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A Review of the *Haliotis rugosa* Lamarck, 1822, Complex of the Western Indian Ocean, with Notes on the Subspecific Status of *Haliotis multiperforata* Reeve, 1846

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ABSTRACT The three taxa *Haliotis rugosa rugosa* Lamarck, 1822, *Haliotis rugosa pustulata* Reeve, 1846, and *H. rugosa rodriguensis* Owen, 2013, are reviewed and illustrated. The confusing taxon *Haliotis multiperforata* Reeve, 1846, recently discovered to be from eastern Yemen, is validated as a fourth subspecies and is illustrated. Possible explanations for the restricted distribution of this subspecies are also explored. A map of the distribution of these taxa is included.

INTRODUCTION

The abalones (Haliotidae) are a family of marine vetigastropod gastropods that include 55 extant species (Geiger & Owen 2012; Owen 2014). Most species are endemic taxa restricted to narrow geographic areas. Some species have extensive distributions with little phenotypic variation amongst individuals (*i.e.*, *Haliotis asinina*). However, some widespread species have a tendency to form isolated subpopulations, representing multiple subspecies, within the larger context of the species. In the Western Indian Ocean *Haliotis rugosa* represents the latter, and consists of three subspecies: *H. rugosa pustulata*, distributed from the Red Sea, along the eastern coast of Africa, and extending to Madagascar, *H. rugosa rugosa* in coastal areas of Mauritius and Réunion, excluding the island of Rodrigues, where another subspecies, *H. rugosa rodriguensis*, occurs (Owen 2013). Here we recognize a new subspecies of *Haliotis rugosa* which is restricted in distribution to the Yemeni Coast in the northern Gulf of Aden. In addition, this new subspecies finally provides a concrete identification and distribution of the taxon, *Haliotis multiperforata*, described in Reeve (1846).

Abbreviations of Collections: BOC: Buzz Owen Collection, Gualala, California, USA; FFC: Franck Frydman Collection, Paris, France; HDC: Henk Dekker Collection, Winkel, The Netherlands; NGC: Norbert Göbl Collection, Gerasdorf near Vienna, Austria; NHMUK: Natural History Museum United Kingdom, London, UK; RKC: Robert Kershaw Collection, Narooma, New South Wales, Australia; SBMNH: Santa Barbara Museum of Natural History, Santa Barbara, California, USA.

Shells examined: *H. rugosa multiperforata* n. ssp. (Figure 1), Broom, Mukalla, to Jabut, Nishtun, Yemen, NHMUK 1950.3.16.32 (Lectotype; Figure 5.A), NHMUK 1950.3.16. 33-34 (Paralectotypes; Figures 5.B-C); 26; *H. rugosa rugosa* (Figure 2), Mauritius and Réunion, >200; *H. rugosa pustulata* (Figure 3), Red Sea to Mozambique, including Madagascar, >200; Tobruk, Libya, 1; *H. rugosa rodriguensis* (Figure 4), various locations, Rodrigues Island, 15.

Genus *Haliotis* Linnaeus, 1758

Type species. *Haliotis asinina* Linnaeus, 1758 (subsequent designation Montfort, 1810)

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***Haliotis rugosa multiperforata* (Reeve, 1846) ssp. nov.**

Type material (as *H. multiperforata* Reeve, 1846): Lectotype: NHMUK 1950.3.16.32 (Figure 5.A), 63 mm. Paralectotypes: NHMUK 1950. 3.16 33-34 (Figure 5.B-C). 35.2 mm, 41.2 mm. Additional non-type specimens as *H. rugosa multiperforata* collected at Broom, Mukalla, Yemen, in 2005 (Figure 1), and Jabut, Nishtun, Yemen, in 2000 (Figure 5.D).

Type locality: *H. multiperforata* Reeve, 1846, Habitat unknown. **Locality** (other)**:** *H. rugosa multiperforata* Reeve, 1846. Near Broom, Yemen, 14^0 18'30"N, 48^0 57'40"E; Nishtun, Yemen, 15^0 49'14"N, 52^0 11'49"E.

Distribution and habitat: The subspecies is distributed along Yemen's Hadhramaut and Al Mahrah coasts between Beer Ali and just north and east of Ras Fartak. Specimens taken on encrusted rocks and crevices in 0.5-5 m mostly, by snorkeling. Animals were preserved but not studied for epipodial or radulae morphology.

Description (diagnostic characters underlined): Shell small to medium (to ~63 mm), medium-weight, oblong, hardly arched, somewhat convex. Anterior margin straight to slightly curved. Spire somewhat elevated and tilted, located approximately 70% towards posterior margin of shell; partially visible in ventral view (Figure 1, top row). Holes fairly small, only slightly elevated, round, usually 7-8 open, rarely 6 or 9. Dorsal surface smooth, spiral ribbing weak to absent – when present usually very narrow, with an occasional broader thread. Spiral ribs with bumps not present on early portion of shell. Periphery between row of holes and columella smooth or with 4-5 extremely weak narrow threads closest to holes. Columella medium width to narrow. Color medium to dark brown often marked with greenish to yellow-white prosocline rays and random patches of same color. No reddish colored specimens observed which are commonly seen in the other three subspecies. Ventral surface highly iridescent silver nacre with reflections of green, pink, and steel blue. Usually very smooth with no visible ribbing present. No muscle scar.

