

Morphology, radula, and shell microstructure of *Cerithidea tonkiniana* Mabille, 1887 (Gastropoda: Potamididae) from Vietnam, with notes on distribution and taxonomic status

Tai Tu NGUYEN^{1*}, Tan Dung PHAM¹, Thi Thuy Duong HOANG¹, Hoang Nam DAO², Duc Sang DO³

¹Joint Vietnam-Russia Tropical Science and Technology Research Center, 63 Nguyen Van Huyen St., Nghia Do, Hanoi, VIETNAM;

²Vietnam Forest Museum, Vietnamese Academy of Forest Sciences, Ngoc Hoi St., Dai Thanh, Hanoi, VIETNAM;

³Department of Applied Zoology, Faculty of Biology, VNU University of Science (Vietnam National University, Hanoi), 334 Nguyen Trai, Thanh Xuan, Hanoi, VIETNAM

*Corresponding author, E-mail: taitu1990@gmail.com, <https://orcid.org/0000-0002-0374-3518>

ABSTRACT. Additional morphological data on *Cerithidea tonkiniana* Mabille, 1887, from Vietnam are presented based on extensive material collected across its currently known national range, including the Gulf of Tonkin and the central coast. This study provides the first SEM documentation of shell microstructure and radula for Vietnamese populations, and additionally presents a detailed description of the operculum of *Cerithidea tonkiniana*. Shell morphology exhibits moderate variation in size but stable proportions among populations, indicating marked morphological cohesion across a broad latitudinal gradient. The outer shell surface displays a compact commarginal microstructure with distinct growth increments consistent among examined localities. The radula conforms to the typical potamidid pattern and closely resembles that of *C. sinensis*, supporting their close affinity while retaining diagnostic differences. Updated distributional data refine northern locality records and confirm the species' extension southward to Da Nang along the north-central coast. These results provide a detailed morphological reference framework for *C. tonkiniana* and facilitate more reliable identification of potamidid gastropods in mangrove ecosystems of the western Pacific region.

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Морфология, радула и микроструктура раковины *Cerithidea tonkiniana* Mabille, 1887 (Gastropoda: Potamididae) из Вьетнама с замечаниями по распространению и таксономическому статусу

Тай Ту НГУЕН^{1*}, Там Зунг ФАМ¹, Тхи Тхюи Зыонг ХОАНГ¹, Хоанг Нам ДАО², Дук Санг ДО³

¹Joint Vietnam-Russia Tropical Science and Technology Research Center, 63 Nguyen Van Huyen St., Nghia Do, Hanoi, VIETNAM;

²Vietnam Forest Museum, Forest Inventory and Planning Institute, Ngoc Hoi St., Dai Thanh, Hanoi, VIETNAM;

³Department of Applied Zoology, Faculty of Biology, VNU University of Science (Vietnam National University, Hanoi), 334 Nguyen Trai, Thanh Xuan, Hanoi, VIETNAM

*Автор-корреспондент, E-mail: taitu1990@gmail.com, <https://orcid.org/0000-0002-0374-3518>

РЕЗЮМЕ. Представлены дополнительные морфологические данные о *Cerithidea tonkiniana* Mabille, 1887, из Вьетнама, основанные на обширном материале, собранном по всему вьетнамскому ареалу,

включая Тонкинский залив и центральное побережье. Впервые приведены SEM микроструктуры периостракума раковины и радулы для вьетнамских популяций, а также дано детальное описание крышечки *Cerithidea tonkiniana*. Морфология раковины демонстрирует умеренную изменчивость размеров, но стабильные пропорции между популяциями, что указывает на заметное морфологическое единство в широком широтном диапазоне. Периостракум имеет компактную коммаргинальную микроструктуру с отчетливыми линиями роста, сходную для всех исследованных местонахождений. Радула соответствует типичному для потамидид строению и близка к таковой у *C. sinensis*, что подтверждает их тесное родство при сохранении диагностических различий. Данные о распространении уточняют северные находения и подтверждают распространение вида к югу до Дананга вдоль северо-центрального побережья. Эти результаты являются детальной морфологической референсной базой для *C. tonkiniana* и способствуют более надежной идентификации потамидидных гастропод в мангровых экосистемах западно-тихоокеанского региона.

Introduction

The genus *Cerithidea* Swainson, 1840 (Gastropoda: Potamididae) comprises amphibious gastropods characteristic of mangrove forests, tidal swamps, and salt marshes throughout the Indo-West Pacific region. Pronounced shell variability and morphological convergence have long obscured species boundaries within the genus [Brandt, 1974; Kobelt, 1890–1898; Wilson, 1993; Reid *et al.*, 2008, 2013]. These taxonomic difficulties were substantially addressed in the revisionary monograph by Reid [2014], which clarified species limits, synonymy, and distribution patterns based on shell morphology and molecular evidence. Nevertheless, fine-scale morphological data and population-level assessments remain limited for several species within the genus. At present, 15 extant species of *Cerithidea* are recognized worldwide, in addition to numerous fossil taxa [Reid, 2014; MolluscaBase, 2026].

Cerithidea tonkiniana Mabilie, 1887, originally described from northern Vietnam, represents a typical mangrove-associated species occurring on trunks and branches of mangrove trees as well as on mud and stones beneath the vegetation, mainly in the upper intertidal zone [Mabilie, 1887]. Owing to its brief and unillustrated original description, the species was consistently misidentified throughout much of the twentieth century, most commonly as *Cerithidea ornata* or *C. balteata* [Habe, Kosuge, 1967; Choe, 1992; Fukuda, 1996; Kojima *et al.*, 2006; Hong *et al.*, 2010], until its taxonomic identity was clarified by Reid *et al.* [2013] and subsequently treated in detail by Reid [2014].

Despite the clarification of its taxonomic status and shell morphology, the species remains insufficiently characterized at a finer morphological level. Data on shell microstructure, radula morphology, and patterns of morphological variation within Vietnamese populations remain undocumented [Fischer, 1891; Fischer, Dautzenberg, 1904].

The present study supplements Reid's [2014] treatment of *Cerithidea tonkiniana* by examining extensive material from Vietnam and providing new information on shell microstructure and radula morphology, based on scanning electron microscopy, along with an assessment of morphological variation, updated distributional records, and ecological observations.

Material and methods

Specimens of *Cerithidea tonkiniana* were examined from multiple localities in Vietnam, covering a substantial part of the known range of the species within the country (Fig. 1). Material was collected in mangrove forests and adjacent brackish habitats. Individuals were found on mangrove trunks, bran-

ches, leaves, and aerial roots, as well as on mudflats, sediment surfaces, stones, boulders, dead wood, and in small tidal creeks, including artificial mangrove plantations in the lower intertidal zone. In addition, radula images of *C. sinensis* from mangrove ecosystems in northern Vietnam were included to facilitate morphological comparison with *C. tonkiniana*. All material is deposited in the Zoological Collection of the Biological Museum, VNU University of Science (Vietnam National University, Hanoi), Vietnam; the Joint Vietnam-Russia Tropical Science and Technology Research Center (VRTC); and the Vietnam Forest Museum, Forest Inventory and Planning Institute, Hanoi, Vietnam (VFM).

