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On the Identity of *Lottia strigatella* (Carpenter, 1864) (Patellogastropoda: Lottiidae)

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Abstract. Nomenclatural confusion has surrounded the northeastern Pacific lottiid currently referred to by the specific names *strigatella* or *paradigitalis* for 135 years. Much of this confusion has resulted because of the supposed range of this nominal taxon (Gulf of California to the Gulf of Alaska), its morphological variation within this range, and its overt similarity to several earlier named taxa. Here we examine the relatedness and distribution of these taxa from localities between Guaymas, Mexico, and the Aleutian Islands, Alaska. Relatedness is established by a maximum parsimony analysis of partial 16S mtDNA genes and distance analyses of cytochrome c oxidase I and 16S. The results of these analyses provide unequivocal evidence of the distinctness of *Lottia strigatella* (Carpenter, 1864), *Lottia paradigitalis* (Fritchman, 1960), and the presence of a third previously unrecognized taxon, *Lottia* ***argrantesta*** Simison & Lindberg, sp. nov. The taxa *L. strigatella, L. paradigitalis,* and *L.* ***argrantesta*** are not members of a species complex, but rather members of three distinct subclades within the northeastern Pacific Lottiidae. Additionally, molecular data from *Lottia borealis* (Lindberg, 1982) revealed that this Alaskan taxon should be synonymized with *L. paradigitalis. Lottia strigatella* and *Lottia paradigitalis* show characteristic Californian distributions with apparent range end points in the vicinity of Point Conception, California. These data and the evolutionary history they reveal provide a compelling demonstration of the levels of morphological variation present in the Patellogastropoda.

INTRODUCTION

Nomenclatural confusion has surrounded the northeastern Pacific lottiid currently referred to by the specific name *strigatella* or *paradigitalis* for 135 years. Much of this confusion has resulted because of the apparent extensive range of this nominal taxon (Gulf of California to the Gulf of Alaska), its morphological variation within this range, and its overt similarity to several other earlier known taxa. Understanding the extent of its distribution in the northern portion of this range was further complicated by the presence in Alaska of the morphologically similar *Lottia borealis* Lindberg, 1982.

The tortured nomenclatural history began with the proposal of two similar specific names for a single nominal taxon—*strigillata* for the California population and *strigatella* for the Gulf of California population by P. P. Carpenter in the 1860s. Palmer (1958) and McLean (1966) gave detailed discussions of the subsequent nomenclatural confusion.

In summary, Carpenter (1864a) proposed *Acmaea strigatella* for a limpet from Cabo San Lucas, Baja California Sur, Mexico. In a second paper (Carpenter, 1864b) this specific name was erroneously spelled *strigillata.* Carpenter (1866:334) proposed *Acmaea patina* Var. b. *strigillata* for a second nominal taxon from the Vancouver-Californian provinces. He compared it to small specimens of *Lottia pelta* (Rathke, 1833), and remarked on the difficulty in distinguishing it from "the *A. strigatella* of Cape St. Lucas." Burch (1946) erroneously referred to the northern species as *Acmaea persona strigillata,* noting the similarity between it and small specimens of *Lottia persona* (Rathke, 1833). Smith & Gordon (1948) and Abbott (1974) followed Burch. Grant (1933) placed *A. persona strigillata* in synonymy with *Lottia digitalis* (Rathke, 1833), but illustrated specimens of Burch's *A. persona strigillata* as "*Acmaea persona.*" Four years later, Grant (1937) illustrated the same shells as supposed hybrids between *L. digitalis* and *L. pelta,* but the name *A. persona strigillata* remained in synonymy with *L. digitalis.* It is interesting to note that Grant, who originally suggested that this taxon was a hybrid, never discussed this decision in any of her texts. The hybrid designation only appeared in figure captions without further comment (see also Light, 1941; Smith et al., 1954).

The name *Acmaea paradigitalis* was proposed by Fritchman (1960) after a study of the radular basal plate morphology of *L. digitalis, L. pelta,* and the supposed

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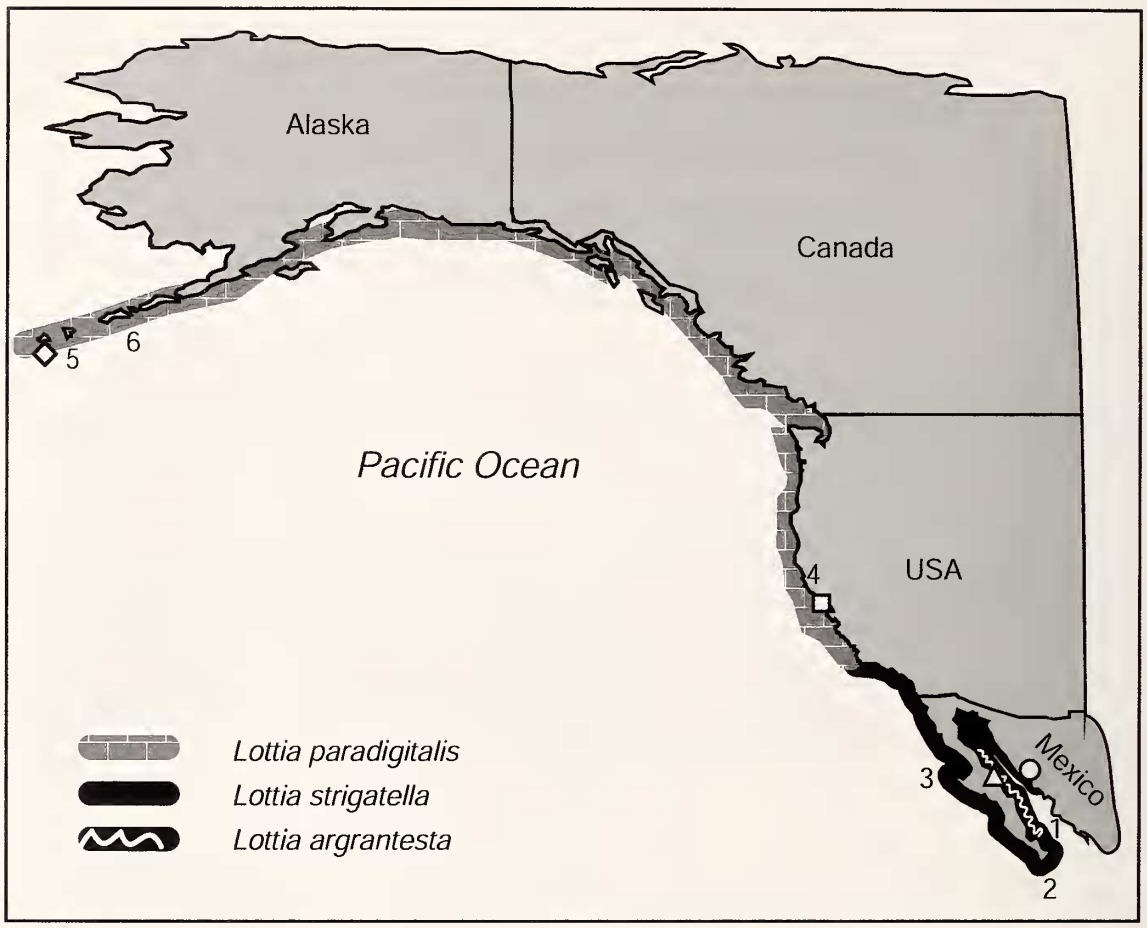


