

Abalone Without Holes: A Photo Iconography and Study of a Rare Morphological Variant of *Haliotis* (Gastropoda: Vetigastropoda)

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ABSTRACT Three different types of imperforate abalone shell morphologies are discussed and photographed and factors leading to imperforation in *Haliotis* are explored. Three plates illustrate this phenomenon. Additional plates examine the unique situation with *Haliotis elegans* Koch in Philippi, 1845, and the soft parts of an imperforate specimen showing the absence of the pallial cleft, in comparison with a normal *Haliotis*. Additionally, three recently discovered small specimens of the black abalone with nacre-filled holes are also discussed and photographed.

KEY WORDS Pallial cleft, imperforate, *Haliotis*, abalone, gastropod.

INTRODUCTION

Among the defining characteristics of abalone (Haliotidae) are a row of respiratory pores, or tremata, distributed along the left side of the shell. The pores are generally thought to be an evolutionary response in primitive vetigastropods to the consequences of torsion: a developmental rotation of the visceral mass that places the mantle cavity, gills and anus over the head. Garstang (1928) and Yonge (1947) suggested that torsion allowed gastropods a protective retreat into the mantle cavity but subsequently created a “sanitation problem” by placing the anus above the head, potentially fouling the gills and sense organs and preventing the discharge of gametes. Respiratory pores are believed to be one solution whereby wastes and gametes are discharged through the holes away from the head and twin bi-pectinate gills in abalone. Other ancestral adaptations involve slits in the shell (pleurotomarids, scissurellids, temnotropids), and the more derived conditions of the

loss of one gill (trochids), or the loss of gills entirely and the development of secondary gills (patellids) (Geiger *et al.*, 2008).

Thus, it is both unusual and intriguing that imperforate abalone occur naturally, although they are extremely rare. Three imperforated shell types occur in abalone: 1) Tremata never developed, even during the initial growth stage. 2) Initial trema development occurred, but an injury of the mantle and pallial cleft prevented later trema development and instead formed an irregular growth line. 3) Initial trema development occurred, but injury created a highly arched shell and distorted growth line lacking tremata. Only three specimens are currently known of Type 1. Type 2 is far more common. Type 3 is restricted to a few rare specimens of the black abalone, *Haliotis cracherodii cracherodii* Leach, 1814. This paper describes the taxonomy of known imperforate abalone, presents evidence that the loss of tremata is maladaptive, and discusses potential reasons why imperforate abalone are

so rare. All three types are illustrated. Additionally, an intriguing species, *H. elegans* is included which often stops developing tremata as it approaches adult size (usually >45–50 mm). Rarely, a particularly large specimen may retain but a single hole closest to the spire after filling in all the earlier formed tremata, as it continued developing shell increment without holes.

ABBREVIATIONS OF COLLECTIONS

BOC: Buzz Owen Collection, Gualala, California, USA; BSC: Bill Snell Collection, Trinidad, California, USA; BTC: Brian Tissot Collection, Trinidad, California, USA; CASIZ: California Academy of Sciences Collection, San Francisco, California, USA; CRC: Chuck Reitz Collection, San Diego, California, USA; NMNH: National Museum of Natural History (Smithsonian), Washington DC, USA; RKC: Robert Kershaw Collection, Narooma, New South Wales, Australia; JCC: Johnathan Centoni Collection, Trinidad, California, USA; JLC: Julian Lee Collection, Los Angeles, California, USA.

MATERIAL & METHODS

All shells, with the exception of the type and syntype specimens, were lightly moistened with mineral oil, the excess oil being removed to prevent glare during photography. The camera used for photographing the type specimen was a Canon EOS 30D, with a 2.5 s exposure at *f*/29. The remainder of the photography was done with a Canon A650 PowerShot at various exposures at *f*/8.

TAXONOMIC REVIEW

TYPES OF IMPERFORATE *HALIOTIS*

TYPE 1. This designation is used to refer to an abalone whose shell never developed a single open hole. There are currently three known specimens, all being *H. cracherodii cracherodii*. A fourth, an 8-10 mm juvenile *H. rufescens* Swainson, 1822, has been reported (Leighton, 1960) but was lost over 50 years ago. It was found alive in a *Macrocystis pyrifera* kelp holdfast.