Shell measurements included shell height (SH), shell width (SW), aperture height (AH), and aperture width (AW), taken using a digital caliper with an accuracy of 0.01 mm. The ratios H/W and H/AH were calculated to assess overall shell shape. The number of whorls was counted to the nearest quarter whorl following Kerney and Cameron [1979]. Shells were photographed using a Canon 6D Mark II camera equipped with a Canon EF 100 mm f/2.8L IS USM Macro lens; images were processed using Adobe Photoshop software. Terminology for shell and soft-body morphology follows Houbriek [1984, 1986] and Reid [2014]. For shell surface microstructure analysis, selected specimens were examined and photographed at designated areas using a scanning electron microscope (SEM; JEOL JSM-IT200) at the Joint Vietnam–Russia Tropical Science and Technology Research Centre (Hanoi, Vietnam).

Live specimens were fixed and preserved in 75% ethanol buffered with sodium carbonate. Radulae were dissected from the buccal mass and treated with 10% NaOH to remove soft tissues. Following digestion, the radulae were rinsed several times in distilled water and gently heated in distilled water for approximately 10 minutes to ensure complete removal of residual NaOH and debris. The samples were then dehydrated through a graded ethanol series (70% and 96%), each step lasting 10–15 minutes. Dehydrated radulae were mounted on carbon conductive adhesive tape attached to aluminum SEM stubs and dried in a Memmert UN55 drying oven at 30°C under controlled low humidity (10%) for 48 hours. Dried samples were sputter-coated with platinum using a JEC-3000FC ion sputter coater (JEOL, Japan) and subsequently examined and photographed with a JEOL JSM-IT200 scanning electron microscope.

Taxonomy

Class Gastropoda Cuvier, 1795
Subclass Caenogastropoda Cox, 1960
Superfamily Cerithioidea Fleming, 1822
Family Potamididae
H. Adams et A. Adams, 1854

Genus *Cerithidea* Swainson, 1840

Cerithidea Swainson, 1840: 198, 203, 342.

Phaenommmia Mörch, 1860: 80 (type species: *Cerithium charbonnieri* Petit de la Saussaye, 1851, M).

Aphanistylus P. Fischer, 1884: 682 (type species: *Aphanistylus moreleti* Wattebled, 1886)

Cerithidea – Reid *et al.*, 2008: 680–699; Reid *et al.*, 2013: 564–576; Reid, 2014: 9.

Type species. *Melania lineolata* Gray in Griffith et Pidgeon, 1833 = *Cerithidea obtusa* (Lamarck, 1822) (type by subsequent designation Makiyama 1936)

Remarks. *Cerithidea* Swainson, 1840 represents a well-defined lineage within Potamididae, extensively treated by Houbriek [1986] and further revised by Reid [2014]. Shell elongate and turreted, light to moderately solid, with variably developed axial and spiral sculpture. Growth determinate, expressed by reduction of axial ribs on the final whorl, formation of a strong ventrolateral varix, and development of a thickened, flared adult aperture. A characteristic feature is spire decollation, resulting from progressive dissolution of early whorls and subsequent sealing of the apical opening by internal shell deposits, representing a derived condition within Potamididae. Anatomy includes a reduced ctenidium and osphradium, a vascularized mantle cavity, and a pallial siphonal eye on the mantle margin [Houbriek, 1986]. Radula conforms to a conserved generic pattern with minor interspecific variation in cusp configuration. A combination of shell and anatomical characters distinguishes *Cerithidea* from related genera such as *Cerithideopsis* and *Pirenella* [Reid *et al.*, 2008; Reid, 2014].

Cerithidea tonkiniana Mabile, 1887
(Figs 1–6)

Cerithidea tonkiniana Mabile, 1887: 158–159; Reid *et al.*, 2013: 564–580, figs 1, 2; Reid, 2014: 47–49, figs 2F, 13N–Y, 14A.

Potamides (*Cerithidea* ?) *tonkinianus* – Fischer, 1891: 79.

Potamides (*Cerithidea*) *tonkinianus* – Fischer, Dautzenberg, 1904: 416.

Cerithidea (*Cerithidea*) *sinensis* var. *tonkiniana* – Dautzenberg, Fischer, 1905: 137–138.

Cerithidea ornata – Habe, Kosuge, 1967: 34, pl. 13, fig. 17; Choe, 1992: 310–311, pl. 65, fig. 103a, b; Kojima *et al.*, 2006: 525–535; Reid *et al.*, 2008: 680–699.

Cerithidea (*Cerithidea*) *ornata* – Fukuda, 1996: 21, pl. 3, fig. 4; 2000: 106–110, 135, fig. 5.4b, fig. 5.5b; Hong *et al.*, 2010: 258, fig. 4b.

Cerithidea morchii – Min *et al.*, 2004: 129, fig. 220.

Cerithidea (*Cerithidea*) *weyersi* – Thach, 2007: 60, pl. 9, figs 173, 181.

Type locality. Tonkin, Vietnam (Northern Vietnam); no precise locality stated in the original description.

Type material examined. Syntypes MNHN 25690, Tonkin, Vietnam.

