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Haliotis kamtschatkana Jonas, 1845 – a Single Species, not a Pair of Subspecies

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ABSTRACT *Haliotis kamtschatkana kamtschatkana* Jonas, 1845, and *Haliotis kamtschatkana assimilis* Dall, 1878, are shown to represent a single species, *Haliotis kamtschatkana* Jonas, 1845. This conclusion is reached by an extensive examination of shell specimens throughout the range of the species and of the animal itself. This conclusion is corroborated by no genetic differentiation existing between the subspecies at the molecular level (Gruenthal and Burton, 2005; Supernault, *et al.*, 2010). Photoplates of specimens illustrate differences in shell morphology and colorations at various locations throughout the range of the species.

KEYWORDS Haliotidae, *Haliotis*, *Haliotis kamtschatkana*, polymorphic, variability.

INTRODUCTION Worldwide, there are over 80 species, subspecies, and forms of Family Haliotidae. As late as 1965, eight of these were species level taxa endemic to the Eastern Pacific coast, ranging from Sitka, Alaska, USA to central Baja California, Mexico including the offshore islands of this area. One species, *Haliotis kamtschatkana* Jonas, 1845, was described from specimens reportedly from Unalaska Island, in the Aleutian Islands, Alaska. However, this was clearly an error, as the species is not found north of Salisbury Sound, about 20 km north of Sitka, Alaska. A second species**,** *Haliotis assimilis* Dall, 1878, was described from specimens from Monterey and San Diego, California. Figure 1 juxtaposes four shell specimens, two from the northern range and two from the southern range. Given the distance separating these localities is roughly 1500 km and they appear significantly different in morphology and coloration, it is understandable how two distinct species were originally designated.

Owen began observing these two species initially as a commercial abalone diver and eventually as an aquaculturalist. One particular trait that Owen observed is that these two species occasionally exhibited a spiral orange band as shown in Figure 1 (specimens 3 and 4). Even with this band, the specimens shown in Figure 1 still exhibit markedly different shell morphologies. Owen also observed very 'intermediate' specimens of the two species in which the animal looked the same but the shell morphology had characteristics of both *H. kamtschatkana* and *H. assimilis* (*see* original species descriptions in Jonas, 1845, and Dall, 1878). In 1959, after five years examining a growing amount of material, Owen became convinced the pair of taxa represented subspecies rather than full species. It was Owen's observations and working with James H. McLean that led to these two species being reclassified as subspecies (*H. kamtschatkana kamtschatkana* and *H. kamtschatkana assimilis*) as captured in McLean's 1966 doctoral dissertation while at Stanford University (McLean, 1966). The epipodia were identical and only morphological shell characteristics were observed to differentiate the two subspecies (McLean, 1966).

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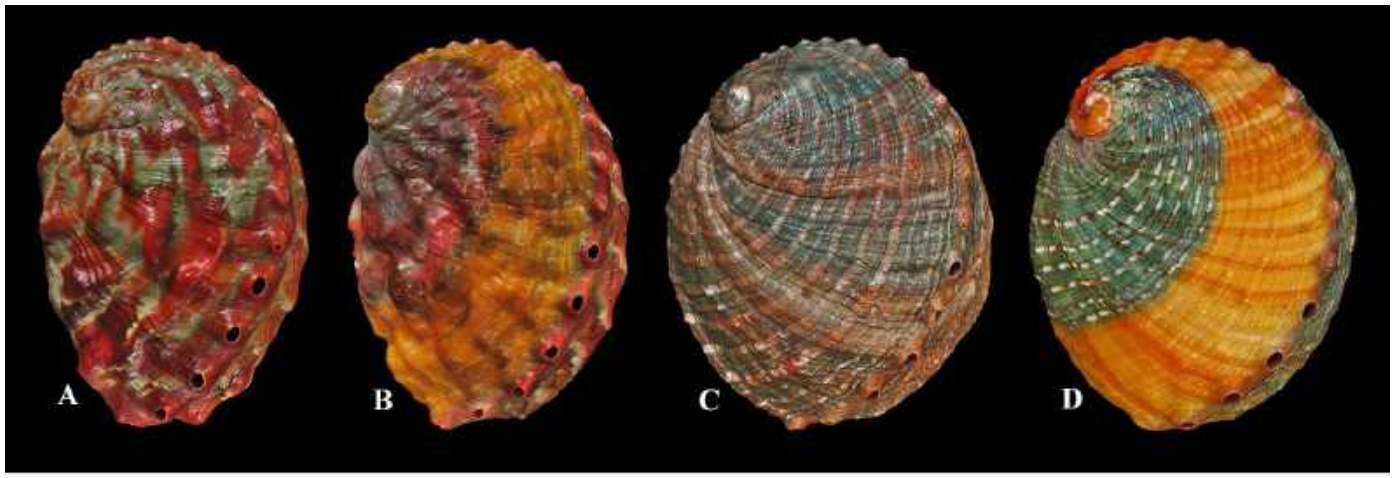

FIGURE 1. ***Haliotis kamtschatkana.*** **A - Denman Island, British Columbia, Canada. 100.5 mm; B - Point Arena, California, USA. 115.4 mm; C - Point Loma, California, USA. 131.2 mm; D - Northern Baja California, Mexico. 101.4 mm. All live-taken by diving. 3-20 m.**

Since then, both authors have endeavored to observe shell specimens in massive quantities throughout the range of the *kamtschatkana* species as well as occasional live specimens encountered in the Pacific Ocean or in marine laboratories. Genetic tests of abalone species among the northeastern Pacific Ocean designed for use in forensic purposes in the British Columbia courts (for enforcement actions against poachers) can distinguish the seven North American species of abalone based upon sequence differentiation (Supernault, *et al.*, 2010). An analysis of lysin and VERL sequences in the eastern Pacific abalone species confirmed the previously hypothesized close evolutionary relationships among North American abalone species (McLean, 1966; Geiger, 2000; Gruenthal and Burton, 2005; Supernault, *et al.*, 2010). Two genetic tests readily differentiate "pinto/threaded" abalone from the remaining six North American abalone species, however *H. kamtschatkana kamtschatkana* and *H. kamtschatkana assimilis* are indistinguishable through molecular analysis of nuclear DNA, lysin, or traditional COI mitochondrial sequences (Gruenthal and Burton, 2005; Supernault, *et al.*, 2010). The fact that these two supposed subspecies cannot be distinguished through molecular analysis suggests that any differences in shell morphology may not reflect a restriction in gene flow, but may result instead from environmental influences or a simple Mendelian polymorphism (Supernault, *et al.*, 2010). The remainder of this paper explains why there are not two species, or even two subspecies at hand, but rather one single species that exhibits a remarkable plasticity in shell attributes including morphology and coloration.