The three definitely known examples are listed chronologically by date of discovery: 1) The first was found near Los Angeles, California, and is the type specimen of *Haliotis cracherodii* form *imperfurata* Dall, 1919. It measures 100 mm and is in the NMNH (Pl. 1, top row). 2) The second specimen is a juvenile found fresh dead in a tide pool at Johnson's Lee, Santa Rosa Island, California, in August 1964. It measures 26.5 mm, and is in the BSC (Pl. 1, 3rd row). 3) The third specimen was a live-taken small adult found at San Quintín, Baja California, Mexico, in July 1987, and kept alive in a marine laboratory for 8 months. It measures 86 mm and is in the BTC (Pl. 1, 2nd row). Its growth rate was monitored and compared to other specimens taken simultaneously from the same area. Three normal shells in the bottom row of Plate 1 serve for comparison.

TYPE 2. This designation refers to specimens that were clearly injured in an early stage of growth, which caused injury to the mantle that deposits shell increment. This injury apparently damaged the pallial cleft region of the mantle, which then prevented the animal from depositing normal shell with holes, forming instead a very irregular wavy imperforate "line". Pl. 5 compares such an animal with a normal abalone – note the absence of the pallial cleft. Only specimens with normal shell proportions are placed in this category. Four such specimens are included on Pl. 2. They are also listed chronologically by date of discovery. 1)

Haliotis cracherodii cracherodii. This first specimen was taken near El Rosario, Baja California, Mexico, in 1952, by a Mexican commercial fisherman. It measures 103.5 mm, and is in the BOC (Pl. 2, top row). 2) The second specimen, *Haliotis walallensis* Stearns, 1899, was found near Anchor Bay, California, in June 1954. It was found fresh dead with part of the animal still attached, apparently the victim of an attack by the seastar *Pycnopodia helianthoides* Brandt, 1835. It measures 93.8 mm and is in the BOC (Pl. 2, 2nd row). 3) The third specimen, *Haliotis rufescens*, was found on the south side of Black Point, Sonoma County, California, in 1989. It measures 224.3 mm and is in the BOC (Pl. 2, bottom row). 4) The fourth specimen, *Haliotis fulgens guadalupensis* Talmadge, 1964, was live-taken at Guadalupe Island, Baja California, Mexico, in 1995. It measures 105.2 mm and is in the CRC (Pl. 2, 3rd row). On shell numbers 1, 2, and 4, the abnormal wavy line pattern, where the holes would have been, is clearly visible, while on shell number 3, a more mature specimen, the line is not visible due to an infestation of marine boring organisms.

TYPE 3. This designation refers to an odd morphological variety of *H. cracherodii cracherodii* described as *H. cracherodii* var. *holzneri* Hemphill, 1907. This unusual morphology occurred due to an injury, which caused the angle of shell growth to radically “shift” downward, forming an oblong, somewhat narrow, and highly arched shell, additionally developing a very distorted “twisted” shell increment in the area where holes would normally be formed. All three of Hemphill’s syntypes are Type 3 imperforate. Two additional specimens are known, which also lack holes. Many other examples of similar shape exist, which do have holes, however. Both morphologies are illustrated on Pl. 3. This variety could be described as a “Type 2”

because it stopped forming holes due to an injury, but because it was described as a “var.” and given a name, this designation was chosen. This variety was discussed in more detail elsewhere (Owen, 2005).

Other Imperforate Variants. An intriguing species, *Haliotis elegans*, endemic to Western Australia, normally stops forming holes as it approaches adult size (>75 mm), with occasional specimens forming a barely visible tiny slit mid-dorsum before stopping trema formation entirely. Of 194 specimens examined over 75 mm, 176 (90.7%) were imperforate in later stages of growth. Close examination of these specimens showed clearly that in no instances was this imperforate state caused by an injury (as is the case with Type 2 specimens). This abnormality is found only in this species, and does not occur in other *Haliotis*. Plate 4 illustrates three such specimens compared to a normal adult shell of 50 mm.

