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Haliotis papulata Reeve 1846 (Vetigastropoda: Haliotidae), the pimpled abalone, is the correct name for the small Indo-West Pacific abalone referred to as *Haliotis thailandis* Dekker & Patamakanthin 2001 and not as a synonym of *Haliotis varia* Linnaeus 1758

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ABSTRACT The syntypes of *Haliotis papulata* Reeve 1846 have been re-examined and are found to not represent specimens of *H. varia* Linnaeus 1758. *Haliotis papulata* appears to be the correct name for specimens that are currently considered *H. thailandis* Dekker & Patamakanthin 2001. The synonymy of *Haliotis thailandis* within *H. papulata* provides a more detailed understanding of the distribution of the species and its probable close phylogenetic relationships with the Indo-Pacific abalone species, *Haliotis unilateralis* Lamarck 1822 and *H. clathrata* Reeve 1846.

KEY WORDS Haliotidae, *Haliotis papulata*, *Haliotis thailandis*, *Haliotis varia*

INTRODUCTION

Haliotis papulata Reeve 1846, the pimpled abalone, was originally described by Reeve (1846). However, since its original description a number of authors have considered the species a synonym of *Haliotis varia* Linnaeus 1758, including Talmadge (1962), Geiger (1998), and Geiger & Owen (2012). Recently, one of the authors (B. Owen) photographed Haliotidae specimens from the Hugh Cuming collection at the Natural History Museum, United Kingdom in London which includes Reeve's *Haliotis* type material (Reeve 1846; Dance 1980). Amongst the collection are three shells belonging to *Haliotis papulata* Reeve 1846, from the 'north coast of Australia', representing the syntypes of the species. (Figure 1: images 1-4). These specimens do not match the characteristics of *Haliotis varia*; especially specimens from northern Australia or the West Pacific, even when taking morphological variability of *H. varia* shells into account (Figure 3: images 1-4). Here we provide evidence that *Haliotis papulata* does not represent *Haliotis varia* and that the recently described species, *Haliotis thailandis* Dekker & Patamakanthin 2001, actually represents *H. papulata* and thus, should be considered a junior synonym of the latter.

MATERIAL

Abbreviations of Collections.
ARC: Arjay Raffety Collection;
BOC: Buzz Owen Collection;
MHNG: Muséum d'Histoire Naturelle, Geneva, Switzerland;
NMHUK: Natural History Museum, London, United Kingdom;
RKC: Robert Kershaw Collection;
FFC: Franck Frydman Collection;
CIE: Conchology Incorporated Encyclopedia;
KSC: Katherine Stewart Collection.

Note: All specimens in figures in BOC unless otherwise indicated.

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Shells Examined. *Haliotis papulata* – 3 (syntypes); *Haliotis thailandis* – >90; *Haliotis unilateralis* – >100*; Haliotis varia* (Northern Territory, Australia) – >75; *Haliotis varia* (other localities) – >1,000.

RESULTS

Haliotis papulata Reeve 1846
Synonyms: *Haliotis thailandis* Dekker & Patamakanthin 2001

Type material. Syntypes: NHMUK 1950.3.16.9 – 11 (Figure 1: images 1-4)

Type Locality. 'North coast of Australia' (Reeve 1846)

Original Diagnosis. 'Hal. testá suborbiculari-ovatá, spiraliter obtuso-liratá, liris subdistantibus, conspicuè tuberculatis; foraminibus subtubiferis, quaternis perviis; corallo-rubidá, flavescente variá (Reeve 1846)'.

Original Translation. 'Shell somewhat orbicularly ovate, spirally obtusely ridged, ridges rather distant, conspicuously tuberculate; perforations sub-tubiform, four open; dark coral-red, variegated here and there with patches of yellow (Reeve 1846b).'

Description. Shell small (to 30 mm) lightweight, oval, flat, little arched. Spire little elevated, visible in ventral view, located approximately 35-40% towards posterior margin of shell. Columella of moderate width. Holes large, usually 3-5 open, somewhat raised. Dorsal surface with rows of relatively large nodules to small pustules in spiral orientation, fine growth lines. Coloration usually overall reddish; apex often pink, dorsal surface bright red to dark orange or purple, somewhat mottled with spots in other shades of red, green, or white, often with blotches in proximity to row of holes. Nacre bright, often with a pink sheen. No muscle scar is present.

