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Two new species of genus *Anceyoconcha* S. Tumpeesuwan & C. Tumpeesuwan, in Nahok et al., 2020 (Gastropoda: Pulmonata: Camaenidae), from northeastern Thailand

Benchawan Nahok[1,3], Chanidaporn Tumpeesuwan[1*] & Sakboworn Tumpeesuwan[1,2]

Abstract. Two new species of the Indochinese tree snail *Anceyoconcha* S. Tumpeesuwan & C. Tumpeesuwan, in Nahok et al., 2020, are described from natural forests and forestry plantations on sandstone and basalt hills in northeastern Thailand. These snails can be found on trees from the foothills to higher elevations, around 1–2 m above ground level. The new species *Anceyoconcha carinata* and *Anceyoconcha elongata* possess the key characters of the genus, namely, a shell that is sinistral, ovate conic to elongate conic with six to nine slightly convex whorls, semi-transparent, and lustrous. The dart sac and mucous glands are absent, and the flagellum long cylindrical and tapering. Both new species differ from all previously described species by unique characters of shell; length of penis, vagina and free oviduct; and flagellum shape. The phylogeny based on the mitochondrial and nuclear DNA and genetic distances suggest that all *Anceyoconcha* species form a well-supported monophyly, and that both new species are differentiated from the rest of the congeners.

Key words. tree snails, genital system, systematics, phylogeny

INTRODUCTION

The Indochinese tree snail genus *Anceyoconcha* S. Tumpeesuwan & C. Tumpeesuwan, in Nahok, Tumpeesuwan & Tumpeesuwan, 2020, was originally proposed by Ancey (1907) as *Giardia*, with *Bulimus siamensis* Redfield, 1853, designated as the type species. According to Schileyko (2003), the genus *Giardia* Ancey, 1907, is classified in the subfamily Camaeninae, which is included in family Camaenidae by Schileyko (2003) and Bouchet et al. (2017). It is endemic to the Indochinese region (Fig. 1), extending across the countries of Cambodia, Laos, Thailand, and Vietnam (Schileyko, 2003, 2011; Sutcharit & Panha, 2008; Srihata et al., 2010; Sutcharit et al., 2017; Thach, 2017, 2018; Inkhavilay et al., 2019; Nahok et al., 2020; Sutcharit et al., 2020). However, *Giardia* Ancey, 1907, is a junior homonym of the protozoa genus *Giardia* Künstler, 1882. Recently, S. Tumpeesuwan & C. Tumpeesuwan, in Nahok et al. (2020), proposed a new replacement name, *Anceyoconcha*, for *Giardia* Ancey, 1907.

Previously, only *Giardia siamensis* was reported in Thailand (Schileyko, 2003, 2011; Sutcharit & Panha, 2008; Srihata et al., 2010; Sutcharit et al., 2017). Other names have been used, such as *Pseudobuliminus* (*Giardia*) *siamensis* and *Pseudobuliminus siamensis* (Solem, 1966; Hemmen & Hemmen, 2001; Boonngam et al., 2008; Nabhitabhata, 2009; Tumpeesuwan & Tumpeesuwan, 2010; Jumlong et al., 2013; Tumpeesuwan et al., 2014). However, the reproductive anatomy of the East Asian *Pseudobuliminus* studied by Habe (1955) and Wu (2004) showed the presence of a dart sac and mucous glands, both of which are absent in all so-called "*Giardia*" and "*Pseudobuliminus*" in Thailand (Nahok, 2020; Nahok et al., 2020). Therefore, these snails might be reassigned to *Anceyoconcha*.

Nahok et al. (2020) proposed an additional species, *Anceyoconcha rhombostoma* (Pfeiffer, 1861), for the genus. This species was formerly reported as a *Ganesella* member (Raheem et al., 2017; Sutcharit et al., 2017, 2019) and *Giardia rhombostoma* in Schileyko (2011). Budha et al. (2016) reported the COI and 28S rDNA sequences of *Ganesella capitium* and *Ganesella rhombostomus*. Lately, the comparison of genital systems of the type species of *Anceyoconcha* and *Ganesella*—between *Anceyoconcha siamensis*, as illustrated by Schileyko (2003, as *Giardia siamensis*), and *Ganesella capitium*, by Budha et al. (2012, as *Darwininitium shiwalikianum*)—suggested that the genital anatomy of "*Ganesella*" *rhombostoma* is similar to that of "*Giardia*" *siamensis*, and the former species was therefore moved to *Anceyoconcha* (see Nahok et al., 2020).

Accepted by: Ng Ting Hui

[1]Department of Biology, Faculty of Science, Mahasarakham University, Kantharawichai District, Maha Sarakham, 44150 Thailand; Email: ctumpeesuwan@yahoo.com (*corresponding author)

[2]Palaeontological Research and Education Centre, Mahasarakham University, Kantharawichai District, Maha Sarakham, 44150 Thailand

[3]Educational Research Development and Demonstration Institute, Srinakharinwirot University, Ongkharak District, Nakhon Nayok, 26120 Thailand

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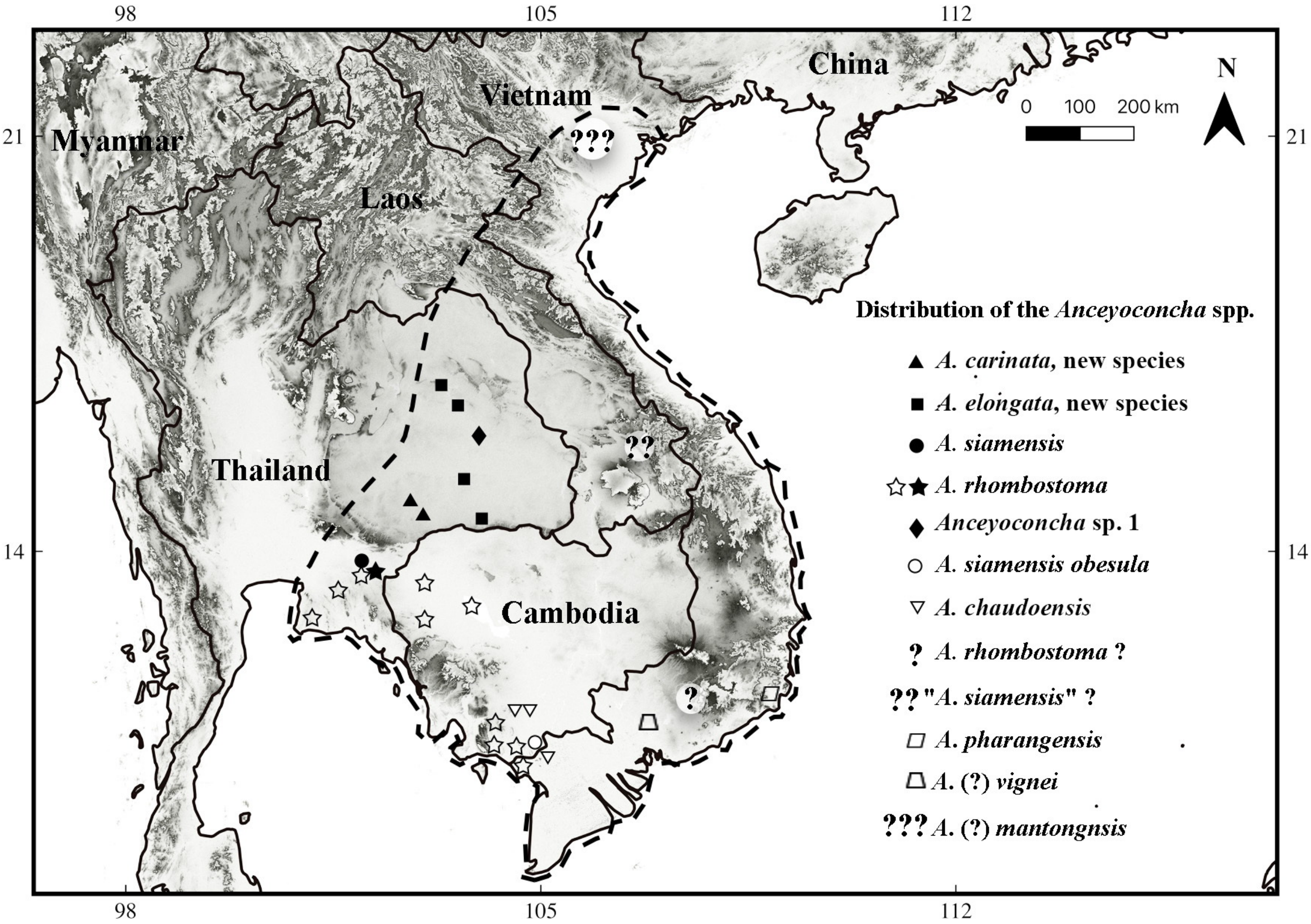

