Identification Guide and Iconography of Eastern Pacific Hybrid Abalone Shells (Genus *Haliotis*) Part 2 of 2

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ABSTRACT There are seven species of *Haliotis* that inhabit the rocky coastline and offshore islands in the Eastern Pacific Ocean and hybridization has been observed, though very rarely, among them. This manuscript along with photo images of known hybrid specimens will serve as a guide to identifying hybrid abalone shells of this area.

KEY WORDS Haliotidae, *Haliotis*, abalone, Eastern Pacific, hybrid abalone

INTRODUCTION The following seven abalone species are found in the Eastern Pacific Ocean coastline from Alaska, USA, to Baja California, Mexico:

<u>Haliotis</u> Common name

corrugata W. Wood, 1828 Pink or Corrugated abalone
cracherodii Leach, 1814 Black abalone (currently an endangered species in USA)
fulgens Philippi, 1845 Green abalone
kamtschatkana Jonas, 1845 Pink or Corrugated abalone
Green abalone (currently an endangered species in USA)
walallensis Stearns, 1899 Pink or Corrugated abalone
Black abalone (currently an endangered species in USA)
Green abalone
Vinter abalone
Flat abalone
Flat abalone

Haliotis corrugata is the only one of the above species that has hybridized with all of the other species listed. Part 1 of this two-part series discussed and illustrated the *Haliotis corrugata* hybrids. Part 2 of this series will address all of the remaining two-species hybrid combinations that have been observed from natural populations and one two-species combination that was created in an aquaculture facility.

For *Haliotis* species with associated subspecies (*corrugata*, *cracherodii*, *fulgens*), any hybrids discussed and shown in the Figures are of the parent's nominate subspecies and for brevity, labeling will be provided only to species hierarchy except in the one hybrid combination (*H. cracherodii* x *H. fulgens*) in which

subspecies are applicable. Also for brevity, all specimens pictured are from California, USA unless from Mexico in which case that will be explicitly labeled within the Figures. All specimens are from Owen's personal collection unless labeled otherwise within Figures.

Abbreviation of collections: BOC: Buzz Owen Collection, Gualala, CA; ARC: Arjay Raffety Collection, Marina del Rey, CA; JLC: Julian Lee Collection, Los Angeles, CA; EOC: Erik Owen Collection, Jenner, CA; BMC: Bob McMillen Collection, Nicasio, CA; DPC: Don Pisor Collection, San Diego, CA; RTC: Ryan Turney Collection, Monte Rio, CA; LTC: Lawrence Thomas Collection, Morro Bay, CA; LACM: Los Angeles County Museum of

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Natural History, Los Angeles, CA. All collections located in USA.

Materials and Methods: Shell specimens photographed were cleaned with any of the following tools: Xacto tool with #11 blade, dental scalers, wire brushes, and/or tooth brushes. Shell specimens were slightly moistened with mineral oil. They were then photographed with either Canon A65OES or Nikon Coolpix 5700 digital cameras. The images were processed in Adobe Photoshop Version 6 and placed on black plates.

Shells Examined: Thousands of shells of each conspecific species.

Haliotis rufescens x H. sorenseni: hundreds Haliotis rufescens x H. kamtschatkana: 35 Haliotis cracherodii cracherodii x H. fulgens fulgens: 7

Haliotis cracherodii californiensis x H. fulgens guadalupensis: 3

Haliotis sorenseni x H. kamtschatkana: 6
Haliotis rufescens x H. walallensis: 6
Haliotis rufescens x H. fulgens: 2
Haliotis walallensis x H. kamtschatkana: 1
(plus one additional cultured specimen)
Haliotis walallensis x H. sorenseni: 2
Haliotis sorenseni x H. fulgens: 2 (cultured only - not from natural populations)

DISCUSSION The most recent comprehensive examination of Family Haliotidae was published in Geiger & Owen (2012) and in that publication, each species was illustrated with at least 10 specimens. The specimens were carefully chosen to show the variability found within a species, subspecies, or form with respect to morphology and coloration.

A hybrid specimen has a blend of *multiple* parent species characteristics such that it does not fall within the normal description of a conspecific species. When abalone are 50 mm

or less in size, it is sometimes difficult to accurately identify the species for conspecific specimens but is even more so for hybrids. For abalone species that form a muscle scar, that development does not begin taking place until the shell is approximately 100 mm. The complexity, coloration, and pattern of the muscle scar can be key factors in identifying which parent species comprise a hybrid specimen. Large mature hybrid shells best demonstrate the characteristics of both parent species.

Sometimes the width of the growing margin is a characteristic that readily identifies species but this factor is dependent on phase of growth (most prominent in juvenile and subadult stages) and environmental conditions (if deposited during calm sea conditions, growth margin may be very wide but in rough waters, it may be eroded and thin). The color of the growth margin can vary and is dependent on the type of algae most recently consumed. Dorsal 'diet bands' refers to base color changes of the shell that reflect change in algae consumed. Sometimes these bands exhibit very stark contrast (Figure 14, Row 1) and sometimes they are more subtle (Figure 1, top row specimen). Diet bands should not be confused with 'color patterning' which are induced by genetic markers and manifest as chevrons and irregular zig-zag areas (Figure 15, Row 4), white flecking (Figure 16, Row 1) spiral orange banding (Figure 5, center row first column) etc.

Table 1 summarizes the number of hybrid abalone shell specimens known to have come from natural populations in the Eastern Pacific Ocean. Part 1 of this two-part hybrid discussion addressed only the hybrids of *Haliotis corrugata* – the first column in the table. Part 2 will address all of the remaining hybrid combinations known to exist in natural populations (grayed entries in Table 1).

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Haliotis							
corrugata	corrugata	_					
cracherodii	1	cracherodii					
fulgens	23	10	fulgens				
kamtschatkana	3	0	0	kamtschatkana			
rufescens	47	0	2	35	rufescens		
sorenseni	10	0	*	6	>1000	sorenseni	
walallensis	25	0	0	1	6	2	walallensis

TABLE 1: Natural population hybrid abalone shell specimen numbers *This hybrid combination has been cultured but no specimens exist from natural populations.