Abbreviation of collections: BOC: Buzz Owen Collection, Gualala, CA, USA; ARC: Arjay Raffety Collection, Marina del Rey, CA, USA; AMC: Athena Maguire Collection, Freestone, CA, USA**;** JLC: Julian Lee Collection, Los Angeles, CA, USA; JCC: Johnathan Centoni Collection, Trinidad, CA, USA.

Materials and methods: Shell specimens photographed were cleaned with any of the following tools: Xacto tool with #11 blade, dental scalers, wire brushes, 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

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Adobe Photoshop Version 6 and placed on black plates.

Shells examined: *Haliotis kamtschatkana*: Alaska, USA, to British Columbia, Canada: >500 specimens; North Coast of California (Fort Ross to Mendocino/Fort Bragg), USA: >250 specimens; Cambria to Point Conception, California, USA: >5,000 specimens; Point Loma, California, USA, to Baja California Norte, Mexico: >20,000 specimens.

DISCUSSION

Haliotis kamtschatkana has an expansive range from Alaska, USA, to Baja California, Mexico, and there are definitely classic 'northern' and 'southern' looking shell morphologies as described immediately below. As the plates are introduced, particular features to note within localized ranges are discussed. Additionally, there are several other Eastern Pacific Gastropods that have expansive ranges similar to *H. kamtschatkana*. These include the following species that range from Alaska, USA, to Baja California, Mexico: *Bathybembix bairdii*, *Cidarina cidaris*, *Nucella ostrina*, *Calliostoma annulatum*, *Astraea (Pomaulax) gibberosus*, *Ceratostoma foliatum*, *Lottia gigantea*, *Ocinebrina interfossa*, and *Ocinebrina lurida*.

The shells which exhibit a 'northern morphology' have a more elongated overall shape, lighter weight, 3 to 6 open holes (tremata), exhibit a somewhat lumpy surface with prosocline ridges/folds emanating from the apex of the shell but not extending to the row of holes, and a spire that is more pronounced rather than flush with the suture. With respect to colors, some shells have a solid color but are generally orange or red. Most shells have some sort of patterning, usually a blotchy white or green, and uncommonly, a shell exhibits a spiral orange band (*e.g.* Figure 1-B) and even more uncommonly a spiral green band (Figures 6-T and 11-D). With respect to sculpture, most shells have ribs that are muted in height, sometimes without minor threads interspersed between major ribs, and sometimes with no discernable ribs or minor threads at all (smooth). The shell is generally much thinner and therefore more lightweight than the 'southern morphology' forms. Though some shells exhibit some very prominent prosocline ridges about the apex, others can exhibit almost no undulations but are still thin. There is usually a fairly deep channel in the peripheral area between the row of holes and the columella.

The shells which exhibit a 'southern morphology' have a more rounded overall shape, medium weight, 4 to 7 open holes (tremata), exhibit a fairly smooth surface with raised and/or colored spiral ribs, and a spire that is more flush with the suture. With respect to colors, some shells have a solid color (orange, red, green, and rarely white), some have variable colored ribs that resemble porcupine quills, some exhibit pinwheel color patterns, and about 5 to 10% of the population exhibit a spiral orange band (*e.g.* Figure 1-D). Rarely, this spiral band is red (Figure 10-R) or green (Figure 10-I), rather than orange. With respect to sculpture, most shells exhibit raised ribs and usually there are 10 to 16 wider ribs with sets of 3 to 4 minor threads in between the major ribs. The shell surface can range from nearly smooth to somewhat lumpy (having prosocline ridges/folds) in a small percentage of specimens. The shell is generally thicker and therefore more medium in weight than the 'northern morphology' specimens. Some southern shells are extremely deep, resembling hemispheres (Figure 10-A, B). There is a groove between the row of holes and the columella but not as pronounced as the deeper channel found in the specimens exhibiting more northern morphology.

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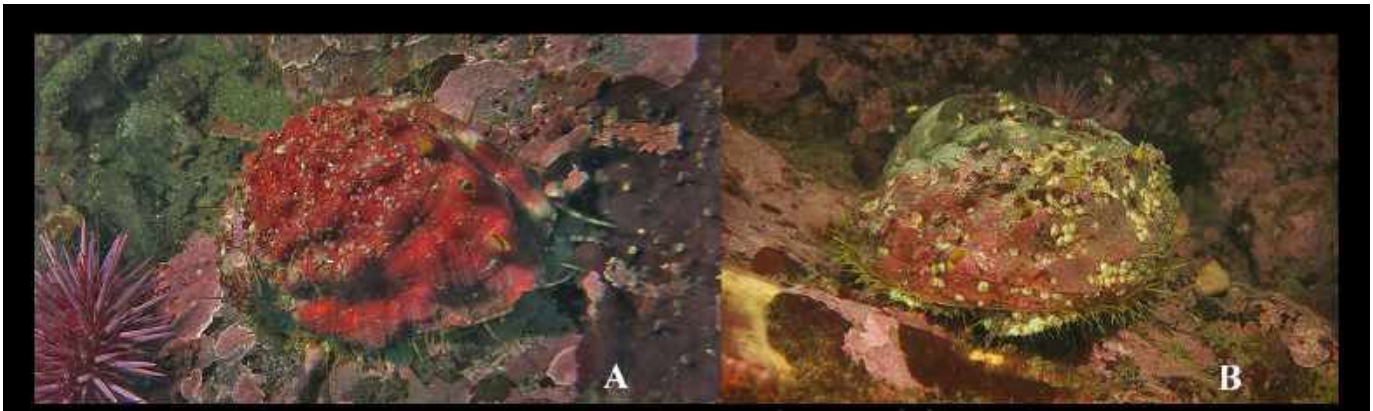

FIGURE 2. *Haliotis kamtschatkana* Jonas, 1845. Live animals photographed *in situ* near Mendocino, California, USA. Estimated size approximately 80-100 mm. 11 m. Photographed by Kevin Joe. August, 2014.