Fig. 1. Geographical range of *Anceyoconcha* (dashed line) and the recorded localities. Filled symbols: data from Nahok et al. (2020) and this study; open symbols: data from Schileyko (2011) and Sutcharit et al. (2019, 2020); ?: recorded localities and taxonomic status could not be traced. Laos data from Inkhavilay et al. (2019); Vietnam data from Schileyko (2011) and Sutcharit et al. (2020).

In previous work, two *Anceyoconcha* species were studied with regard to their shell characters, radula, and genital system. In the present work, we collected more material of this genus in Thailand for an integrative approach, which combined the external shell morphology, radula, genital organ, and DNA sequences. Here, we describe two new species of *Anceyoconcha*.

MATERIAL AND METHODS

Morphological studies. Specimens were collected from seven localities throughout the distribution range in northeastern Thailand (Fig. 1). Adult snails were drowned in water for 24 hours, then fixed and preserved in 70% ethanol to examine their genital anatomy. The dissections for the examination of the reproductive system were performed using a stereo microscope. Radulae were extracted from the buccal mass and examined under a scanning electron microscope. Empty shells were counted for whorl number and measured for shell height (SH), shell width (SW), aperture height (AH), and aperture width (AW) using digital vernier calipers. Specimens were primarily identified following Nahok (2020). The examined specimens were deposited in the land snail collection of the Natural History Museum, Mahasarakham University, Thailand (NHMSU 00036–00046).

Abbreviations.
at = atrium
p = penis
prm = penial retractor muscle
ep1 = proximal part of epiphallus
ep2 = distal part of epiphallus
fl = flagellum
vd = vas deferens
v = vagina
gs = gametolytic sac
fo = free oviduct
ut = uterus
pro = prostate gland
hd = hermaphroditic duct
ag = albumen gland

DNA extraction and amplification. DNA was extracted from the foot muscle tissue of an adult snail (one specimen per population) using a GF-1 Nucleic Acid Extraction Kit (Vivantis Technologies Sdn. Bhd, Malaysia). The COI and 16S rRNA mitochondrial genes and 28S rRNA nuclear gene were amplified by PCR using the primer pairs L1490 and H2198 (Folmer et al., 1994), 16Scs1 (Chiba, 1999) and 16S_MN3R (Neiber et al., 2017), and 28SF4 and 28SR5 (Morgan et al., 2002), respectively. Reaction conditions were as follows: an initial denaturation step at 94°C for 2 min;

Table 1. Specimens included for molecular analysis, with their GenBank accession numbers. Species identities of sequences obtained from GenBank follow the respective sources.

Species	Localities	Specimen voucher	GenBank accession numbers			References
			COI	16S rRNA	28S rRNA	
Pseudobuliminus incertus	Wulai, Taipei	Kameda Y:2968	AB852705	-	-	Hirano et al. (2014)
Pseudobuliminus meiacoshimensis	Ishigaki, Okinawa	Kimura K:psd02	AB852706	-	-	Hirano et al. (2014)
Ganesella capitium	Nepal	-	KX228489	-	KX228496	Budha et al. (2016)
"*Ganesella rhombostomus*"	-	KB-2017	KX228490	-	KX228497	Budha et al. (2016)
"*Ganesella rhombostomus*"	-	KB-2017	KX228491	-	KX228498	Budha et al. (2016)
Anceyoconcha siamensis	Khao Chakan, Sa Kaeo, Thailand	NSKKC1060	MN433674	OK138720	OK138713	This study
Anceyoconcha rhombostoma	Phet Pho Thong, Sa Kaeo, Thailand	NSKPT1060	MN433675	OK138721	OK138714	This study
Anceyoconcha carinata, new species	Khao Plai Bat, Buri Ram, Thailand	NBRPB560	MN433669	OK138722	OK138715	This study
Anceyoconcha elongata, new species	Phu Po, Kalasin, Thailand	NKSPP660	MN433670	OK138723	OK138716	This study
Anceyoconcha elongata, new species	Phu No, Kalasin, Thailand	NKSPN960	MN433671	OK138724	OK138717	This study
Anceyoconcha elongata, new species	Phanom Sawai, Surin, Thailand	NSRPS1060	MN433673	OK138725	OK138718	This study
Anceyoconcha sp.1	Pha Nam Yoi, Roi Et, Thailand	NREPY960	MN433672	OK138726	OK138719	This study
Bradybaena similaris	Japan	KC8276	AB852697	LC472125	AB852967	Hirano et al. (2019)

36 cycles of 94°C for 30 s, 50°C for 45 s, and 72°C for 45 s; and a final extension step at 72°C for 5 min for COI and 16S rRNA. The same conditions were followed for 28S rRNA, except for the annealing temperature, which was at 53°C. The PCR products were checked with 1% agarose gel electrophoresis. Successful PCR products were sent for NGS-based sequencing at Celamics DNA Sequencing Services (Seoul, Korea) and 1st BASE DNA Sequencing Services (Selangor, Malaysia).

Phylogenetic analysis. Forward and reverse sequences were checked by Bioedit version 7.0.9 (Hall, 1999, 2001). Sequences were aligned using the Clustal W algorithm in MEGA X (Kumar et al., 2018). All new sequences were deposited in GenBank under the accession numbers MN433669–MN433675 for COI, OK138720–OK138726 for the 16S rRNA fragment, and OK138713–OK138719 for the 28S rRNA, and are shown in Table 1. Additional sequences of *Pseudobuliminus* proposed by Hirano et al. (2014) and *Ganesella* proposed by Budha et al. (2016) were downloaded from GenBank for comparison. *Bradybaena* proposed by Hirano et al. (2019) were included as outgroups. The pairwise genetic distances were calculated by the measured distances (p-distances). Phylogenetic trees were obtained using Bayesian inference (BI), neighbour joining (NJ), and maximum likelihood (ML).

The aligned COI, 16S rRNA, and 28S rRNA sequences were concatenated into one partitioned dataset, which we analysed using the programme EMBOSS seqret (Madeira et al., 2019). The programme jModeltest version 2.1.10 (Posada, 2008; Darriba et al., 2012) was used to select the best-fit DNA substitution model for BI analysis based on the Bayesian information criterion (BIC) algorithm. Additional BI analysis was performed using MrBayes version 3.2.6 (Ronquist et al., 2012) and run for two million generations, with a sampling frequency of 100 generations. Trees sampled before this point were discarded as burn-in. Support for nodes was defined as posterior probabilities. The NJ analysis was estimated in MEGA X (Kumar et al., 2018) and branch support was calculated using the bootstrapping method with 1,000 replicates. The ML analysis was performed

Table 2. Pairwise p-distance values for different species in this study based on mitochondrial COI sequences.

