pupoid, red-brown. Periostracum thick, corneous; shell surface smooth. Whorls 5-6; sutures moderately impressed; apex obtuse; spire short. Last whorl large about two-thirds of shell height, distorted and flattened in front, ventrally rounded. Aperture rounded, shallow to absent posterior angled groove present. Peristome continuous, with thin parietal declining shoulder internally. Lip thickened, little expanded, margin moderately duplicated with thin growth ridges; umbilicus narrow. Operculum concentric, thick, calcareous, multi-spiral plate.

Radula: Taenioglossate radula, teeth arrangement with marginal teeth shape similar to *P. myersii*. Major differences are in the central teeth which have multiple cusps: the central cusp relatively short and small, flanked by 1-3 tapered lateral cusps; and inner marginal teeth with 3 cusps: the central cusp large with a convex tip, flanked by small and pointed inner cusps, the outer lateral cusp very small to nearly wanting.

Distribution. The previous records of this species were from Tonkin (Mabille 1887a, b); Babe National Park, Bac Kan, Vietnam (Yamazaki et al. 2007)

Remarks. Based on the similarity in shell morphology, Pain (1974) placed *P. rochebruni* into the synonymy of *P. gravida*. However, examination of the type specimens of *P. rochebruni* indicate that it is a distinct species (see also *P. gravida*). *P. rochebruni* can be distinguished from the latter species by having a larger red-brown to purple-black shell with flattened whorls and shallow sutures, while *P. gravida* usually has smaller pale orange shell with convex whorls and impressed sutures (Tables 1, 2). *P. rochebruni* differs from the sympatric *P. crossei* in both shell size and colour (Tables 1, 2, Fig. 5F) as well as having a distinct karyotype pattern (see Kongim et al. 2010).

***Pollicaria crossei* (Dautzenberg and dHamonville, 1887)**

http://species-id.net/wiki/Pollicaria_crossei

Figs 5F, G; 6F; Tables 1, 2

Hybocystis crossei Dautzenberg and dHamonville, 1887: 220, pl. 8, fig. 4. Type locality:

Than Moi, Tonkin. Kobelt and Möllendorff 1899: 137. Kobelt 1902: 290.

Pollicaria crossei—Kobelt, 1902: 290.

Material examined. Single specimens of the syntype deposited in MNHN, the figured specimen in original publication is designated here as the lectotype of *Hybocystis crossei* Dautzenberg and dHamonville, 1887 MNHN 21304 (Fig. 5F), and paralectotype RBINS 525390 (3 shells; the biggest one excluded). Cuc Phuong National Park, Ninh Binh, Vietnam: CUMZ 1521, 1522, 1588 (Fig. 5G), 1593. Hulien Nature reserve, Vietnam: CUMZ 1590.

Description. Shell: Shell small, pupoid, bright orange. Periostracum thin, corneous; shell surface smooth. Whorls 5-6; sutures moderately impressed; apex obtuse; spire short. Last whorl large about two-thirds of shell height, distorted and flattened in front, ventrally rounded. Aperture rounded, with shallow to absent posterior angled groove. Peristome continuous, with thin parietal declining shoulder internally. Lip thickened, little expanded and duplicated; umbilicus narrow. Operculum thick, calcareous, concentric.

Radula: Taenioglossate radula, teeth arrangement with central, lateral and marginal teeth similar in shape to *P. myersii*.

Distribution. The previous records of *P. crossei* was from Than-Moi, Tonkin and Cuc Phuong National Park, Ninh Binh, Vietnam (Dautzenberg and dHamonville 1887, Vermeulen and Maassen 2003).

Remarks. *Pollicaria crossei* has long been recognized as a subjective synonym of either *P. rochebruni* or *P. gravida* (Kobelt 1902, Pain 1974). However, the relatively smaller bright orange shell with thick, brown periostracum of *P. crossei* are a combination of characters that distinguish it from *P. rochebruni*. The bright orange shell with flattened whorls and shallow sutures distinguish it from *P. gravida* (Table 1, Fig. 3A). Moreover, the karyotypic study of the smaller shell form of *P. gravida* sensu lato indicated a distinct species recognized as *P. crossei* (see Kongim et al. 2010).

Acknowledgements

We are grateful to M. Siddal and S. Watson (AMNH, New York); P. Bouchet, V. Héros and P. Maestrati (MNHN, Paris); J. Ablett and H. Taylor (NHM, London); T. Backeljau (RBINS, Brussel); R. Janssen (SMF, Frankfurt); R.C. Preece (UMCZ, Cambridge); R.G. Moolenbeek (ZMA, Amsterdam); M. Glaubrecht, F. Köhler and T. von Rintelen (ZMB, Berlin) for their assistance and kind permission to examine specimens and the type materials used in this study. We are also indebted to S. Tumpeesuwan and members of Animal Systematics Research Unit for their field assistance and also thank anonymous reviewers for providing helpful suggestions. This project was funded by an award from the Darwin Initiative Project (no. 14-653). Additional funding was provided by the MRG 5080405 to BK, the TRF Senior Research Scholar Grant from the Thailand Research Fund (TRF) 2012-2015 (RTA5580001) to SP. Other supports are from The National Research Council of Thailand and The National Research University Project (NRU) FW0646A-56.