Distribution and habitat. The Indo-West Pacific extending from the Laccadive Sea in the northwest to the northern coast of Australia and New Guinea in the southeast. The species is particularly notable in the coastal waters near Phuket Province in southern Thailand and the Camotes Sea region of the Philippines archipelago. Specific localities include: Arippu (Aripo), Sri Lanka; Olango Island, Philippines; Ko(h) Racha Yai Island (also known as Racha Island), Mai Thon Island, and Phuket Island, Thailand; southeast of Nuakata Island, Milne Bay, Milne Bay Province, Papua New Guinea (Dekker & Patamakanthin 2001; Geiger & Owen 2012; personal observation).

This species occurs in sublittoral environments, typically found between 10-25 meters in depth (Dekker & Patamakanthin 2001; Geiger & Owen 2012). Dekker & Patamakanthin (2001) record that in southern Thailand, this species occurs on bivalves that are cemented to the sea floor and appears to feed on the encrusting or epizoan flora and/or fauna located on them and on the associated hard benthic substrates.

DISCUSSION / REMARKS

Resurrection of *Haliotis papulata* as a valid species

Talmadge (1962) synonymized several species described by Reeve (1846), including *Haliotis papulata*, into *Haliotis varia* based on the observations by S.P. Dance of the Hugh Cuming malacological collection at the British Museum of Natural History (now the Natural History Museum, London, United Kingdom; Dance 1980). Talmadge (1962), however, did not directly observe these type specimens. Reeve (1846) used these 3 specimens from this

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collection as his syntypes of *Haliotis papulata* and these differ greatly from *Haliotis varia* in a number of characteristics. The *Haliotis papulata* syntypes range in size from 23.7-30 mm in length while *H. varia* can reach up to sizes of 86 mm, and are typically larger than 40 mm in length (Figure 3: images 1-2; Geiger & Owen 2012). The *Haliotis papulata* shells are slightly arched, forming a relatively flattened convex profile, while *H. varia* shells are arched, forming convex to highly convex shells (Geiger & Owen 2012). The shell spire position of *Haliotis papulata* is located more medially in contrast to *H. varia*, with the spire located more distally towards the posterior portion of the shell (Figure 1: images 1-4 & 18-20; Figure 2: images 1-20). In addition, discrete spirally-arranged rows of nodules are not formed in *Haliotis varia*, although some thickened ridges can form areas with swellings that look somewhat reminiscent of nodules (Figure 3: images 3-4).

Synonymy of *Haliotis thailandis*

Haliotis thailandis was originally described based on shells collected from the Andaman Sea, specifically coastal and insular waters around Phuket and Krabi Provinces, Thailand (Dekker & Patamakanthin 2001). Dekker & Patamakanthin (2001) defined the species based on the small size of the shells, generally 3-4 prominent spirally oriented rows of nodules, weak growth lines, 3-5 opened tremata, and shell coloration. Although four animals were available for study and imaged, Dekker & Patamakanthin (2001), did not describe them in detail or make one of these specimens with a preserved animal as the holotype, or include them among the paratypes.

The *Haliotis papulata* syntype specimens are small in size (23.7-30 mm), oval in shape, have low apices, possess 3-4 rows/spirals of nodules, and have 4-5 open tremata (Figure 1: images 1-4). These shell characteristics align well with *Haliotis thailandis* described by Dekker & Patamakanthin (2001). Although *Haliotis thailandis* was originally described based on material only known from the Andaman Sea around southern coastal Thailand (considered endemic to that area at the time of the study), additional specimens sharing morphological characteristics with the species and attributed to it have been recovered from other areas of the Indo-West Pacific since 2001 including the Laccadive Sea and Bay of Bengal around coastal Sri Lanka, the Camotes Sea (Olango Island, Visayas, Philippines) and New Guinea in the West Pacific (Figure 2: images 16-20; Dekker & Patamakanthin 2001; Geiger & Owen 2012; personal observations). Based on the examination of Reeve's material and the more widespread Indo-West Pacific distribution of the taxon Dekker & Patamakanthin (2001) described, *Haliotis papulata* appears to be the correct name for this taxon due to the much earlier date of publication. *Haliotis thailandis* is designated here as a junior synonym based on the rules of International Commission on Zoological Nomenclature.