No.	Species	1	2	3	4	5	6	7	8	9	10	11
1	*Pseudobuliminus incertus*											
2	*P. meiacoshimensis*	0.178										
3	*Ganesella capitium*	0.225	0.219									
4	"*Ganesella rhombostomus*"	0.217	0.217	0.194								
5	"*Ganesella rhombostomus*"	0.215	0.215	0.194	0.005							
6	*Anceyoconcha siamensis*	0.210	0.233	0.196	0.160	0.160						
7	*A. rhombostoma*	0.214	0.218	0.193	0.002	0.007	0.156					
8	*A. carinata*, new species	0.201	0.220	0.203	0.174	0.175	0.177	0.171				
9	*A. elongata*, new species, Phu Po	0.214	0.229	0.191	0.170	0.170	0.191	0.176	0.171			
10	*A. elongata*, new species, Phu No	0.193	0.216	0.188	0.155	0.155	0.188	0.157	0.166	0.063		
11	*A. elongata*, new species, Phanom Sawai	0.206	0.225	0.188	0.149	0.153	0.180	0.156	0.168	0.105	0.090	
12	*Anceyoconcha* sp.1	0.216	0.223	0.194	0.155	0.158	0.188	0.156	0.171	0.113	0.121	0.113

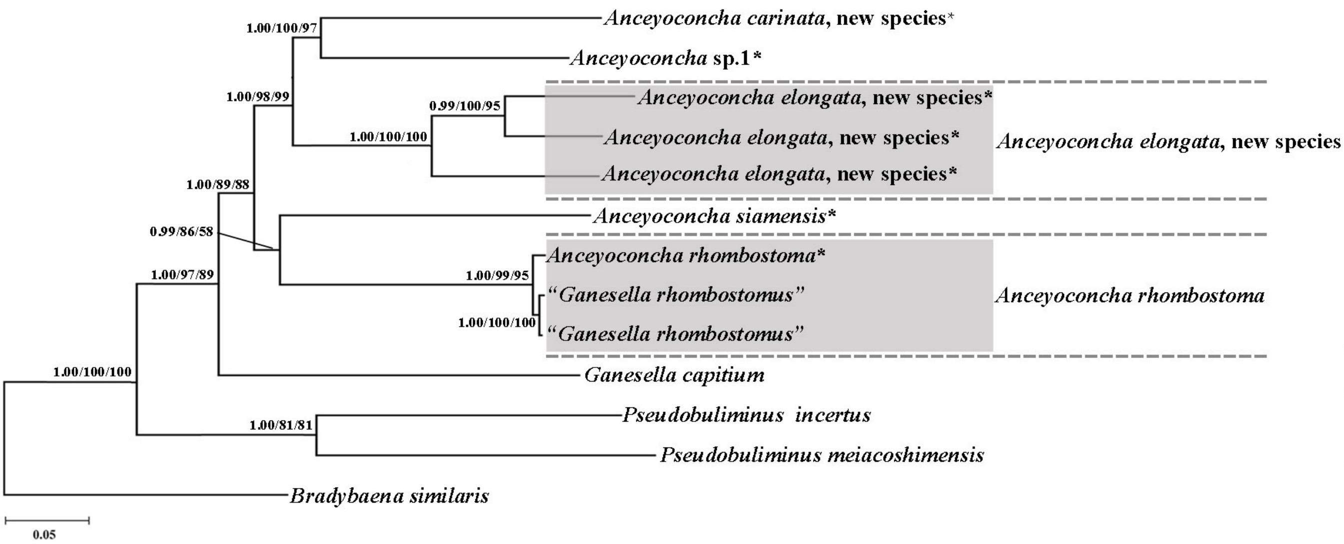

Fig. 2. Bayesian inference (BI) tree of genera *Anceyoconcha*, *Ganesella*, and *Pseudobuliminus* based on the mitochondrial and nuclear DNA (concatenated genes of COI, 16s rRNA, and 28S rRNA). Numbers at nodes indicate branch support based on posterior probability (BI) / bootstrapping (neighbour joining) / bootstrapping (maximum likelihood). *sequences of this study.

using the programme RAxML version 0.9.0 (Kozlov et al., 2019) conducted under GTR+FO+G, and support values by bootstrapping with 1,000 replications. Phylogenetic trees were arranged and edited using FigTree version 1.4.0 (Rambaut, 2012). Following Hirano et al. (2014), nodal support values were considered to be meaningful if ≥ 70% for bootstrapping or ≥ 0.95 for posterior probabilities.

RESULTS

Sequences of the COI, 16S rRNA, and 28S rRNA genes were generated from seven individuals from seven localities of *Anceyoconcha* spp. in northeastern Thailand. In addition, we included six Genbank sequences of COI, one Genbank sequence of 16S rRNA, and four Genbank sequences of 28S rRNA (Table 1). Five missing 16S rRNA sequences and two missing 28S rRNA sequences were coded as missing data in the concatenated dataset.

A total of 13 sequences (655 bp) of COI gene fragment had nucleotide frequencies of 0.285, 0.133, 0.175, and 0.407 for A, C, G, and T, respectively, and there were 263 variable sites and 190 were parsimony informative. The uncorrected p-distance of the intraspecific distances among *Anceyoconcha* spp. ranged from 0.002 to 0.105, whereas interspecific distances among species ranged from 0.113 to 0.191 (Table 2). A total of eight sequences (460 bp) of 16S rRNA gene fragment had nucleotide frequencies of 0.365, 0.121, 0.122, and 0.392 for A, C, G, and T, respectively, and there were 440 variable sites and 238 were parsimony informative. A total of 11 sequences (560 bp) of 28S rRNA gene fragment had nucleotide frequencies of 0.204, 0.292, 0.322, and 0.182 for A, C, G, and T, respectively, and there were 555 variable sites and 477 were parsimony informative. The concatenated dataset (1,675 bp) had nucleotide frequencies of 0.269, 0.199, 0.231, and 0.301 for A, C, G, and T, respectively, and there were 1,318 variable sites and 765 were parsimony informative.

The phylogenetic trees reconstructed using the BI, NJ, and ML methods were highly congruent, with almost identical topologies and the same supported nodes for all major clades, and with all datasets. The BI phylogenetic tree based on the concatenated dataset of COI, 16S rRNA, and 28S rRNA is shown in Fig. 2.

Based on the phylogenetic analyses, *Anceyoconcha* is strongly supported as a separate clade from *Ganesella* and *Pseudobuliminus* (Fig. 2).

Anceyoconcha carinata, new species, is clearly separate from other congeners and forms a sister group to *Anceyoconcha* sp.1, with very strong support (1.00 for BI posterior probability, and 100% and 97% bootstrap support for NJ and ML, respectively).

Anceyoconcha elongata, new species, from three localities were grouped in the same subclade with very strong support (1.00 for BI posterior probability, and 98% and 99% for NJ and ML bootstrap replicates), and form a sister group to the clade containing *A. carinata*, new species, and *Anceyoconcha* sp., with very strong support from BI, NJ, and ML analyses.

"*Ganesella rhombostomus*" proposed by Budha et al. (2016) is the most closely related to *A. rhombostoma* from Sa Kaeo, with very strong support (1.00 for BI posterior probability, and 99% and 95% bootstrap support for NJ and ML, respectively); while *A. siamensis* is sister to the *A. rhombostoma* subclade, with high support from BI with posterior probability of 0.99, but no significant support from NJ and ML (86% and 58% bootstrap support, respectively).

SYSTEMATICS

Family Camaenidae Pilsbry, 1895

Anceyoconcha S. Tumpeesuwan & C. Tumpeesuwan, in Nahok, Tumpeesuwan & Tumpeesuwan, 2020

Anceyoconcha S. Tumpeesuwan & C. Tumpeesuwan, in Nahok et al., 2020: 81 (replacement name for *Giardia* Ancey, 1907, not *Giardia* Künstler, 1882 (Metamonada)).

Type species. *Bulimus siamensis* Redfield, 1853.