Three small black abalone shells (size range 43.8–47.0 mm) purchased from a shell collector in Los Angeles have all of their holes closed with nacre clear to the ventral margin. The specimen on Pl. 4, Figs. 1 & 2, has a normal growing edge (not “ground off”) and the closed holes are formed from concentric rings as the animal filled it with nacre (Plate 4, Fig. 3). Plate 4, Fig. 4, illustrates the identical morphology of the last closed hole of the specimen of the *H. rufescens* Type 2 imperforate illustrated on the bottom row of Pl. 2. Although we don’t know what caused this condition one possibility is that they may have been filled by the animal to protect itself from barnacles, sponges, worms, etc. growing over the holes and the shell collector polished the epibionts off while cleaning them.

BIOLOGICAL REVIEW

As Type 1 imperforate abalone are exceedingly rare, imperforation may reduce survival during the initial growth stage, greatly slow growth rate, and ultimately reduce evolutionary fitness. That all of the known field specimens belong to one species that occurs in wave-swept intertidal habitats further suggests some adaptive reasons why respiratory pores are crucial for proper abalone growth and development. What then, is the functional significance of the pores?

In addition to the “waste problem” hypothesis, another idea has developed in the last few decades - that of induced water flow through the mantle cavity. Until relatively recently, the pores of abalone were assumed to be exclusively exhalant structures for mantle cavity water propelled by ctenidial cilia and laden with digestive wastes and reproductive products Crofts (1929). However Voltzow (1983) revealed that elevated respiratory pores in the Pinto abalone, *H. kamtschatkana kamtschatkana* Jonas, 1845, facilitate a completely passive circulation of mantle cavity water in response to the dynamics of water flowing over the shell surface. Diversity among abalone in respiratory pore structure, therefore, may be of functional significance in a manner similar to the apical pore of keyhole limpets (Murdock & Vogel, 1978) and the raised ostia of marine sponges (Vogel, 1974). Tissot (1992) investigated induced flows in 13 species of abalone and found that the extent of induced flow varied significantly among species. Overall, large, elevated pores, which are common in subtidally distributed species (e.g., *H. rufescens*) were more efficient at promoting passive mantle cavity circulation than the small unelevated pores of intertidal species like *H. cracherodii cracherodii*. The passive circulation may represent considerable energetic savings as animals don't have to continually pump water

through their gills and out their respiratory pores. Tissot (1992) found that black abalone experienced little induced flow and suggested this was in response to its wave-swept intertidal habitat, which naturally circulated water through the mantle cavity and out the pores. Moreover, Voltzow and Collin (1995) showed that keyhole limpets (*Diodora aspera* Rathke, 1833), whose apical openings were naturally or experimentally blocked, exhibited no evidence of damage to the mantle cavity or associated organs. Instead, water flowing naturally over the gill tips and head, indicated that the apical pore is not necessary for the effective removal of wastes. Thus, the real functional challenge for imperforate abalone is likely to be the energetic disadvantage of not being able to use external currents to move water through the mantle cavity and over the gills. Below we discuss two experiments that test this hypothesis.

Field experiments. Tissot (1991) experimentally tested the idea that the closure of open pores would influence growth and survivorship relative to normal individuals in black abalone. During 1987–1989 at Santa Cruz Island, California, pores were experimentally closed by covering all openings with marine epoxy putty (Z-Spar splash zone compound). Although splash zone compound is toxic while curing, which takes about one hour, fully cured putty is non-toxic. To control for this initial toxic effect epoxy putty was momentarily applied to all pores and subsequently removed on control individuals. Overall a total of 108 individuals in three separate experiments were tagged and followed in the field for two years. Although there were no significant statistical differences among the results of these experiments, trends in the data suggest that individuals with open or experimentally-closed pores had lower survivorship (33% vs. 44%), lower growth rates (1.7 vs. 2.5 mm/month), and a smaller percentage of individuals exhibiting

shell growth (20% vs. 39%) than abalone with naturally open pores, suggesting that tremata may have functional value to black abalone and the lack of open pores may influence growth and survivorship and perhaps evolutionary fitness.

