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A New Species of Abalone (*Haliotis*) from Greece

BUZZ OWEN[1], SHARON HANAVAN[2] AND STEWART HALL[2]

[1] P.O. Box 601, Gualala, California, USA 95445

[2] 115 Oakwood Place, Scotts Valley, California, USA 95066

Abstract. An undescribed species of *Haliotis* has been discovered in the Aegean and Ionian Seas. It is described herein as *Haliotis* ***mykonosensis***, sp. nov. Although shell morphology of this new species is often similar to the sympatric *Haliotis tuberculata lamellosa* Lamarck, 1822, characteristics of the epipodium and other anatomical features of the soft body parts and analysis of shell measurements show that the two species are clearly distinct. Furthermore, differences in behavior and in the reproductive cycles of these two species have been observed. Epipodial characteristics are also compared with the other Mediterranean taxa *Haliotis stomatiaeformis* Reeve, 1846, and the immigrant *Haliotis pustulata* Reeve, 1846. In addition to epipodial comparisons, shell measurement comparisons have been made with the above three species.

INTRODUCTION

Haliotis tuberculata lamellosa Lamarck, 1822, a variation of *H. tuberculata* Linnaeus, 1758, previously recognized as a subspecies (Geiger, 1998), collected throughout the Mediterranean Sea is known to have highly variable shell characteristics (Ubaldi, 1987). This is also true in the Aegean, Adriatic, and Ionian seas (B. Owen, personal observation). The new species described herein closely resembles *H. t. lamellosa* in shell morphology, and has probably been overlooked in previous collections due to the lack of studies involving the intact animal. The soft parts of *H.* ***mykonosensis*** differ most conspicuously in the epipodium, a tentacle-bearing structure, which has a sensory function, and originates from the side of the foot, projecting laterally beyond the edge of the shell (Owen et al., 1971; Cox, 1962). This structure is highly species-specific in its detail and has been used as a primary identifying feature for species (Ino, 1952; Cox, 1962).

Between 1981 and 1997, Owen made a series of trips to study the abalone populations on 11 Greek Islands (Table 1). In 1992, while on the island of Mykonos, Owen observed that some of the abalone had epipodia that were very different from the common *Haliotis tuberculata lamellosa* they were living beside. Epipodial characteristics were also compared with the other Mediterranean taxa *Haliotis stomatiaeformis*[1] Reeve, 1846, and the immigrant *Haliotis pustulata* Reeve, 1846.

MATERIALS AND METHODS

Live abalone were usually found at depths of 1–3 m. Rarely were they found at depths greater than four m. Owen collected a total of 154 *Haliotis* ***mykonosensis*** during the same period that he observed or collected approximately 3000 *Haliotis tuberculata lamellosa.* The live specimens were either kept alive in containers of seawater or preserved in 70% isopropyl alcohol. Living material was transported to Gualala, California in 1988, 1991, 1996, and 1997 and maintained by author Owen in several 13 liter aquariums with filtered seawater collected from the local shoreline. A total of 46 *H.* ***mykonosensis*** and 45 *H. t. lamellosa* have been studied in aquaria.

Morphological comparisons between the two species involved 154 *Haliotis* ***mykonosensis*** and more than 200 *H. t. lamellosa* specimens collected live from the same localities. Radular preparations were examined by scanning electron microscopy. Behavioral contrasts and differences in gonadal development with season were observed in live specimens. Comparisons of epipodia were also made with alcohol-preserved *H. stomatiaeformis* and *H. pustulata.*

Thirty *H.* ***mykonosensis*** and 32 *H. t. lamellosa* shells, similarly lacking lamellae formation and comparable in size, were measured for length, width, spire height, and several measurements associated with the suture line (the line formed by the respiratory pores). Data collected on shell measurements are listed in Table 2. Statistical analysis of the above measurements was performed. In the analysis, the size of the shell was normalized by dividing

[1] In a 1998 manuscript on the genera and species of Haliotis, Geiger listed a second Mediterranean species *Haliotis neglecta* Philippi, 1848, as both a separate species (Geiger, 1998: table 2) and as a subspecies of *H. tuberculata* (Geiger, 1998: note 5) based only on seven shells. Additional material provided by B. Owen (personal observation) clearly shows the species to be distinct from *H. tuberculata* and that the correct name for this second Mediterranean species should be *H. stomatiaeformis* (Geiger & Owen, manuscript in progress). The correct name for this species is used herein.