Figure 1. Sketch map of a section of temperate North America showing expected distributions of *Lottia paradigitalis, Lottia strigatella, Lottia* ***argrantesta*** Simison & Lindberg, sp. nov. respective type localities of nominal taxa (symbols in column 5, Table 1), and localities of molecular samples (reference numbers in column 5, Table 1). Expected distributions of haplotype groups are based on associated shell morphologies.

hybrid. McLean (1966) synonymized *L. paradigitalis* with the Panamic species *L. strigatella* based on the similar shell characters of the two taxa. The similarities had been noticed first by Carpenter (1866) but were subsequently ignored by most workers. McLean's treatment was followed by later workers including Seapy & Hoppe (1973), Carlton & Roth (1975), Christiaens (1975), and Morris et al. (1980). This nomenclature remained relatively stable until Lindberg (1981:75) revived the use of the specific name *paradigitalis* for northern California specimens of *L. strigatella* based on radular differences that distinguished the northern and southern California taxa from one another.

The advent of molecular techniques provides new data to examine levels of relatedness and to determine the distributions of populations and species-rank taxa. The *strigatella/paradigitalis* question is an ideal problem for such study. The debate has been ongoing for 135 years, and character analysis of morphological characters as well as ecological studies have provided conflicting answers to the distinctness and distributions of these nominal species. Clearly, a new data set is needed to address these questions.

Here we examine the phylogeny and distribution of the lottiid taxa formerly known as *strigatella, paradigitalis,* and *borealis* from localities between Guaymas, Mexico, Bodega Bay, California, and the Aleutian Islands, Alaska. Phylogeny was established by maximum parsimony analysis of a partial sequence of the mitochondrial large ribosomal subunit (16S) (Simison, 2000). After delimiting these taxa with molecular characters, shell and radular characters were examined to determine the range of morphological variation within each taxon. These morphological characters were then used to identify and delimit the regional occurrences of the taxa and associate existing type specimens with specimens from known haplotype groups.

Table 1

Specimens and localities examined in the course of this study. Symbols and numbers refer to type and additional sampling localities, respectively. Shell and radula numbers refer to illustrated specimens and checkmarks to recovered molecular sequences. Genbank accession numbers: *L. **argrantesta*** COI = AF295537, 16S = AF295540. *L. paradigitalis* COI = AF295538, 16S = AF295541. *L. strigatella* COI = AF295539, 16S = AF295542.