Diagnosis. Shell sinistral, ovate trochoid to elongate conic, with 6–9 slightly convex whorls, semi-transparent, and lustrous. Genital system without dart sac and mucous glands. Flagellum long cylindrical and tapering, distally relatively hook-shaped (Figs. 4A, B, 5A, B, 6A, B). Vas deferens long, thin, entering epiphallus laterally. Free oviduct short. Vagina long, stout. Gametolytic duct thickened at base, proximal part wider than distal part; gametolytic sac spear- or droplet-shaped. Radula, central tooth symmetric unicuspid, narrowly rounded to lanceolate; lateral teeth oblique unicuspid (Fig. 5J) or bicuspid with indistinct or distinct blunt ectocone (Figs. 4H, 6H); marginal teeth tricuspid-tetracuspid with finger-shaped ectocone.

Anceyoconcha carinata, new species
(Figs. 3A, B, 4; Tables 1–3)

Anceyoconcha sp.1 – Nahok, 2020: 72–73, figs. 25C, D, 39, 46, 47, 50, 53, tables 3, 5, 7–10.

Material examined. Holotype: NHMSU-00036, Khao Plai Bat (basalt hill), Prakhon Chai District, Buri Ram Province, Thailand (14°28′55.36″N, 102°58′11.00″E), alt. 211 m, 30 May 2017, SH = 19.0 mm, SW = 7.6 mm, AH = 5.4 mm, AW = 3.3 mm (Fig. 3A). Paratypes: 6 shells, 4 living specimens preserved in ethanol (NHMSU-00037), same data as for holotype. 1 shell (NHMSU-00038), Khao Angkhan (basalt hill), Chaloem Phra Kiat District, Buri Ram Province, Thailand (14°32′27.36″N, 102°50′13.60″E), alt. 251 m, 31 May 2017 (Fig. 3B).

Diagnosis. Shell slightly ovate conic, last whorl with strong ridge around umbilicus (Fig. 3A, B). Penis and vagina shorter than flagellum. Flagellum long cylindrical, divided into two portions (Fig. 4A, B).

Etymology. Specific epithet 'carinata' derived from Latin word 'carina', meaning 'keel' and referring to the shell of this new species having a periumbilical keel.

Description. Shell (Fig. 3A, B; Table 3): slightly ovate conic, whorls 6½, shell height 18.5–22.0 mm, shell width 7.2–8.8 mm, aperture height 5.4–7.1 mm, and aperture width 3.3–6.1 mm. Brownish colour; semi-transparent and lustrous. Apex obtuse, acute with light colour; embryonic shell smooth. Last whorl straight, rounded; with a periumbilical keel near aperture. Peripheral keel and peripheral band absent. Aperture large, irregularly rounded or ovoid, quite oblique, with thin, reflexed margins. Peristome expanded and reflexed. Umbilicus, a minute perforation, narrow and deep.

Genital system (n = 3) (Fig. 4A–F): atrium short. Penis short cylindrical. Epiphallus divided into two portions, proximal part (ep1) stout and swollen, distal part (ep2) long cylindrical. Penial retractor muscle present. Flagellum approximately almost the same length as distal part of epiphallus (ep2); with proximal part twisted and distal part S-shaped. Vas deferens long. Vagina short cylindrical but longer than penis. Gametolytic duct thickened at base and gradually slender to small tube distally. Gametolytic sac small swollen gland at

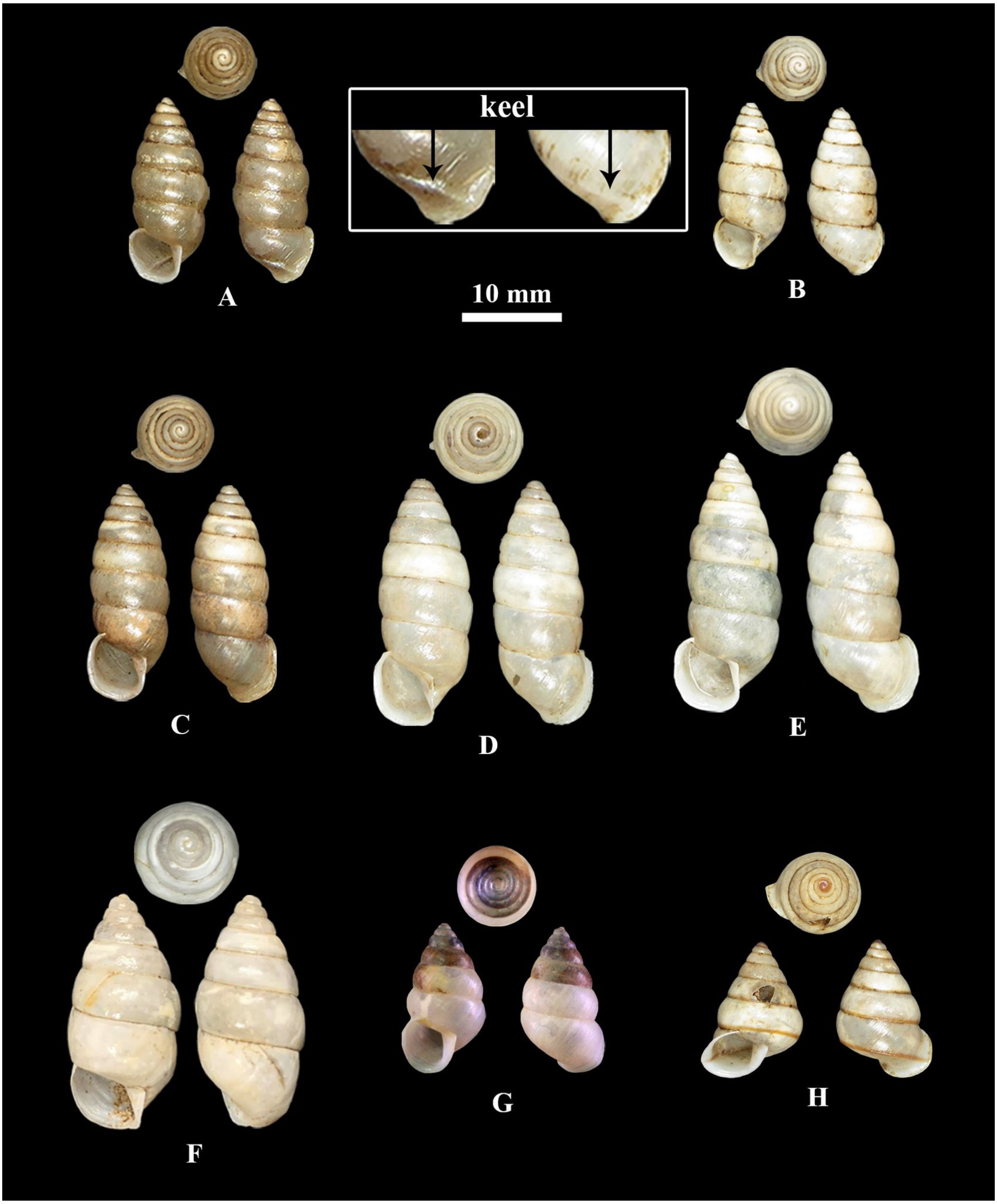

Fig. 3. Shell morphology of *Anceyoconcha* spp. in northeastern Thailand. A, B, *A. carinata*, new species; A, holotype (NHMSU-00036) from Khao Plai Bat, Buri Ram; B (NHMSU-00038) from Khao Angkhan, Buri Ram. C–E, *A. elongata*, new species; C, holotype (NHMSU-00039) from Phu Po, Kalasin; D (NHMSU-00041) from Phu No, Kalasin; E (NHMSU-00045) from Phanom Sawai Forest Park, Surin. F, *A.* sp.1 (NHMSU-00043) from Pha Nam Yoi, Roi Et. G, *A. siamensis* (ZRCBUU-0325). H, *A. rhombostoma* (NHMSU-00022). Fig. 3G photograph courtesy of Pongrat Dumrongrojwattana.

distal end of gametolytic duct. Free oviduct short. Uterus and prostate gland long and stout. Inner wall of penis with short, stout, and smooth longitudinal pilaster (Fig. 4C). Inner wall of ep1 with four corrugated longitudinal pilasters (Fig. 4C); inner wall of ep2 with three smooth longitudinal pilasters (Fig. 4D). Inner wall of flagellum with three stout and smooth longitudinal pilasters (Fig. 4E). Inner wall of vagina with two longitudinal pilasters (Fig. 4F).