Table 1

Specimen Collection Data

Locale	Years	Number of dive sites	Hours dived (Approx.)	Total *H.t. lamellosa*	Total ***H. mykonosensis***
Hydra	1981, 1992	3	8	30	0
Mykonos	1981, 1991, 1992, 1996	6	50	150[1,2]	46[3]
Skiathos	1988	3	20	20[4]	0
Rhodes	1988	2	11	15[4]	0
Paros	1991, 1992	5	25	50[5]	5
Santorini	1991, 1996	4	12	12	0
Corfu	1992, 1997	12	25	260[1,6]	94[7]
Chios	1992	3	12	30[5]	3
Samos	1992	5	12	100[5]	6
Naxos	1992	4	10	75[5]	0
Crete	1996	4	15	200[8,9]	9
Totals	6	51	> 200	942	154

[1] > 500 observed alive but not taken
[2] 37 brought to U.S. alive in 1991
[3] Seven brought to U.S. alive in 1991 (5) and 1997 (2)
[4] Three brought to U.S. alive (from each island)
[5] > 250 observed alive but not taken
[6] Seven brought to U.S. alive in 1997.
[7] 41 brought to U.S. alive in 1997
[8] > 1000 observed alive but not taken
[9] Two brought to U.S. alive in 1996

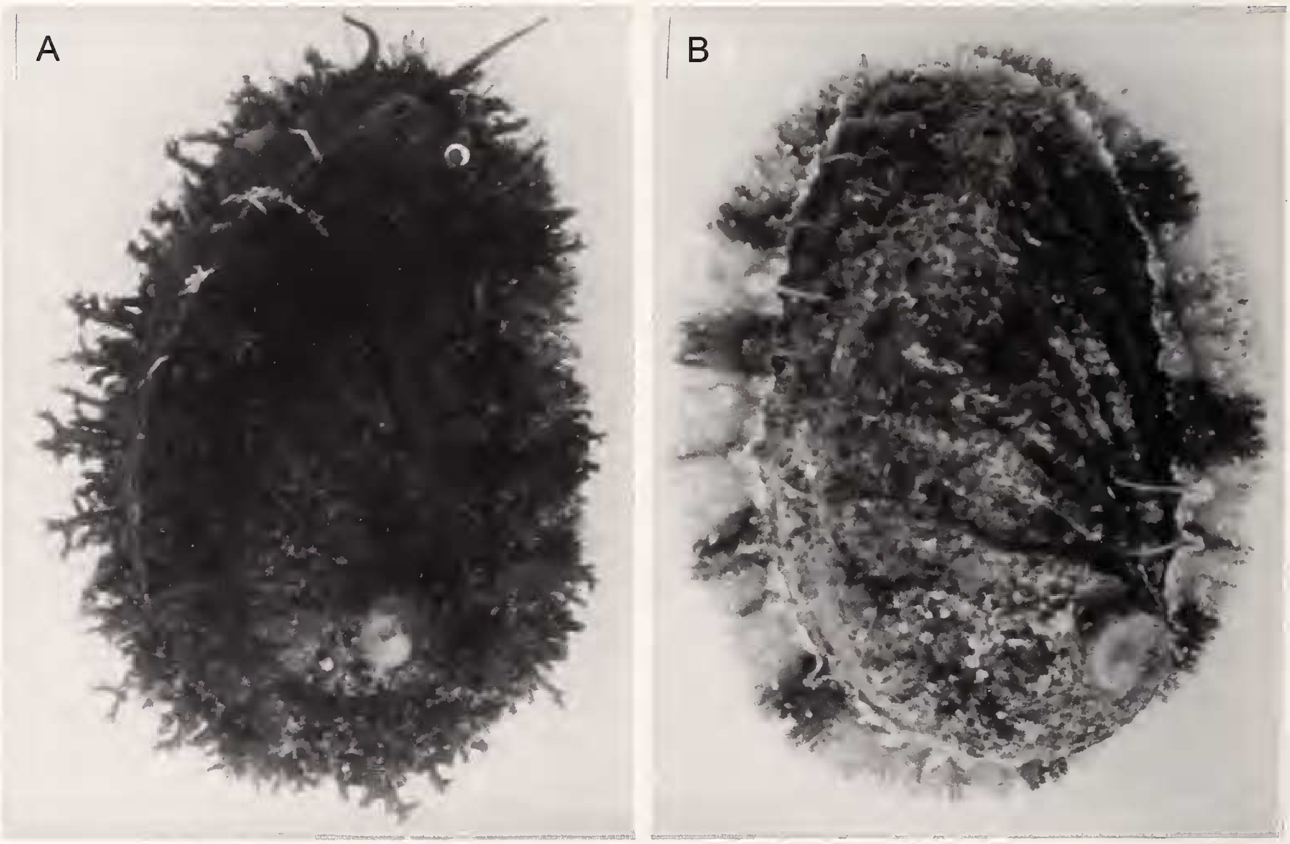

Figure 1. Live animals dorsal view. A. *H.* ***mykonosensis*** Owen, Hanavan & Hall, sp. nov., 39 mm long. B. *H. t. lamellosa,* 45 mm long. Photographs by B. Owen.