Description of other *H. rugosa* subspecies:

***Haliotis rugosa rugosa* (diagnostic characters underlined):** (Endemic to Mauritius and Réunion). Shell small (to ~58 mm), oblong, depressed, light to medium weight, hardly arched, somewhat convex. Anterior margin straight to slightly curved. Spire low to somewhat elevated, visible in ventral view (Figure 2, top row), located approximately 70% towards posterior margin. Holes slightly larger than average, round, slightly raised, usually 5-6 open. Dorsal surface with very distinct and often deeply cut, square-profile spiral cords differing in width up to three-fold, cords often more pronounced and tightly spaced close to suture, with irregular radial growth marks. Spiral ribs with bumps often present on early portion of shell. Periphery between row of holes and columella with 2-3 very strong thick cords, occasionally with 1-2 weak threads immediately below holes. Central cord usually largest, often expanding to create a slight shelf-like ridge. Columella wide. Coloration variable; often brown to reddish-brown with fairly large areas of white, green and occasionally purple and red. Weak prosocline rays visible on some specimens. Interior usually with strong wide ribbing pattern showing through from dorsum. Nacre bright silver-white. No muscle scar. Shells from Mauritius (Figure 2.1-12) often have deeper cut, more pronounced cords than those from Réunion (Figure 2.13-15).

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***H. rugosa pustulata* (diagnostic characters underlined):** (Distributed from Red Sea down east coast of Africa, including Madagascar, to Park Rynie, South Africa. Very rarely migrates into the Mediterranean Sea, though most accounts may be spurious [F. Crocetta, pers. comm.]. May occur in Socotra and extend east into Oman and Muscat, but confirmation awaits positive identification of material collected from these areas [Bosch, *et al.*, 1995]). Shell small (to ~56 mm), oblong, depressed, light to medium weight, hardly arched, somewhat convex. Anterior margin straight to slightly curved. Spire low to somewhat elevated, visible in ventral view (Figure 3, top row), located more towards center of shell (~60% towards posterior margin). Holes slightly larger than average, round, slightly raised, usually 5-6 open. Dorsal surface usually with spiral cords differing in width up to three fold (in a few specimens cords are hardly visible), cords often being more pronounced and tighter spaced close to suture, may bear regularly spaced pustules; pustules may be lined up radially to form prosocline radial folds. Periphery between row of holes and columella with 2-3 rather prominent cords, occasionally with 1-2 weak threads immediately below holes. Central cord often largest, sometimes expanding to create a slight shelf-like ridge. Columella medium width. Coloration variable; most frequently sepia to dark olive base color with sharp transitions to sand and creamy blotchy markings with superimposed tenting and fine spiral mottling. Other known colors include orange, red, rust, grass green, dark cyan. Entire shell usually of same coloration; occasionally changing during ontogeny. Color pattern also has fine tenting only, watercolor transitions, no pattern. Weak prosocline rays seen on some specimens. Interior often irregular with protuberances and cording showing through from dorsum. Nacre bright white. No muscle scar.

***H. rugosa rodriguensis* (diagnostic characters underlined):** (Endemic to Rodrigues Island). Shell small (to ~50 mm), fairly light-weight, oblong, hardly arched, somewhat convex. Anterior margin straight to slightly curved. Spire somewhat elevated and tilted, located approximately 70% towards the posterior margin of shell; partially visible in ventral view (Figure 4, top row). Holes medium large, fairly elevated, somewhat elongate, usually 5-6 open. Dorsal surface usually with strong bumpy spiral cords alternating with narrower ribs crossing deep, prominent lamellae-like folded ridges, giving shells very jagged irregular sculpture (ribs may appear slightly scaly on some specimens). Periphery between row of holes and columella with 2-3 very strong thick cords, occasionally with 1-2 weak threads immediately below holes. Central cord usually largest, often expanding to create a wide shelf-like ridge. Columella quite narrow. Shell very brightly colored with lime green, bright white, and purple-maroon brown; occasional specimens bright red or yellow. Colors arranged as irregular banding or patches. No prosocline rays. Ventral surface highly iridescent silver nacre with reflections of steel blue, pink, and green; usually highly irregular due to very jagged sculpture on dorsum. No muscle scar.

Comparison of *H. rugosa multiperforata* to other *H. rugosa* subspecies:

Haliotis rugosa rugosa (Figure 2) has wide and often deep spiral cords, sometimes interspaced with narrow ribbing which is often deep, flat, and has a squarish profile. The columella is wide. The periphery between the row of holes and columella has a strong major cord and several narrower ribs. The colors are widely variable and often include white, red, maroon, and green. There are usually 5-6 open holes. The ventral surface is marked with smooth but

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strong parallel ribs that normally show weakly developed irregular bumps or folded ridges.