Other material examined. NHMUK 20130260, Hai Phong, Vietnam. ZVNU.MOL, 11 specimens, Vietnam, Quang Ninh Province, Van Don Special Administrative Zone, Dai Xuyen mangrove forest (21°10'54.5"N, 107°27'40.0"E), coll. T.T. Nguyen & H.N. Dao, 25 June 2024; VRTC.MOL, 23 specimens, Vietnam, Quang Ninh Province, Van Don Special Administrative Zone, Quan Lan Island, upper intertidal mangrove fringe (20°54'54.3"N, 107°31'49.9"E), coll. T.T. Nguyen & H.N. Dao, 19 June 2024; ZVNU.MOL, 30 specimens, Vietnam, Quang Ninh Province, Co To Special Administrative Zone, Truong Xuan mangrove forest (20°59'46.7"N, 107°46'19.9"E), coll. T.T. Nguyen & D.S. Do, 14 February 2025; VFM.MOL, 09 specimens, Vietnam, Quang Ninh Province, Hai Lang, Dong Rui mangrove forest (21°14'43.2"N, 107°23'5.2"E), coll. T.T. Nguyen & H.N. Dao, 14 April 2024; VRTC.MOL, 03 specimens, Vietnam, Quang Ninh Province, Van Don Special Administrative Zone, Cai Lim mangrove forest (21°06'18.6"N 107°34'18.7"E), coll. T.T. Nguyen & T.D. Pham, 10 August 2024; VRTC.MOL, 5 specimens, Vietnam, Quang Ninh Province, Mong Cai 3, Hai Yen mangrove forest (21°30'28.2"N 107°55'22.1"E), coll. T.T. Nguyen & T.D. Pham, 10 February 2025; VRTC.MOL, 07 specimens, Vietnam, Hai Phong City, Cat Ba National Park, Phu Long mangrove forest (20°49'8.9"N, 106°54'56.5"E), coll. T.T. Nguyen & H.N. Dao, 5 July 2025; VRTC.MOL, 11 specimens, Vietnam, Hai Phong City, Nam Do Son, Bang La mangrove forest (20°42'51.3"N, 106°45'55.5"E), coll. T.T. Nguyen & T.D. Pham, 7 February 2025; VRTC.MOL, 22 specimens, Vietnam, Ninh Binh Province, Xuan Thuy National Park, mangrove forest (20°14'53.5"N, 106°34'40.3"E), coll. T.T. Nguyen & H.N. Dao, 29 January 2026; VRTC.MOL, 30 specimens, Vietnam, Ninh Binh Province, Kim Dong, Binh Minh mangrove forest (19°55'01.3"N 106°04'24.2"E), coll. T.T. Nguyen & T.D. Pham, 5 March 2025; VRTC.MOL, 22 specimens, Vietnam, Hung Yen Province, Nam Cuong, Nam Tinh mangrove forest (20°20'44.7"N, 106°34'42.4"E), coll. T.T. Nguyen & H.N. Dao, 31 January 2026; VRTC.MOL, 30 specimens, Vietnam, Thanh Hoa Province, Nghi Son, Hai Binh mangrove forest (19°23'43.6"N, 105°46'03.4"E), coll. T.T. Nguyen, 16 August 2024 (Fig. 1C); ZVNU.MOL, 06 specimens, Vietnam, Nghe An Province, Hai Chau Commune, mangrove forest (18°59'40.26"N 105°36'32.29"E), coll. D.S. Do, 25 November 2025 (Fig. 1A); ZVNU.MOL, 16 specimens, Vietnam, Ha Tinh Province, Tran Phu, mangrove forest (18°24'24.48"N 105°54'16.63"E), coll. D.S. Do, 24 November 2025 (Fig. 1B); VRTC.MOL, 13 specimens, Vietnam, Da Nang City, Hoi An Dong Ward, Bay Mau nipa palm forest (15°52'27.3"N, 108°22'17.8"E), coll. T.T. Nguyen, 28 August 2024.

Description. Shell medium-sized (H 21.6–43.0 mm), thin to moderately solid, elongate-conical, usually decollate, with 5–8 remaining whorls. Spire profile mostly straight; periphery rounded to slightly angled. Axial sculpture prominent, with 11–25 rounded ribs on penultimate whorl; 4–11 ribs persisting beyond ventrolateral varix. Ventrolateral varix is strong, positioned at 180–220°. Spiral sculpture is weak, visible as faint ridges on preserved spire whorls. Base with 9–13 spiral lirae. Aperture flared and slightly thickened in adult; apertural margin slightly sinuous in lateral view; short anterior canal present. Colour pale brown with darker spiral bands and lines; a pale band is usually present at the shoulder and below the periphery.

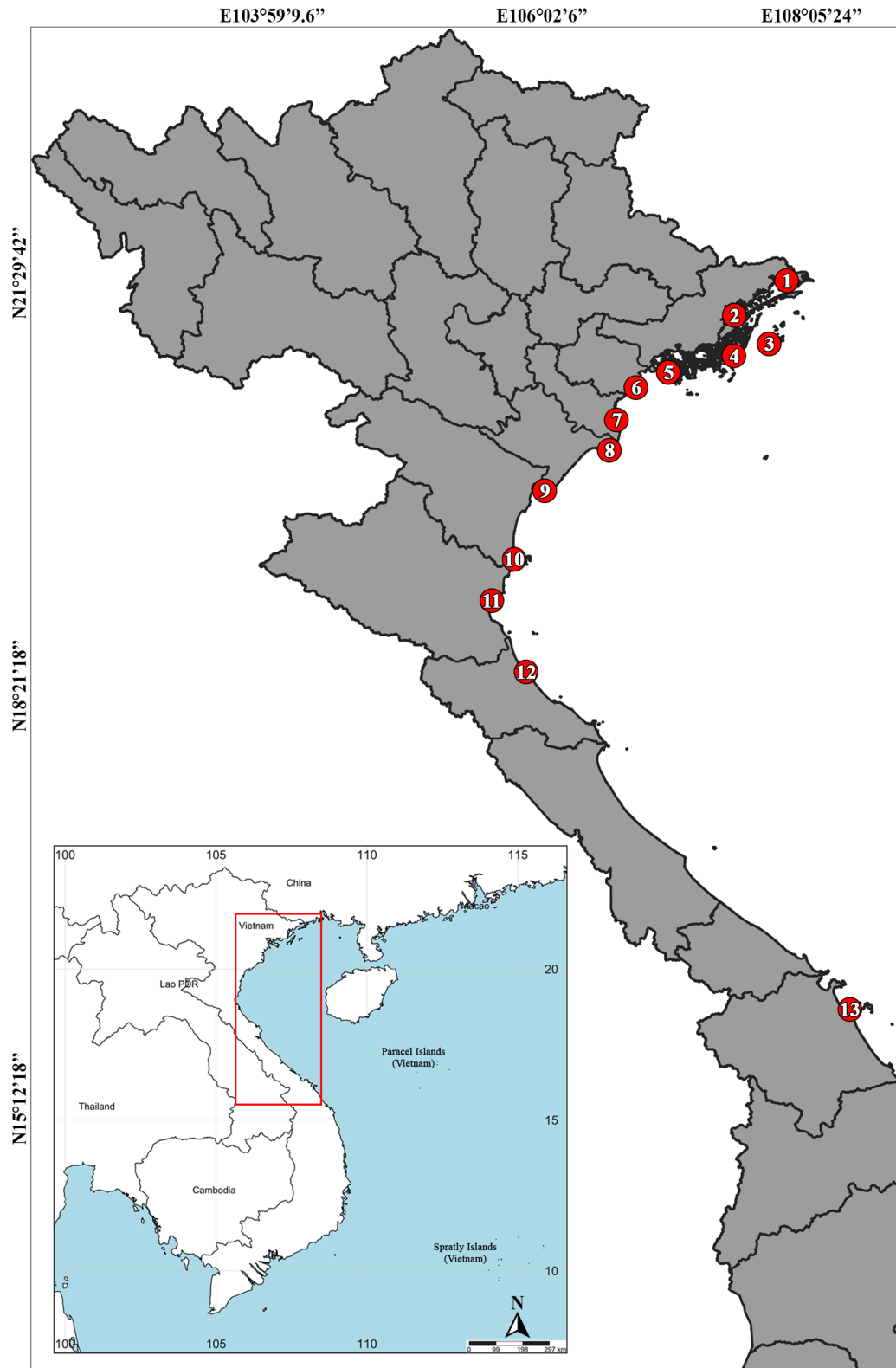


FIG. 1. Distribution of *Cerithidea tonkiniana* in Vietnam 1: Mong Cai Ward 3, 2: Hai Lang Commune, 3: Co To Special Zone, 4: Van Don Special Zone (Quang Ninh Province); 5: Cat Ba National Park, 6: Nam Do Son Ward (Hai Phong City); 7: Nam Cuong Commune (Hung Yen Province); 8: Xuan Thuy National Park, 9: Kim Dong Commune (Ninh Binh Province); 10: Nghi Son Ward (Thanh Hoa Province); 11: Hai Chau Commune (Nghe An Province); 12: Tran Phu Ward (Ha Tinh Province); 13: Hoi An Dong Ward (Da Nang City).