The animal appears similar throughout the range with the only variable being the intensity of color particularly around the outer margin of the foot (which is a more intense orange in northern populations). Epipodial characteristics are commonly used to delineate abalone species, however there are no observable differences throughout northern or southern populations of the animal. This is true of the radulae as well (Geiger & Owen, 2012).

Figures 3 through 5 exhibit images of shell specimens from Alaska, USA, to British Columbia, Canada. Within this northernmost range, almost all of the shells maintain the 'northern morphology' and the presence of a spirally oriented orange band is very rare. Solid orange specimens are commonly found within these populations. The shells examined in this range exhibit extensive variability (some smooth, some wavy, varied color patterns, etc.) and are usually very thin and lightweight likely due to the fact that they exist in inland passages and do not endure surf conditions.

Figures 6 and 7 contain images of shell specimens from the north coast of California, USA. These specimens more frequently resemble the 'northern morphology' though there are some that exhibit a more southerly aspect**.** There is less color variability in this range (mostly red and orange base color with white/green blotches) and this is due to the consistent diet of various species of red algae, though occasional specimens exhibit bands of shell increment of a lighter color due to a change in diet to a species of brown algae (probably *Nereocystis luetkeana*) Figure 7-B. The spiral orange band color form is found a little more often in this range though usually only around 10% of shells exhibit it. The shells are generally more rugged and heavy likely due to the surf conditions along the rocky coastline in which they exist.

Figure 8 exhibits a number of shell specimens collected in Cambria, California, USA. At this point in the species distribution, there is more variability in shell coloration and patterns. Some of the specimens have a very 'northern morphology' (Figure 8 A-H) while others maintain a more 'southern morphology' as exhibited on the bottom two rows of this Figure (Figure 8 M-T); additionally, there are also many intermediate specimens demonstrating a combination of southern and northern characteristics (Figure 8 I-L)**.** The orange band

color form as well as solid orange specimens are also found in this range.

Figure 9 exhibits images of shell specimens from the Channel Islands and the Point Conception area of California, USA. Most of the shells from this area adhere to the 'southern morphology' in that they are fairly round in shape, lack waviness, are fairly heavy, and have well defined ribs. The color forms show wide variability with orange banded and solid orange color forms distributed throughout these localities. It should be noted, that the largest specimens of the species have been found in the area five to eight kilometers southeast of Point Conception likely due to the abundance of kelp that exists in this region.

Figure 10 contains images of shell specimens collected in Baja California, Mexico. The authors note the extreme variability in shell coloration and patterns exhibited by these specimens. Anywhere from 5 to 10% of the specimens examined from the range contain a spiral orange band and solid orange specimens are also found. The sculpture of the shell can also be quite variable ranging from smooth to strongly ribbed and sometimes with prosocline folds/ridges. More significantly, the authors emphasize that though uncommon, some specimens exhibit the 'northern morphology' with respect to prosocline waviness emanating from the spire but not reaching the row of holes and are somewhat more elongated (*see* Figure 11 G-L). Additionally, the channel (groove) located in the peripheral area between the row of holes and columella is deeper and more pronounced. Figure 11 reveals that specimens of the 'northern morphology' can be found *throughout* the species distribution from Alaska, USA, to Baja California, Mexico, that include the spiral orange banded color form (Alaska, USA: Figure 3-N, Baja California, Mexico: Figure 11-L).

It should be noted that shell specimens of *H. kamtschatkana*, particularly the 'northern morphology', are sometime confused with *H. discus* (particularly subsp. *hannai*), which is found in the northwestern Pacific Ocean. This species is also a member of the Nordotis group of *Haliotis* along with *H. kamtschatkana* (Geiger & Owen, 2012). Although *H. discus* currently consists of 2 subspecies, it is also very variable in morphology (similar to *H. kamtschatkana*) and subspecific designation may not be required for the species.

CONCLUSION

It has been demonstrated that shells exhibiting both 'southern' and 'northern' morphology are observed throughout the species distribution from at least southern Oregon, USA, to its southern-most point in central Baja California, Mexico. The Alaska, USA, population consists predominantly of shells which exhibit the 'northern' morphology and share marked similarity to shells found in Canada and Washington, USA. Both southern and northern looking shells exhibit the spiral orange band but the propensity for this to occur varies from roughly 10% in the southernmost range to almost 0% in the northernmost range. Intermediate specimens of the 'northern' and 'southern' morphologies are found throughout the entire range as well. In conclusion, *Haliotis kamtschatkana* is a single highly polymorphic and color variant species that exhibits most variability in its southern range and significant but less variability in the northernmost range.

Gruenthal and Burton, 2005, and Supernault, *et al.*, 2010, corroborate the authors' conclusion that the two formerly recognized subspecies are a single species and cannot be distinguished at a molecular level between animal specimens examined throughout the distribution range of

Haliotis kamtschatkana from Alaska, USA, to central Baja California, Mexico.