Haliotis rugosa pustulata (Figure 3) often has spiral cords, which frequently may bear regularly spaced pustules which are often lined up radially to form prosocline radial folds. The periphery between the row of holes and columella has a strong major cord and several narrower ribs. The colors are widely variable and often include orange, red, and green. There are usually 5-6 open holes. The ventral surface is usually irregular with bumps, folded ridges and parallel ribs visible from dorsal surface.

H. rugosa rodriguensis (Figure 4) has strong bumpy spiral cords alternating with narrower ribs crossing deep, prominent lamellae-like folded ridges, giving shells very jagged irregular sculpture. Most specimens have spiral ribs with bumps present on early spire. The periphery between the row of holes and columella has a strong major cord and several narrower ribs. The colors are widely variable and often include white, red, green, and yellow. There are usually 5-6 open holes. The ventral surface is extremely irregular due to very jagged sculpture on dorsum.

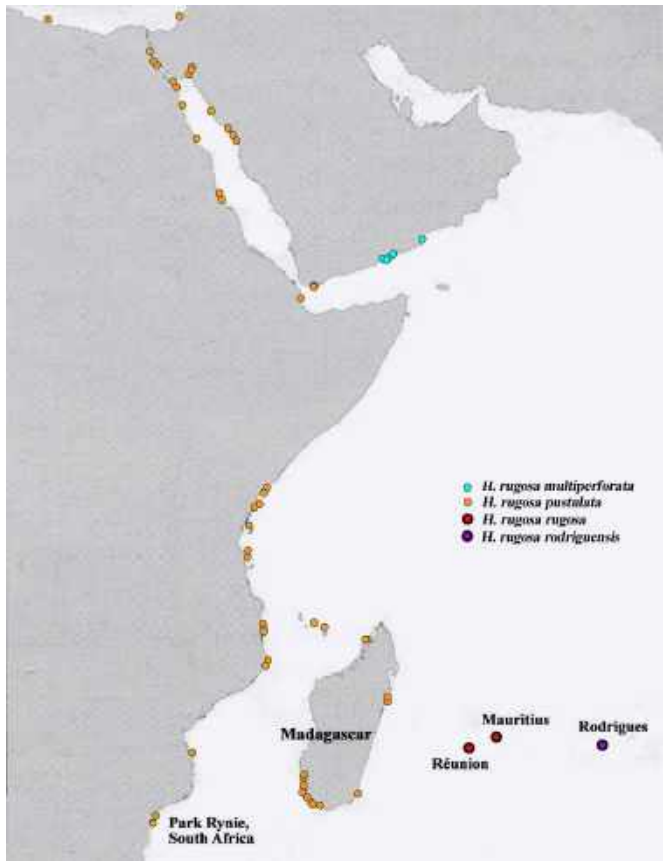

Figure 7. Map showing distribution of the four *H. rugosa* subspecies.

DISCUSSION / REMARKS

The distribution of *Haliotis rugosa multiperforata* is relatively unusual, being located within a very restricted area along the continental coastline, as opposed to an isolated island (or island group) like the majority of *Haliotis* subspecies. The subspecies' location in the northern portion of the Gulf of Aden along Yemen's Hadhramaut and Al Mahrah coasts, lies within an area that is not as greatly affected by the Somali Current as other portions of the southern coastline of the Arabian Peninsula further east (Schott & McCreary 2001; Al Saafani 2008; Ali, *et al.* 2009). Part of this may be attributed to the presence of the anticyclonic Socotra Gyre and 'Great Whirl', which direct waters during the summer months along the southern coast of the Horn of Africa, eastward past Socotra towards the coast of Oman, diverting currents from the Yemeni Coast. These strong eddies may prevent the mixture of *Haliotis rugosa pustulata* populations along the East Coast of Africa with *H. rugosa multiperforata*. This portion of the northwestern Gulf of Aden is also generally isolated from the Red Sea by the narrow strait of Bab-el Mandeb. In addition, the study on reproductive biology of this subspecies, considered *H. pustulata* at the time (Ali, *et al.* 2009), noted that the majority of gravid individuals spawn between March and

April. Interestingly, this time period coincides with shallow Ekman drifts, within the western Gulf of Aden, flowing towards the Yemeni Coast (Al Saafani 2008). The co-occurrence of the synchronized spawning with the onshore Ekman Drifts may provide a mechanism that prevents dispersal of this subspecies from expanding to the Omani coast further east. However, more studies need to be done on the reproductive biology of *H. rugosa pustulata* along the East African coast and the Red Sea to determine if spawning times are similar to those of *H. rugosa multiperforata*, or if differences in spawning times may maintain the Yemeni subspecies.