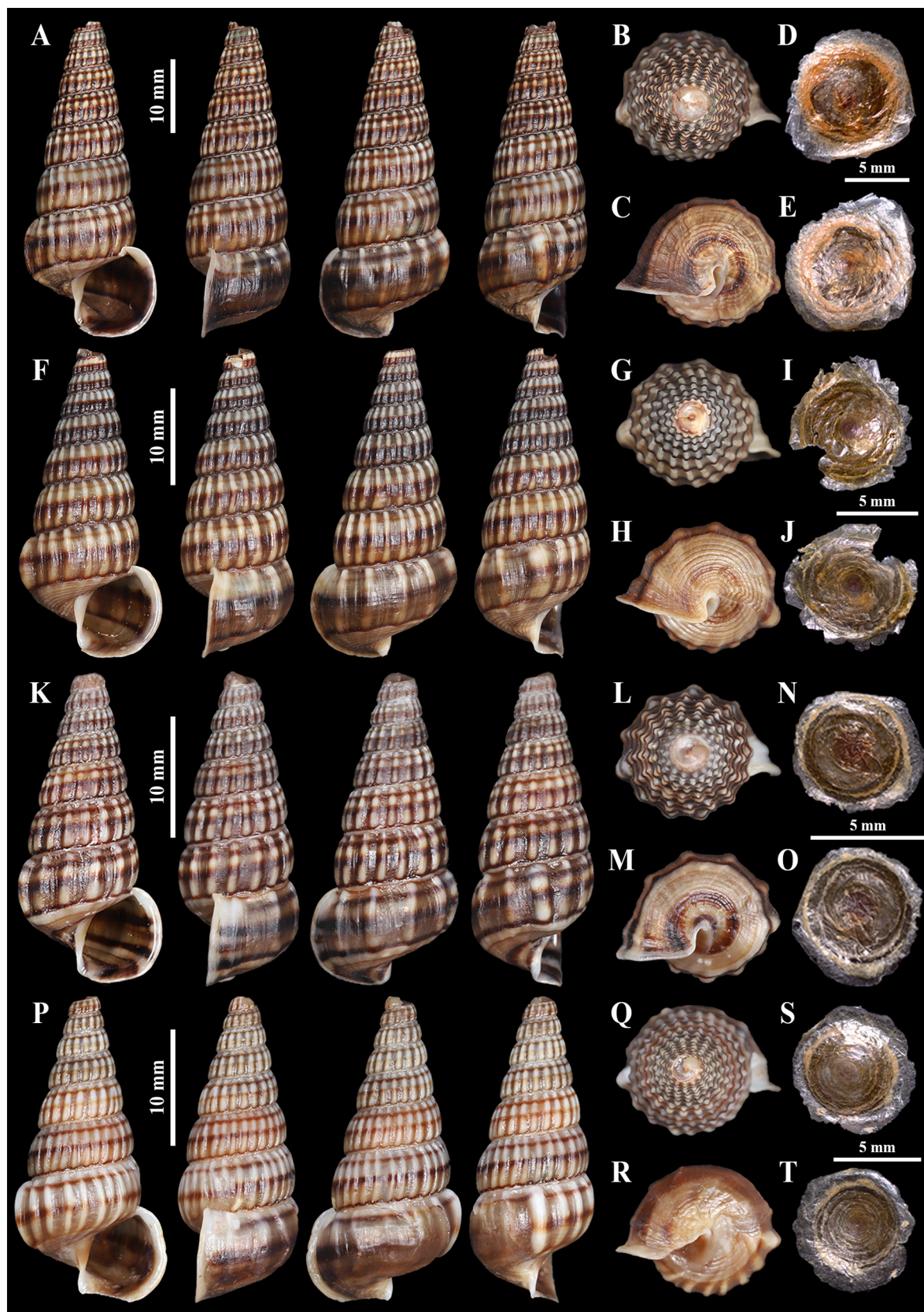


FIG. 2. Shells and operculae of *Cerithidea tonkiniana* Mabilie, 1887 from Vietnam. A-E: VRTC, Van Don, Quang Ninh; F-J: VRTC, Hai Binh, Thanh Hoa; K-O: ZVNU, Hai Chau, Nghe An; P-T: ZVNU, Tran Phu, Ha Tinh. For each specimen: apertural, dorsal and lateral views (A, F, K, P); apical view (B, G, L, Q); basal view (C, H, M, R); operculum, inner view (D, I, N, S); operculum, outer view (E, J, O, T).

Table 1. Shell measurements and number of whorls of *Cerithidea tonkiniana* from Vietnam (number of adult specimens in parentheses).