ACKNOWLEDGEMENTS

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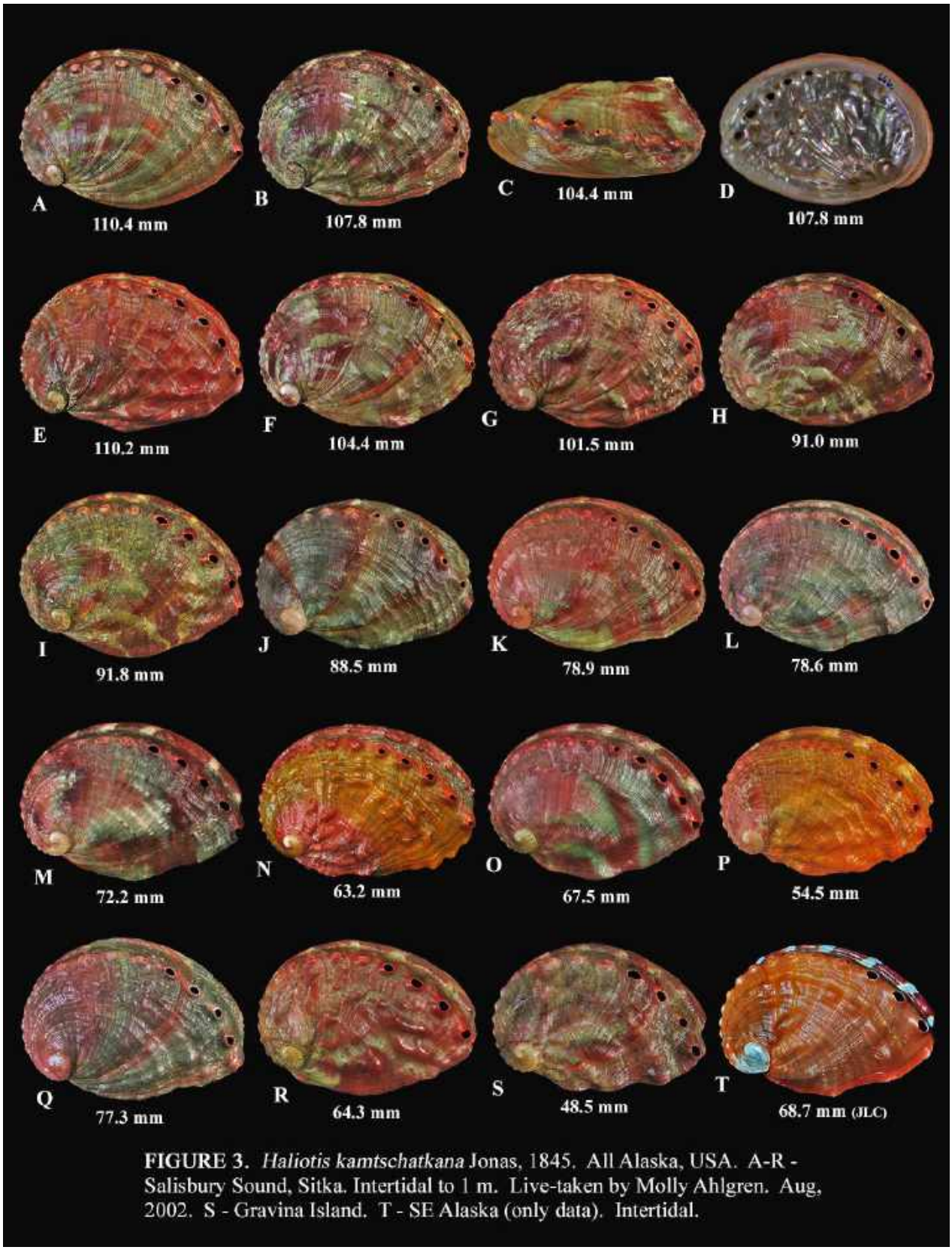

FIGURE 3. *Haliotis kamtschatkana* Jonas, 1845. All Alaska, USA. A-R - Salisbury Sound, Sitka. Intertidal to 1 m. Live-taken by Molly Ahlgren. Aug, 2002. S - Gravina Island. T - SE Alaska (only data). Intertidal.

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FIGURE 4. *Haliotis kamtschatkana* Jonas, 1845. All Strait of Georgia, British Columbia, Canada. A-G - Denman Is. H-I - Prince Rupert. J-M - Nanoose Bay. N-P - Near Nanaimo Mar. Sta. Q - Victoria Breakwater. R-T - .5 km north of USA-Canadian border. All live-taken intertidal to 15 m. 1960-1964.

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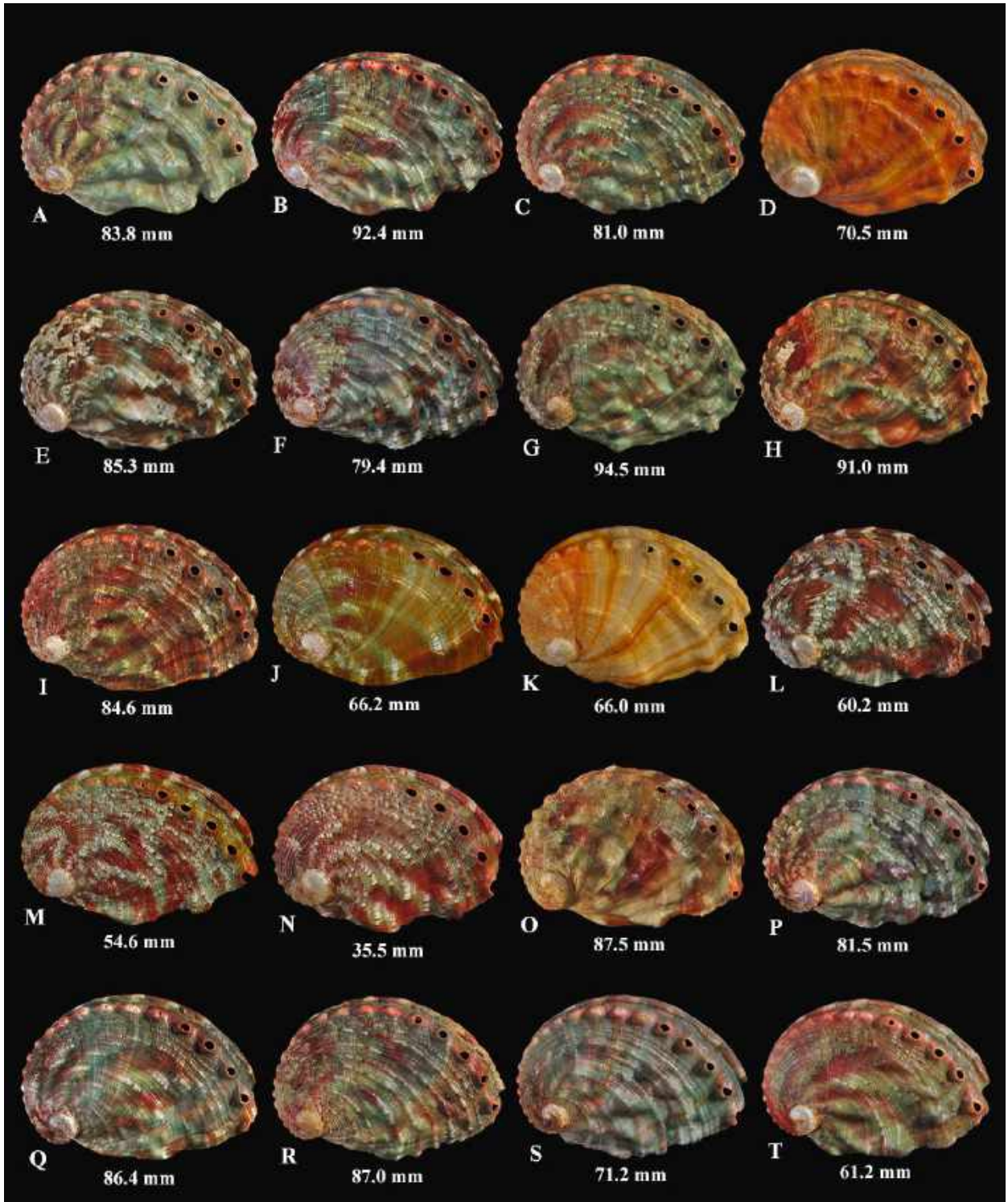