Hybrids of Haliotis corrugata are the most readily identified due to this species being the most sculpted of the Eastern Pacific Ocean abalone taxa. Some of the remaining hybrid combinations are quite readily identifiable as the shells of the parent species exhibit such different features that a blending of multiple traits is evident. Some combinations are much more difficult to discern by shell alone because the parent species share many common characteristics. In most crosses that shall be discussed, the hybrid animal was examined and the epipodial structures confirmed the identity of both parent species. However, there are some combinations in which a live animal was not examined yet the shell implies that parents of two different species were involved.

Haliotis rufescens x H. sorenseni

Though this cross is the most common of all the Eastern Pacific hybrids with over a thousand specimens known to exist, it is still considered This hybrid is only found in Baja rare. California, Mexico, and Southern California, as Point Conception is the northernmost range of H. sorenseni. While this combination is readily evident from the epipodial characteristics of a live animal (Owen et al. 1971), it is not necessarily easily distinguished by shell morphology until the specimen is quite large (>175mm) and is approaching maturity. The share several parent species characteristics which also persist in the hybrid: usually a red or salmon base-colored dorsum often with diet induced color bands, 3 to 5 open holes, and generally a wavy or lumpy sculpture. However, they also often possess some marked differences: H. rufescens usually exhibits a fairly heavy and low elongated shell with moderately thick red growing margin while H. sorenseni is generally characterized by a thinner and more oval shell with a very thin growing margin - this being the case it can make it difficult to confirm hybridization by shell alone - particularly with subadult and juvenile hybrids of the two taxa. What confounds identification when only the shell is available, is that some hybrids (verified by epipodial characteristics) are thick-shelled while others are thin, some have a fairly thick growing margin while others are rather thin, some have a dorsum that more resembles *H. rufescens* while others appear more like *H. sorenseni*. The most useful diagnostic characteristic is if a larger mature shell (>175 mm) has little or no muscle scar, or a rather irregular broken up scar pattern with less of the bright red and green colored nacre of H. rufescens. Even this can be a bit deceiving as H. rufescens that grow very quickly in a food-rich environment can sometimes have minimal muscle scar development. columella tends to flare out in large specimens of *H. sorenseni* and this attribute is observed in some of the hybrids of this combination. A single specimen of this hybrid is shown with representative parent species in Figure 1. Figures 2 and 3 illustrate 20 additional examples of this cross.

Haliotis rufescens x H. kamtschatkana

There are 35 specimens of this hybrid combination known to exist and almost all have come from Southern California and northern Baja California, Mexico. Until recently the northernmost specimens came from near Cambria and San Simeon, California, but recently a shell specimen was dead-collected in Elk, Northern California. This particular hybrid combination is somewhat easier to identify because the parent species have more differing characteristics. Haliotis rufescens exhibits a fairly heavy and low elongated shell with thick red growing margin, diet bands on some specimens, 3 to 5 holes, and a muscle scar in mature adults. Haliotis kamtschatkana exhibits a light to medium weight inflated shell with thinner growing margin and spiral cords/threads, diet bands as well as genetic color patterns (to include a spiral orange band in 5 to 10% of specimens), 5 to 7 holes, no muscle scar, and sometimes color banding between the row of holes and the columella. The hybrid usually possesses a blending of these traits with an intermediate shell weight, shape, red growing margin, spiral cords, diet banding and some zigzag color patterning particularly in the juvenile phase. There are generally 4 to 5 holes, a hint of a muscle scar, and sometimes color banding exists between the row of holes and the columella. Three of the specimens exhibit the orange spiral color band inherent to H. kamtschatkana. A single specimen of this hybrid combination is shown with representative parent species in Figure 4. Figures 5 and 6 illustrate 20 more examples of this cross

NOTE: This particular hybrid is sometimes difficult to differentiate from *H. rufescens* x *H. sorenseni* but there are some criteria that assist identification. *Haliotis rufescens* x *H. kamtschatkana* usually has more open holes that are more tightly spaced, and there is often

genetic patterning on the dorsal surface and possibly banding between the row of holes and the columella, especially during the juvenile growth phase. Additionally, there is generally a more distinct and wider spiral cording texture (rather than thin threading) evident.

Haliotis cracherodii x H. fulgens

Thus far, a live specimen of this particular hybrid combination has not been observed so it is the shell characteristics alone that imply two species are involved. This hybrid would only be found in Baja California, Mexico, and as far north as Santa Rosa Island, California, which is the northernmost range of *H. fulgens*. This is a cross where the hybrid does not adhere to shell features of conspecific species thus by a process of recognition and elimination of characteristics, the parent species are deduced. This is also a combination in which subspecies of both nominate species exist at Guadalupe Island, Mexico. The subspecies designations are explicitly identified in the Figures (7-9) pertaining to this hybrid. While this hybrid exhibits a blend of multiple parent species characteristics, there are some traits that clearly dominate from each parent. During the juvenile phase, this hybrid appears to more resemble Haliotis fulgens and it is understandable how specimens might be viewed merely as darkcolored H. fulgens. However, at the mature stage, this hybrid exhibits the rounded shape and heavy weight of Haliotis cracherodii, darkto-black color diet bands, softened spiral ribbing, less elevated holes, a wider columella, a thin growing margin that is not finely serrated like H. fulgens, yet a very distinctive muscle scar and nacre color akin to H. fulgens. With respect to holes, Haliotis fulgens of all subspecies typically have 5 to 7, Haliotis cracherodii cracherodii 5 to 8, Haliotis cracherodii californiensis 9 to 16, and the hybrids 4 to 9 (however several hybrid shells were damaged during early shell growth and developed

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abnormal morphology with fewer open holes). Figure 7 features *H. cracherodii cracherodii* x *H. fulgens fulgens* along with representative parent species while Figure 8 provides a similar illustration for *H. cracherodii californiensis* x *H. fulgens guadalupensis*. Figure 9 illustrates all remaining specimens that strongly exhibit this hybrid's shell characteristics.