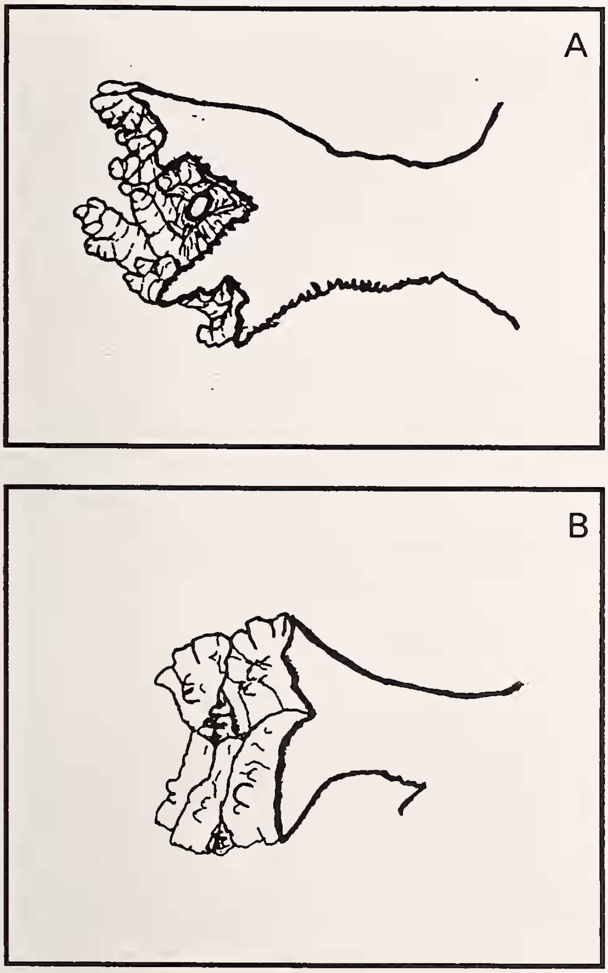

Figure 2. Vertical cross sectional drawing of epipodia of alcohol-preserved specimens. A. *H. **mykonosensis*** Owen, Hanavan & Hall, sp. nov., ×10. B. *H. t. lamellosa,* ×10.

each shell measurement by the shell's length. A one-way analysis of variance with 95% confidence intervals of the mean based on the pooled standard deviations was used to analyze width and spire placement (the ratio of the distance from the spire to the end of the suture line and the shell length).

The spire inflation was measured by the ratio of the shell's height at ⅕ the distance from the spire to the end of the suture line and the spire height (R1). The length measurement was not used to normalize this ratio. The distance from suture line to the widest edge of the columella when viewed from the top of the shell was measured and divided by the length (R2). These ratios were graphed against each other and analyzed using a statistical technique called discriminant analysis for multivariate statistics. A detailed discussion of this method can be found in Anderson (1984).

Other Animal Material Examined

Haliotis pustulata. D. L. Geiger collection, date 17 January 1987, Na'Ama Bay, Sinai, Egypt, Gulf of Aquaba; California Academy of Sciences, CASIZ 071896, 5 km SSW of Mora Mora Village, Madagascar, and CASIZ 102287, Tanzania, Zanzibar, north end, Ras Nunswi.

Haliotis tuberculata. D. L. Geiger collection, taken 24 March 1988, Banyuls-sur-mer, southern France, on rock at 0.5 m, brown; D. L. Geiger collection, taken 24 March 1988 Banyuls-sur-mer, southern France, on rock at 0.5 m, green; D. L. Geiger collection, taken 19 August 1989 Isla del Aire, Balearic Islands, Spain; California Academy of Sciences, CASIZ 102314, Ilha Sao Miguel, Azore Islands and CASIZ 099125, Cadiz, Strait of Gibraltar, Isla Tarifa.

Haliotis stomatiaeformis. B. Owen collection, #523 (with animal), Malta; D. L. Geiger Collection, AAB51a, Malta (shell only).

SYSTEMATICS

Family Haliotidae Rafinesque, 1815

Haliotis **mykonosensis** Owen, Hanavan & Hall, sp. nov.

(Figures 1A, 2A, 3 [left], 4 [left])

Type material: Holotype, California Academy of Sciences, CASIZ 112121. Platy Yialos, Mykonos, Greece, 2 m depth under small flat rock, 19 May 1996, collected by B. Owen. The dimensions of the holotype are: length 38.0 mm, width 23.5 mm, and height 7.8 mm. Paratypes (2), California Academy of Sciences, CASIZ 112122. Platy Yialos, Mykonos, Greece, 2–4 m depth under small flat rock, 19 May 1996, Collected by B. Owen. Paratype #1 measures length 34.5 mm, width 20.0 mm, and height 7.5 mm. Paratype #2 measures length 35.5 mm, width 21.0 mm, and height 7.2 mm.