FIGURE 5. *Haliotis kamtschatkana* Jonas, 1845. All Queen Charlotte Islands, British Columbia, Canada. A-E - Bauke Island, Barkley Sound. F-H - Tasu Sound. I-N - Hope Island, near Bull Harbor entrance. O-T - Sivart Island, East coast of Moresby Island. All live-taken 10-12 m. 1960-1965.

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FIGURE 6. *Haliotis kamtschatkana* Jonas, 1845. All California, USA. A-Q - Live-taken Little River, August, 1955. 8-10 m. R - Live-taken S.E. Farallon Island, July, 1959. 20 m. S - N. Farallon Island, 1962. 15 m. Dead collected. T - Fort Bragg. 15 m. Dead collected. 8-10 m.

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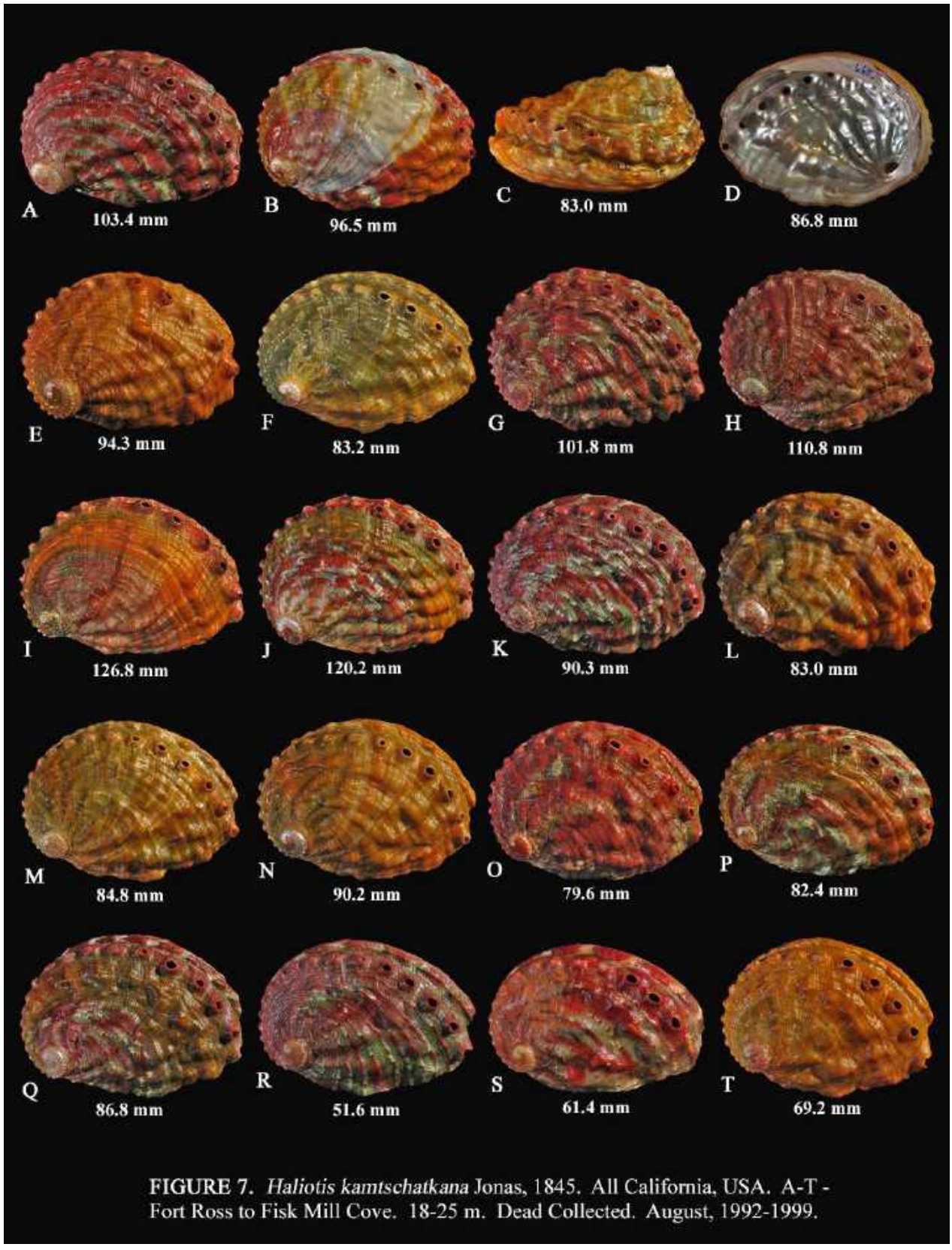

FIGURE 7. *Haliotis kamtschatkana* Jonas, 1845. All California, USA. A-T - Fort Ross to Fisk Mill Cove. 18-25 m. Dead Collected. August, 1992-1999.