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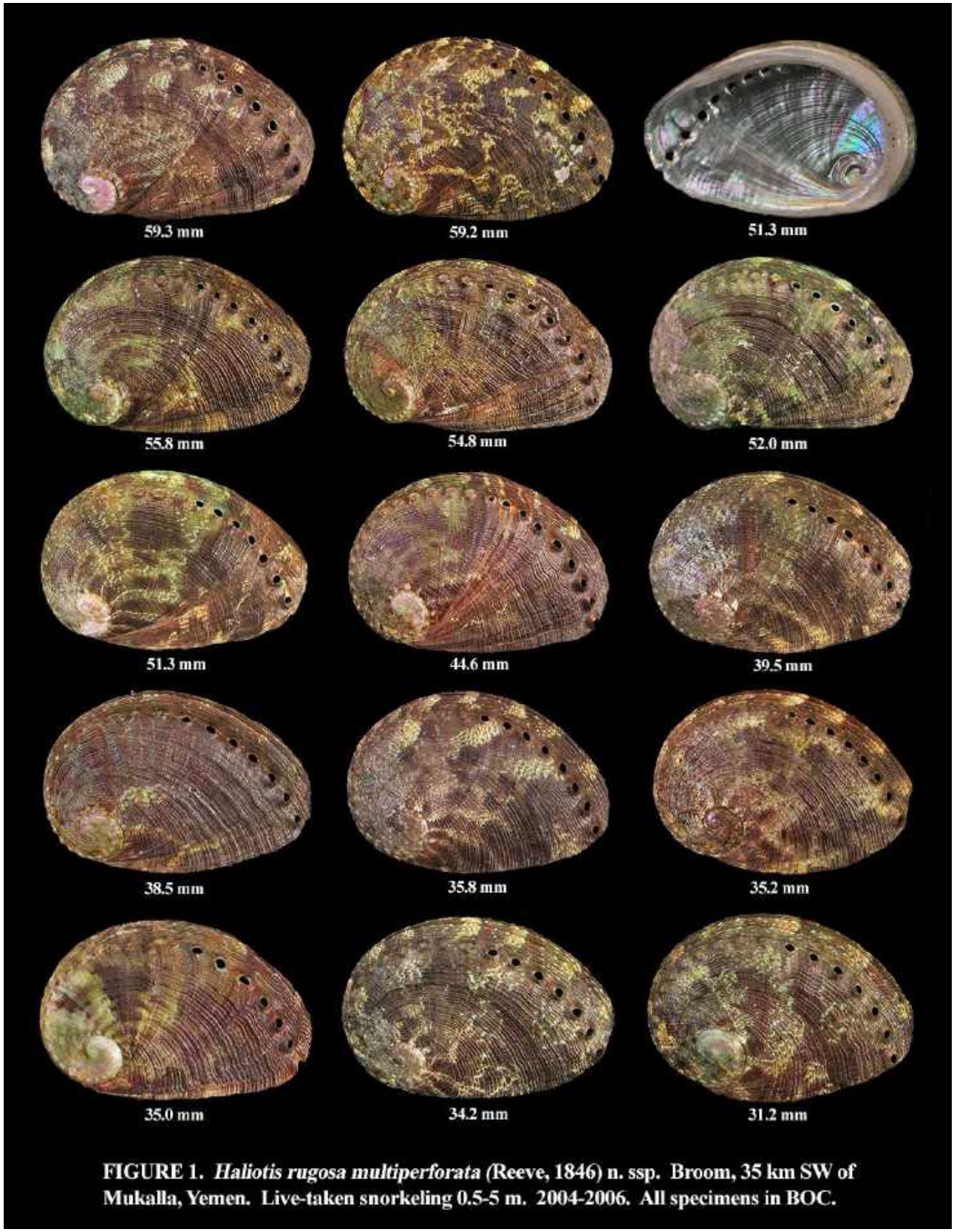

FIGURE 1. ***Haliotis rugosa multiperforata*** **(Reeve, 1846) n. ssp. Broom, 35 km SW of Mukalla, Yemen. Live-taken snorkeling 0.5-5 m. 2004-2006. All specimens in BOC.**