Radula (n = 3) (Fig. 4G–I): comprises 126–128 transverse rows of teeth, each row containing 65–73 teeth, (22–24) + (10–12) + 1 + (10–12) + (22–24). Central teeth symmetric and unicuspid, narrowly rounded. Lateral teeth oblique rounded, bicuspid with indistinct or distinct blunt ectocone (Fig. 4H), larger than central teeth. Marginal teeth gradually changing from broadly tricuspid (13th–28th) to tetracuspid (29th–36th) with two small ectocones.

Remarks. The shell morphology of *A. carinata*, new species, differs from that of many other congeners in the presence of a strong keel around the umbilicus (Fig. 3A, B). *Anceyoconcha rhombostoma* also possesses the keel, but its shell is ovate trochoid, shorter than that of *A. carinata*, new species, and the presence of a keel on its periphery runs to an angle of the rhomboid-shaped aperture (see Sutcharit et al., 2019: fig. 3C–I; Nahok et al., 2020: fig. 4B; Sutcharit et al., 2020: fig. 12C, D). The genitalia of *A. carinata*, new species, possess three characters that are distinct from those of all other congeners in that the vagina and penis are shorter than the flagellum, and the flagellum is divided into two sections with a twining proximal part and S-shaped distal part (Fig. 4A, B).

Distribution. *Anceyoconcha carinata*, new species, is currently known from the basalt hill areas in Prakhon Chai and Chaloem Phra Kiat Districts, Buri Ram Province.

Anceyoconcha elongata, new species

Figs. 3C–E, 5; Tables 1–3

Giardia siamensis – Srihata et al., 2010: 364–365, 367, fig. 2. Phu No, Kalasin.

Pseudobuliminus siamensis – Jumlong et al., 2013: 72–76, fig. 2. Phanom Sawai Forest Park, Surin.

Anceyoconcha sp.5 – Nahok, 2020: 77–78, figs. 25H, 41, 46–47, 50, 53, tables 3, 5, 7–10. Phanom Sawai Forest Park, Surin.

Anceyoconcha sp.6 – Nahok, 2020: 79–80, figs. 25I, 42, 46–47, 50, 53, tables 3, 5, 7–10. Phu No, Kalasin.

Anceyoconcha sp.7 – Nahok, 2020: 81–82, figs. 25J, 43, 46–47, 50, 53, tables 3, 5, 7–10. Phu Po, Kalasin.

Material examined. Holotype: NHMSU 00039; Phu Po (sandstone hill), Mueang District, Kalasin Province, Thailand (16°37′10.42″N, 103°37′55.59″E); alt. 241 m; 17 June 2017; SH = 21.8 mm, SW = 7.8 mm, AH = 6.5 mm, AW = 4.1 mm (Fig. 3C). Paratypes: 55 shells, 6 living specimens preserved in ethanol (NHMSU-00040), same data as for holotype. 1 shell (NHMSU 00041), 1 living specimen preserved in ethanol (NHMSU-00042), Phu No (sandstone hill), Tha Khantho District, Kalasin Province, Thailand (16°51′42.33″N, 103°14′45.20″E); alt. 264 m, 27 September 2017 (Fig. 3D); 18 shells (NHMSU 00045), 1 living specimen preserved in ethanol (NHMSU-00046), Phanom Sawai Forest Park (basalt hill), Mueang District, Surin Province, Thailand (14°45′34.88″N, 103°21′56.62″E), alt. 206 m, 14 October 2017 (Fig. 3E); 1 shell (NHMSU 00047), Khao Sala, Buachet District, Surin Province, Thailand (14°25′44.87″N, 103°56′3.34″E), alt. 312 m, 14 October 2017.

Diagnosis. Shell elongate conic. Flagellum equal to or longer than epiphallus.

Etymology. Specific epithet derived from Latin word ‘elongatus’, meaning prolonged and referring to the elongate shell of the new species.

Description. Shell (Fig. 3C–E; Table 3): elongate conic, whorls 7¾, shell height 21.6–28.1 mm, shell width 7.6–9.7 mm, aperture height 6.1–7.8 mm, and aperture width 4.1–7.6 mm. Pale grey to light brown or white to light yellow, transparent, and lustrous. Apex obtuse. Embryonic shell smooth. Last whorl large, evenly rounded, polished. Peripheral keel and peripheral band absent. Aperture half-moon-shaped to sub-ovate. Peristome expanded, parietal callus transparent. Umbilicus narrowly opened.

Genital system (n = 5, comprising three specimens from Phu Po, one specimen from Phu No, one specimen from Phanom Sawai) (Fig. 5A–D): atrium short. Penis long cylindrical shape. Penial retractor muscle present, swollen at base. Epiphallus is equal to or half of penis length. Flagellum is equal to or slightly longer than epiphallus length, cylindrical, and slender hook-shaped or sickle-shaped at distal end. Vas deferens long. Vagina length is equal to or slightly longer than penis length. Gametolytic duct swollen and thickened at base, and gradually slender to small tube distally. Gametolytic sac small, swollen, balloon-shaped gland at distal end of gametolytic duct. Free oviduct very short. Uterus and prostate gland very long. Inner wall of penis rather smooth (Fig. 5E). Proximal part of epiphallus (ep1) inner wall with five corrugated longitudinal pilasters (Fig. 5E); distal part of epiphallus (ep2) inner wall with smooth longitudinal pilaster (Fig. 5F). Inner wall of flagellum with two longitudinal pilasters, one very thin and smooth, and the other robust and smooth (Fig. 5G). Inner wall of vagina with six slightly undulating longitudinal pilasters (Fig. 5H).

Radula (n = 4, comprising three specimens from Phu Po, one specimen from Phanom Sawai Forest Park) (Fig. 5I–K): comprises 76–80 transverse rows of teeth in specimens from Phu Po, and 100 rows in one specimen from Phanom Sawai; each row containing 51–59 teeth, (16–18) + (9–11) + 1 + (9–11) + (16–18). Central teeth symmetric unicuspid, lanceolate. Lateral teeth similar to central tooth, large, and oblique unicuspid. Teeth on both sides begin to transform into indistinct, bicuspid marginal teeth with tiny ectocone at numbers 10–12. Marginal teeth gradually change to broad tricuspid, starting at numbers 13–17, and begin to transform into tetracuspid with two cusp ectocones from numbers 18–27 to edge of radula plate.

Table 3. Comparison of shells, radulae, and genital systems of *Anceyoconcha* spp. from northeastern Thailand.