References

- Abbott RT (1989) Compendium of Landshells. American Malacologists, Inc., MA, 240 pp.
- Benson WH (1856) Characters of seventeen new of the Cyclostomacea from the British Provinces of Burmah, collected by Theobald W, jun., Esq. Annals and Magazine of Natural History, Series 2, 17: 225–233.
- Benson WH (1859) Observation of shell and animal of *Hybocystis*, a new genus of Cyclostomidae, base on *Megalostoma gravidum* and *Otopoma blennus*, B.; with notes on other living shells from India and Burmah. Annals and Magazine of Natural History, Series 3, 4: 90–93.
- Benson WH (1860) Notes on the subgenus *Corilla* H. & A. Adams, and on the group *Plectopylis* Benson; also on *Pollicaria* Gould, and *Hybocystis* Benson. Annals and Magazine of Natural History, Series 3, 6: 98–100.
- van Benthem Jutting WSS (1960) Some notes on land and freshwater Mollusca of Malaya. Basteria 24: 10–20.
- Blanford WT (1864) On the classification of the Cyclostomacea of eastern Asia. Annals and Magazine of Natural History, Series 3, 13: 441–465.
- Chan SY (1997) On *Pollicaria elephas* (de Morgan, 1885) West Malaysia. The Papustyla 11: 11–12.
- Cox LR (1964) Gastropoda, general characteristic of Gastropoda. In: Moore RC and Pitrat CW (Eds) Treatise on Invertebrate Palaeontology. Geological Society of America Inc., and University of Kansas Press. pp. I85–I169.
- Crosse H (1885) Etude monographique sur les espèces du genre *Hybocystis* de Benson. Journal de Conchyliologie 33: 180–193.
- Dautzenberg P, d'Hamonville L (1887) Description des espèces nouvelles du Tonkin et observations sur quelques autres mollusques de la même région. Journal de Conchyliologie 35: 213–225.
- Fischer P (1885) Note sur l'animal de *Hybocystis elephas* de Morgan. Journal de Conchyliologie 33: 174–179.

- Gould AA (1856) Descriptions of shells. Proceedings of Boston Society of Natural History 6: 11–16.
- Gould AA (1862) Otia conchologica: descriptions of shells and mollusks from 1839 to 1862. Freeman and Bolles, Boston, 256 pp.
- Gude GK (1921) Mollusca III, Land Operculates (Cyclophoridae, Truncatellidae, Assimineidae, Helicinidae). In: Shipley AE (Ed) The fauna of British India including Ceylon and Burma, 386 pp.
- Habe T (1964) Operculate land molluscs from Southeast Asia. Nature and Life in Southeast Asia, Kyoto 4: 111–128.
- Haines WA (1855) Descriptions of four new species of terrestrial shells from Siam. Annals of the Lyceum of Natural History of New York 6: 157–158. doi: 10.1111/j.1749-6632.1858.tb00358.x
- Hanley S, Theobald W (1870) Conchologica Indica: illustrations of the land and freshwater shells of British India. L. Reeve & Co., London. 65 pp, 160 pls.
- International Commission on Zoological Nomenclature (ICZN) (1999) International Code of Zoological Nomenclature, 4th. London, International Trust for Zoological Nomenclature, 306 pp.
- Johnson RI (1964) The recent Mollusca of Augustus Addison Gould, illustration of the types described by Gould, with a bibliography and catalogue of his species. United State National Museum Bulletin 239: 1–182. doi: 10.5479/si.03629236.239
- Kobelt W (1902) Cyclophoridae. Das Tierreich, 16 Lieferung. Verlag von R. Friedländer und Sohn, Berlin, 663 pp.
- Kobelt W, Möllendorff OF (1899) Katalog der gegenwärtig lebend bekannten Pneumonopomen. Nachrichtenblatt der Deutschen Malakozoologischen Gesellschaft 31: 129–151.
- Kongim B, Sutcharit C, Tongkerd P, Panha S (2009) Karyotype differentiation within the Elephant Pupinid snail, *Pollicaria mouhoti* (Pfeiffer, 1862) (Caenogastropoda: Pupinidae). The Natural History Journal of Chulalongkorn University 9: 201–208.
- Kongim B, Sutcharit C, Tongkerd P, Tan SHA, Quynh NX, Naggs F, Panha S (2010) Karyotype variation in the genus *Pollicaria* (Caenogastropoda: Pupinidae). Zoological Studies 49: 125–131.
- Laidlaw FF (1928) A list of land and freshwater Mollusca of the Malay Peninsular with notes. Journal Malayan Branch Royal Asiatic Society 6: 25–37.
- Mabille MJ (1887a) Molluscorum Tonkinorum Diagnoses. Imprimé par A. Masson, Meulan, 18 pp.
- Mabille MJ (1887b) Sur quelques mollusques du Tonkin. Bulletin de la Société Zoologique de France 4: 73–164.
- von Martens E (1860) On the molluscs of Siam. Proceedings of the Zoological Society of London 1860: 6–18.
- von Martens E (1867) Die preussische Expedition nach Ost-Asien. Zoologischer Theil, zweiter Band. Verlag der Königlichen Geheimen Ober-Hofbuchdruckerei, 477 pp.
- Möllendorff OF (1886) The land shells of Perak. Journal of the Asiatic Society of Bengal 55: 299–316.
- Möllendorff OF (1891) On the land and freshwater shells of Perak. Proceedings of the Zoological Society of London 1891: 330–348.
- Morgan J de (1885a) Mollusques terrestres et fluviatiles du royaume de Perak. Bulletin de la Société Zoologique de France 10: 353–428.
- Morgan J de (1885b) Note sur quelques espèces nouvelles de mollusques terrestres récoltés dans la Peninsula Malaise. Le Naturaliste 7: 68–70.