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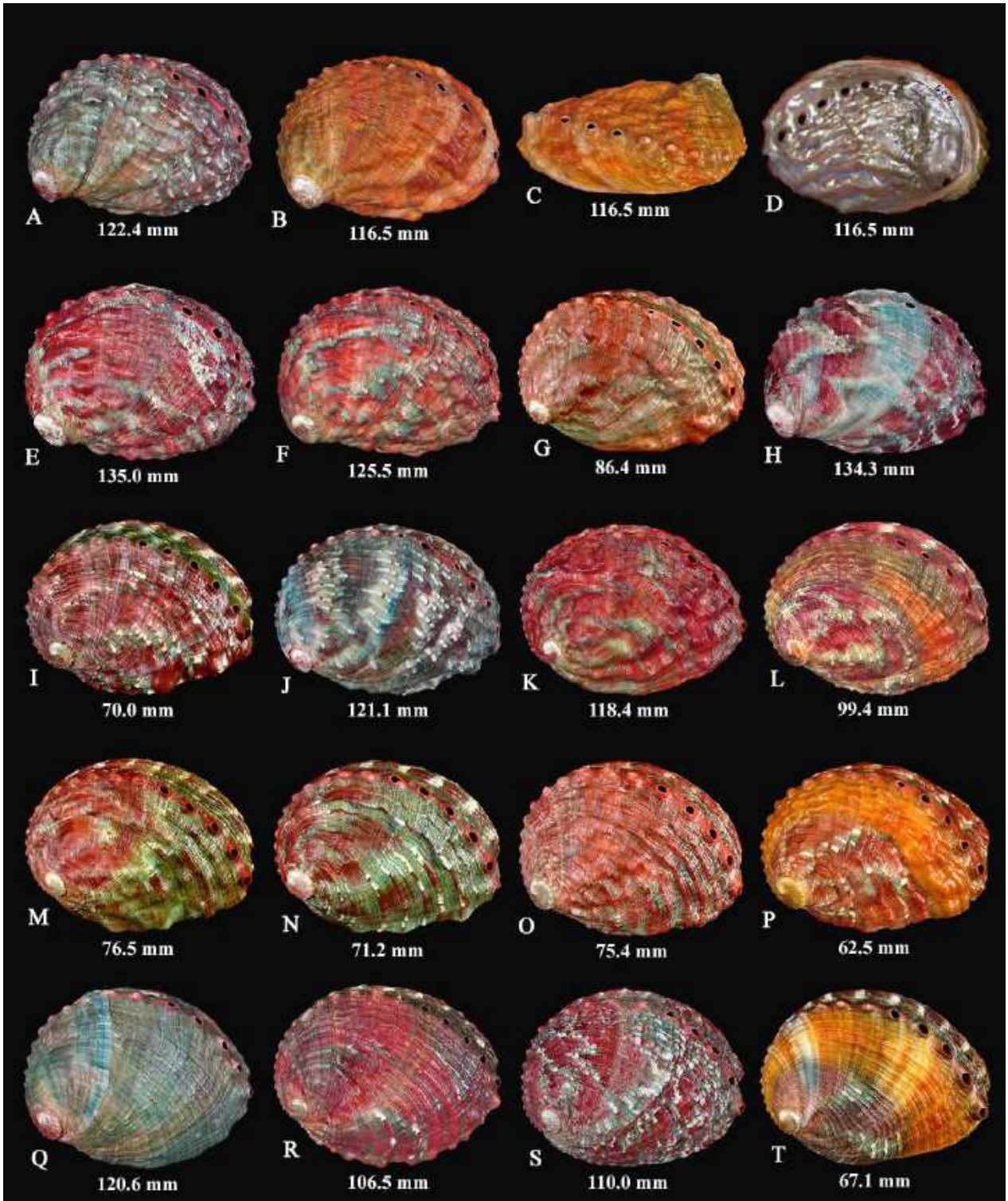

FIGURE 8. *Haliotis kamtschatkana* Jonas, 1845. All California, USA. Cambria to Pt. Estero. 1962-1965. 20-25 m. A-H: Specimens selected illustrating more "northern" morphology. I-L: Non-selected specimens. M-T: Specimens selected illustrating more "southern" morphology. Collected by Buzz Owen.