Etymology: This species is named for the type locality, Mykonos.

Distribution: Thus far found only on five of the 11 islands surveyed. Most common at the more northern Greek islands studied, particularly Corfu. Less common at Mykonos (type locality) and rare at Paros, Chios, and Samos. Thus far found only in areas of *Poisidenea oceanica* (L.) (Riedl, 1983; Larkum et al., 1989), a broad-leafed (~1.5 cm wide) green "eel grass."

Shell morphology: The species exhibits a thin, oblong-ovate, flatly convex shell with between four and seven open respiratory pores. The exterior has fine, smooth spiral cording, with a shallow post-syphonic groove, infrequently found with lamellae at shell sizes smaller than 25 mm. The exterior shell coloration is variegated olive green, brown, and beige with an occasional totally orange form. The shell exterior often forms a fine radial tenting pattern of the other colors against the beige background.

Table 2

Shell Measurements

Specimen number	Length	Width	Spire to suture line end	Spire height	Shell height[1]	Distance from suture line[2]
H. mykonosensis						
90	38	28.5	30.9	7.25	5.8	4.5
37	38.5	23.8	30.4	7.95	5.8	5
13	33.8	19.3	26.45	6.95	5.6	4.2
14	35.5	21.4	28.7	7.05	6.2	4.65
20	38.6	23.1	30.4	9.1	6.9	5.25
8	45.85	28.6	39.5	9	7.7	4.85
34	29.5	18.75	23.7	6.8	5.15	4.5
12	34.8	20.65	26.95	6.7	4.75	4.2
16	35.8	21.95	30	8.2	5.9	4.2
35	28.5	17.5	23.3	6.2	5.05	3.2
24	37	20.4	29.95	7	6	4.5
10	38.5	22.4	29.95	8.4	7.05	5.3
22	31.6	19.15	26.2	6.8	5.1	4.0
7	32.95	19.4	27.6	6.8	5.1	4.2
21	35	19.8	27.35	7.05	6.1	5.3
31	22.7	14.5	18.6	5.1	4.1	3.6
23	38.6	22.35	34.2	9.9	8.2	5.0
18	28.35	17.9	22.8	5.85	4.8	3.4
Unk	30.8	17.55	25.1	6	5.2	4.3
19	29.4	17.25	22.95	6.2	5.3	4.2
36	28.1	27.05	23	6.2	5.25	3.5
15	42.5	26.2	33.85	8.7	7.1	5.8
94	38.35	23.3	31.1	8.9	6.6	4.8
95	40.65	27.3	31.25	9	7.75	4.7
93	36.7	22.5	28.85	8.7	6.95	4.8
16	41.1	24.45	35.1	8.85	6.6	4.5
17	44.4	25.3	36.2	9.5	8.3	ND[3]
22	39.8	24.25	31.75	9.4	8.2	ND
7	34.15	21.1	29	7.7	6	ND
19	40.25	24.5	33.45	8.7	8.2	ND
H. tuberculata lamellosa						
1	30.85	18.3	26	7.8	4.3	5.4
2	38.1	23.55	31.5	7.9	5.1	4.8
3	37.95	24.3	30.4	8.8	6.6	5.95
4	34.3	20.75	26.35	7.8	5.7	5.2
5	31.2	29.8	22.4	7.1	5.2	5.2
6	41.8	25.3	33.85	9.2	8.1	6.6
7	32.55	31.8	25.85	6.4	5.1	5.1
8	27.6	17.4	23.4	7.2	5.15	6.05
9	30.85	19.95	25.35	7.6	5.05	4.75
10	35.6	22.1	29.2	7.1	5.2	5.5
11	35.95	21.6	27.3	7.5	4.95	5.0
12	38.6	32.9	31	7.9	5.8	6.0
13	31.1	18.95	25	7.1	5.1	4.6
14	31.7	19.3	25.05	6.8	5.25	4.6
15	31	19.35	25.3	6.7	4.3	4.3
16	33.5	20.8	27.3	8	6.8	4.8
17	31.1	18.3	25.65	7.3	5.9	5.5
18	33.3	19.8	27.4	7.8	6.7	4.6
19	29.4	17.75	24.9	6.9	6.6	5.6
20	27.7	17.3	23.2	6.2	5	4.8
21	30.75	19.4	24.4	7.9	4.75	4.3
22	29.2	17.5	23.25	6.1	3.8	5.6
23	25.1	16.25	20.6	6.15	4.85	4.7

Table 2

(Continued)