Specimen no.	Taxon	Locality	Tables 2&3	Figure 1	Shell	Radula	COI	16S
UCMP No. 157003	*Lottia **argrantesta***	Califin, La Paz, BCS, Mexico	1	1	17	23	√	√
UCMP No. 157008	*Lottia **argrantesta***	Bahía de San Francisquito, BCS, Mexico	2	△	18	24	√	√
UCMP No. 157005	*Lottia **argrantesta***	Tecolate, La Paz, BCS, Mexico	3	1			√	√
UCMP No. 157006	*Lottia **argrantesta***	Tecolate, La Paz, BCS, Mexico	4	1	19		√	√
UCMP No. 157007	*Lottia **argrantesta***	Bahía de San Francisquito, BCS, Mexico	5	△	16	25	√	√
UCMP No. 157036	*Lottia paradigitalis*	Attu, Aleutian Is., Alaska, U.S.A.	6	◇				√
UCMP No. 157037	*Lottia paradigitalis*	Attu, Aleutian Is., Alaska, U.S.A.	7	◇				√
UCMP No. 157038	*Lottia paradigitalis*	Attu, Aleutian Is., Alaska, U.S.A.	8	◇				√
UCMP No. 157039	*Lottia paradigitalis*	Attu, Aleutian Is., Alaska, U.S.A.	9	◇				√
UCMP No. 157040	*Lottia paradigitalis*	Attu, Aleutian Is., Alaska, U.S.A.	10	◇				√
UCMP No. 157041	*Lottia paradigitalis*	Attu, Aleutian Is., Alaska, U.S.A.	11	◇				√
UCMP No. 157042	*Lottia paradigitalis*	Attu, Aleutian Is., Alaska, U.S.A.	12	◇				√
UCMP No. 157043	*Lottia paradigitalis*	Amchitka, Aleutian Is., Alaska, U.S.A.	13	5				√
UCMP No. 157044	*Lottia paradigitalis*	Adak, Aleutian Is., Alaska, U.S.A.	14	6				√
UCMP No. 157045	*Lottia paradigitalis*	Adak, Aleutian Is., Alaska, U.S.A.	15	6				√
UCMP No. 157046	*Lottia paradigitalis*	Adak, Aleutian Is., Alaska, U.S.A.	16	6				√
UCMP No. 157047	*Lottia paradigitalis*	San Francisco Bay, CA, U.S.A.	17	□				√
UCMP No. 157020	*Lottia paradigitalis*	San Francisco Bay, CA, U.S.A.	18	□	6	26	√	√
UCMP No. 157023	*Lottia paradigitalis*	Bodega Bay, CA, U.S.A.	19	4				√
UCMP No. 157019	*Lottia paradigitalis*	San Francisco Bay, CA, U.S.A.	20	□	8	28	√	√
UCMP No. 157018	*Lottia paradigitalis*	San Francisco Bay, CA, U.S.A.	21	□	7	27	√	√
UCMP No. 157021	*Lottia paradigitalis*	Bodega Bay, CA, U.S.A.	22	4	5			√
UCMP No. 157022	*Lottia paradigitalis*	Bodega Bay, CA, U.S.A.	23	4	3			√
UCMP No. 157001	*Lottia strigatella*	Guaymas, Sonora, Mexico	24	○	12		√	√
UCMP No. 157009	*Lottia strigatella*	Sta Maria, Cabo San Lucas, BCS, Mexico	25	2		22		√
UCMP No. 157002	*Lottia strigatella*	Guaymas, Sonora, Mexico	26	○	15		√	√
UCMP No. 157010	*Lottia strigatella*	Cabo San Lucas, BCS, Mexico	27	2		21		√
UCMP No. 157014	*Lottia strigatella*	Chileno, Cabo San Lucas, BCS, Mexico	28	2		20	√	√
UCMP No. 157004	*Lottia strigatella*	Califin, La Paz, BCS, Mexico	29	1			√	√
UCMP No. 157017	*Lottia strigatella*	Bahía Tortugas, BCN, Mexico	30	3			√	√
UCMP No. 157015	*Lottia strigatella*	Bahía Tortugas, BCN, Mexico	31	3	14		√	√
UCMP No. 157016	*Lottia strigatella*	Bahía Tortugas, BCN, Mexico	32	3			√	√
UCMP No. 157011	*Lottia strigatella*	Cabo San Lucas, BCS, Mexico	Na	2	9			
UCMP No. 157012	*Lottia strigatella*	Cabo San Lucas, BCS, Mexico	Na	2	11			
UCMP No. 157013	*Lottia strigatella*	Cabo San Lucas, BCS, Mexico	Na	2	13			

MATERIALS AND METHODS

In the course of this study we examined the morphology of over 1500 putative specimens of *Lottia strigatella, Lottia paradigitalis,* and *Lottia borealis* from the Gulf of Alaska to the Gulf of California, Mexico. In addition, nearly 100 specimens from 10 arbitrary localities between Guaymas in the Gulf of California, Mexico and Alaska, California were collected for molecular sequencing (Figure 1). Specimens collected for sequencing were biased to represent as much morphological variation as possible from each locality. All specimens were labeled with a locality-based code and preserved in 70% ethanol (ETOH).

In the laboratory the coded specimens were sorted into morphologically similar groupings irrespective of locality, and several specimens were then randomly chosen from each group for sequencing. This approach increases the possibility that all phenotypes present in a taxon will be sampled as well as providing multiple sequences for similar individuals in each "lot." After reconstituting the groupings by locality it was discovered that 32 specimens from 13 localities had been selected for sequencing (Table 1).

Institutional abbreviations used herein are as follows: LACM—Malacology Section, Natural History Museum of Los Angeles County, Los Angeles, California; UCMP—Museum of Paleontology, University of Califor-

Table 2

Uncorrected P pairwise comparison of 16S from specimens of the nominal strigatella-paradigitalis "complex." Specimen numbers correspond to numbers in Table 1.