Haliotis sorenseni x H. kamtschatkana

There are 6 specimens of this hybrid combination confirmed but there could be many more that have gone unrecognized because these two species share many common characteristics that are difficult to delineate when combined. This hybrid is found only in California. Mexico and Southern Baia as Point Conception is California, the northernmost range of H. sorenseni. Both of these species have fairly thin and deep shells with an inward-sloping columella, do not form muscle scars, and exhibit thin growing margins. Additionally, both usually exhibit diet banding, may possess variable width threads/cords, and often have highly variable lumpiness and shell One marked difference between sculpture. these species is that *H. sorenseni* usually has 3 large fluted holes whereas kamtschatkana has 5 to 7 smaller less-fluted holes that are more tightly spaced. Another difference is that H. kamtschatkana often exhibits extreme variations in color patterning whereas H. sorenseni displays very little (limited to peppered white speckling). Haliotis kamtschatkana usually exhibits 10 to 16 spiral cords with 3 to 5 spiral threads between each (although there are occasional completely smooth specimens). In contrast, H. sorenseni tends to have a spiral threaded pattern throughout. The hybrid has a very inflated lightweight shell with 4 to 5 elevated holes, very thin margin, lacks a muscle scar though nacreous clumps may exist, and usually exhibits spiral cords. Note that five of the six shells illustrated are near the extreme length of *H. kamtschatkana* so it is the *H. sorenseni* parent that has influenced the size of these specimens. It may well be very difficult to discern juvenile and subadult specimens of this particular hybrid by shell alone. A single specimen of this hybrid combination is shown with representative parent species in Figure 10, and Figure 11 illustrates the remaining specimens of this hybrid currently known.

Haliotis rufescens x H. walallensis

There are 6 known specimens of this hybrid that were found ranging from Point Loma to Point Arena, California, though both parent species range much farther south and north from Baja California, Mexico, into Oregon. The parent species have sufficient dissimilar characteristics make this combination more discernible. Haliotis rufescens possesses a fairly heavy and low elongated shell usually with a thick red growing margin, is often diet banded, has 3 to 5 holes, and a well developed muscle scar in mature specimens. walallensis exhibits a thinner, lighter weight, elongated vet flat shell with thin growing margin and imbricate structure (resembling scales) linking cords/threads, often with chevron or zigzag patterning, 5 to 7 open holes, and no muscle scar. The hybrid of these two species exhibits a medium to heavy weight shell with an intermediately wide red growing margin, 4 to 6 holes that are tighter spaced and only slightly fluted, and possesses only a hint of a muscle scar. Some imbricate structure is evident in the hybrid particularly during the early growth phase of the shell. Some of the specimens exhibit the chevron patterning inherent to the H. walallensis parent. A single specimen of this combination is hvbrid shown with representative parent species in Figure 12 and Figure 13 illustrates the remaining specimens of this hybrid combination.

Haliotis rufescens x H. fulgens

There are only two known specimens of this hybrid which were observed with live animal and both came from Santa Cruz Island. This species has been readily cultured in laboratories, so the rareness of this combination in nature may stem from the two species having different spawning/gonad maturation cycles in localities where both species exist, or the two taxa inhabiting significantly different depths (H. rufescens distributed in deeper, colder water with H. fulgens existing at shallower depths - a number of exceptions to the latter possibility exist, however). The ranges of the two parent species coincide from Baia California Norte to Santa Rosa Island, California. As with all hybrids, multiple characteristics of both species are observed and in this case, the dorsal coloration of the hybrid (burgundy) is atypical of either of the conspecific parents. In the juvenile phase, the sculpturing of this hybrid more resembles H. fulgens but cording characteristics are clearly subdued upon maturity. The growing edge is reddish-brown and slightly wide like H. rufescens, being definitely wider than the usually thin-margined H. fulgens. The growing edge is also somewhat serrated which more resembles the H. fulgens parent. The shell is a bit lumpier than a typical H. fulgens and this demonstrates the influence of *H. rufescens*. Both parent species may exhibit diet banding and this is also the case with the hybrid, though this is more subtle than in many other crosses. While both species form muscle scars, this hybrid's muscle attachment pattern more resembles *H. fulgens* and the nacre has a bluish color that is not nearly as intense in H. rufescens. Haliotis rufescens usually has 3 to 5 holes and *H. fulgens* typically has 5 to 7. The two hybrid specimens have 5 holes. The hybrid shells are a little heavier than the typical medium-weight *H. fulgens* but not as robust as H. rufescens. Figure 14 illustrates both specimens of this hybrid with representative parent species.

Haliotis walallensis x H. kamtschatkana

Only one specimen of this hybrid has been positively identified from natural populations and was live-taken at Point Conception in June. 1963. However, three others have been cultured only one of which is mature (the latter specimen is included on Figure 15). Because the parent species share some characteristics, this is another combination that may be very hard to discern by shell alone and would likely be mistaken as H. kamtschatkana. Both of these species do not form muscle scars, possess thin growing margins, exhibit diet banding, have 5 to 7 holes, and can have significant dorsal color patterning. The most significant difference between the parent species is H. walallensis produces a very flat shell while H. kamtschatkana possesses a very inflated morphology. Another differential diagnostic is H. walallensis exhibits an imbricate structure that is somewhat scaly in texture on the dorsum. Haliotis kamtschatkana exhibits a strong channel or groove (dorsal perspective) between the row of holes and columella. The specimen from natural populations is a fairly lightweight shell of intermediate height relative to its parent species, has 6 holes, exhibits a groove in the peripheral area between the row of holes and the columella, and displays imbricate structure particularly during the early phase of growth. It also exhibits no muscle scar, and tends to more resemble the *H. kamtschatkana* parent. Figure 15 illustrates both the natural populations and adult cultured hybrid with both parent species.

Haliotis walallensis x H. sorenseni

There have only been two specimens of this hybrid combination identified from natural populations – one taken at Santa Cruz Island and the second at Point Loma. One is fully mature and the other is a fairly young sub-adult.