Specimen number	Length	Width	Spire to suture line end	Spire height	Shell height[1]	Distance from suture line[2]
24	35.2	21.45	28.3	8.3	6.3	5.1
25	29.75	18.15	23.1	6.25	4.6	4.2
26	32.45	20.15	26.75	8.3	5.6	4.7
27	38.6	24.95	33.5	9.2	6.95	6.1
28	41.2	26.35	32.4	11.5	6.7	6.6
29	38.7	24.65	31.5	8.8	6.3	4.8
30	37	21.7	29.8	8.9	6.6	6.3
31	35.4	21.7	29.2	8.4	6.3	5.4
32	33.85	19.4	27.15	8.9	5.9	5.8
H. stomatiaeformis						
1	29.5	27.6	25.85	6.1	6.7	ND
2	24.5	14.55	22.5	6.2	6.05	ND
3	28.5	18	25.75	7.9	7.3	ND
4	26.5	16.05	24.3	6.9	6.9	ND
5	34.5	20.5	30.85	8.2	8	ND
H. pustulata						
1	35.05	22.45	22.5	7.7	5.8	ND
2	38.35	24.75	28.3	8.1	7.2	ND
3	28.4	18.6	21.3	6.2	5.8	ND
4	40.9	25.55	30	8.8	7.3	ND
5	32.85	21.65	23.45	7.2	6.2	ND

[1] Shell height at ⅕ the distance from spire to the end of the suture line.
[2] Distance from suture line to the widest edge of the columnella.
[3] ND = not done.

Epipodium: The species has a thick epipodial structure with an elongated dorsal margin and smaller ventral margin. The ventral surface is covered with small wartlike papillae and is pigmented. The mid-epipodial region, also pigmented, is covered with large, highly ramified projections, which often subdivide into complex non-symmetrical branching structures. The number and spacing of these large projections vary from one specimen to the next. The basic color of pigmented areas is brown to almost black.

Discussion: When examining the soft body parts of *Haliotis **mykonosensis*** and *Haliotis tuberculata lamellosa,* anatomical differences between the species are most evident in the epipodium. The side-by-side comparison of live specimens of these two species in Figure 1 clearly shows that the large, highly ramified epipodial projections between the upper and lower epipodial margins of *H. **mykonosensis*** (Figure 1A) are very different from the small digiform projections of *H. t. lamellosa* (Figure 1B). In *H. **mykonosensis***, the projections subdivide into complex non-symmetrical branching structures, which give the living animal a unique appearance. Larger specimens (> 25 mm) have highly developed projections, which can be more than 6 mm in length. *Haliotis tuberculata lamellosa* has small digiform projections, which are simple, blunt, and seldom more than 1 mm. Infrequently, a specimen will have longer projections (up to 1.5 mm) with a small stellate structure visible at the tip when viewed under a hand magnifier. In addition, the lower epipodial margin of *H. **mykonosensis*** is not visible from the top view (Figure 1A) in contrast to the clearly visible lower epipodial margin of *H. t. lamellosa* (Figure 1B).

Differences in the epipodium can also be seen in the comparison of alcohol-preserved specimens of *Haliotis **mykonosensis*** (Figure 2A) and *H. t. lamellosa* (Figure 2B). *Haliotis **mykonosensis*** has an elongated dorsal margin and the presence of papillae and pigment on the ventral surface. *Haliotis tuberculata lamellosa* has a more elongated ventral margin, clearly visible in Figure 1B, with a smooth unpigmented ventral surface. The pigmented areas of the epipodium of *Haliotis **mykonosensis*** are brown to almost black, whereas those of *H. t. lamellosa* are grayish green, dispersed in a series of vertical bands.

Comparisons to *Haliotis pustulata* and *Haliotis stomatiaeformis* further support the uniqueness of the epipodial characteristics of *H. **mykonosensis***. The epipodium of *H. pustulata* is a thin structure, which has ventral and dorsal margins composed of closely packed fingerlike projections (Geiger, 1996). *Haliotis stomatiaeformis* has an extremely thin epipodium with small digiform structures on the upper and lower margins, and unlike *H. **my-***