Characters	***A. siamensis***	***A. rhombostoma***	***A. carinata*, new species**	***A. elongata*, new species**	***Anceyoconcha* sp.1**
Characters of shell	n = 1	n = 36	n = 8	n = 76	n = 1
Shell shape	Ovate conic	Ovate trochoid	Slightly ovate conic	Elongate conic	Ovate conic
Shell height (mm)	13.0–23.0	7.6–14.6	18.5–22.0	21.6–28.1	19.1
Shell width (mm)	6.0–7.0	3.3–8.6	7.2–8.8	7.6–9.7	9.2
Number of whorls	7–9	6	6½	7¾	7¾
Peripheral keel	Absent	Absent or present	Absent	Absent	Absent
Peripheral band	Absent	Absent or present	Absent	Absent	Absent
Periumbilical keel	Absent	Absent	Present	Absent	Absent
Characters of radula	n = 1	n = 3	n = 3	n = 4	n = 1
Number of rows	89	104–106	126–128	76–100	100
Number of teeth in rows	45–53	57–65	65–73	51–59	51–59
Lateral teeth	6–8	9–11	10–12	9–11	6–8
Marginal teeth	16–18	19–21	22–24	16–18	19–21
Central teeth shape	Lanceolate	Broadly rounded	Narrowly rounded	Lanceolate	Broadly rounded
Characters of genitalia	n = 1	n = 3	n = 3	n = 5	n = 1
Flagellum	Tiny hook-shaped at distal end	Hook-shaped at distal end	Twining proximal part and S-shaped at distal end	Slender hook-shaped or sickle-shaped at distal end	Hook-shaped at distal end
Penis shape	Short cylindrical	Long cylindrical	Short cylindrical	Long cylindrical	Long cylindrical with proximal bend
Penis length	Shorter than flagellum	Slightly shorter than flagellum	Shorter than flagellum	Longer than flagellum	Longer than flagellum
Vagina length	Longer than flagellum	Equal to flagellum	Shorter than flagellum	Longer than flagellum	Longer than flagellum
References	Schileyko (2003); Nahok et al. (2020)	Sutcharit et al. (2019); Nahok et al. (2020)	Nahok (2020); this study	Nahok (2020); this study	Nahok (2020); this study

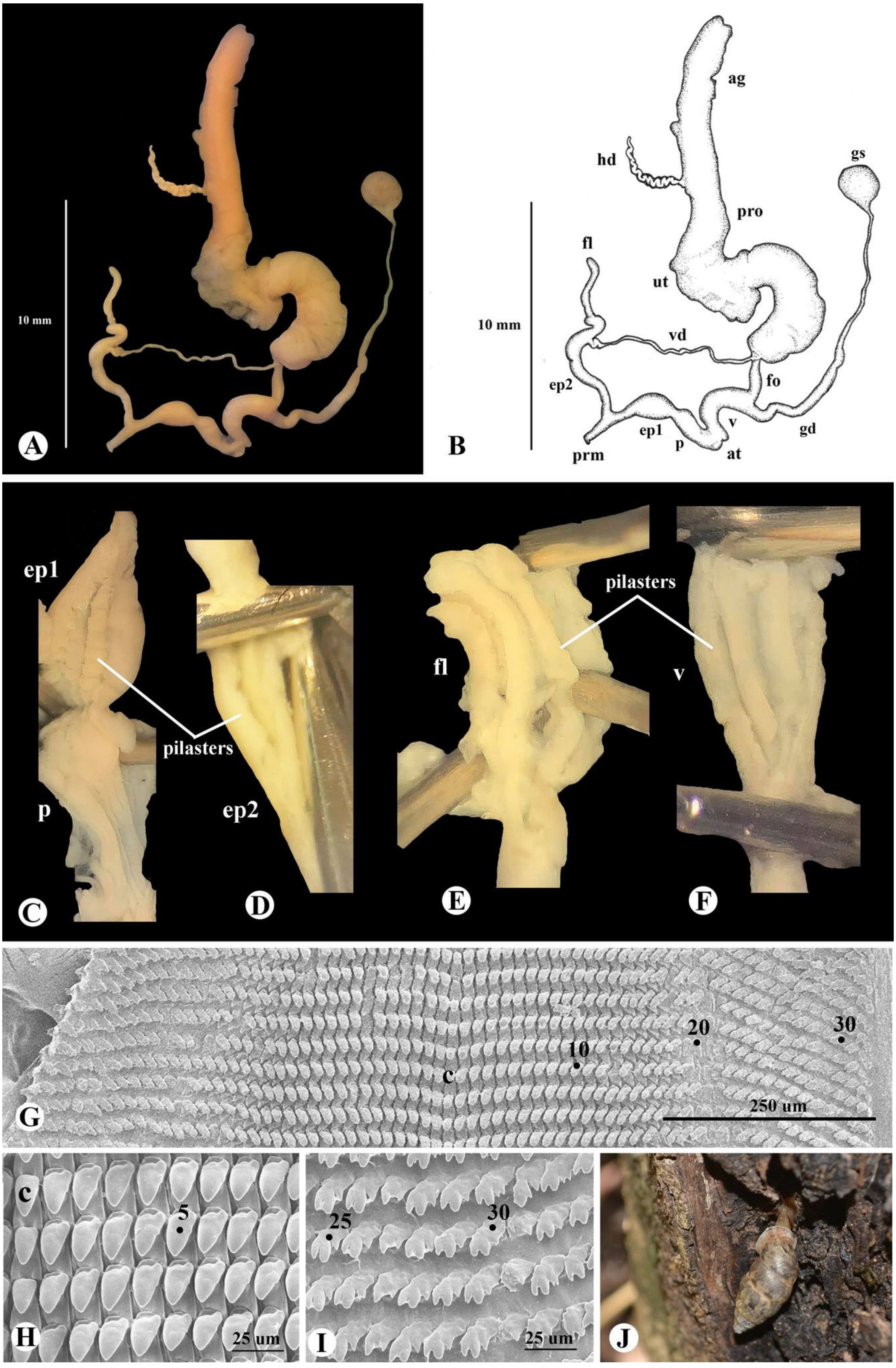

Fig. 4. *Anceyoconcha carinata*, new species. A, B, genital system, paratype (NHMSU-00037). C–F, inner wall of genital system; C, penis (p) and proximal portion of epiphallus (ep1); D, distal portion of epiphallus (ep2); E, flagellum (fl); F, vagina (v). G, view of transverse rows of radula, with number of lateral and marginal teeth indicated (c = central tooth); H, right side of central tooth and lateral teeth; I, right side of marginal teeth. J, natural habitat and living adult.