Lab experiments. A group of black abalone were live-taken together with an 86 mm imperforate specimen from San Quintín, Baja California, Mexico, and grown out for eight months in the same aquarium tank at 15C with an *ad libitum* algal diet. The shell growth rate of the imperforate individual was not significantly different than those of other individuals with pores and indicated that in a laboratory environment the pores may not be as functionally important as in their natural environment. Also, the time frame of <1 year may be insufficient to detect effects on animals that can easily live for 20 or more years.

Hatchery observations. An apparently unique phenomenon occurred in a commercial abalone culture facility in the late 1970's. A single spawning of a pair of adult *H. rufescens* produced a number of juveniles that were clearly Type 1 imperforates. The number was not recorded, but was estimated to be as many as 8–10 (Owen, pers. obs.). Conversations with other *Haliotis* aquaculturists of many years experience confirmed the apparent uniqueness of this event (D. Leighton, E. Ebert, J. McMullen, pers. comm., Owen, pers. obs.). Specimens of this group were cultivated at a California Department of F&G lab in addition to their lab of origin (Owen, pers. obs.). To our combined knowledge, no such event has occurred since.

DISCUSSION AND CONCLUSIONS

There are several possible hypotheses that could explain both the occurrence of imperforate

abalone and their rarity in nature. The extreme rarity of Type 1 imperforates, even under laboratory conditions, suggests that the mechanism whereby they occur is unusual. One possibility is that it is caused by a rare recessive gene; a gene not normally expressed but occasional crosses between two individuals that have the gene results in an imperforate individual. This could be one possible explanation for the laboratory cohort of imperforate abalone: both parents had the gene in a heterozygous, non-expressed state.

Another possibility is that some environmental cue or event influences a developmental process, which prevents the growth of normal mantle tissue and a pallial cleft. In this case, it may not be genetic in origin but purely phenotypic.

If the imperforate condition is maladaptive then these individuals would also have a low survival rate as well. Evidence to support the maladaptive nature of the Type 1 imperforate condition include: 1) they have only been observed in the field in black abalone, which occupy wave-swept environments where the tremata may have reduced functional advantage; 2) all known individuals have been relatively small (< 100 mm); 3) Type 2 and 3 imperforates are also uncommon, suggesting they may suffer from the lack of respiratory pores as well.