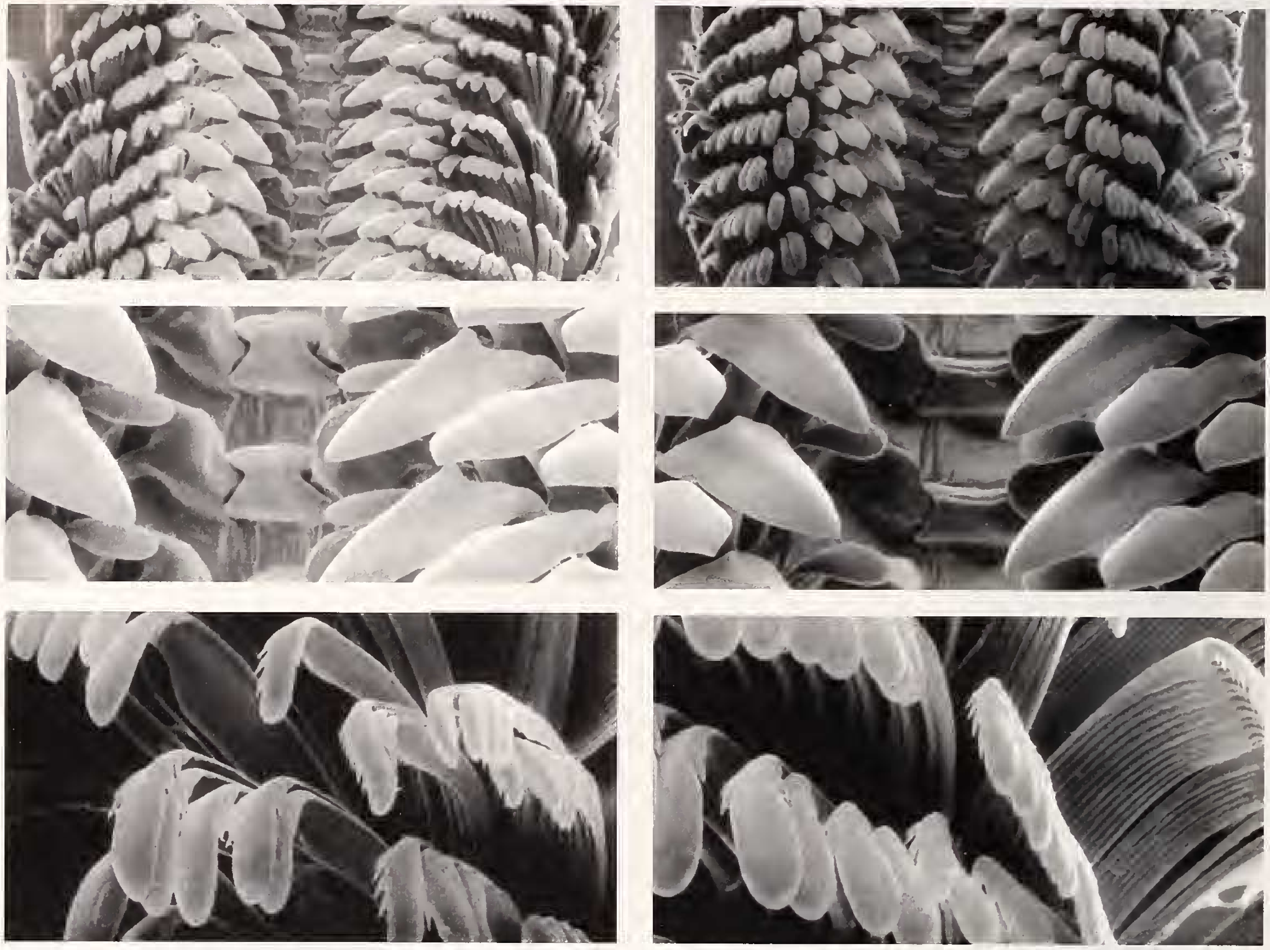

Figure 3. Scanning electron micrographs of radular teeth. Left. *H.* ***mykonosensis*** Owen, Hanavan & Hall, sp. nov. Right. *H. t. lamellosa.* Top. Radular teeth ×40. Middle. Rachidian and inner lateral teeth ×120. Bottom. Lateral teeth ×200.

konosensis does not have any large, highly ramified projections between the margins. *Haliotis* ***mykonosensis*** has a very thick epipodium with an elongated dorsal margin, which differs from the other species described herein, in which the ventral margin is more elongated than the dorsal margin.

Another notable anatomical difference was observed in the color of the male gonad. The mature male gonad of *Haliotis* ***mykonosensis*** is a dull grayish white color. In *Haliotis tuberculata lamellosa* it is a bright pinkish cream color.

Scanning electron micrographs of the radula of *H.* ***mykonosensis*** and *H. t. lamellosa* (Figure 3) show the radula of the two species to be similar.

Haliotis ***mykonosensis*** resembles *H. t. lamellosa* exclusively in shell morphology. The shell of *H. t. lamellosa* is highly variable with respect to many characteristics of shell sculpture, presence or absence of lamellae, and color patterns (Ubaldi, 1987). To a lesser extent, this is also true of *H.* ***mykonosensis***, which closely resembles *H. t. lamellosa* in shell size, shape, and number of open respiratory apertures (Figure 4). Both *H.* ***mykonosensis*** and *H. t. lamellosa* from Greece possess between four and seven open respiratory apertures, and greater than 90% of the specimens examined have five or six open holes. However, subtle differences in shell sculpture, spire inflation, and color patterns have been observed in a large percentage of shells. *Haliotis tuberculata lamellosa* typically has stronger and wider cording than *H.* ***mykonosensis***, which has fine narrow cording. The spire of *H. t. lamellosa* is typically more inflated than the spire of *H.* ***mykonosensis*** as shown in the shell measurements discussed below. The radially placed markings in *H.* ***mykonosensis***, when present, tend to be finer and more consistent throughout growth than in *H. t. lamellosa.*