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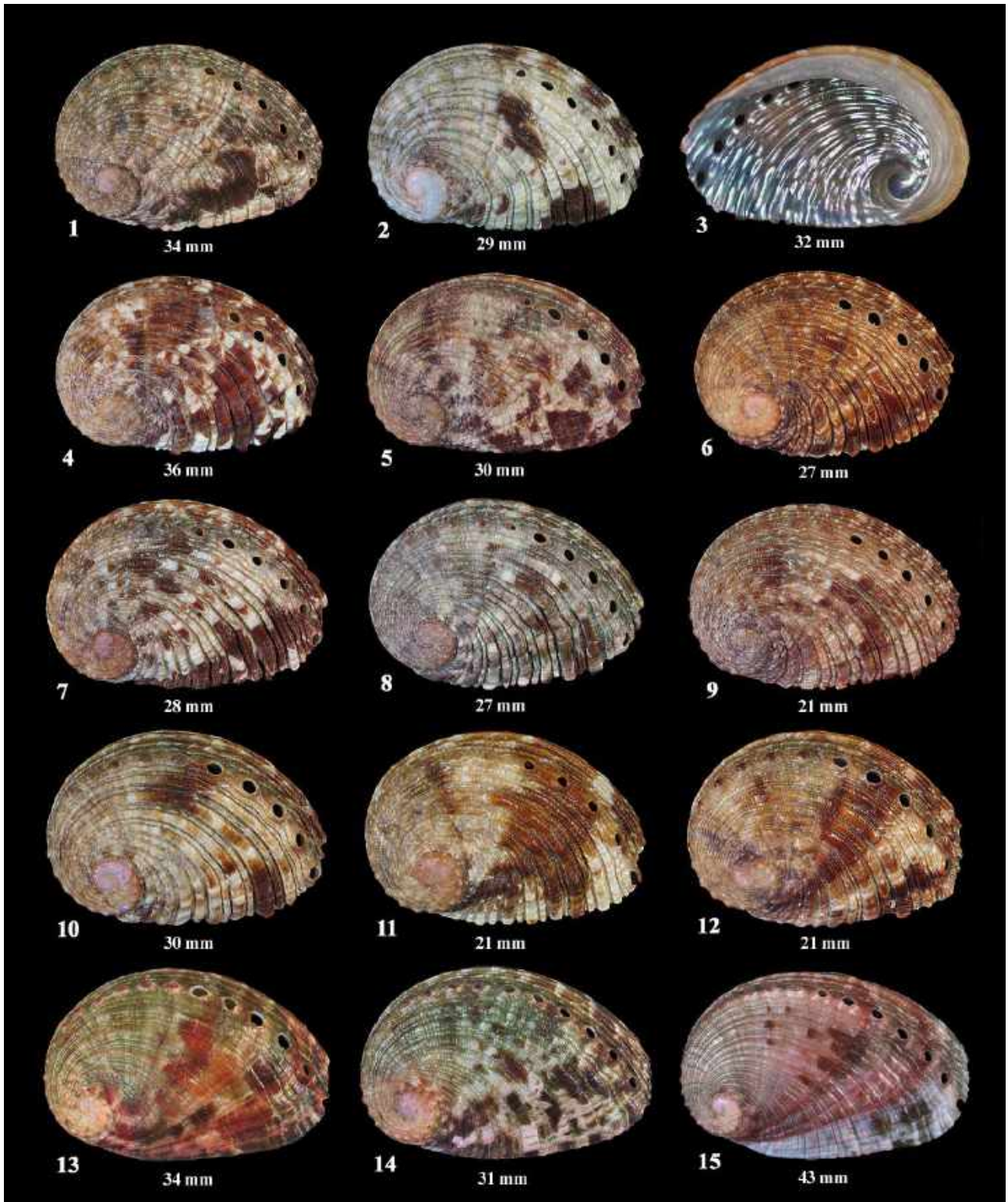

FIGURE 2. ***Haliotis rugosa rugosa*** **Lamarck, 1822. Numbers 1-12 from Mauritius; 13-15 from Réunion. 5-10 m. All live-taken. All specimens in RKC.**

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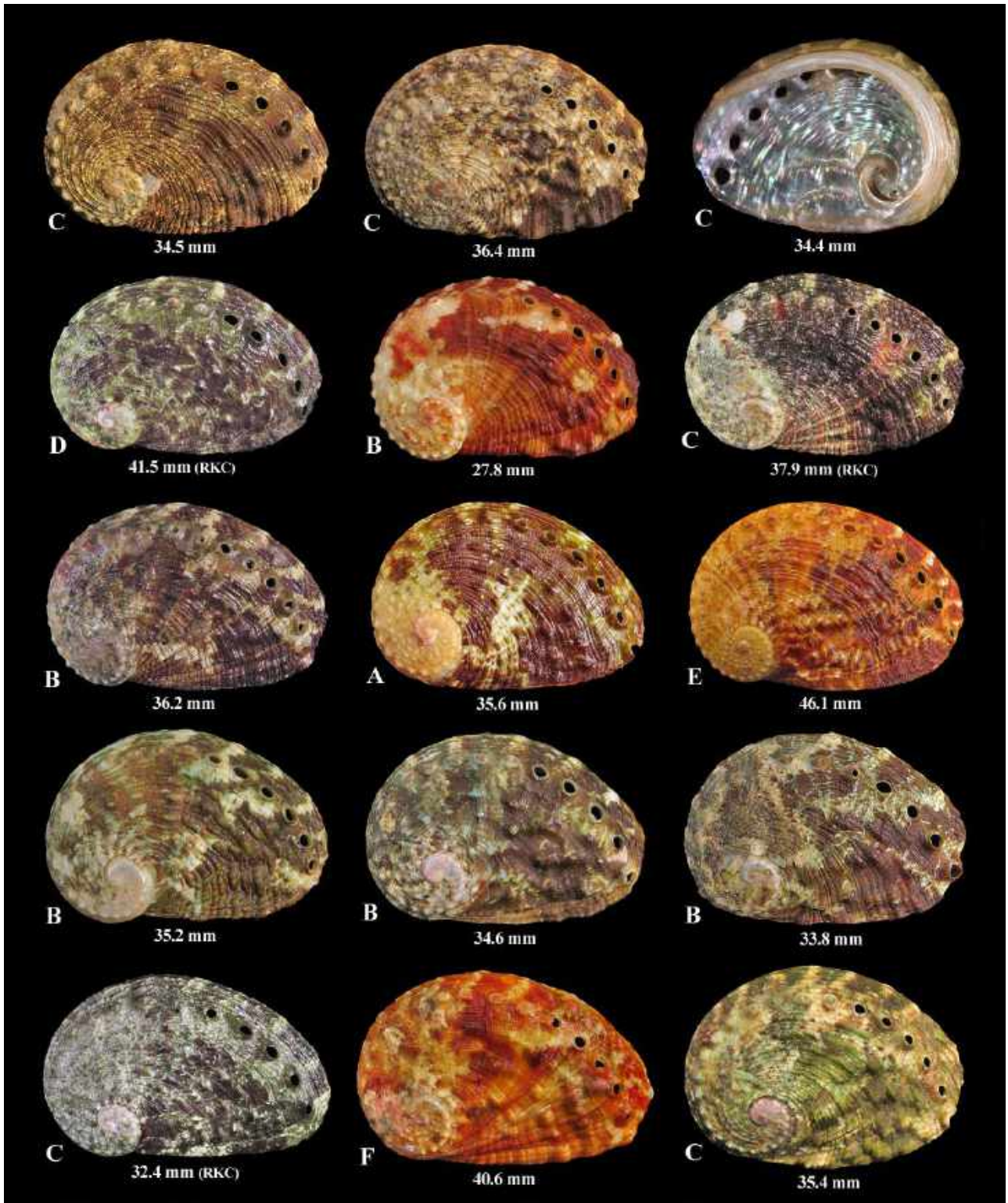