In addition, with the synonymy of *Haliotis thailandis* within *H. papulata*, the images of the live animals in Dekker & Patamakanthin (2001) and habitat provide further evidence that *H. papulata* does not represent *H. varia*. The live animals of *Haliotis papulata* possess elongate filamentous epipodial tentacles with alternate light-dark band coloration, a characteristic also found in *H. clathrata* Reeve 1846 and *H. unilateralis* Lamarck 1822 (Figure 1: images 16-17; Stewart & Geiger 1999; Dekker & Patamakanthin 2001; Geiger & Owen 2012). The epipodial tentacles of *Haliotis varia* do not possess alternate light-dark color banding on the epipodial tentacles and the tentacles are not filamentous (Geiger 1999; Dekker &

Patamakanthin 2001; Geiger & Owen 2012). Moreover, *Haliotis varia* usually occurs in shallower environments than *H. papulata*, typically found in the intertidal zone and shallower portions of the subtidal zone (Geiger & Owen 2012).

Possible Evolutionary Relationships and Biogeography

Although molecular phylogenetic studies have sampled and analyzed a number of species of abalone, *Haliotis papulata* (syn. *H. thailandis*) has not been part of such studies (Lee & Vacquier 1995; An *et al.* 2005; Degnan *et al.* 2006; Streit *et al.* 2006; Bester-van der Merwe *et al.* 2012). The small size, flattened to slightly convex shape of the shell, prominent spirally oriented rows of nodules, spire orientation, shell coloration, and filamentous epipodial tentacles with light-dark band coloration provides evidence of a probable close relationship with *Haliotis unilateralis* (which has also not been sampled in any molecular phylogenetic analyses; Figure 1: images 16–17; Geiger & Owen 2012; Owen & Pan 2016).

Haliotis unilateralis is endemic to the Western Indian Ocean (WIO), including the Red Sea, and allopatric divergence between *Haliotis papulata* and *Haliotis unilateralis* across the Indian Ocean basin is possible (Geiger & Owen 2012; Owen & Pan 2016). While the resemblance of the shell morphology and epipodial characteristics of *Haliotis papulata* and *Haliotis unilateralis* specimens from the Western Indian Ocean, particularly coastal portions of Mozambique, are very similar and likely indicate a close relationship, we currently do not consider them to represent the same species due to the significant spatial distance between populations of these two taxa and the likely absence of gene flow between them (Geiger & Owen 2012; Owen & Pan 2016). The easternmost population of *Haliotis unilateralis* is located at the northern end of the Gulf of Oman, while the westernmost population of *Haliotis papulata* appears to be located in the northeastern portion of the Laccadive Sea near Arippu, Sri Lanka (Geiger & Owen 2012; Owen & Pan 2016). In addition, populations of abalone with shell morphological features similar to either of these two taxa have not been recovered from coastal or island areas along the Arabian Sea coastlines of India, Pakistan, Iran, or the Maldives. It is interesting to note that a number of other marine organisms show similar distributions and possible allopatric speciation between closely related taxa that occur either in the Western Indian Ocean or the Eastern Indian Ocean (EIO) and/or Western Pacific Ocean. One example is within the genus *Callistocypraea* (Cypraeidae), with two sister species *Callistocypraea broderipii* and *C. nivosa* (Meyer 2004; Lorenz 2017). *Callistocypraea broderipii* is endemic to the Western Indian Ocean, occurring along the African coast from KwaZulu-Natal northward to the Horn of Africa and extending across to the Mascarenes (Meyer 2004; Lorenz 2017). *Callistocypraea nivosa* is found in the Andaman Sea and the Bay of Bengal in the EIO (Meyer 2004; Lorenz 2017). Evidence can also be found within marine mammals. A recent study by Chanfana (2018) indicates that closely-related humpback dolphin species, *Sousa plumbea* and *S. chinensis*, show no evidence of gene flow, with *Sousa plumbea* occurring in the WIO and the Arabian Sea and *S. chinensis* distributed in the Bay of Bengal, Laccadive Sea, and EIO (Chanfana 2018). Other examples can be found in the Strombidae, Mullidae, and scarine labrids (Uiblein 2011; Choat *et al.* 2012; Wilson 2013).