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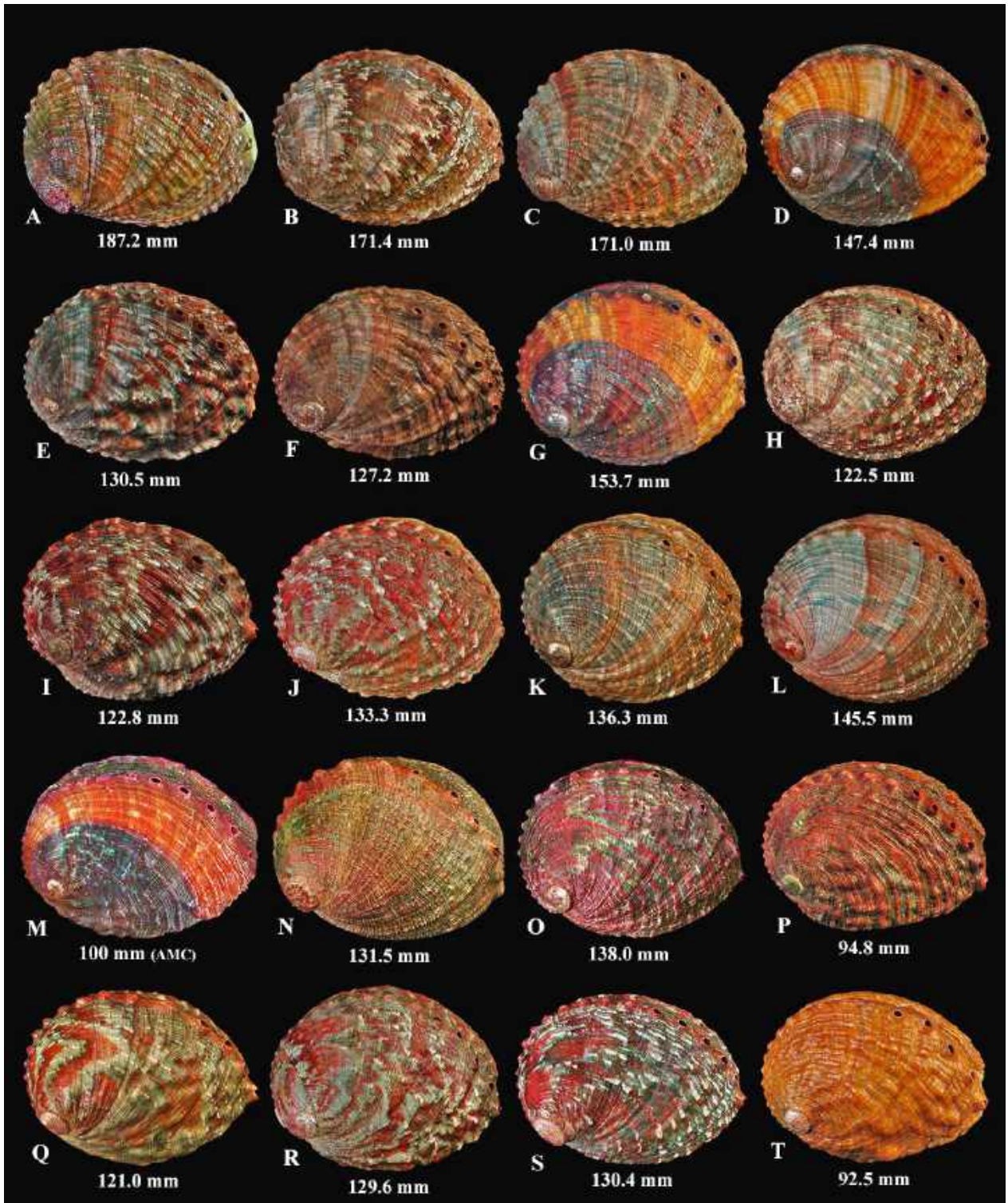

FIGURE 9. *Haliotis kamtschatkana* Jonas, 1845. All California, USA. A-J - 6 km E. of Pt. Conception. K - Pt. Loma. L - Bird Rock, La Jolla. M - Palos Verdes. N - So. side Anacapa Is. O - Yellowbanks, Santa Cruz Is. P - Ford Pt., Santa Rosa Is. Q - Sand spit, San Nicolas Is. R-S - San Miguel Is. T - Pt. Arguello. All live-taken 1959-1962 except M & O dead 2016. 20-25 m.

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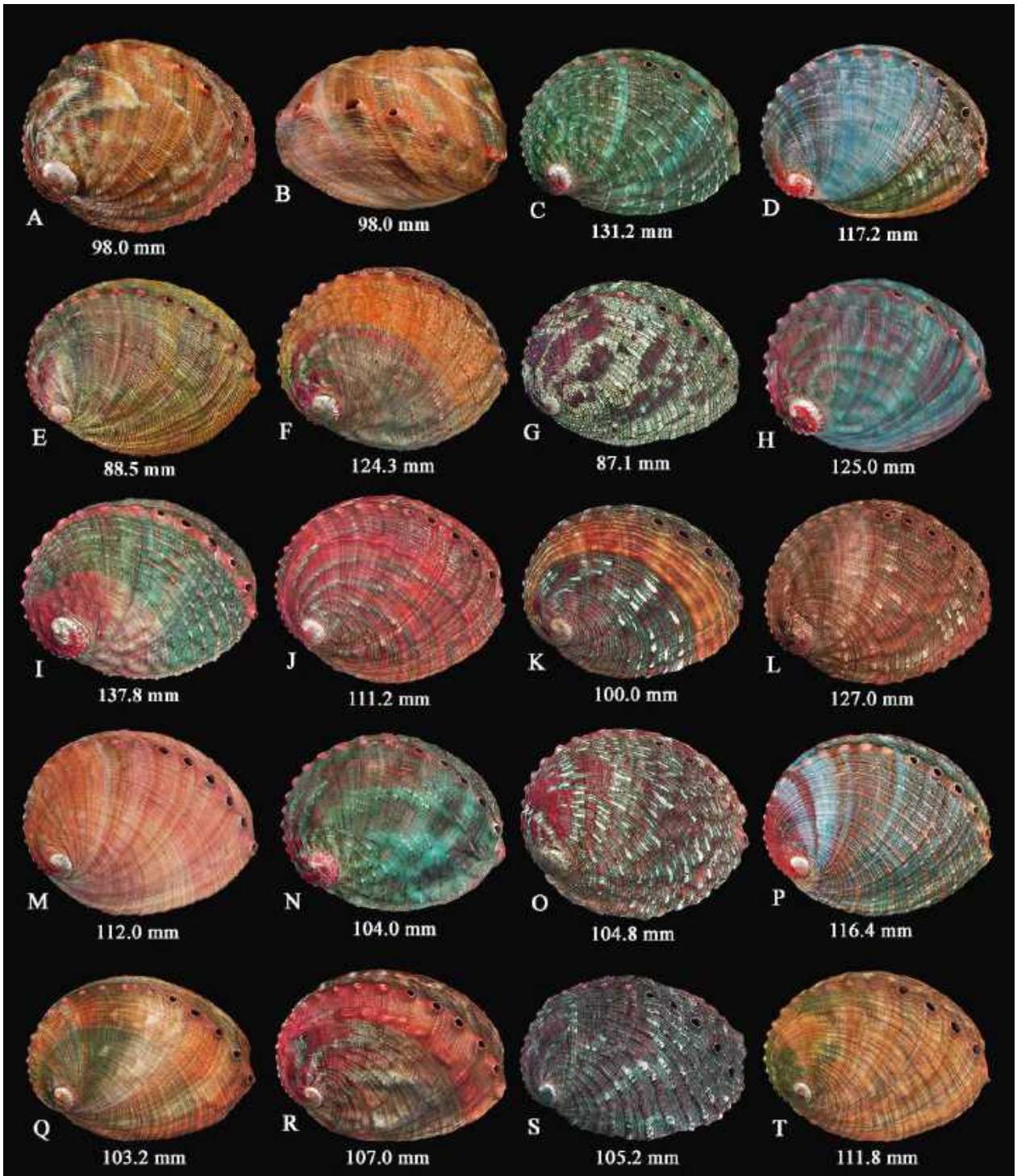