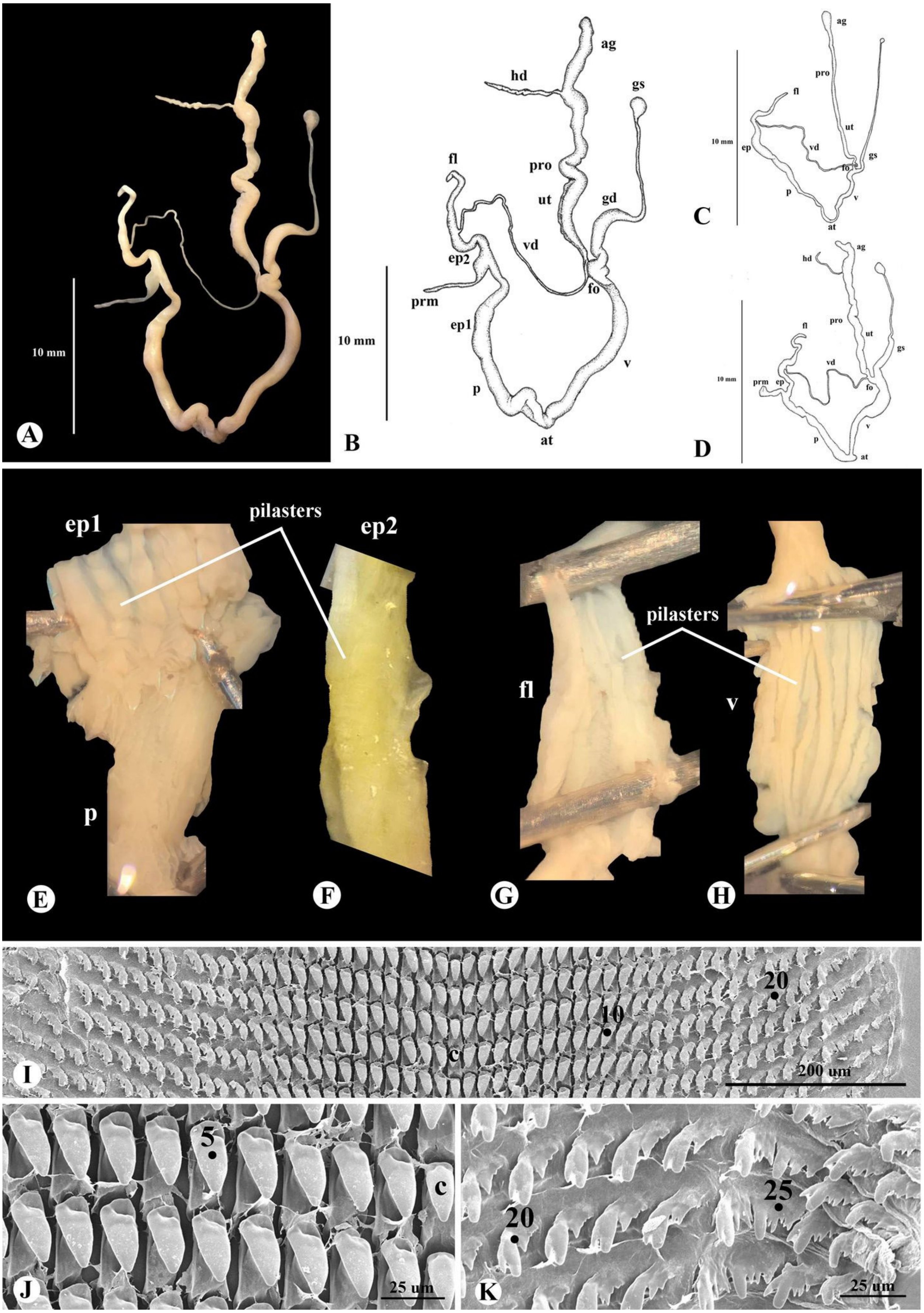

Fig. 5. *Anceyoconcha elongata*, new species. A, B, genital system, paratype (NHMSU-00040) from Phu Po, Kalasin. C, genital system (NHMSU-00042) from Phu No, Kalasin. D, genital system (NHMSU-00046) from Phanom Sawai, Surin. E–H, inner wall of genital system; E, penis (p) and proximal portion of epiphallus (ep1); F, distal portion of epiphallus (ep2); G, flagellum (fl); H, vagina (v). I, view of transverse rows of radula, with number of lateral and marginal teeth indicated (c = central tooth); J, left side of central tooth and lateral teeth; K, right side of marginal teeth.

Remarks. *Anceyoconcha elongata*, new species, was discovered from Phu Po and Phu No in Kalasin, and Phanom Sawai and Khao Sala in Surin. These four populations resemble each other in shell morphology, reproductive anatomy, and radula morphology, but differ slightly in size, colour, and shape of aperture (Fig. 3C, D, F; Table 3). The penial retractor muscle is present in specimens from Phu Po and Phanom Sawai, but is absent in the specimen from Phu No. The penis is long and cylindrical in the specimen from Phanom Sawai, notably different from those in the specimens from Phu Po, which have a proximal twist at the base, and those in specimens from Phu No, which have a thin proximal end. *Anceyoconcha elongata*, new species, has a similar elongate conic shell to that identified in *A. chaudoensis* (Rochebrune, 1882) from Southern Cambodia (see Sutcharit et al., 2020: fig. 12E, F). However, the shell of *A. elongata*, new species, is bigger than that of *A. chaudoensis*, with shell height of the new species ranging from 21.6 to 28.1 mm, whereas shell height in *A. chaudoensis* ranges approximately from 16.1 to 21.4 mm. The peristome at the columella side is straight on both inner and outer sides in *A. elongata*, new species, but concave on the outer side in *A. chaudoensis.* These similarities in shell shape need further clarification, and should be supported by comparisons of genital anatomy, radula morphology, and phylogeny based on mitochondrial and nuclear DNA and genetic distances.

There exists one lot of five specimens in the Muséum national d'Histoire naturelle (MNHN) that has been attributed to the species and may possibly have been part of material provided by Harmand to Rochebrune (1882). However, these may not have been the specimens on which Rochebrune based his description, because of 1) the lack of information on the original label (compared to other species described in the same paper, which had detailed labels providing solid evidence that they are types), and 2) discrepancies between the measurement of the largest shell in the MNHN lot (21 mm) and that in the original description (24 mm in Rochebrune, 1882) (Virginie Héros, pers. comm., 2021). As the types cannot be traced, we consider *Anceyoconcha chaudoensis* a nomen inquirendum.

Distribution. *Anceyoconcha elongata*, new species, is currently known from Phu Po and Phu No in Kalasin Province, and Phanom Sawai Forest Park and Khao Sala in Surin Province.

***Anceyoconcha* sp.1**

Figs. 3F, 6; Tables 1–3

Anceyoconcha sp.2 – Nahok, 2020: 74–75, figs. 25E, 40, 46–47, 50, 53, tables 3, 5, 7–10. Pha Nam Yoi, Roi Et.

Material examined. 1 shell (NHMSU-00043) (Fig. 3F), Pha Nam Yoi, Nong Phok District, Roi Et Province, Thailand (16°19′39.38″N, 104°19′1.69″E), alt. 278 m, 3 September 2017, SH = 19.1 mm, SW = 9.2 mm, AH = 5.2 mm, AW = 5.7 mm; 1 living specimen preserved in ethanol (NHMSU-00044), same locality as previous lot.

Diagnosis. Shell ovate conic and stout. Flagellum shorter than epiphallus. Flagellum ⅓ of penis length.

Description (empty shell = 1, living specimen = 1). Shell (Fig. 3F; Table 3): broadly rounded and stout, whorls 7¾, shell height 19.1 mm, shell width 9.2 mm, aperture height 5.2 mm, and aperture width 5.7 mm. Pale grey to light yellow, transparent, and shining. Apex obtuse. Aperture half-moon-shaped.

Genital system (n = 1) (Fig. 6A, B): atrium short. Penis long cylindrical shape with proximal bend. Penial retractor muscle short. Epiphallus longer than penis. Flagellum length is half of penis length, and hook-shaped at distal end. Vas deferens long. Vagina is longer than penis. Gametolytic duct thickened and swollen at base, and gradually slender to small tube distally. Gametolytic sac is small swollen gland at distal end of gametolytic duct. Free oviduct very short. Uterus and prostate gland long and stout. Inner penial wall with oblique lamellae (Fig. 6C). Proximal part of epiphallus (ep1) inner wall with five corrugated longitudinal pilasters (Fig. 6C). Distal part of epiphallus (ep2) inner wall with rather smooth surface (Fig. 6D). Inner wall of flagellum with smooth and robust longitudinal pilasters (Fig. 6E). Inner vaginal wall with six slightly undulating longitudinal pilasters (Fig. 6F).

Radula (n = 1) (Fig. 6G–I): comprises 100 transverse rows of teeth, each row containing 51–59 teeth, (19–21) + (6–8) + 1 + (6–8) + (19–21). Central teeth symmetric unicuspid, broadly rounded. Lateral teeth similar to central tooth, but are oblique and cusps are wider and longer. Teeth on both sides begin to transform into indistinct bicuspid marginal teeth with tiny ectocone at numbers 7–9. Marginal teeth gradually change to broad tricuspid, starting at numbers 10–18, and begin to transform to tetracuspid with two small cusp ectocones from numbers 19–27 to edge of radula plate.