The light-dark band colored, elongate epipodial tentacles also suggest a close relationship with *Haliotis clathrata*, although shell characteristics differ between the two taxa (Dekker &

Patamakanthin 2001; Geiger & Owen 2012). Future molecular phylogenetic studies of the abalones need to include comprehensive sampling of *Haliotis clathrata*, *H. papulata*, and *H. unilateralis* (including individuals from the Arabian Peninsula, the Mascarenes, Mozambique, and the Red Sea population that displays a distinctive rut between the row of tremata and the columella on the dorsal side of the shell) and determine if the hypothesis that these taxa are closely related and possibly form a species complex is confirmed. In addition, it is likely that with more molecular phylogenetic studies, it will be possible to determine if some of the Indo-Pacific species turn out to either be paraphyletic or represent complexes with numerous cryptic and/or ecological species, particularly with the amount of Neogene tectonism, sea level changes, and evolutionary divergence that has occurred within numerous other marine organisms in the Indo-West Pacific (Meyer 2004; Renema *et al.* 2008; Williams & Duda 2008; Bromfield & Pandolfi 2011; Bowen *et al.* 2013; Briggs & Bowen 2013; Gaither & Rocha 2013; Lorenz 2017).

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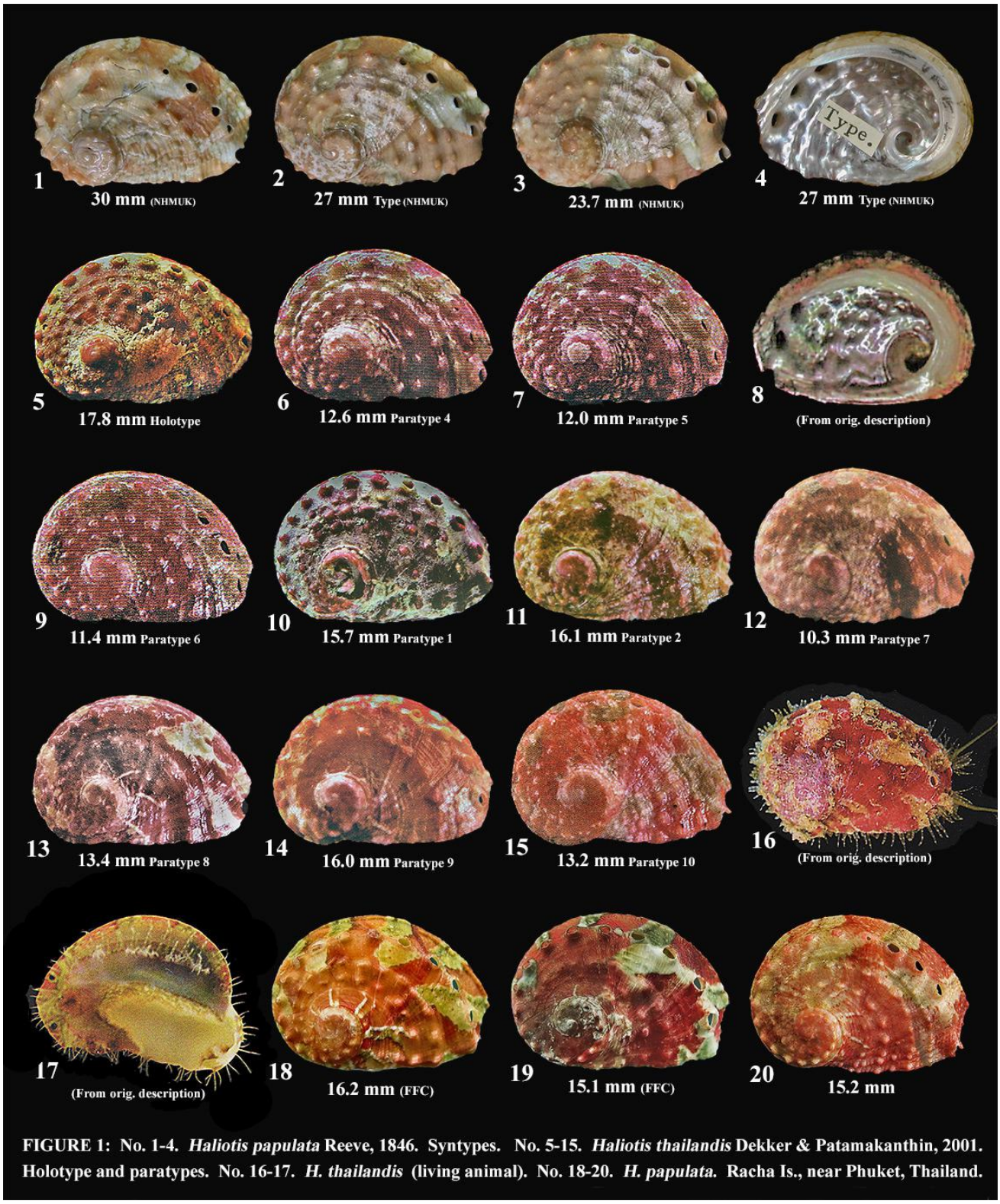

FIGURE 1: No. 1-4. *Haliotis papulata* Reeve, 1846. Syntypes. No. 5-15. *Haliotis thailandis* Dekker & Patamakanthin, 2001. Holotype and paratypes. No. 16-17. *H. thailandis* (living animal). No. 18-20. *H. papulata*. Racha Is., near Phuket, Thailand.