The most notable difference between the shells of the two species is in the presents of lamellae. *Haliotis tuberculata lamellosa* often has lamellae, and, when present, they can begin to form on the shell starting as small as 3 mm in length. *Haliotis* ***mykonosensis*** infrequently devel-

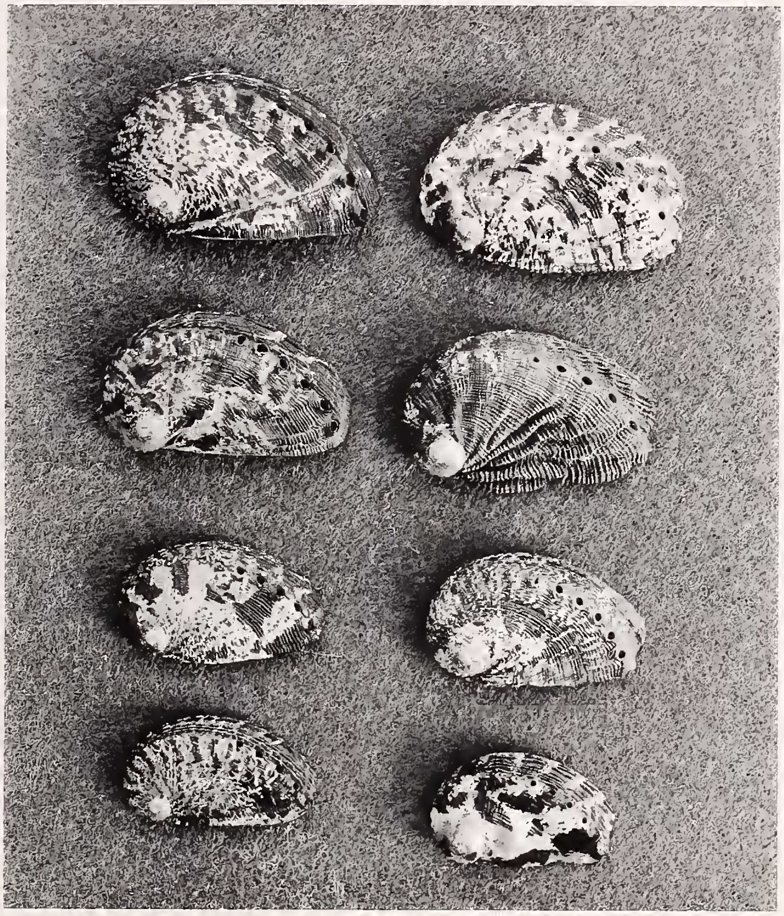

Figure 4. Shell exteriors. Left. *H. **mykonosensis*** Owen, Hanavan & Hall, sp. nov. (B. Owen collection) Right. *H. t. lamellosa* (B. Owen collection). Length of top left specimen is 44 mm.

ops lamellae. When lamellae are present, they are less pronounced and rarely form at a shell length smaller than 25 mm.

Table 2 presents the shell measurements of *H. **mykonosensis***, *H. t. lamellosa*, *H. stomatiaeformis*, and *H. pustulata*. The ratio of the width divided by length showed no significant difference between any of the four species. Statistical analysis of the measure of spire placement distinguishes *H. **mykonosensis*** and *H. t. lamellosa* from both *H. stomatiaeformis* and *H. pustulata* with 95% confidence intervals of the mean (Table 3). *Haliotis **mykonosensis*** does not differ from *H. t. lamellosa* in this comparison.

There are two shell measurements that can distinguish *H. **mykonosensis*** and *H. t. lamellosa* from one another.

Table 3

Spire placement one-way graphic analysis of variance.

Species	N	Mean	SD*	Individual 95% CIs for Mean Based on pooled SD
				-----+----------+----------+----------+------
H. pustulata	5	71.545	4.310	(----*----)
H. stomatiaeformia	5	90.187	1.744	(----*----)
*H. **mykonosensis***	30	81.150	2.804	(-*)
H. t. lamellosa	32	80.894	2.858	(-*)
				-----+----------+----------+----------+------
Pooled SD = 2.889				70.0 77.0 84.0 91.0