FIGURE 3. ***Haliotis rugosa pustulata.*** **A - Tobruk, Libya. B - Tulear, Madagascar. C - Fernão Veloso, Mozambique. D - Nuieba, Sinai. E - Northern Red Sea, Egypt. F - Park Rynie, South Africa. Only data. All BOC unless otherwise indicated.**

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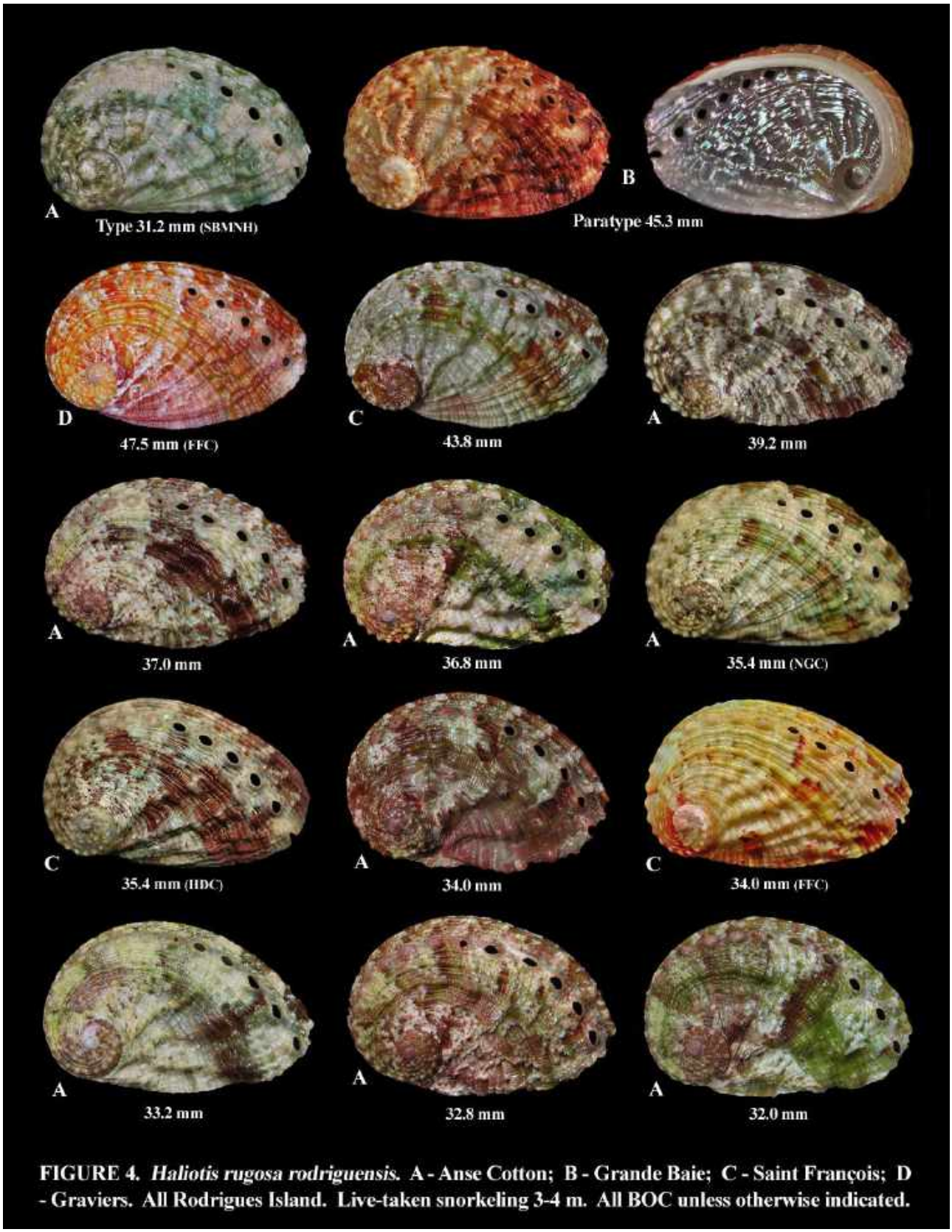