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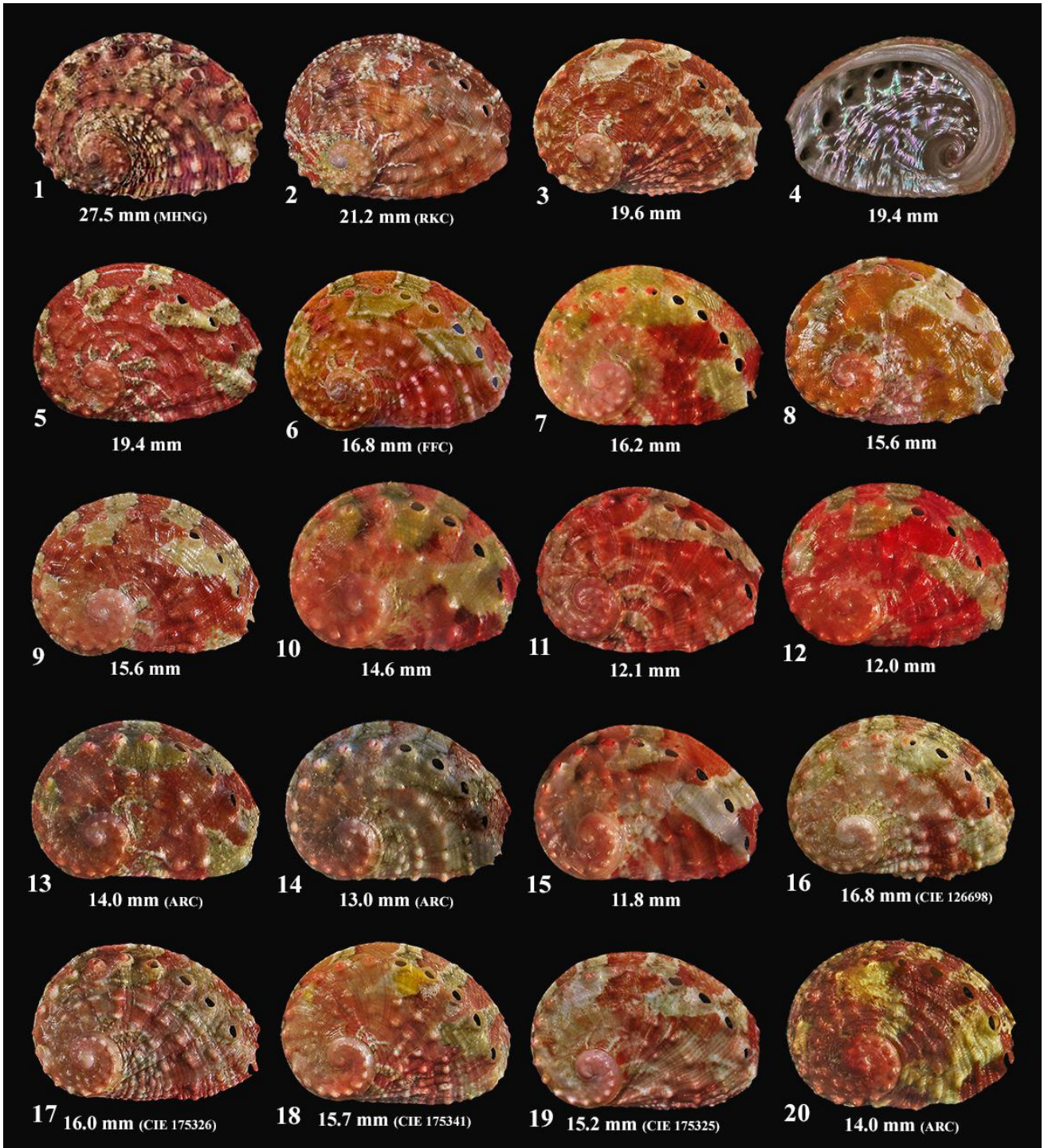