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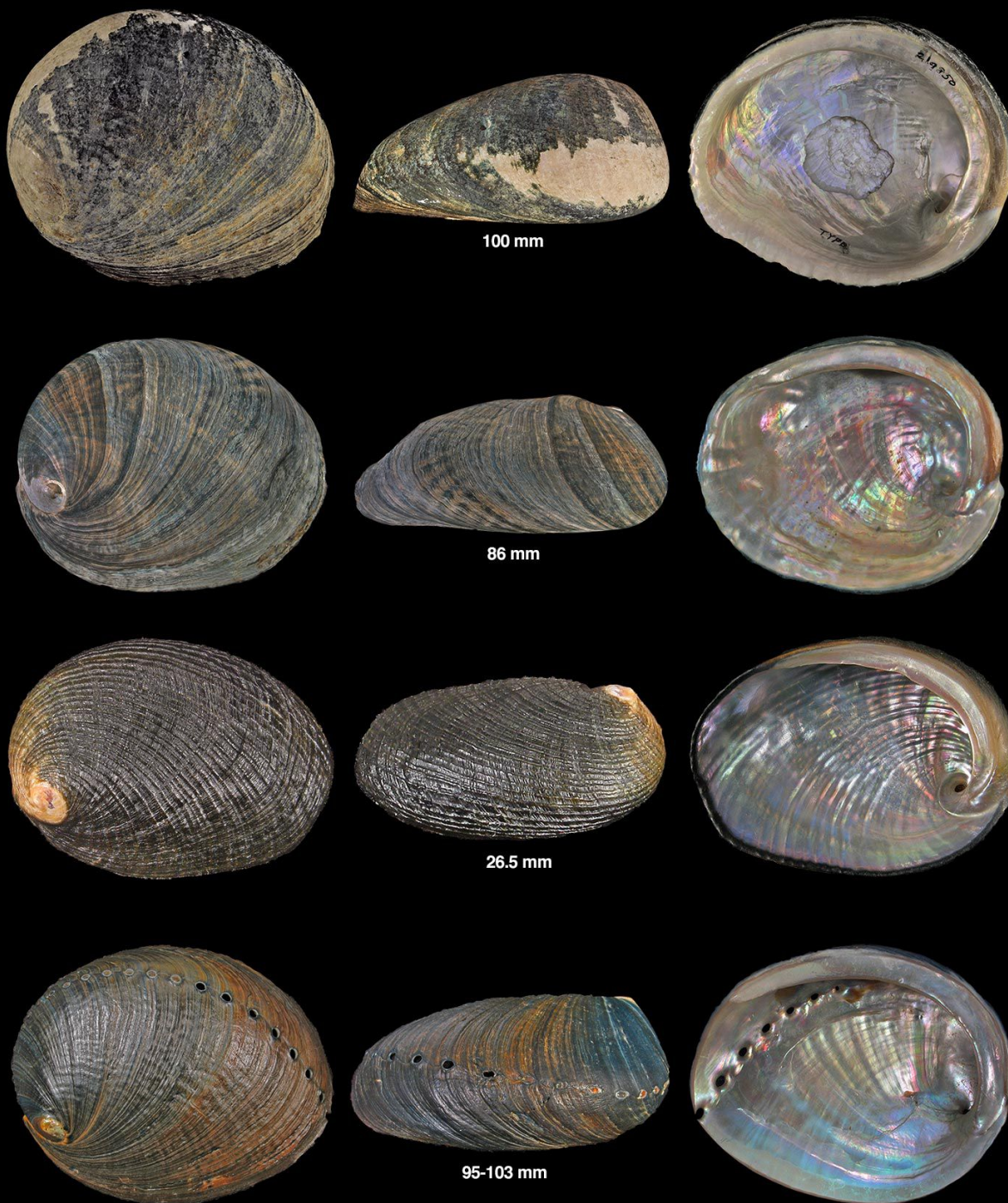
We wish to thank Yolanda Villacampa of the NMNH for photographing the type specimen of *H. cracherodii* form *imperforata*, and Liz Kools of the CASIZ for permitting the photography of the syntype of *H. cracherodii* var. *holzneri*. We acknowledge and thank Daniel Geiger for editing the manuscript and offering helpful suggestions. We also want to thank Aaron Pan for proof reading the manuscript and offering helpful comments and would especially like to