Localities and number of specimens	Ranges, mean \pm S.D. in mm of:			H/W ratio	H/AH ratio	Number of whorls
	Shell height (H)	Shell width (W)	Aperture height (AH)			
Dai Xuyen, Van Don, Quang Ninh (n = 11)	28.0–39.8 33.7 \pm 3.82	12.0–16.9 14.8 \pm 1.53	8.3–11.6 10.3 \pm 1.14	2.01–2.46 2.18 \pm 0.16	2.88–3.56 3.19 \pm 0.20	6–7
Quan Lan, Van Don, Quang Ninh (n = 23)	22.7–39.0 28.6 \pm 4.42	10.0–18.0 12.8 \pm 2.06	7.0–12.3 8.6 \pm 1.49	2.00–2.50 2.19 \pm 0.12	2.93–3.79 3.31 \pm 0.21	5–7
Co To, Van Don, Quang Ninh (n = 30)	25.1–39.7 31.4 \pm 3.90	11.0–16.1 13.5 \pm 1.42	7.0–11.0 8.9 \pm 0.96	2.05–2.79 2.29 \pm 0.16	3.08–3.90 3.52 \pm 0.21	6–8
Dong Rui, Hai Lang, Quang Ninh (n = 9)	29.4–39.0 33.0 \pm 3.54	13.1–17.0 15.1 \pm 1.65	9.0–12.0 10.4 \pm 1.26	2.12–2.29 2.20 \pm 0.06	2.96–3.33 3.20 \pm 0.12	6–7
Cai Lim, Van Don, Quang Ninh (n = 3)	31.2–38.4 34.2 \pm 3.75	15.0–19.0 16.6 \pm 2.14	10.0–12.0 11.0 \pm 1.0	2.02–2.10 2.07 \pm 0.04	3.00–3.20 3.11 \pm 0.10	6
Hai Yen, Móng Cái 3, Quang Ninh (n = 5)	25.0–37.8 29.0 \pm 5.48	10.8–15.9 12.7 \pm 2.53	6.9–10.6 8.2 \pm 1.74	2.11–2.39 2.28 \pm 0.11	3.29–3.68 3.55 \pm 0.15	6–7
Cat Ba NP, Hai Phong (n = 7)	30.4–43.0 35.5 \pm 4.53	15.5–19.0 16.7 \pm 1.25	10.0–12.7 11.5 \pm 1.05	1.96–2.47 2.09 \pm 0.17	2.84–3.58 3.12 \pm 0.27	5–7½
Xuan Thuy NP, Ninh Binh (n = 22)	21.6–40.1 29.3 \pm 5.07	9.8–17.9 13.5 \pm 2.42	6.3–12.6 8.9 \pm 1.67	1.79–2.67 2.15 \pm 0.19	2.85–4.16 3.26 \pm 0.31	6–8
Binh Minh, Ninh Binh (n = 30)	24.0–37.0 29.3 \pm 3.43	9.5–16.0 13.1 \pm 1.54	6.5–11.0 8.4 \pm 1.09	1.93–2.69 2.26 \pm 0.18	2.91–3.70 3.34 \pm 0.19	6–7
Hai Binh, Thanh Hoa (n = 30)	24.2–35.3 29.22 \pm 3.16	10.2–17.1 13.31 \pm 1.59	7.3–11.8 9.05 \pm 0.98	1.86–2.43 2.21 \pm 0.14	2.79–3.55 3.25 \pm 0.18	6–7½
Hai Chau, Nghe An (n = 6)	23.8–34.1 28.17 \pm 3.02	10.0–16.8 12.56 \pm 1.42	7.4–10.9 9.26 \pm 0.91	1.88–2.38 2.24 \pm 0.13	2.80–3.52 3.22 \pm 0.17	6–7½

Operculum. Very thin, corneous, discoid, almost flat; yellowish brown to dark brown, peripheral margin extremely thin and nearly transparent. Central area, slightly depressed. Outer surface bearing distinct concentric growth lines (Figs 2E, J, O, T). The inner surface is smooth and glossy (Figs 2D, I, N, S).

Measurements. Shell measurements of *Cerithidea tonkiniana* from eleven localities in northern Vietnam are summarized in Table 1. A total of 176 adult specimens were examined, covering coastal areas from Quang Ninh and Hai Phong southward to Ninh Binh and Thanh Hoa (Fig. 2). Shell height ranged from 21.6 to 43.0 mm. Mean shell height varied moderately among populations, with the largest averages recorded in Cat Ba and the smallest in Xuan Thuy and several Red River delta localities; however, the size ranges overlapped broadly across all samples. Shell width (9.5–19.0 mm) and aperture height (6.3–12.7 mm) increased proportionally with shell height.

Shell proportions remained comparatively stable across the examined range. Mean H/W ratios ranged from 2.09 to 2.29, indicating a consistently elongate-conical shell form, whereas H/AH ratios showed slightly greater dispersion (approximately 3.11–3.55) but remained within a narrow interval across the sampled range. The number of whorls ranged from 5 to 8, most frequently 6–7, without a detectable geographic pattern. Overall, the examined

material reveals moderate variation in shell size but limited variation in shell proportions throughout the studied range.

Periostracum microstructure. The shell surface examined under SEM shows well-developed spiral cords separated by broad interspaces. At low magnification ($\times 15$ – $\times 45$), the peripheral region of the last whorl exhibits regularly arranged cords with smooth to slightly uneven surfaces.

At higher magnifications ($\times 60$ – $\times 250$), the surface of the spiral cords displays fine longitudinal microsculpture. This microsculpture appears as closely spaced, parallel elements oriented along the direction of shell growth. No nodules, granules, or reticulate patterns are observed. Interspaces between cords lack distinct secondary sculpture at the examined magnifications (Fig. 3).

The observed features represent external shell microsculpture only.

Animal. Head brownish grey, densely mottled with cream, oval to rounded spots of nearly uniform size; surface finely granulose. Anterior half of snout distinctly darker, sharply demarcated from posterior half; tip bearing three yellow spots, two larger and one smaller, the latter slightly displaced laterally. Tentacles grey, with a distinct dark subterminal ring and blackened tip. Lateral surfaces of the foot are dark grey to blackish; the sole is grey. Mantle pale grey (Figs 4C, D, F).