	L. agrantesta					*L. paradigitalis*										
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
L. argrantesta																
1																
2	0.15%															
3	0.15%	0.30%														
4	0.00%	0.15%	0.15%													
5	1.05%	1.20%	1.20%	1.05%												
L. paradigitalis																
6	15.95%	16.10%	15.91%	15.91%	16.09%											
7	16.06%	16.22%	16.02%	16.03%	16.21%	0.0%										
8	14.75%	14.89%	14.71%	14.72%	14.87%	0.00%	0.00%									
9	14.94%	15.08%	14.90%	14.91%	15.06%	0.00%	0.00%	0.15%								
10	15.79%	15.94%	15.76%	15.76%	15.94%	0.00%	0.00%	0.00%	0.16%							
11	15.15%	15.29%	15.11%	15.12%	15.29%	0.00%	0.00%	0.00%	0.15%	0.00%						
12	15.79%	15.94%	15.76%	15.76%	15.94%	0.00%	0.00%	0.00%	0.16%	0.00%	0.00%					
13	15.18%	15.32%	15.14%	15.15%	15.31%	0.48%	0.16%	0.46%	0.46%	0.48%	0.46%	0.48%				
14	14.82%	14.95%	14.78%	14.79%	14.94%	0.00%	0.00%	0.00%	0.15%	0.00%	0.00%	0.00%	0.46%			
15	15.24%	15.39%	15.20%	15.21%	15.37%	0.00%	0.00%	0.00%	0.15%	0.00%	0.00%	0.00%	0.48%	0.00%		
16	15.95%	16.10%	15.91%	15.91%	16.10%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.48%	0.00%	0.00%	
17	15.28%	15.42%	15.25%	15.25%	15.41%	0.00%	0.00%	0.44%	0.44%	0.32%	0.31%	0.32%	0.62%	0.44%	0.46%	0.16%
18	14.90%	15.03%	14.86%	14.87%	15.02%	0.16%	0.17%	0.29%	0.44%	0.16%	0.15%	0.16%	0.61%	0.29%	0.31%	0.16%
19	16.25%	16.40%	16.21%	16.22%	16.38%	0.65%	0.66%	0.77%	0.92%	0.64%	0.64%	0.64%	1.13%	0.77%	0.77%	0.65%
20	14.72%	14.87%	14.72%	14.72%	14.86%	0.82%	0.50%	0.89%	1.05%	0.81%	0.78%	0.81%	0.31%	0.90%	0.93%	0.82%
21	14.90%	15.05%	14.90%	14.90%	15.05%	0.00%	0.00%	0.15%	0.30%	0.00%	0.00%	0.00%	0.46%	0.15%	0.15%	0.00%
22	14.97%	15.11%	14.94%	14.94%	15.09%	0.00%	0.00%	0.15%	0.30%	0.00%	0.00%	0.00%	0.46%	0.15%	0.15%	0.00%
23	14.79%	14.93%	14.75%	14.76%	14.91%	0.00%	0.00%	0.00%	0.15%	0.00%	0.00%	0.00%	0.46%	0.00%	0.00%	0.00%
L. strigatella																
24	18.89%	19.05%	18.99%	19.01%	19.17%	12.04%	12.15%	11.39%	11.44%	11.94%	11.45%	11.94%	11.57%	11.46%	11.95%	12.03%
25	18.23%	18.37%	18.32%	18.34%	18.48%	12.51%	12.19%	11.68%	11.89%	12.38%	12.06%	12.38%	12.20%	11.74%	12.04%	12.53%
26	18.76%	18.89%	18.85%	18.87%	19.01%	12.89%	12.60%	12.03%	12.24%	12.76%	12.43%	12.76%	12.88%	12.09%	12.41%	12.91%
27	17.96%	18.10%	18.06%	18.08%	18.22%	12.44%	12.13%	11.48%	11.69%	12.32%	11.86%	12.32%	12.00%	11.54%	11.98%	12.46%
28	18.31%	18.46%	18.41%	18.43%	18.59%	12.43%	12.12%	11.73%	11.94%	12.30%	11.85%	12.30%	11.99%	11.79%	12.26%	12.45%
29	18.32%	18.46%	18.42%	18.43%	18.58%	12.54%	12.24%	11.57%	11.78%	12.41%	11.95%	12.41%	12.40%	11.63%	12.07%	12.56%
30	18.21%	18.35%	18.31%	18.33%	18.47%	12.15%	11.83%	11.43%	11.49%	12.19%	11.73%	12.19%	12.03%	11.49%	11.94%	12.17%
31	18.20%	18.34%	18.30%	18.31%	18.46%	12.34%	12.02%	11.55%	11.59%	12.37%	11.91%	12.37%	12.21%	11.59%	12.04%	12.35%
32	17.97%	18.11%	18.07%	18.08%	18.23%	12.49%	12.01%	11.68%	11.74%	12.53%	12.06%	12.53%	12.36%	11.74%	12.19%	12.51%

Table 2

Continued

	L. paradigitalis							*L. strigatella*								
	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
L. paradigitalis																
17																
18	0.44%															
19	0.76%	0.46%														
20	1.05%	0.89%	1.40%													
21	0.29%	0.15%	0.61%	0.75%												
22	0.30%	0.15%	0.61%	0.75%	0.00%											
23	0.44%	0.29%	0.77%	0.90%	0.15%	0.15%										
L. strigatella																
24	11.63%	11.39%	12.52%	11.59%	11.11%	11.46%	11.43%									
25	12.18%	11.90%	12.72%	12.07%	11.54%	11.89%	11.72%	0.84%								
26	12.54%	12.30%	12.78%	12.73%	11.89%	12.24%	12.07%	0.33%	1.03%							
27	11.99%	11.69%	12.67%	11.88%	11.35%	11.69%	11.52%	0.67%	0.15%	0.89%						
28	12.12%	11.80%	12.82%	11.92%	11.46%	11.80%	11.77%	0.67%	0.15%	0.92%	0.00%					
29	12.08%	11.78%	12.75%	12.27%	11.44%	11.78%	11.61%	0.49%	0.59%	0.73%	0.44%	0.45%				
30	11.80%	11.71%	12.63%	12.05%	11.31%	11.64%	11.47%	0.99%	0.89%	1.33%	0.74%	0.76%	0.89%			
31	11.89%	11.84%	12.72%	11.96%	11.43%	11.74%	11.57%	0.82%	0.74%	1.18%	0.59%	0.61%	0.74%	0.45%		
32	12.03%	11.94%	12.87%	12.08%	11.54%	11.89%	11.72%	0.82%	0.89%	1.33%	0.74%	0.76%	0.88%	0.60%	0.15%	

Table 3

Uncorrected P pairwise comparison of COI from specimens of the nominal strigatella paradigitalis "complex." Specimen numbers correspond to numbers in Table 1.

	L. agrantesta				*L. paradigitalis*				*L. strigatella*					
	1	3	4	5	17	18	20	22	24	26	28	29	30	31
L. agrantesta														
1														
3	0.57%													
4	0.00%	0.56%												
5	2.12%	2.68%	2.11%											
L. paradigitalis														
17	25.66%	25.66%	25.52%	26.52%										
18	25.80%	25.92%	25.77%	26.81%	0.00%									
20	25.57%	25.61%	25.47%	26.40%	0.28%	0.29%								
22	25.69%	25.67%	25.53%	26.55%	0.00%	0.00%	0.28%							
L. strigatella														
24	26.57%	26.55%	26.38%	26.27%	16.91%	17.02%	16.89%	16.91%						
26	26.01%	26.04%	25.90%	25.84%	16.46%	16.67%	16.43%	16.49%	0.00%					
28	27.29%	27.43%	27.27%	27.32%	17.15%	17.16%	17.13%	17.15%	1.20%	1.18%				
29	27.61%	27.75%	27.59%	27.62%	17.13%	17.14%	17.12%	17.13%	0.46%	0.46%	1.08%			
30	26.15%	26.28%	26.13%	26.16%	16.53%	16.54%	16.50%	16.53%	3.28%	3.17%	2.96%	2.91%		
31	26.33%	26.45%	26.15%	26.19%	17.05%	17.16%	17.02%	17.04%	3.69%	3.79%	3.55%	3.52%	1.18%	
32	25.73%	25.90%	25.62%	25.56%	16.61%	16.82%	16.57%	16.64%	3.68%	3.51%	3.40%	3.36%	1.01%	0.14%

nia, Berkeley, California; and USNM—Division of Mollusks, U.S. National Museum of Natural History, Washington, D.C.