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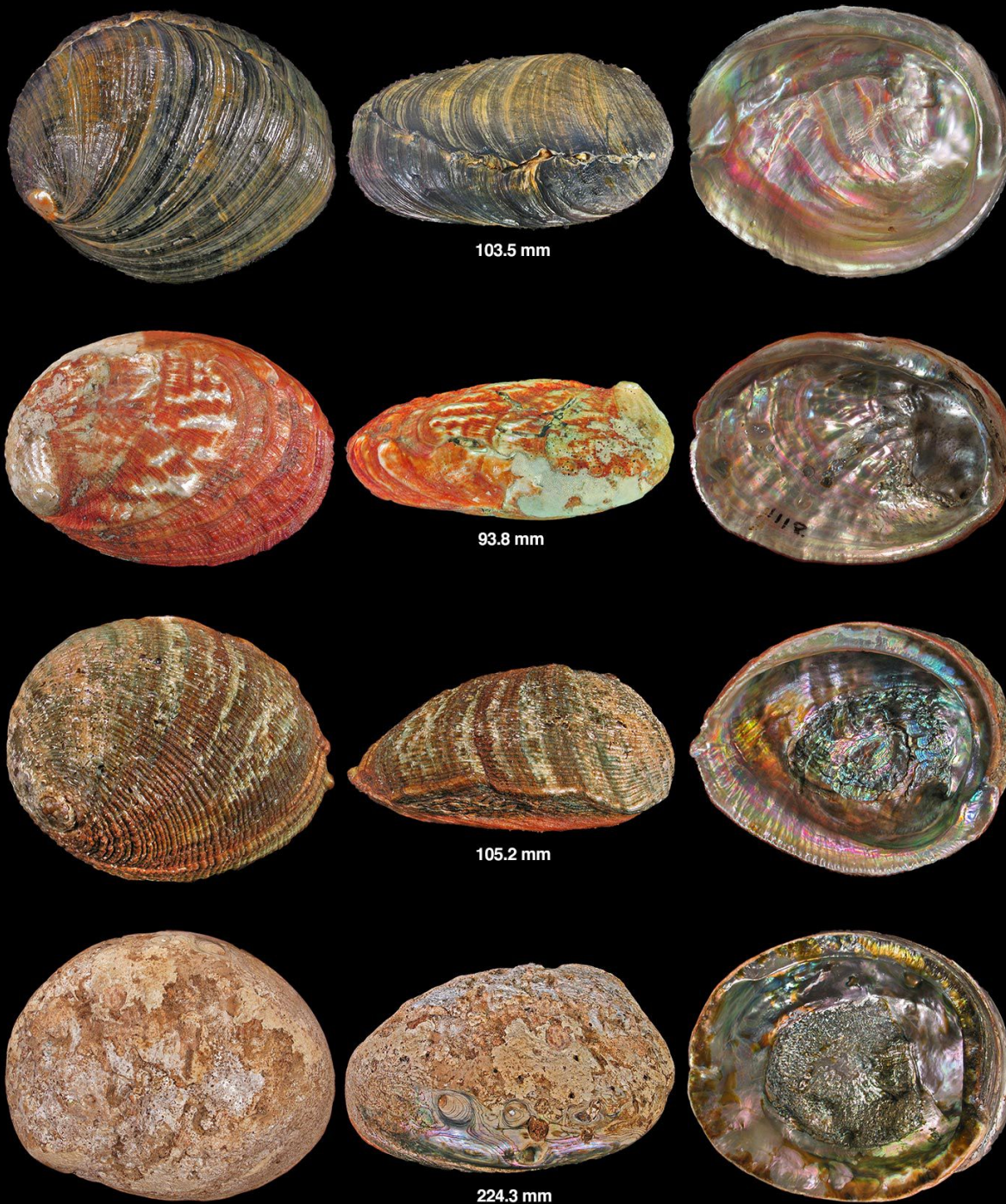
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PLATE 1