FIGURE 10. *Haliotis kamtschatkana* Jonas, 1845. A-B - Guerrero Negro area , Baja California Sur, Mexico. C-T - Northern Baja California, Mexico. **NOTE:** The deep "hemisphere" proportion (A-B) may demonstrate the extreme southern form commonly found in the Guerrero Negro area of central Baja California. Guerrero Negro is hundreds of kilometers south of where specimens C-T were likely taken. Further study of additional Guerrero Negro shells is needed to better understand this population, which may be very near the southern limit of the species.

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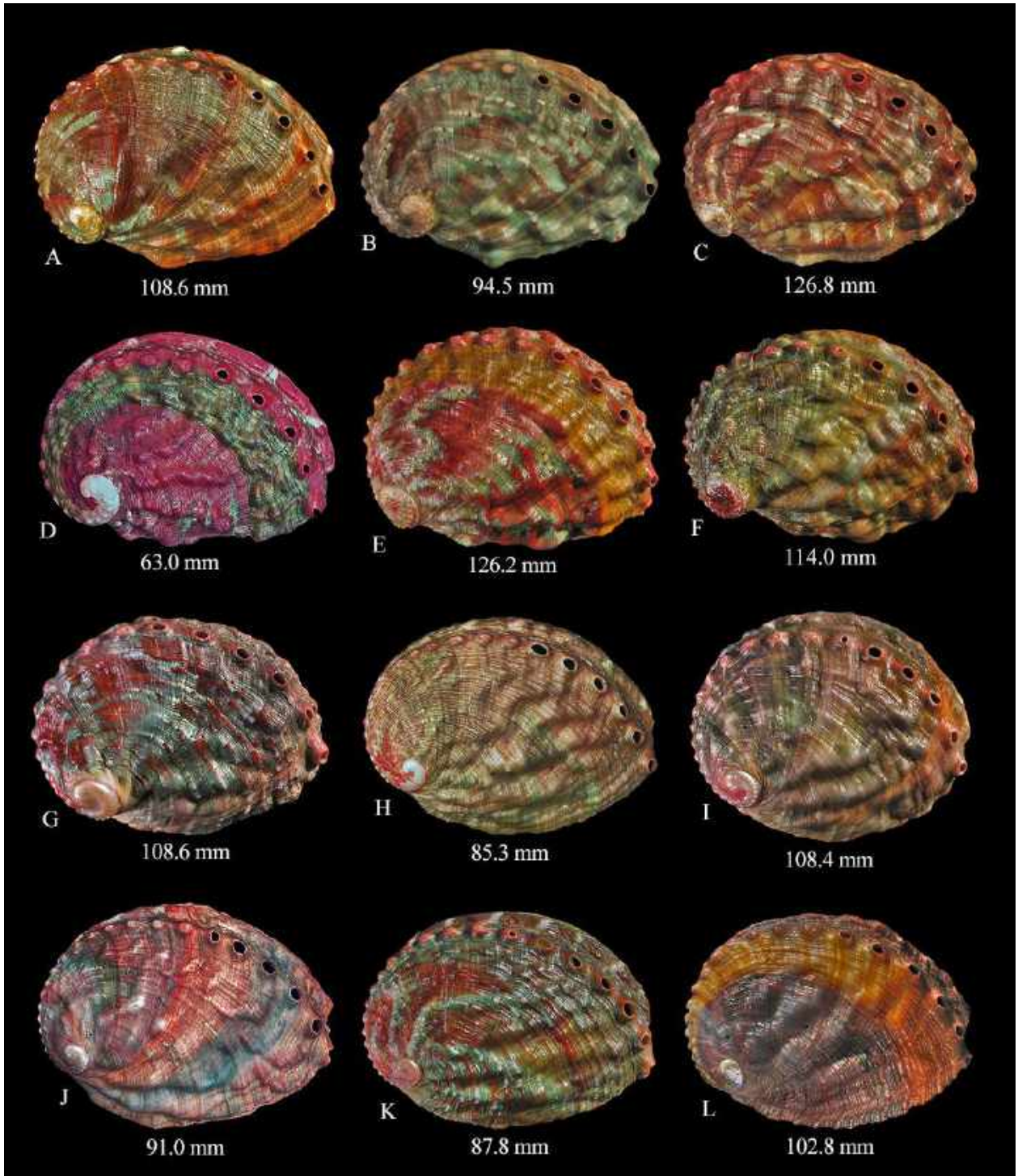

FIGURE 11. A - Salisbury Sound, Sitka, Alaska, USA. B - Nanaimo, Strait of Georgia, British Columbia, Canada. C - Prince Rupert, Strait of Georgia, British Columbia, Canada. D - Elk, California, USA. E-F - Fisk Mill Cove, California, USA. G-L - Northern Baja California, Mexico. Note deep folded ridges in the Baja California specimens which are remarkably similar to specimens A-F from Alaska to Northern California. USA.