FIGURE 4. ***Haliotis rugosa rodriguensis.*** **A - Anse Cotton; B - Grande Baie; C - Saint François; D - Graviers. All Rodrigues Island. Live-taken snorkeling 3-4 m. All BOC unless otherwise indicated.**

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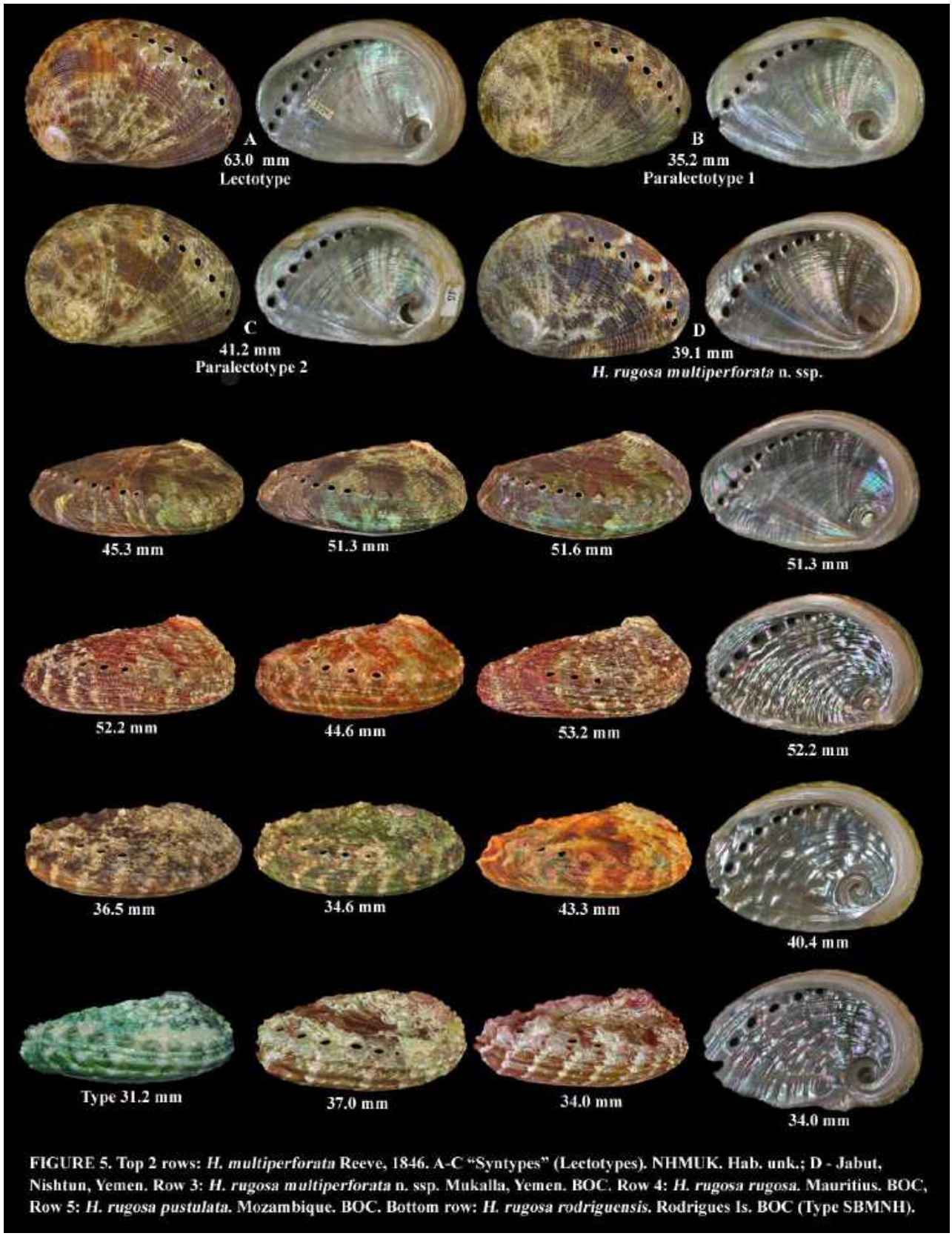

FIGURE 5. Top 2 rows: *H. multiperforata* Reeve, 1846. A-C "Syntypes" (Lectotypes). NHMUK. Hab. unk.; D - Jabut, Nishtun, Yemen. Row 3: *H. rugosa multiperforata* n. ssp. Mukalla, Yemen. BOC. Row 4: *H. rugosa rugosa.* Mauritius. BOC, Row 5: *H. rugosa pustulata.* Mozambique. BOC. Bottom row: *H. rugosa rodriguensis.* Rodrigues Is. BOC (Type SBMNH).