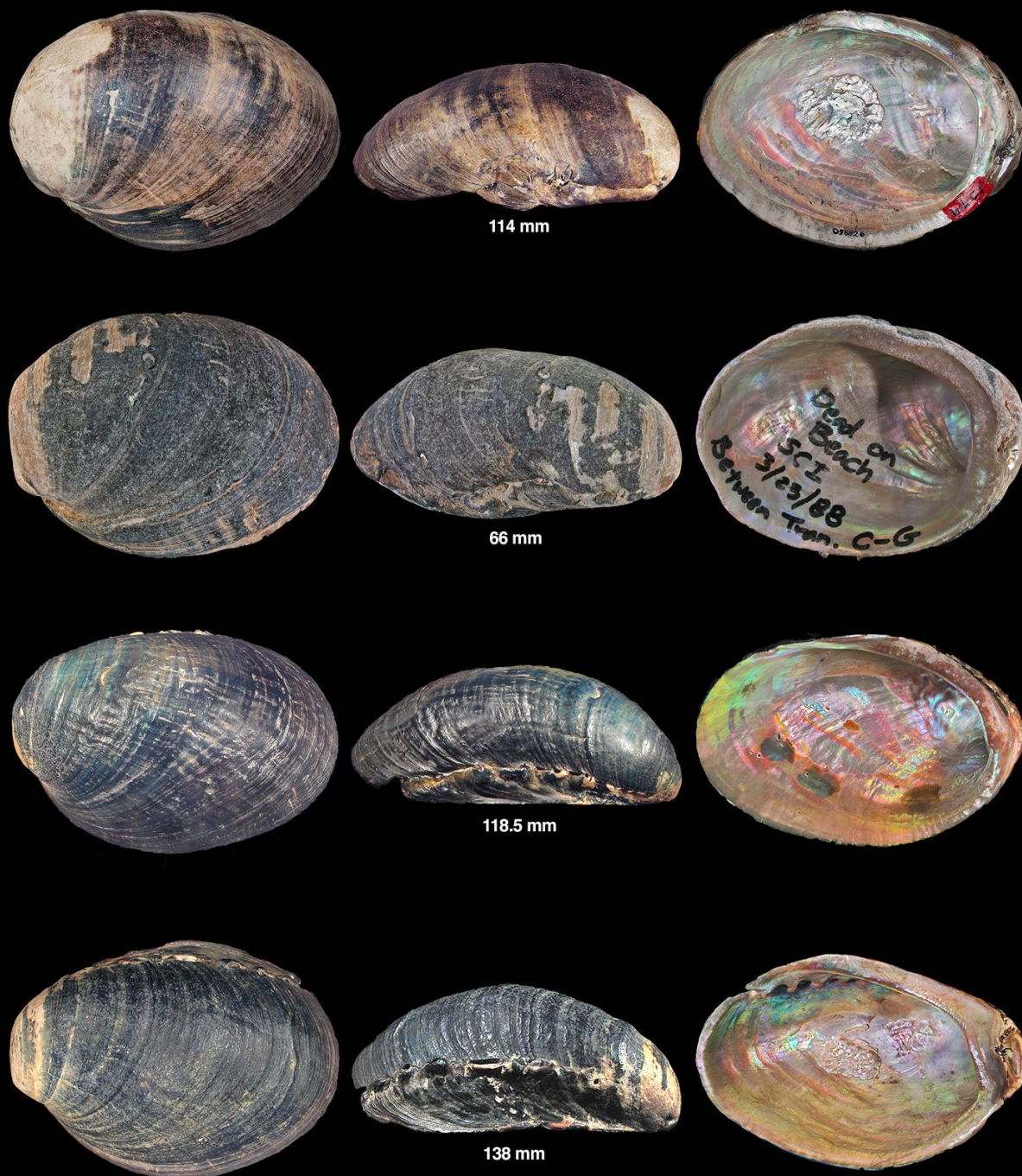
Top Row: *H. cracherodii* form *imperfiorata* Dall, 1919. Type. Coast of Los Angeles County, California. NMNH
 2nd Row: *H. cracherodii* form *imperfiorata*. San Quintín, Baja California, Mexico. Live-taken intertidally. 1987. BTC
 3rd Row: *H. cracherodii* form *imperfiorata*. Johnson's Lee, Santa Rosa Is., California. Live-taken intertidally. 1964. BSC
 Bottom Row: *H. cracherodii* *cracherodii*. La Jolla, California. Live-taken intertidally. 1951. BOC