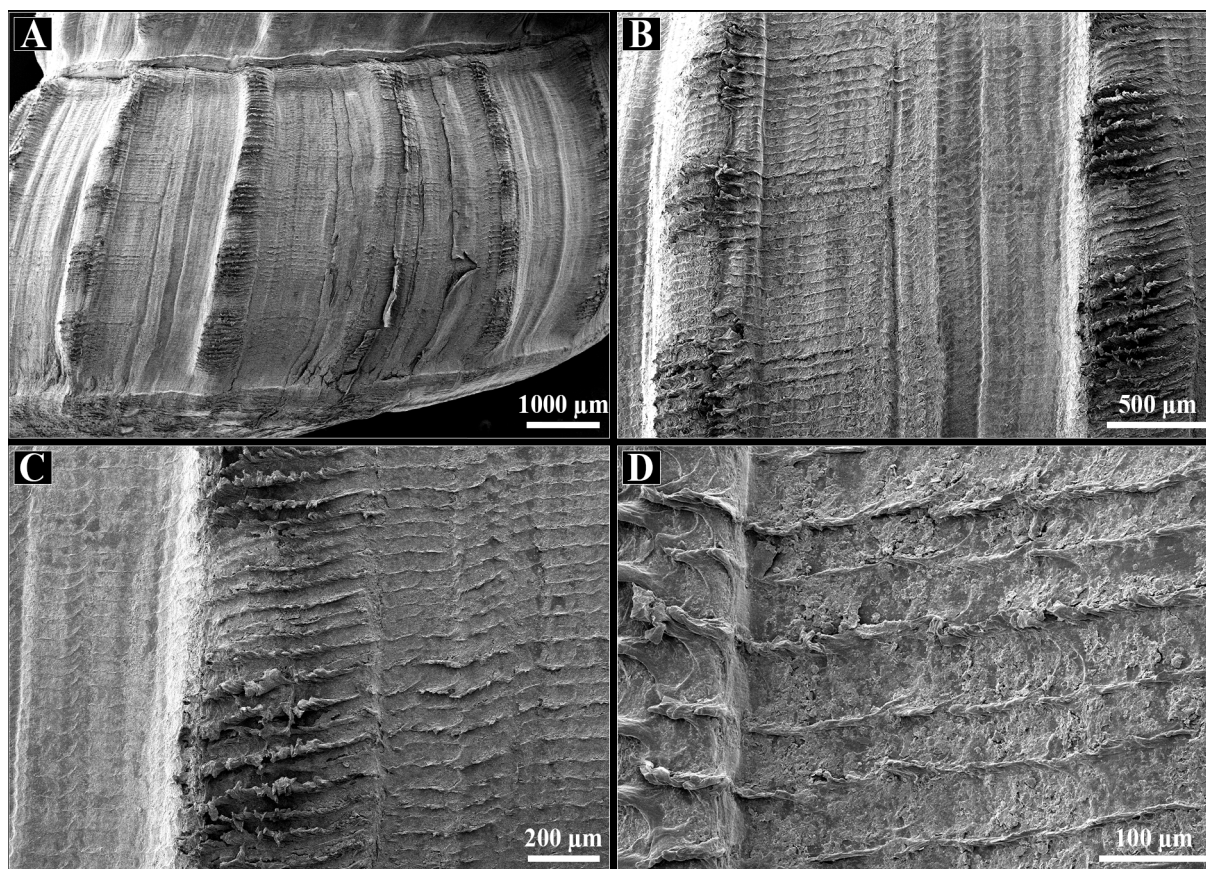


FIG. 3. Scanning electron micrographs of shell periostracum microsculpture of *Cerithidea tonkiniana* from Xuan Thuy National Park, Ninh Binh, Vietnam (VRTC); peripheral region of the last whorl. **A.** Prominent spiral cords separated by wide interspaces (SEM, $\times 15$). **B.** Same area at $\times 45$. **C.** Same area at $\times 60$. **D.** Same area at $\times 250$.

Radula. Taenioglossate, approximately one-seventh of shell length. Rachidian tooth narrow, elongate, tapering, and bilaterally symmetrical; distal end slightly pointed and curved; cutting edge bearing one large central cusp and two blunt cusps on each side, outer cusp minute and sometimes indistinct. Lateral tooth with broad basal plate and broad, oblique cutting edge; grooves deep and conspicuous; cutting edge bearing one long, blunt inner cusp and three smaller outer cusps decreasing in size from inner to outer. Inner marginal tooth broad and very large, elongate, with tapering distal end; cutting edge bearing 1–3 small inner cusps or lacking distinct cusps. Outer marginal tooth very large, broad and plate-like, with large lateral flange extending along entire outer side and partly covering outer marginal tooth of adjacent row; cutting edge bearing 6–7 rather sharp, subequal cusps (Figs 5 A–D).

Habitat and ecological notes. Field observations confirm the occurrence within a mangrove ecosystem, specifically at the upper intertidal zone along the landward margin of the forest. The substrate consists of firm mud mixed with fine sand, which is exposed at low tide and penetrated by numerous pneumatophores. Low mangrove shrubs and halophytic grasses dominate the vegetation. Individuals

occur on exposed mud surfaces around the bases of shrubs and among pneumatophores (Fig. 6).

Early records from Tonkin (northern Vietnam) documented the species in brackish environments along the Song Tam-Bac and Cua-Cam rivers near Haiphong, where specimens were collected on mudbanks exposed at low tide and were observed climbing on grasses growing on these banks; additional material originated from Ha Long Bay [Dautzenberg, Fischer, 1905].

Across its geographic range, the species shows a strong association with mangrove habitats. Previous studies documented individuals climbing mangrove trunks and branches at upper tidal levels, often attached by mucus above the mean tide mark during emersion [Wells, 1985; Reid, 2014]. Taken together, available evidence indicates that the species primarily inhabits mangrove forests, occupying both arboreal substrates and adjacent intertidal mud surfaces within the upper mangrove belt.

Fecal material forms a long, rope-like strand on the mud surface. The cylindrical strand shows nearly uniform diameter and a gently sinuous course, producing an uninterrupted trail aligned with the direction of movement. This pattern reflects continuous