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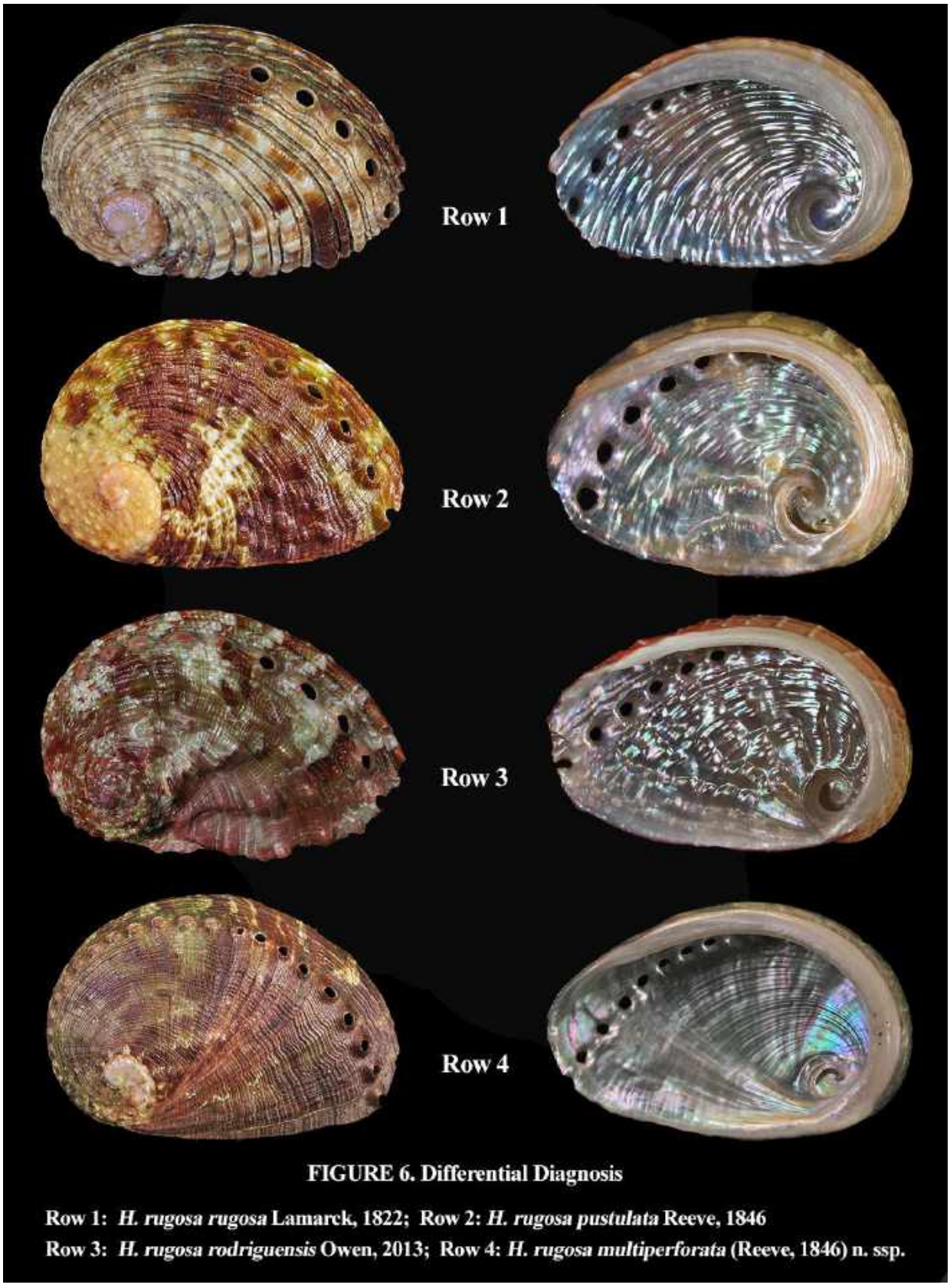

FIGURE 6. Differential Diagnosis

Row 1: *H. rugosa rugosa* Lamarck, 1822; Row 2: *H. rugosa pustulata* Reeve, 1846
Row 3: *H. rugosa rodriguensis* Owen, 2013; Row 4: *H. rugosa multiperforata* (Reeve, 1846) n. ssp.