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Both of the parent species do not form muscle scars, possess thin growing margins, often display diet banding, and can have dorsal color mottling (chevrons or zigzag patterns for H. walallensis and peppered white speckling for H. sorenseni). Perhaps the most significant differences between the parent species is H. walallensis possesses a very flat shell with usually 6 to 8 holes and H. sorenseni exhibits a very inflated shell with 3 to 5 large fluted holes. Another diagnostic difference is H. walallensis exhibits an imbricate structure that is somewhat scaly in texture on the dorsum. The hybrid specimen from Point Loma is young, very flat, fairly lightweight, and has 4 holes, while the Santa Cruz Island specimen is quite mature, more arched, of medium weight, and also has 4 holes. Neither hybrid has a developed muscle scar. Both crosses more resemble the H. sorenseni parent somewhat. phenomenon occurs with other hybrids as well. Figure 16 illustrates both specimens of this hybrid with its parent species.

Haliotis sorenseni x H. fulgens

Two specimens of this hybrid combination were cultured in a laboratory and grown to maturity. None have been encountered in natural populations but since this cross does exist, it will be described and illustrated. Haliotis sorenseni produces a very inflated and lightweight shell, the dorsum usually being salmon colored and often having diet banding as well as a white fleck pattern. There are usually 3 to 5 large fluted holes. Typically, no muscle scar is present, but there may often be nacreous clumps in more mature specimens. Additionally, the columella often tends to flare out in larger individuals. Haliotis fulgens produces a flatter yet medium-weight shell, the dorsum is usually brown colored but can have diet banding as well as a white stippled pattern in a spiral band between the row of holes not extending to the apex. There are usually 5 to 7 somewhat raised

medium sized holes, and typically a muscle scar in mature specimens that becomes more vibrantly blue/green with age. Both parents exhibit thin growing margins. The two hybrid shells are of intermediate height and weight, exhibit a predominantly light green dorsum (due to a diet high in the brown alga Macrocystis pyrifera with diet banding caused by inclusion of various amounts of red algae), but no white fleck patterning. The larger of the two shells has 5 holes; the smaller 4 holes, and both exhibit a confused and complex muscle scar pattern more similar to *H. fulgens*. Both hybrid specimens exhibit flared columellae. Figure 17 illustrates the two specimens of this hybrid with the representative parent species. A probable reason this cross has not been found in natural populations is due to the extreme differences in depth the two parent species normally occur.

CONCLUSION

Hybrid abalone specimens are known to occur very rarely in natural populations. They can be created in a laboratory setting and involve more than just two parent species (Owen & Meyer, 2015). The epipodial characteristics of the live animal provides the strongest indications that hybridization has occurred provided specimen has matured to the point that characteristics of both parent species have become evident (usually about 50-75 mm). This paper has provided diagnostic information for abalone shells that do not adhere to conspecific characteristics. Part 1 of this 2-part series illustrated examples of the Eastern Pacific Ocean abalone species that have hybridized with Haliotis corrugata. Part 2 of this series has addressed the remaining two-species hybrid combinations. It should be noted that shell specimens exist that indicate parentage of more Furthermore, four-species than two species. hybrids have been cultured. Hybrids of more

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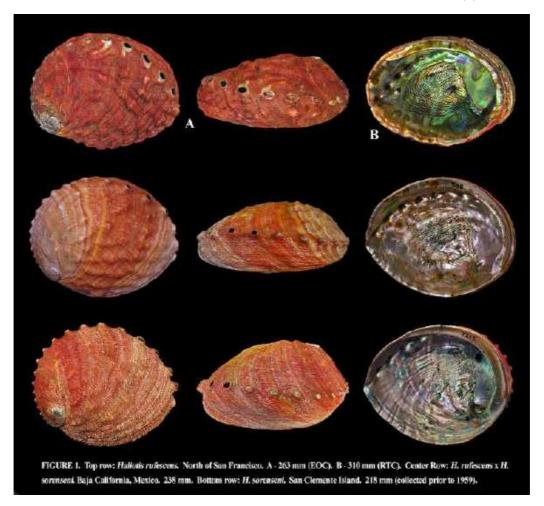
than two-species combinations are a subject for a future manuscript.