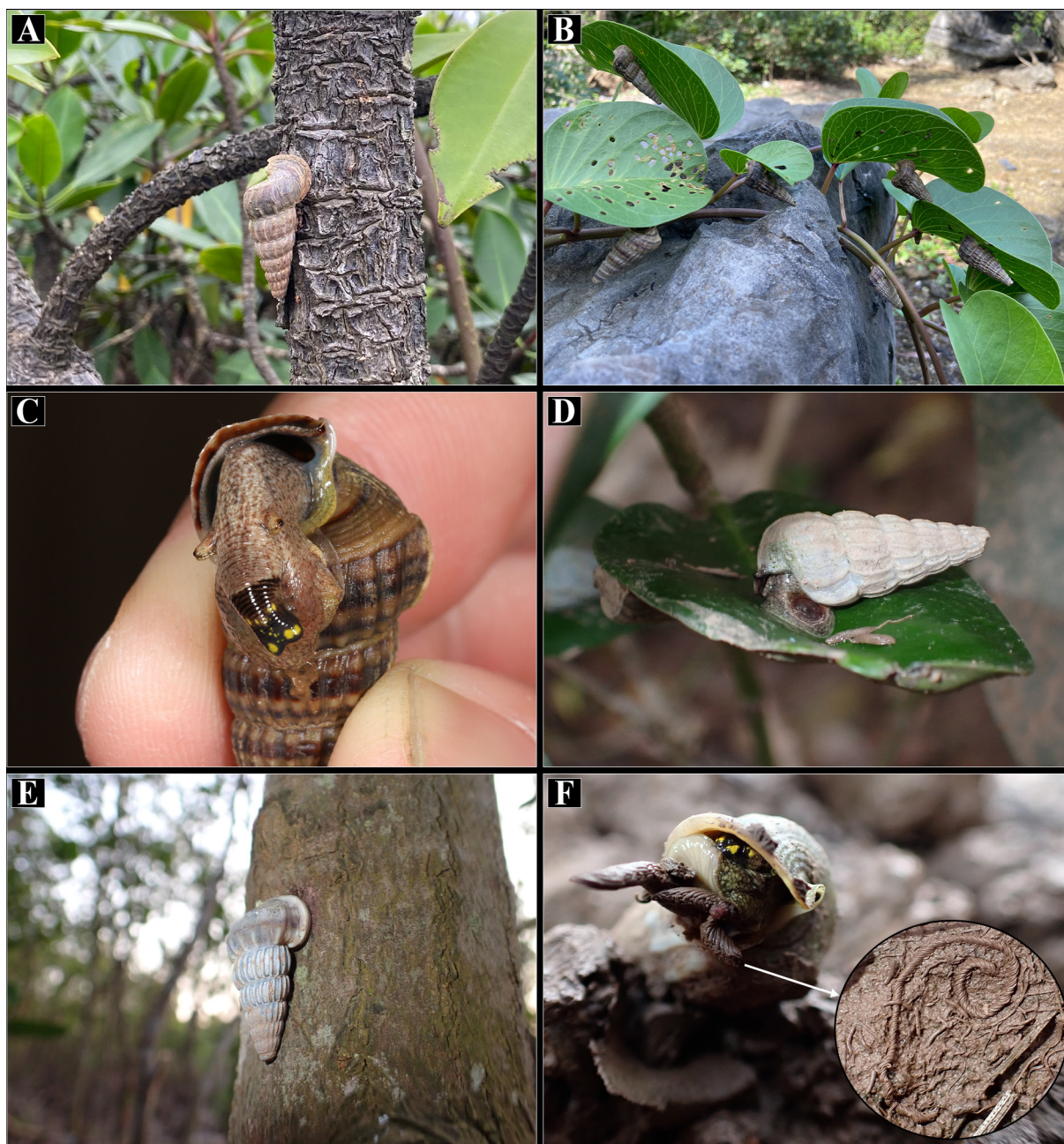


FIG. 4. Live specimens of *Cerithidea tonkiniana* from different localities in Vietnam. **A.** Hai Lang, Quang Ninh. **B, C.** Cat Ba National Park, Hai Phong. **D.** Nam Cuong, Hung Yen. **E, F.** Rang Dong, Ninh Binh. The circled and magnified area in Fig. F shows the fecal morphology of *Cerithidea tonkiniana*.

deposit-feeding activity during locomotion on soft mangrove sediment (Fig. 4F).

Distribution. Vietnam: northern coastal region (Quang Ninh, Hai Phong, Ninh Binh) and north-central region (Thanh Hoa, Nghe An, Ha Tinh); the range extends southward to Da Nang City, the southernmost confirmed record, located south of the Gulf of Tonkin [Fischer, 1891; Dautzenberg, Fischer, 1905; this study] (Fig. 1). Elsewhere: southern China (Zhejiang–Guangxi, including Hong Kong: Tolo Harbour), southern Japan (Shikoku, Kyushu), and South Korea (Suncheon Bay) [Choe, 1992; Fukuda,

2000; Kojima *et al.*, 2006; Hong *et al.*, 2010; Reid, 2014].

Remarks. The taxonomic status of *Cerithidea tonkiniana* Mabille, 1887 has historically remained unsettled. Dautzenberg and Fischer [1905] treated the Tonkin material as a variety of *C. sinensis* (Philippi, 1848), attributing observed differences to intraspecific variation in shell size and shape and assuming the presence of intermediate forms between northern Vietnamese and Chinese populations. Their interpretation relied exclusively on shell morphology.

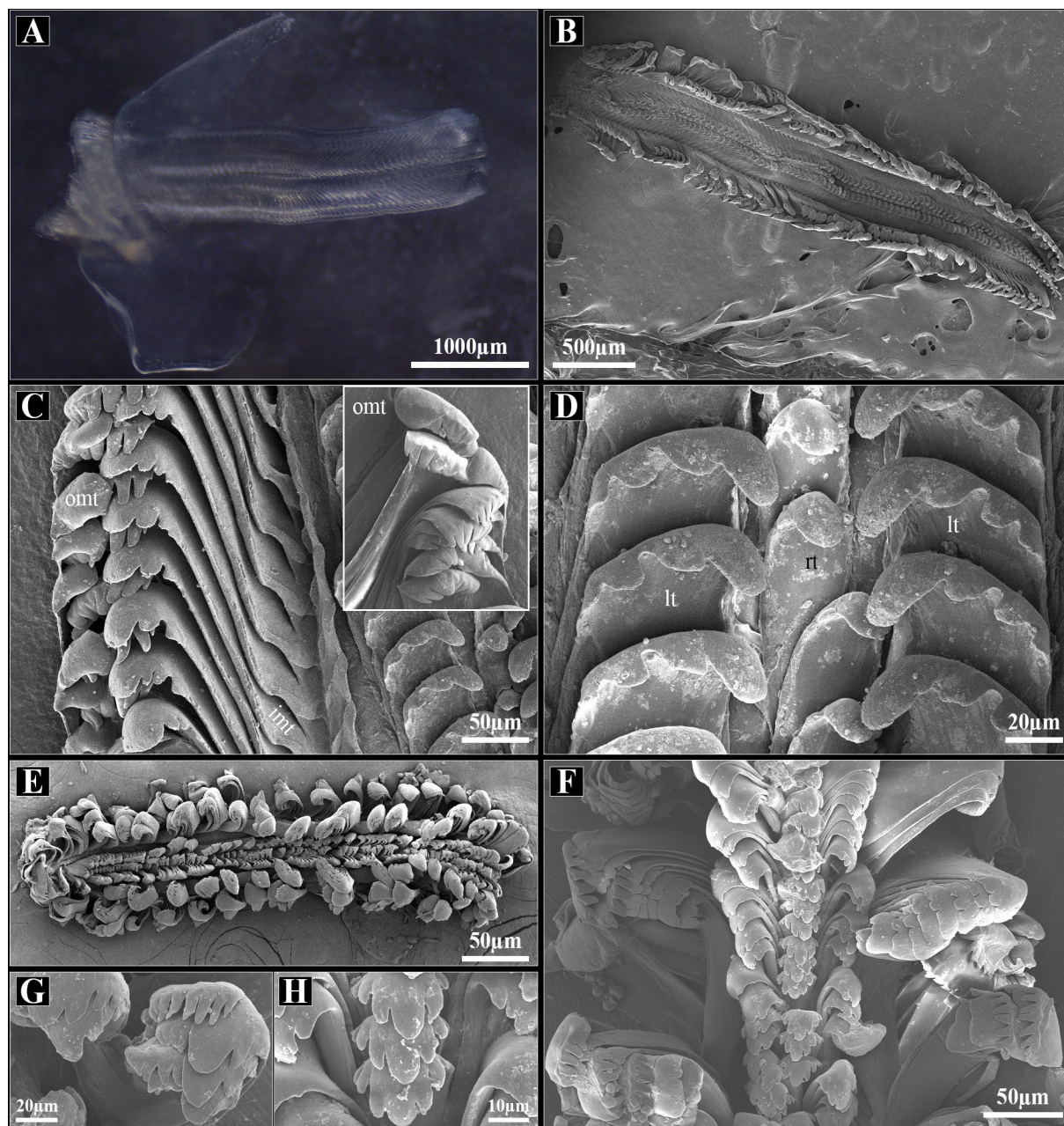


FIG. 5. A–D. Radula of *Cerithidea tonkiniana*. A. General view of the radula. B. General view of the radula (SEM). C. Detail of marginal teeth. D. Detail of rachidian tooth and lateral teeth. E–H. Radula of *Cerithidea sinensis*. E, F. General view of the radula (SEM). G. Detail of marginal teeth. H. Detail of rachidian tooth: rt – rachidian tooth, lt – lateral tooth, omt – outer marginal tooth.

Reid [2014], in a comprehensive revision of Potamididae, recognized *C. tonkiniana* as a distinct species. The present material from northern Vietnam provides independent morphological evidence supporting that interpretation.