FIGURE 2: ***Haliotis papulata*** **Reeve, 1846. No. 1. Aripo, Ceylon. No. 2-15. Racha Island, near Phuket, Thailand. No. 16-19. Olango Island, Philippines. No. 20. Near Milne Bay, Papua New Guinea (dead shell).**

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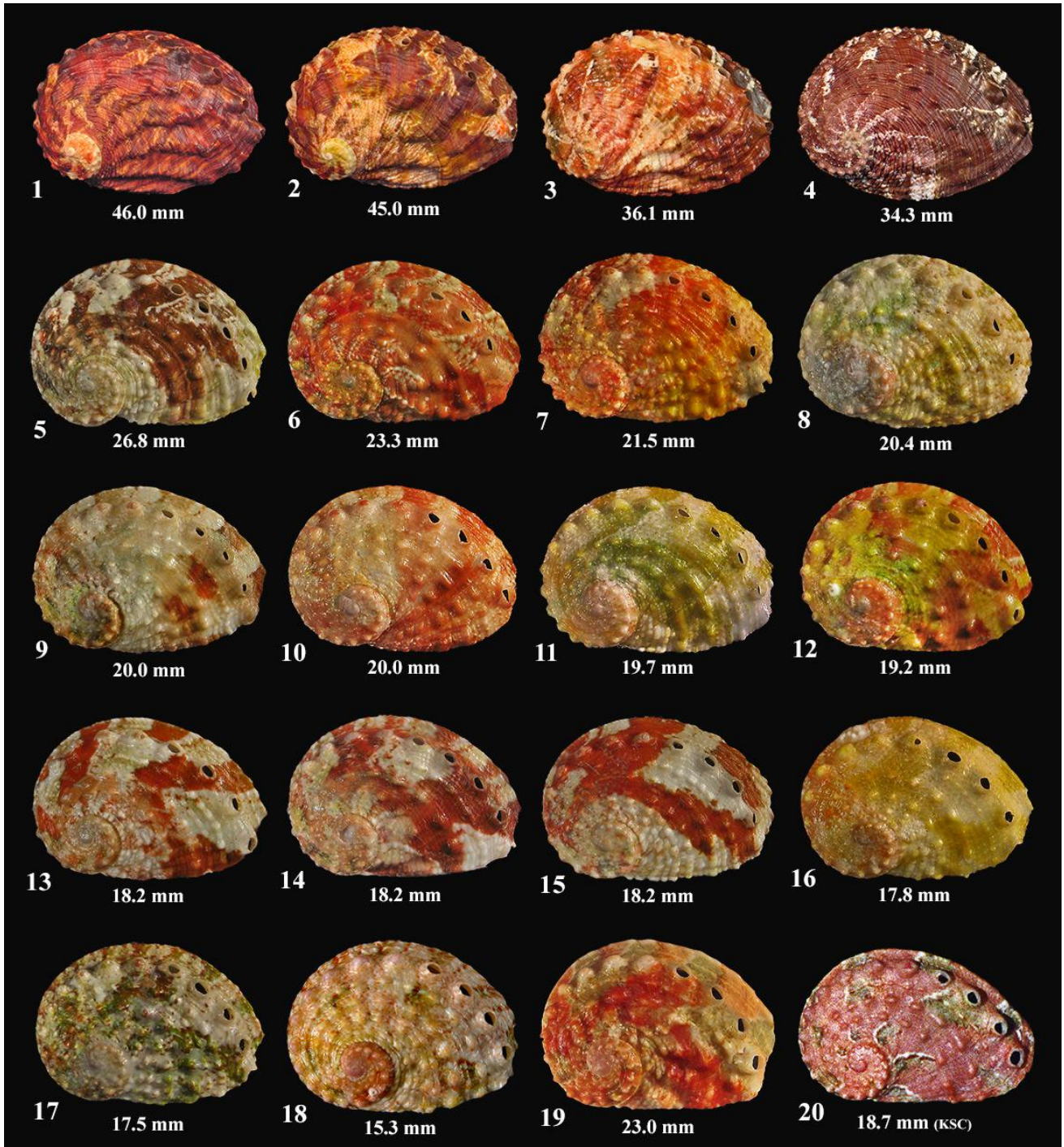

FIGURE 3: No. 1-4. *Haliotis varia* Linnaeus, 1758. Northern Territory, Australia. No. 5-18. *Haliotis unilateralis* Lamarck, 1822. Fernão Veloso, Nacala Bay, Mozambique. No. 19. *H. unilateralis.* Inhaca Island, Southern Mozambique. No. 20. *H. unilateralis.* Bassas da India.