Molecular Sequence Data

Cytochrome c oxidase I (COI) and 16S mtDNA genes were partially sequenced and compared among 15 and 32 individuals, respectively, from 13 localities (Table 1). COI and 16S were chosen for this study based on their interspecific and intraspecific levels of variation found among sequences of eastern Pacific patellogastropods (Simison, 2000).

Extraction. Two equally successful DNA isolation protocols were used: (1) saturated salt/chloroform extraction, and (2) CTAB/phenolchloroform extraction. For each extraction, pedal tissue was cut from the foot margin approximately 3–5 mm along the margin and 3–5 mm toward the center of the foot. The tissue was soaked in deionized water to remove any residual ETOH and finely diced to bits. For the saturated salt technique, the diced tissue was digested in a 1.5 ml tube containing 250 µL isolation buffer (100 mM TRIS, 10 mM EDTA and 400 mM NACL), 60 µl 10% SDS, and 10 µL proteinase K. The mixture was then vortexed and stored on a shaker at 37°C overnight. Following tissue digestion, 175 µL of saturated NaCl solution was added. The samples were inverted for 5 minutes and centrifuged at 13 k rpm for 30 minutes. The supernatant was washed with chloroform using 2 times supernatant volume and mixed by inversion for 2 minutes. The supernatant DNA was precipitated using two volumes of ice cold 100% ETOH, centrifuged at 13 k rpm for 15 minutes and discarded, the remaining pellet was washed twice with two volumes of 70% ETOH. The 70% ETOH wash was discarded and the pellet dried for five minutes in a speed vac. The DNA was eluted in 50 µL of double-distilled water and stored at −20°C.

For the CTAB technique, diced tissue was digested in a 1.5 mL tube containing 600 µL 2XCTAB and 9 µL of proteinase k then incubated at 37°C overnight. 600 µl of phenol:chloroform:isoamyl alcohol (25:24:1) was added to the tissue mixture and mixed via inversion for 5 minutes. The solution was then centrifuged at 13 k rpm for 15 minutes. The supernatant was added to 600 µL of chloroform: isoamyl alcohol (24:1), mixed for 5 minutes and centrifuged at 13 k rpm for 15 minutes. DNA was precipitated using 600 µL isopropanol and stored at −20°C for 2 hours. The precipitate was centrifuged at 13 k rpm for 30 minutes at 4°C. The supernatant was discarded and the pellet washed twice with two volumes of 70% ETOH and centrifuged at 13 k rpm for 20 minutes. The ETOH was discarded and the pellet dried by speed vac for 5 minutes and eluted in 100 µL of deionized water.

Amplification. Amplification of a 700+ bp coding region of COI was achieved with the HCO-2193 and LCO-1490 primers described by Folmer et al. (1994). For the 16S mtDNA region, a 680+ bp fragment was amplified using the 16Sar and 16Sbr primers described by (Palumbi, 1996; Kocher et al., 1989). In a 0.5 mL gene amp tube, on ice, 36.45 µL double-distilled water, 5 µl 10× PCR buffer (Perkin Elmer), 2.5 µl 10µM dNTP's (Pharmacia), 2.5 µL 25 µM MgCl2 (Perkin Elmer), 1 µL each of the 10 µM primers, 1 µL of template, and 0.25 µL of taq (Perkin Elmer) were combined. A negative control containing all reagents except the template was run in parallel. The tube was then transferred to a Perkin Elmer 9600 geneamp. The cycling parameters began with an initial denaturation at 95°C for 2 minutes followed by 36 cycles with three temperature plateaus of 95°C for 50 seconds, 45°C for 50 seconds, and 72°C for 90 seconds, ending with a 7 minute extension at 72°C. PCR products were purified using Wizard® PCR preps DNA Purification System.

Cycle Sequencing. Direct double-stranded cycle sequencing of 20 to 30 ng of PCR product was performed in both directions using the aforementioned primers and the ABI® cycle sequencing kit following a half reaction ABI® cycle sequencing protocol. Cycle sequencing was performed using a Perkin Elmer 9600 geneamp. The cycling parameters were 25 cycles at 96°C for 10 seconds, 50°C for 5 seconds, and 60°C for 4 minutes. Cycle sequencing product was purified using Princeton Separations Centrisep spin columns, then dried in a speed vac. The dried, purified cycle sequencing product was resuspended in 2.5 µl loading solution of 5:1 deionized formamide: 25 mm MEDTA with 50 mg/ml Blue Dextran. 1.5 µl of sample and loading solution was loaded on a 36 cm 4% acrylaminde gel. The gel was run and analyzed on an ABI Prism® 377 DNA sequencer.

Alignment & Analysis. The 16S and COI sequences were aligned by hand using the PAUP 4.0b3a text editor. An uncorrected *P* value, pairwise comparison of the 16S and COI partitions was calculated (Tables 2 and 3). We used the 16S northeast Pacific lottiid dataset generated by Simison (2000) to compare the phylogenetic relationship of the members within the nominal *strigatella-paradigitalis* "complex." This dataset was chosen because it includes a representative of each of the nominal taxa under study here. COI data was not included in Simison's (2000) phylogenetic analysis because of poor sample size.