Shell proportions remain consistent across examined populations and do not approach the morphology attributed to *C. sinensis*. Radular characters further reinforce this distinction: rachidian tooth with a 3–1–3 cutting edge lacking basal cusps; lateral teeth with a 1–1–3 denticle formula and elongate lateral projection; marginal teeth structurally uniform

(Fig. 5E–H). This configuration closely matches the material from southern China illustrated by Li and Xu [2013]. These results suggest that Reid [2014] made an incorrect taxonomic interpretation in considering the specimens identified as *C. sinensis* by Li and Xu [2013] from southern China to represent *C. tonkiniana*.

Combined shell and radular evidence supports the application of the name *C. tonkiniana* to northern Vietnamese populations and confirms its status as a morphologically distinct species within Potamididae.

Discussion

The examined material demonstrates pronounced morphological cohesion of *Cerithidea tonkiniana* along the northern and central Vietnamese coastline, from Quang Ninh and Hai Phong southward to Da Nang. The present description is consistent with Reid [2014] in all major morphological characters, with additional data on the radula and shell surface microstructure. Shell height exhibits moderate variation among localities, whereas shell proportions remain stable, and morphometric ranges broadly overlap. Variation, therefore, primarily involves size rather than shape, and no geographically structured differentiation emerges within the studied range.

All examined populations inhabit intertidal mangrove systems and adjacent brackish mudflats. Such environments are characterized by relatively homogeneous physical conditions, including soft sediments, regular tidal inundation, and moderate hydrodynamic exposure. These factors may constrain shell architecture and promote functional stability. The elongate-conical shell form likely facilitates locomotion on cohesive mud substrates and vertical mangrove surfaces, while maintaining structural resistance to mechanical stress [Reid *et al.*, 2008; Reid, 2014].

The absence of clear geographic structuring suggests effective connectivity among mangrove systems along the Gulf of Tonkin and the central coast. Potamidids possess planktonic larval stages capable of alongshore dispersal, and such dispersal potential likely promotes gene flow across this coastal corridor. The morphological similarity across the sampled range gives reason to suggest that ongoing gene flow may contribute to maintaining uniformity.

The close similarity of the radula to that of *C. sinensis* further supports their close affinity within the genus, while consistent shell and radular differences remain diagnostically informative. Comprehensive documentation of shell morphology, radular structure, and updated distributional data thus establishes a stable morphological reference framework for *C. tonkiniana* in Vietnam and provides a foundation for future comparative and taxonomic studies of mangrove-associated Potamididae.

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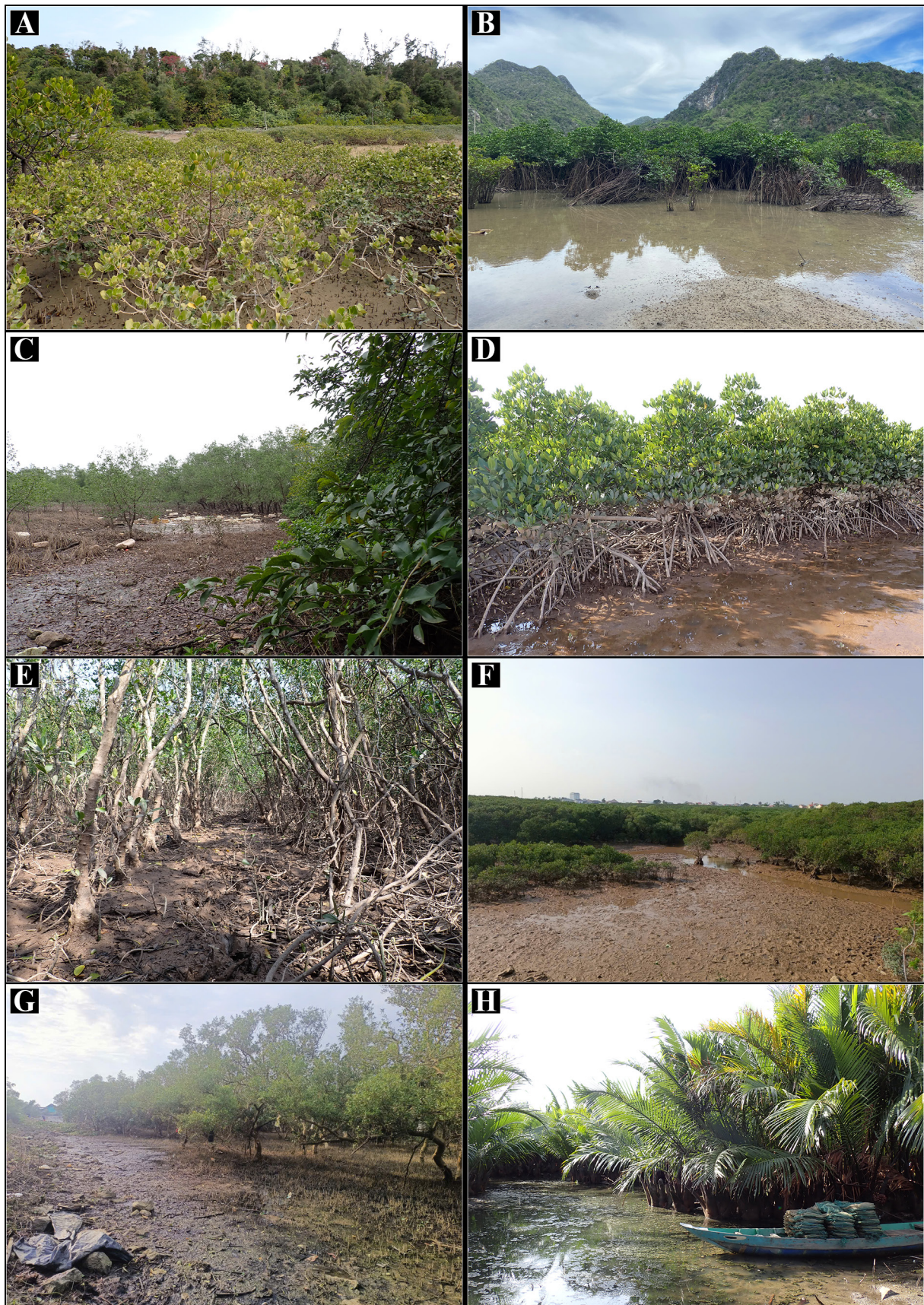


FIG. 6. Representative habitats of *Cerithidea tonkiniana* in Vietnam. **A.** Co To Islands, Quang Ninh. **B.** Cat Ba National Park, Hai Phong. **C.** Nam Cuong, Hung Yen. **D.** Xuan Thuy National Park, Ninh Binh. **E.** Rang Dong, Ninh Binh. **F.** Hai Chau, Nghe An. **G.** Tran Phu, Ha Tinh. **H.** Hoi An Dong, Da Nang.

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