- Naggs F, Raheem D (2005) Sri Lankan snail diversity: faunal origins and future prospects. Records of the Western Australia Museum Supplement No. 68: 11–29.
- Pain T (1974) The land operculate genus *Pollicaria* Gould (Gastropoda), a systematic revision. Journal of Conchology 28: 173–178.
- Pfeiffer L (1852) Descriptions of eighteen new species of land shells, from the collection of Cuming H, Esq. Proceedings of the Zoological Society of London 1852: 156–160.
- Pfeiffer L (1856a) Novitates Conchologicae. Series prima. Mollusca extramarina. Beschreibung und Abbildung neuer oder kritischer Land- und Süßwasser Mollusken. Tome 1, Lief. 5–8: 49–90, pl. 13–24.
- Pfeiffer L (1856b) Verzeichniss der bisher bekannt gewordenen gedeckelten Landschnecken von Cuba. Malakozoologische Blätter 2: 118–150.
- Pfeiffer L (1860) Novitates Conchologicae. Series prima. Mollusca extramarina. Beschreibung und Abbildung neuer oder kritischer Land- und Süßwasser Mollusken. Tome 1, Lief. 12: 121–138, pl. 34–36.
- Pfeiffer L (1862) Descriptions of thirty-six new land shells, from the collection of Cuming H, Esq. Proceedings of the Zoological Society of London 1862: 268–278.
- Pfeiffer L (1863) Novitates Conchologicae. Series prima. Mollusca extramarina. Beschreibung und Abbildung neuer oder kritischer Land- und Süßwasser Mollusken. Tome 2, Lief. 20: 223–234, pl. 58–60.
- Sandberger F (1870–1875) Die Land- und Süßwasser-Conchylien der Vorwelt. Kreidel, Wiesbaden, 950 pp.
- Solem A (1959) Zoogeography of the land and fresh water Mollusca of the New Hebrides. Fieldiana: Zoology 43: 241–359.
- Solem A (1966) Some non-marine mollusks from Thailand. Spolia Zoologia Musei Hauniensis 24: 9–13.
- Sowerby GB (1878) Monograph of the genus Pupinidae. In: Sowerby GB (Ed.) Conchologia Iconica: or, Illustration of the Shells of Molluscous Animals. Vol. 20, 10 pls. Reeve and Benham, London.
- Stanisic J (1998) Superfamily Cyclophoridae, pp. 703–706. In: Beesley PL, Roos GJB, Wells A (Eds) Mollusca: The Southern Synthesis, Fauna of Australia. Vol. 5. CSIRO Publishing, Melbourne. Part. B. 565–1234 pp.
- Stanisic J, Shea M, Potter D, Griffiths O (2010) Australian land snails. Volume 1. A field guide to eastern Australian species. (Bioculture Press: Mauritius). 596 pp.
- Stoliczka F (1871) Notes on terrestrial Mollusca from the neighborhood of Moulmein (Tenasserim Provinces), with descriptions of new species. Journal of the Asiatic Society of Bengal 40: 143–177.
- Tielecke H (1940) Anatomie, Phylogenie und Tiergeographie der Cyclophoriden. Archiv für Naturgeschichte 9: 317–371.
- Vaught K (1989) A Classification of the Living Mollusca. American Malacologists, Inc., Florida, USA. 189 pp.
- Vermeulen JJ, Maassen WJM (2003) The non-marine mollusks 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), 35 pp.
- Wenz W (1938–1944) Gastropoda. Teil 1, Allgemeiner Teil [pp. 1–84] und Prosobranchia [pp. 85–231]. In Schindewolf OH (Ed.) Handbuch der Paläozoologie. Vol. 6 Gebrüder Bornträger: Berlin, 1639 pp.
- Yamazaki K, Yako M, Hung HQ, Ueshima R (2007). Operculate land snails from North Vietnam. Part I: Babe National Park, Bac Kan Province. Chiribotan 38: 48–54.