Morphology

Digital images of the ventral, dorsal, and profile views of 18 shells were captured with a digital camera connected to a Scion LG-3 Scientific Frame Grabber system. In addition, an anterior portion of the radular ribbon from nine specimens (Table 1) was dissected from the head region posterior to the odontophore and placed in a 0.5% sodium hypochlorite solution for 5 minutes or less to dissolve associated organic material and rinsed in distilled water. The radular ribbon was examined using an

Table 4

Summary of range of distances for interspecific and intraspecific pairwise comparisons.

16S			COI		
Taxon	Intraspecific distances	n	Taxon	Intraspecific distances	n
strigatella	0.15%–1.33%	9	*strigatella*	0.0%–3.79%	7
paradigitalis	0.0%–1.4%	18	*paradigitalis*	0.0%–0.29%	4
argrantesta	0.0%–1.2%	5	***argrantesta***	0.0%–2.68%	4
Comparison	Interspecific distances		Comparison	Interspecific distances	
strigatella v. *paradigitalis*	11.11%–12.91%		*strigatella* v. *paradigitalis*	16.43%–17.16%	
strigatella v. ***argrantesta***	17.96%–19.17%		*strigatella* v. ***argrantesta***	25.56%–27.75%	
paradigitalis v. ***argrantesta***	14.71%–16.4%		*paradigitalis* v. ***argrantesta***	25.47%–26.55%	

ElectroScan Model E3 Environmental Scanning Electron Microscope (ESEM).

RESULTS

Molecular Sequence Data

Uncorrected pairwise comparisons of 32 specimens of the nominal *strigatella-paradigitalis* "complex" and the Simison (2000) 16S phylogeny of northeast Pacific lottiids reveal three distinct lineages among the specimens. Sequence divergence within lineages was low while sequence divergence among lineages was greater (Table 4). The three lineages are each nested in different clades of the Simison 16S phylogeny. The geographic distributions of these lineages are sympatric over portions of their ranges; the San Francisco Bay group (*L. paradigitalis*) overlaps with the Baja California group (*L. strigatella*) in southern California, while the Baja California group co-occurs with the Gulf group (*L. argrantesta* n. sp.) in the southern Gulf of California (Figure 1).

Morphology

Examination of radular and shell morphologies of taxa sorted by genotype revealed previously unsuspected morphological differences, especially between Gulf specimens of *L. strigatella* and *L. **argrantesta***. Although both taxa have a wide range of shell pattern variation, specimens of *L. **argrantesta*** (Figures 16 and 19) tend to be lower in profile than specimens of *L. strigatella* (Figures 9 and 15). *Lottia strigatella* specimens also tend to have more convex posterior shell profiles. Both taxa have variegated forms that are similar in shell color and pattern (compare Figures 9 and 16) as well as dark tessellate forms with random white markings (compare Figures 12 and 19). In many cases *L. **argrantesta*** can be distinguished from *L. strigatella* by the presence of low coarse ribs on its shell, but relatively smooth specimens also occur (Figure 17). *Lottia **argrantesta*** appears to lack strongly demarcated shell patterns such as found in *L. strigatella* (e.g., Figures 11–13).

Lottia paradigitalis and *L. strigatella* are substantially more similar to one another than either is to *L. **argrantesta***. Both taxa have a wide range of overlapping shell pattern variation (compare Figures 7, 8 with 9, 13), strongly demarcated shell patterns (compare Figures 3, 5 with 11, 15), and dark tessellate forms (compare Figure 5 [central area] and 12). A solid, yellow-tan form has been found only in *L. strigatella* (Figure 14). Both taxa lack ribbing, and primarily concentric growth lines texture the exterior shell surface although microscopic radial treads are sometimes present; shell profiles are virtually identical in both taxa. One discernible difference between *L. paradigitalis* and *L. strigatella* shell color patterns is the stronger bifurcating patterns of the white markings present in *L. paradigitalis* (compare Figures 3, 5, 7 with 9, 11, 13).

The radula of *L. **argrantesta*** is readily distinguishable from those of both *L. paradigitalis* and *L. strigatella*. In *L. paradigitalis* (Figures 26–28) and *L. strigatella* (Figures 20–22) the inner margins of the second lateral teeth appear convex, while in *L. **argrantesta*** the edges appear concave (Figures 23–25). This places the cusps of the second lateral teeth of *L. paradigitalis* and *L. strigatella* closer to the cusps of the first lateral teeth than they are in *L. **argrantesta***. *Lottia paradigitalis* and *L. strigatella* radulae are very similar in overall morphology. One possible difference we noted was that radular segments in *L. paradigitalis* appear slightly shorter than in *L. strigatella*. There is minor radular variation in *L. paradigitalis* (compare Figures 27 and 28), but it is not as marked as that reported in the Panamic taxon *Lottia fascicularis* (Simison & Lindberg, 1999).

DISCUSSION

After 135 years of conjecture, the results of this study provide unequivocal evidence of the distinctness of *Lottia strigatella*, *Lottia paradigitalis*, and a third previously unrec-

ognized taxon, *Lottia* ***argrantesta***, sp. nov. Moreover, these taxa are not members of a "species complex" or even sister taxa, but rather members of three distinct subclades within the northeastern Pacific Lottiidae (see below). These data and the evolutionary history they reveal provide a compelling demonstration of the levels of morphological convergence present in the Patellogastropoda.

Without the molecular data *Lottia* ***argrantesta*** would likely have gone unrecognized. And while Lindberg (1981:75) revived the use of the specific name *paradigitalis* for northern California specimens of *L. strigatella* based on radular differences, it was thought at that time that *Lottia strigatella* and *Lottia paradigitalis* likely represented a species pair which transitioned at Point Conception, California. This scenario was consistent with the range of morphological shell and radular variation shared by these two taxa, their similar habitats, and their contiguous ranges. Moreover, allopatric divergence during a glacial or interglacial period provided a plausible mechanism.