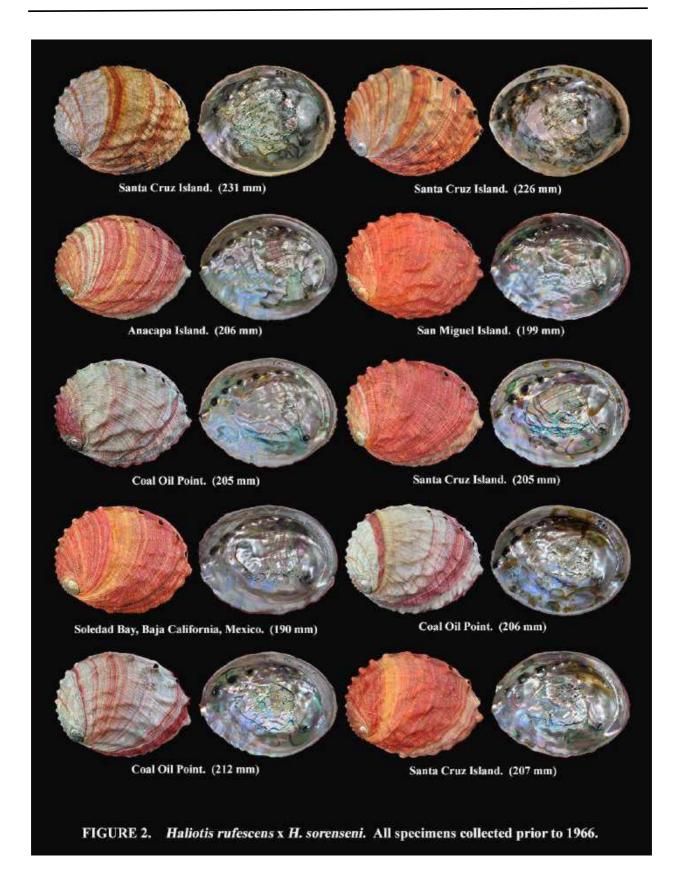
ACKNOWLEDGEMENTS

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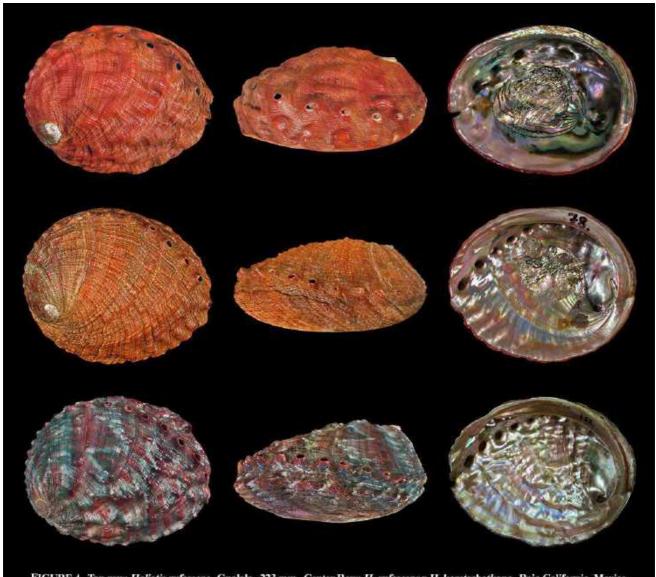
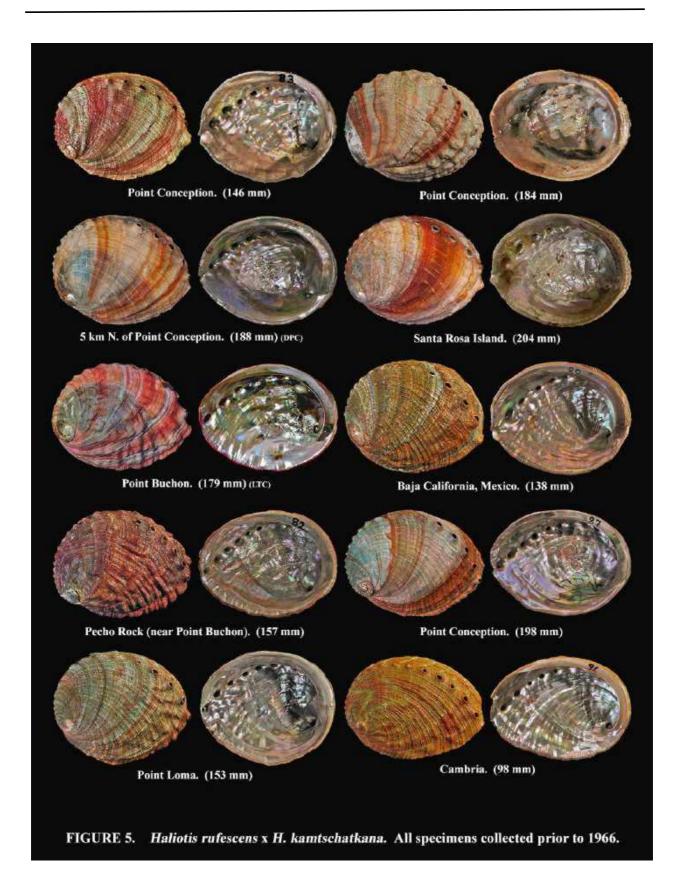


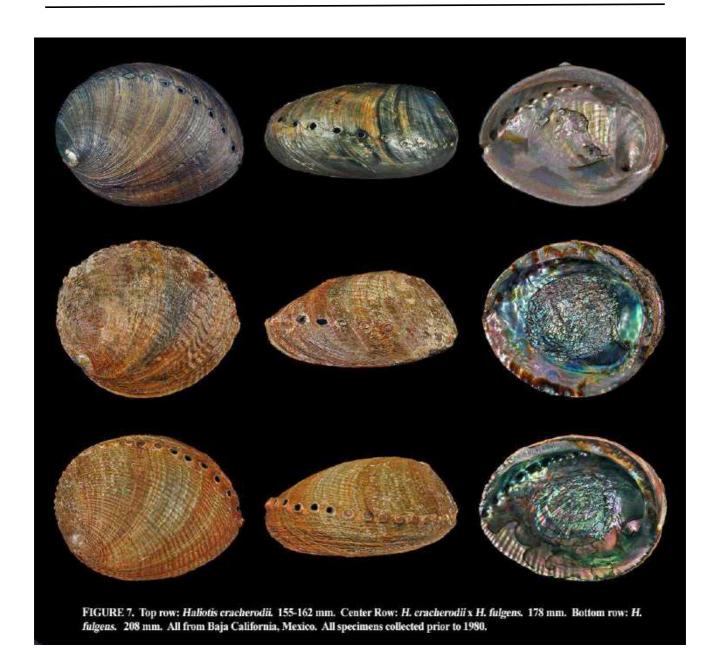
FIGURE 4. Top row: Haliotis rufescens. Gualala. 223 mm. Center Row: H. rufescens x H. kamtschatkana. Baja California, Mexico. 163 mm. Bottom row: H. kamtschatkana. Point Conception. 123 mm. All specimens collected prior to 1966.