* Standard deviation

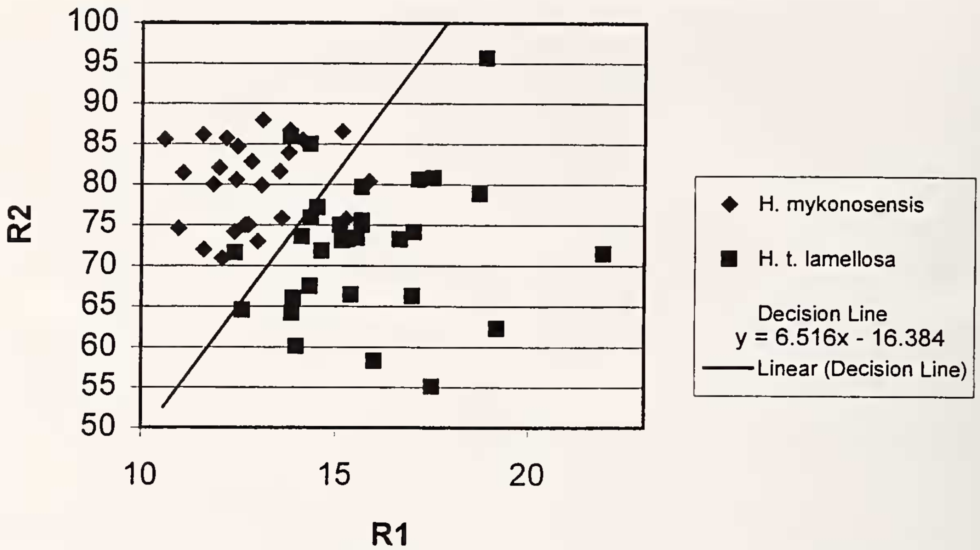

Figure 5. Discriminant analysis of shell measurements. R1 represents the ratio between the shell height at ⅕ the distance from spire to the end of the suture line and the spire height. R2 represents the ratio of the distance from suture line to the widest edge of the columnella and the shell length. The decision line represents the separation of the two species.

The first is that *H. lamellosa* tends to be more inflated in the spire than ***H. mykonosensis*** as shown by the ratio of the shell height at ⅕ the distance from spire to the end of the suture line/spire height (R1). The second difference noted was that the outer edge of the columella extends farther from the suture line in *H. t. lamellosa* than on ***H. mykonosensis*** as represented by the ratio of the distance from suture line to the widest edge of the columnella divided by the length (R2). When plotted against each other, these two ratios distinguish the two species quantitatively. As can be seen in Figure 5, a graphical presentation of the data along with the decision line, the two species clearly separate according to where these statistics fall on the graph when R1 is plotted on the X axis and R2 is plotted on the Y axis. Statistically, the line optimally separating the two species is $R1 = -16.4 + 6.5*R2$. This is called the decision line. If $R1 > -16.4 + 6.5*R2$, then classify the species as ***H. mykonosensis.*** If $R1 < -16.4 + 6.5*R2$, then classify the species as *H. t. lamellosa.* Therefore, if the data collected so far are representative of the population as a whole, the correct decision will be made over 90% of the time using this classification scheme alone.

In addition to differences in anatomical and shell features, differences in feeding behavior and locomotion have been observed in aquarium specimens. For 6 years, a group of *H. t. lamellosa* ignored a species of encrusting red algae building up in their aquarium, whereas ***H. mykonosensis*** actively and preferentially consumed the algae immediately upon introduction into this aquarium. When disturbed into movement by a flashlight at night, there is a substantial difference in speed of locomotion. *Haliotis* ***mykonosensis*** almost detaches from the aquarium walls, and with a very fluid undulating motion of the foot moves across the aquarium rapidly. Similarly disturbed, *H. t. lamellosa* is less active and moves much more slowly and deliberately. *Haliotis* ***mykonosensis*** has also been observed to move rapidly backward when disturbed by a beam of light at night. *Haliotis tuberculata lamellosa* has never been observed to exhibit this behavior, nor has any other species of *Haliotis* studied in aquaria (B. Owen, D. Leighton, personal observation).

A curious observation, which might provide a possible direction for further study, is the difference in seasonal maturity of the male gonad in the two species. In 4 separate years (1981, 1988, 1991, and 1992), *H. t. lamellosa* was observed in the field with very mature gonads, and was actively spawning in October. The mature gonad is easily visible when the animal is removed from the surface to which the animal is attached. The gonad lies alongside the epipodium on the growth side of the shell. None of the ***H. mykonosensis*** observed had mature gonads in October/November of 1992. Only one specimen of 79 had perceptible evidence of gonad maturation (a male from Samos). *Haliotis* ***mykonosensis*** was observed with mature gonads and was actively spawning in May of 1996 and 1997. At the same time, more than 500 adult *H. t. lamellosa* examined had immature gonads and were not observed to spawn, with a single exception of one male from Corfu. This animal spawned minimally (brief expulsion of a trace of sperm) after conditioning in 20–25°C water for 5 days. As these observations included a large number of animals from 11 different islands, in 6 different years, it may suggest that the two species have different reproductive cycles.

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LITERATURE CITED

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