However, this scenario is falsified by the 16S phylogeny. Instead, the shared morphology and habitats of these taxa appear to result from convergence, not common ancestry, and range size is characteristic of the larger, more inclusive clades to which each taxon belongs and not the outcome of a recent divergence from a common ancestor. While disconcerting relative to the more familiar scenario, this result suggests that deeper divergences are also affected by modern day Point Conception. This barrier is possibly thermal in nature and acts to limit the distributions of either larvae or adults. For members of the *Collisella* and "A" subclades (Figure 2) potential southern limiting temperatures appear to occur near the southern California Bight; northern limiting temperatures do not appear to be reached until the northern Gulf of Alaska or Aleutian Islands. For members of the sister clade that contains *L. strigatella, Macclintockia,* and *Nomaeopelta* (Figure 2), northern limiting temperatures are seldom found north of central California, and the majority are south of the Bight. Possible southern limiting temperatures in the *L. strigatella* + *Macclintockia* + *Nomaeopelta* clade occur at the mouth of the Gulf of California. Thus ranges in *Collisella* + subclade A average about 7900 km, while ranges in the *L. strigatella* + *Macclintockia* + *Nomaeopelta* clade average only about 1600 km. Moreover, these different thermal tolerances appear to be clade-level traits that first appeared in their respective common ancestors in the Late Miocene or Early Pliocene, long before glacial and interglacial sequences provided a plausible mechanism for divergence. Subsequent divergences in both clades produced taxa with similar tolerances, suggesting that thermal tolerance was heritable in these clades and this trait constrained descendents to similar range sizes. This finding offers a deeper historical view of the potential makeup of latitudinal barriers and range size than is attainable through classical taxonomic studies. Moreover, the pattern has implications for clade selection (Jablonski, 1987; Lloyd & Gould, 1993; Vermeij, 1996).

SYSTEMATICS

Patellogastropoda Lindberg, 1986

Lottiidae Gray, 1840

Although this taxon is the most diverse and abundant of all patellogastropod clades in the world, it is diagnosed by few characters, and most notably by an absence of calcitic foliated shell microstructures and the presence of fibrillar ones. Foliated shell structures are present in the Patelloidea, Nacelloidea, and many Acmaeoidea, but are absent in the Lottiidae. The remaining anatomical and shell characters of the Lottiidae are all found in different combinations in one or more of the outgroups.

Two major subclades, Lottiinae and Patelloidinae, have been previously recognized on radular and shell microstructure characters; they are also delimited by molecular characters (Simison, 2000). Both groups contain numerous subclades that have been named, as well as previously unrecognized ones. In North America, Australia, Japan, and South America, members of the Lottiidae compose the vast majority of the species in the nearshore patellogastropod guilds. Unlike the Acmaeoidea, members of the Lottiidae are not found in the deep sea. Instead, they are primarily intertidal in habitat and rarely occur deeper than 30 meters. They occupy a wide range of intertidal heights and habitat types. Some species are tolerant of brackish water and can be found in estuarine habitats. Several species are associated with algae and marine angiosperms while others are found only on carbonate substrates.

The Lottiidae are distributed worldwide with the exception of Antarctica. There are no strong biogeographical trends within the global distribution of Lottiidae, and different taxa in a single clade may range from cool temperate to subtropical environs. Members of the Lottiidae are identifiable in the Cretaceous based on shell microstructure and radular characters (Akpan et al., 1982; Lindberg, 1988). By the Eocene, circulatory characters that diagnose living taxa are visible as impressions preserved on the interior of fossil shells (Lindberg & Squires, 1990).

Lottia Gray, 1833

Lottia Gray, 1833:800. Type species, by subsequent designation of Dall, 1871: *Lottia gigantea* Sowerby, 1834. Northeastern Pacific.

Tecturella Carpenter, 1860:3. Type species, by monotypy: *Tecturella grandis* Gray (= *Lottia gigantea* = Sowerby, 1834) (not Stimpson, 1853:36).

Tecturina Carpenter, 1861:219. Type species by original designation: *Tecturina grandis* "Gray" (= *Lottia gigantea* Sowerby, 1834).