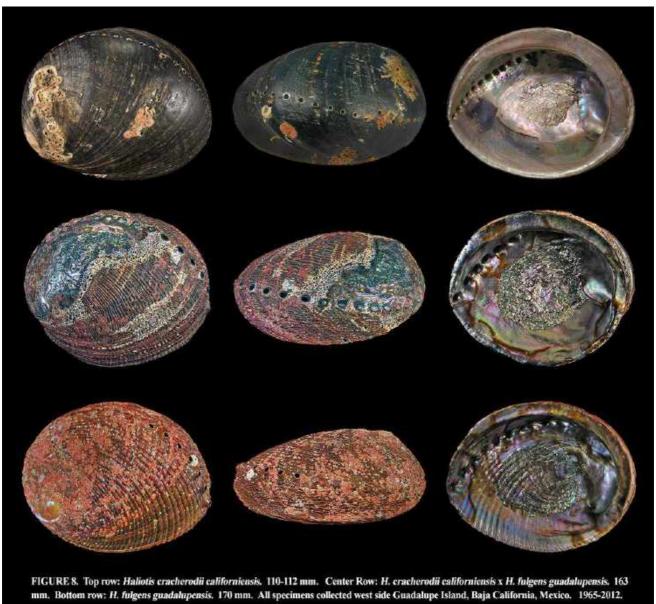
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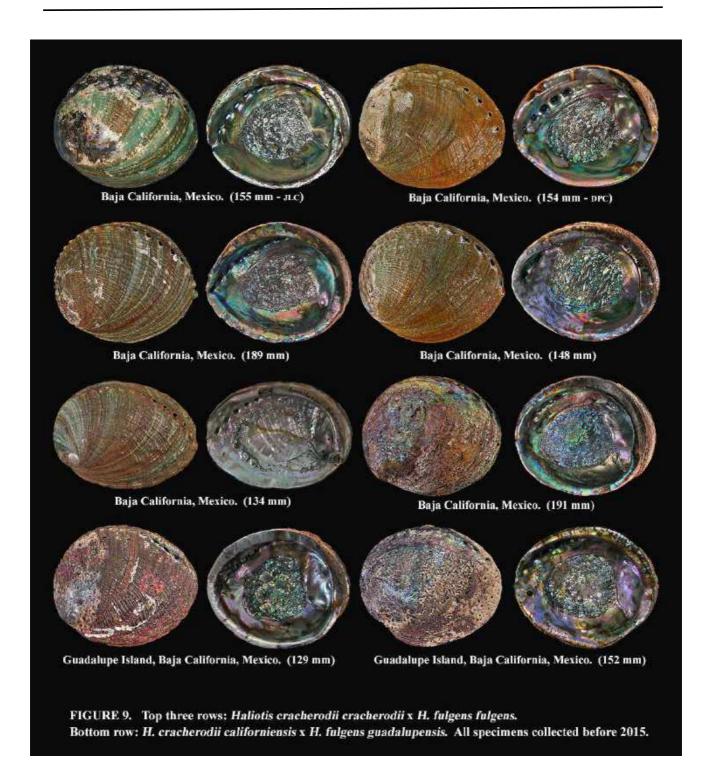


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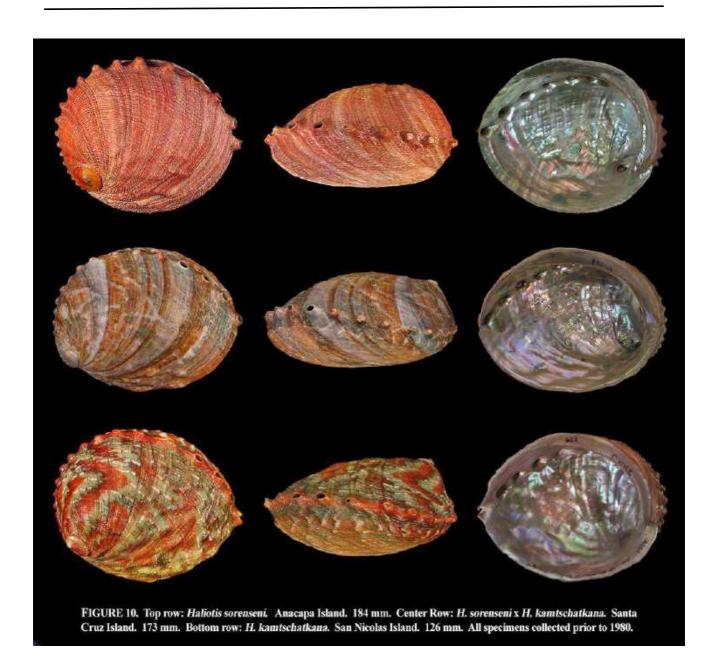