Remarks. *Anceyoconcha* sp.1 differs from all *Anceyoconcha* species by its ovate conic and stout shell. Although the shell of *Anceyoconcha* sp.1 looks similar to that of "*Pseudobuliminus*" *ovoideus* Thach & Huber, in Thach, 2018, the former possesses inflated whorls, rather deep suture, a calloused inner lip, and inclined columella side, whereas the latter possesses flat whorls, simple suture, calloused inner lip, and straight columella side. Moreover, "*Pseudobuliminus*" *ovoideus* was described from the area between Dalat and Phan Rang, Southern Vietnam, approximately 700 km away from the locality of *Anceyoconcha* sp.1, which is found in the center of northeastern Thailand. We propose that both taxa are different species. The genitalia of *Anceyoconcha* sp.1 resemble that of *A. elongata*, new species from Phu Po, with its long, cylindrical penis with a proximal twist at its base, and a gametolytic duct that is thickened and curved at its base (Figs. 5, 6). According to the Bayesian inference tree based on the concatenated genes of COI, 16S rRNA, and 28S rRNA, *Anceyoconcha* sp.1 is clearly separated from *A. carinata* with very strong support (1.00 for BI posterior probability, and 100% and 97% bootstrap support for NJ and ML, respectively), and belongs to a different clade from *A. elongata*, new species (Fig. 2). However, the number of

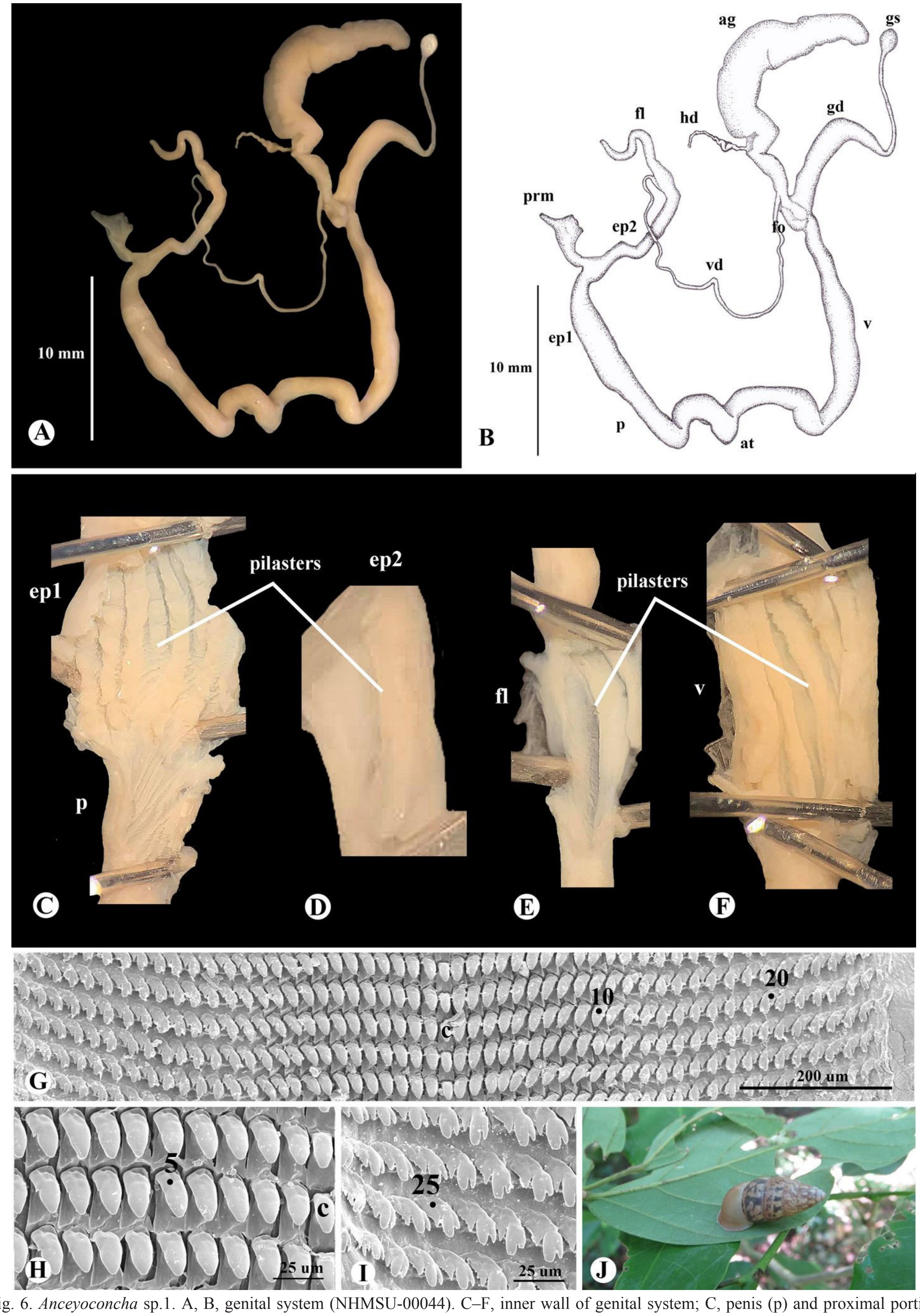

Fig. 6. *Anceyoconcha* sp.1. A, B, genital system (NHMSU-00044). C–F, inner wall of genital system; C, penis (p) and proximal portion of epiphallus (ep1); D, distal portion of epiphallus (ep2); E, flagellum (fl); F, vagina (v). G, view of transverse rows of radula, with number of lateral and marginal teeth indicated (c = central tooth); H, left side of central tooth and lateral teeth; I, left side of marginal teeth. J, natural habitat and living adult.

examined specimens of this species is only one living snail and one empty, incomplete shell, which is insufficient for an assessment of intraspecific variation or to distinguish different species. Therefore, '*Anceyoconcha* sp.1' is used for *Anceyoconcha* from this locality for the time being, until more complete specimens can be found and studied.

Distribution. *Anceyoconcha* sp.1 is currently known from Pha Nam Yoi, Nong Phok District, Roi Et Province.

DISCUSSION

The two new species of *Anceyoconcha* are similar to the type species in terms of external shell morphology, radula, and genital system (Schileyko, 2003; Nahok et al., 2020). However, each new species differs from the previously described species in shell shape, shell ornamentation, flagellum shape, and length of penis, vagina, and free oviduct. *Anceyoconcha carinata*, new species, can be distinguished from other species by the presence of a periumbilical keel, a penis and vagina that are shorter than the flagellum, and a flagellum divided into two parts, comprising a twisted proximal part and S-shaped distal end (Fig. 4A, B). *Anceyoconcha elongata*, new species, has an elongate conic shell, and a long, slender flagellum equal to or longer than the epiphallus (Fig. 5A, B).

The phylogenetic analysis in this study revealed that the formerly confused tree snail genera *Pseudobuliminus* and *Anceyoconcha* are clearly separated in different clades with very strong support (1.00 for BI posterior probability, and 100% bootstrap support for both NJ and ML; Fig. 2). It supports the hypothesis of Nahok et al. (2020), which proposed that *Pseudobuliminus* is non-existent in Thailand, distributed only in mainland China, Taiwan, and Japan (Chang & Hwang, 1999; Schileyko, 2004; Hirano et al., 2014). *Ganesella capitium* is also separated from the *Anceyoconcha* clade with strong support (1.00 for BI posterior probability, and 97% and 89% bootstrap support for NJ and ML, respectively). Moreover, the COI and 28S rRNA sequences of *Ganesella* sp. (Table 1), which was proposed by Budha et al. (2016) as *Ganesella rhombostomus*, form a sister group to *Anceyoconcha rhombostoma* with strong support (1.00 for BI posterior probability, and 99% and 95% bootstrap support for NJ and ML, respectively). With this analysis, we conclude that "*Ganesella rhombostomus*" in Budha et al. (2016) is *Anceyoconcha rhombostoma* (Fig. 2).

Our investigation of the external shell morphology, radula, and genital system, as well as mitochondrial and nuclear DNA sequences of *Anceyoconcha* specimens from northeastern Thailand, has presented two new species. Sutcharit et al. (2020) reviewed and summarised the new combination of *Anceyoconcha*, which comprises 15 nominal taxa. Reproductive anatomy and radula morphology have been studied only in Thai taxa, specifically, *A. siamensis siamensis* and *A. rhombostoma rhombostoma* by Nahok et al. (2020), and the two species described in this paper. There are 13 nominal taxa left that need to be clarified.

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