PLATE 2



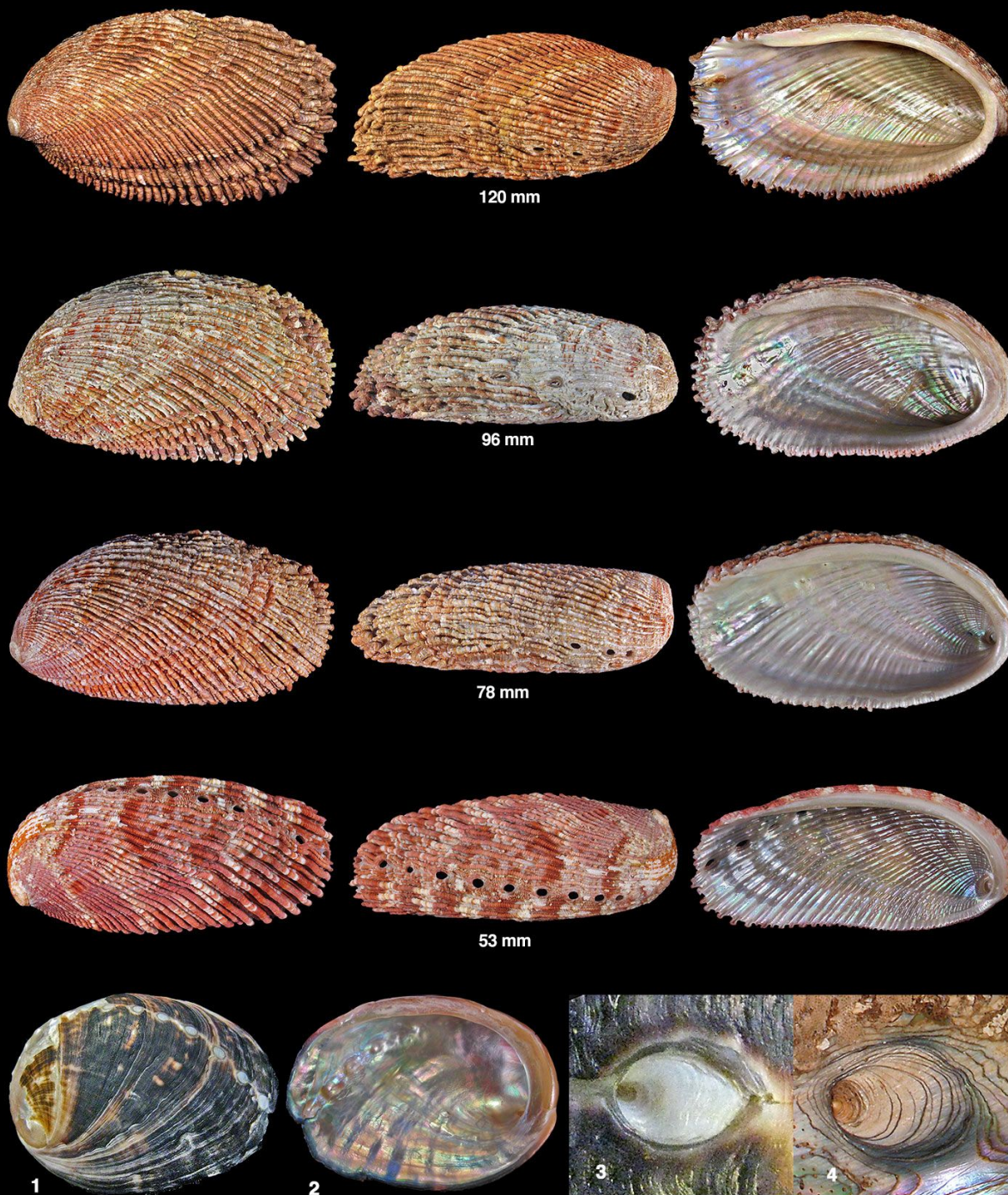
Top Row: *H. cracherodii cracherodii*. Santo Tomás, Baja California, Mexico. 1952. Intertidal zone. BOC
 2nd Row: *H. walallensis*. Near Point Arena, California. 1955. Intertidal zone. BOC
 3rd Row: *Haliotis fulgens guadalupensis*. Guadalupe Island, Baja California, Mexico. 1995. 8-10 m. CRC
 Bottom Row: *Haliotis rufescens*. Black Point, Sea Ranch, Sonoma Co., California. 1989. 5-8 m. BOC

PLATE 3



Top Row: *H. cracherodii* var. *holzneri* Hemphill, 1907. Syntype. Baja California, Mexico. CASIZ
 2nd Row: *H. cracherodii* var. *holzneri*. Imperforate like syntypes. Santa Cruz Island, California. Dead shell. BTC
 3rd Row: *H. cracherodii* var. *holzneri*. Imperforate like syntypes. El Rosario, Baja California, Mexico. 1952. BOC
 Bottom Row: *H. cf. cracherodii* var. *holzneri* (not imperforate). Cuyler Harbor, San Miguel Is., California. 1959. Intertidal. BOC

PLATE 4



Top 4 Rows: *Haliotis elegans*. Between Perth and Freemante, WA, Australia.
 Bottom Row: 1 & 2 - *H. cracherodii cracherodii* with holes filled with nacre by animal. 47.0 mm.
 3 - Closed hole of *H. cracherodii cracherodii*.
 4 - Closed hole of Type 2 imperforate *H. rufescens* (from bottom row of Pl. 2).

PLATE 5



Top: Normal *Haliotis* animal showing pallial cleft where holes are formed (*H. fulgens fulgens* Philippi, 1845. 49 mm)
Bottom: Imperforate *Haliotis* animal showing absence of pallial cleft (*H. fulgens fulgens*. 42 mm)