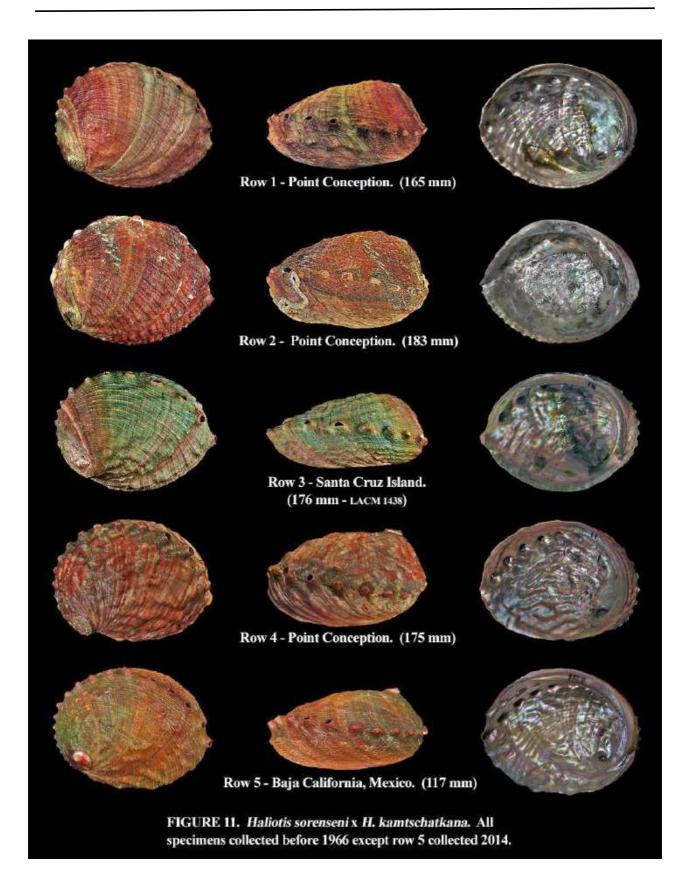


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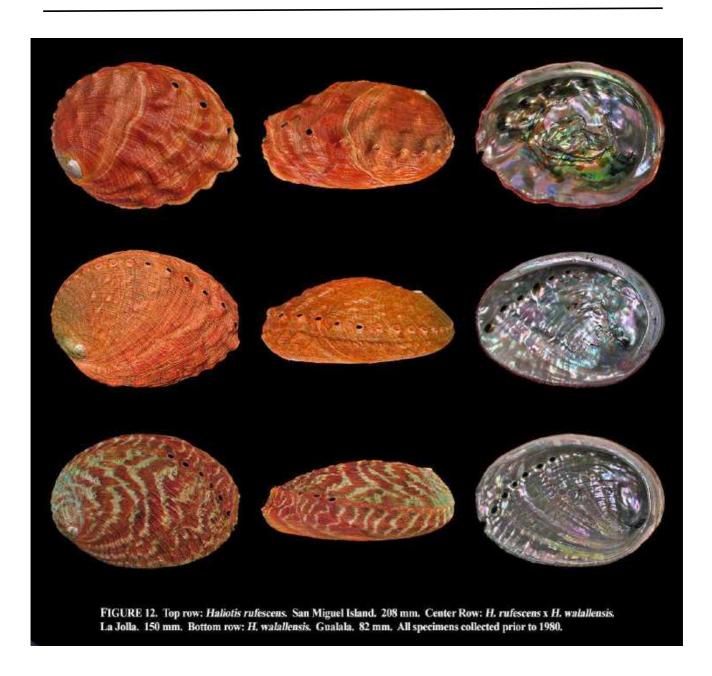


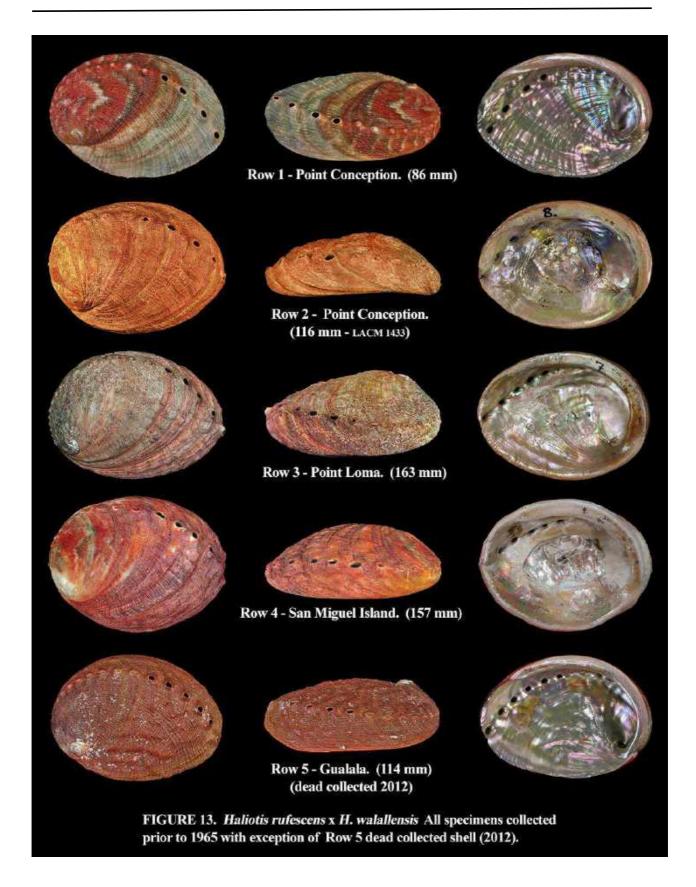
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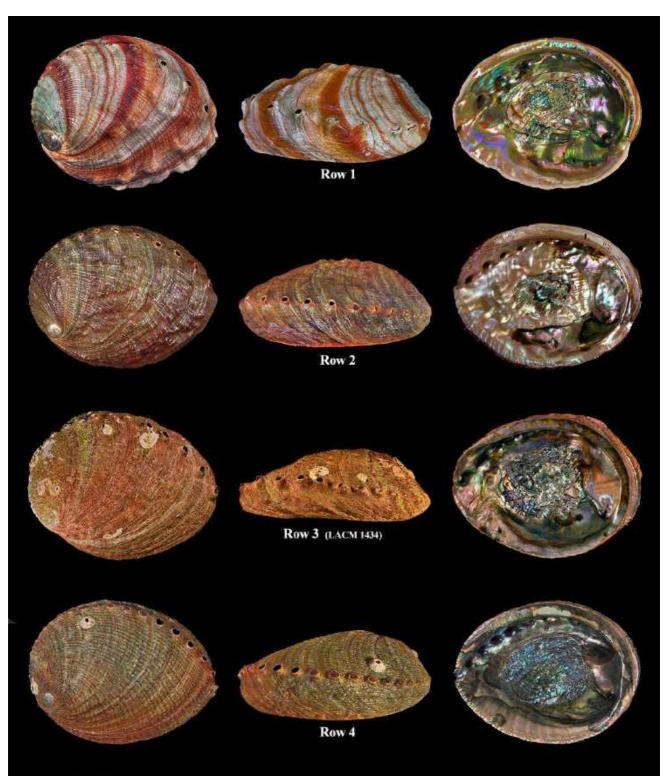
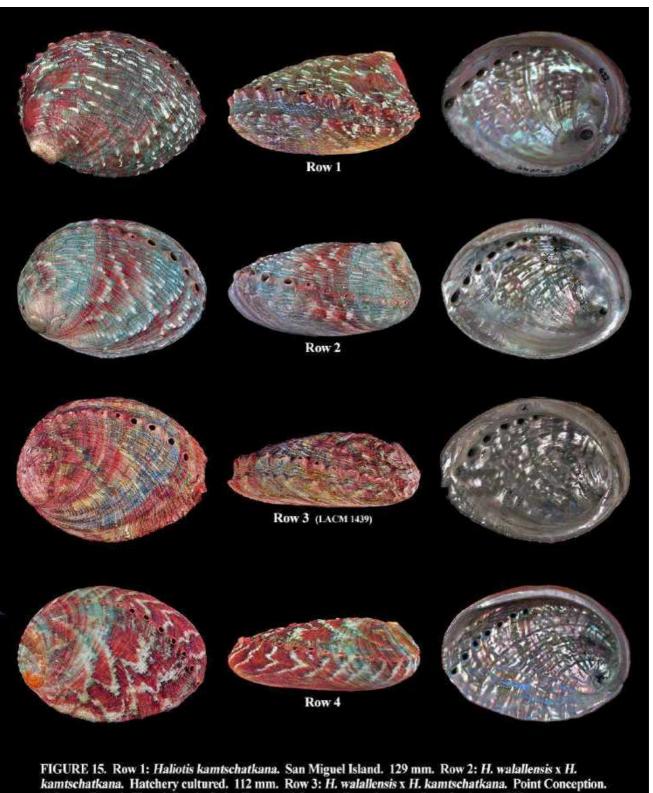


FIGURE 14. Row 1: Haliotis rufescens. Point Estero. 204 mm. Santa Barbara Island. 165 mm. Row 2: H. rufescens x H. fulgens. Gull Rock, Santa Cruz Island. 177 mm. Row 3: H. rufescens x H. fulgens. Santa Cruz Island. 200 mm. Row 4: H. fulgens. La Jolla. 210 mm. All specimens collected prior to 1965.



116 mm. Row 4: H. walallensis. Point Estero. 106 mm. All specimens collected prior to 1980.

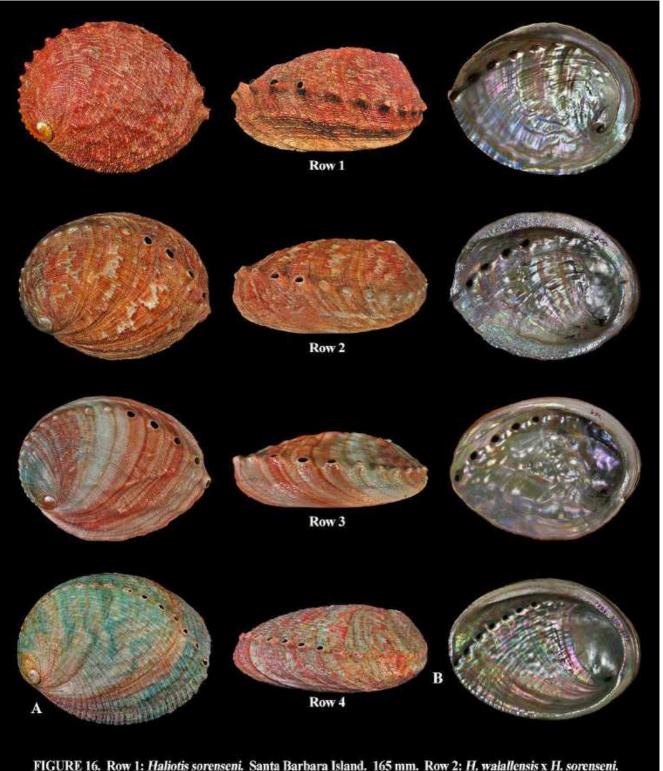


FIGURE 16. Row 1: Haliotis sorenseni. Santa Barbara Island. 165 mm. Row 2: H. walallensis x H. sorenseni. Santa Cruz Island. 157 mm. Row 3: H. walallensis x H. sorenseni. Point Loma. 126 mm. Row 4: H. walallensis. Baja California, Mexico. A - 136 mm. B - 145 mm. All specimens collected prior to 1985.

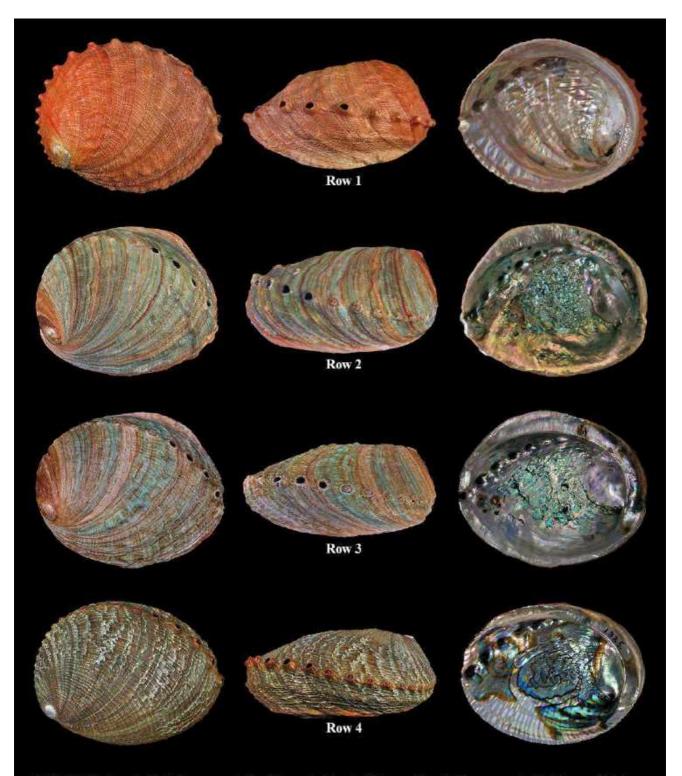


FIGURE 17. Row 1: Haliotis sorenseni. San Clemente Island. 209 mm. Row 2: H. sorenseni x H. fulgens. Hatchery cultured by David Leighton. 141 mm. Row 3: H. sorenseni x H. fulgens. Hatchery cultured by David Leighton. 163 mm. Bottom row: H. fulgens. Santa Cruz Island. 158 mm. All specimens collected or cultured prior to 1980.