Shell profile varies from high to low with the apex

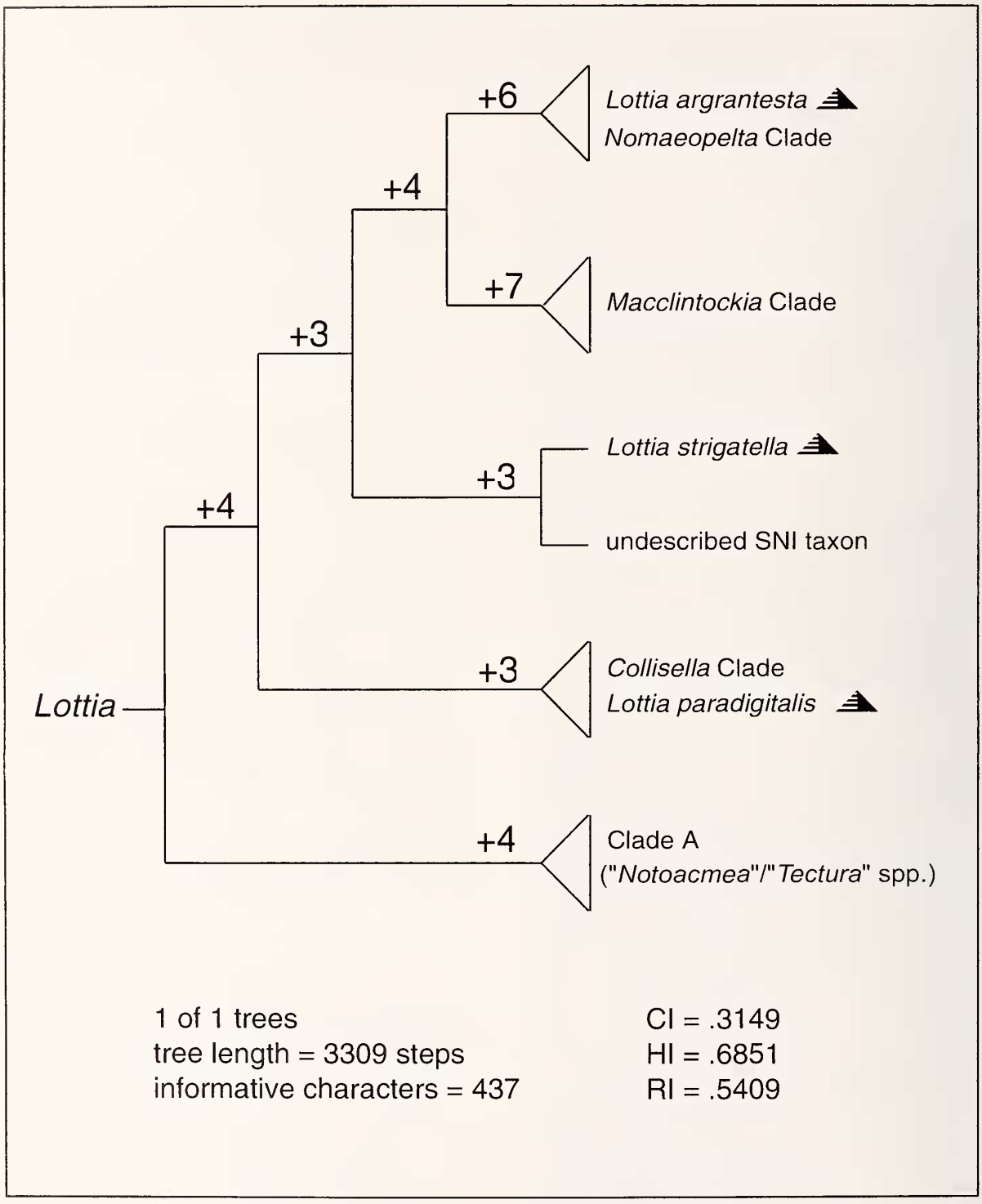


Figure 2. Simison's (2000) 16S maximum parsimony (PAUP 4.0b3a: Swofford, 2000) phylogenetic hypothesis of the relationships among the major clades of temperate northeastern Pacific patellogastropods showing the placement of the three taxa discussed herein (▲). Numbers on branches = decay values. SNI is an unidentified San Nicholas Island, California taxon with a unique haplotype. CI = consistency index, HI = homoplasy index, RI = retention index.

positioned anterior of center of shell. Shell sculpture consists of combinations of ribs, riblets, and concentric growth lines. Radular configuration consists of three pairs of lateral teeth. If present, one pair of marginal teeth (or uncini) is located on the radular membrane at the posterior edge of the ventral plates; they are substantially smaller than the third lateral teeth and non-mineralized. The first and second inner pair of radular teeth are approximately equal in height, but the second pair is usually wider than the first. The outermost third lateral teeth are typically reduced in size relative to the inner teeth. In coralline feeding species all three lateral teeth are approximately equal to one another in size and shape. The ventral plates underlying the lateral teeth are complex with distinct plates for each tooth; however the tooth plates for the second and third lateral teeth may be partially fused anteriorly. A complete or partial secondary gill may be present in the mantle groove. In most taxa, the fibrillar layer dominates the shell microstructure.

This temperate taxon reaches its zenith in the North Pacific especially in the northeastern Pacific. Some Australasian taxa have been assigned to the taxon *Collisella* (e.g., Ponder & Creese, 1980)—a subclade within *Lottia*. However, the presence of *Collisella* (or *Lottia*) taxa in Australia is problematic. The Australian taxa are clearly outliers and whether they share common ancestry with the *Lottia* of the North Pacific has not been convincingly demonstrated. Alternatively, they could represent an independent derivation from a distantly related Australasian lottiid ancestor.

A complete nomenclatural revision of the taxon *Lottia* is beyond the scope of this paper. However, there is sufficient data and sampling to present an overview of our current working classification. This classification provides a framework upon which to place the taxa discovered, described, and discussed herein. It also resolves several longstanding nomenclatural issues surrounding "generic" assignments with the northeastern Pacific Patellogastropoda. A more detailed nomenclatural treatment will be published elsewhere.

In the northeastern Pacific we recognize five subclades within *Lottia* based on molecular characters (Figure 2). An unnamed taxon (Figure 2, subclade A) is composed primarily of taxa previously assigned to the *Notoacmea* by McLean (1966) and *Tectura* by Lindberg (1986b). The taxon *Collisella* is restricted from its previous usage by McLean (1966) and others to correspond to those taxa that share a more recent common ancestor with *Lottia paradigitalis* than with *Lottia strigatella* or members of subclade A (e.g., *Lottia persona*). Another subclade currently consists of an undescribed species from the southern California Islands and *Lottia strigatella*. The crown group consists of two taxa—Macclintockia (Lindberg MS in Kozloff, 1987) and a clade composed primarily of Californian taxa and the Nomaeopelta (Berry, 1958) of the Gulf of California, Mexico. The taxa formerly known collectively as *Lottia strigatella* and *Lottia paradigitalis* actually reside in three of these five clades. Based on examination of their shell and radular morphology it is surprising that they do not share a most recent common ancestor.

Equivalent, hierarchical phylogenetic nomenclature for these taxa is as follows:

Linnean		Phylogenetic
Lottia strigatella	=	*Lottia strigatella*
Lottia paradigitalis	=	*Lottia Collisella paradigitalis*[1]
Lottia ***argrantesta***	=	*Lottia Nomaeopelta* ***argrantesta***

Lottia paradigitalis (Fritchman, 1960)

(Figures 3–8, 26–28)

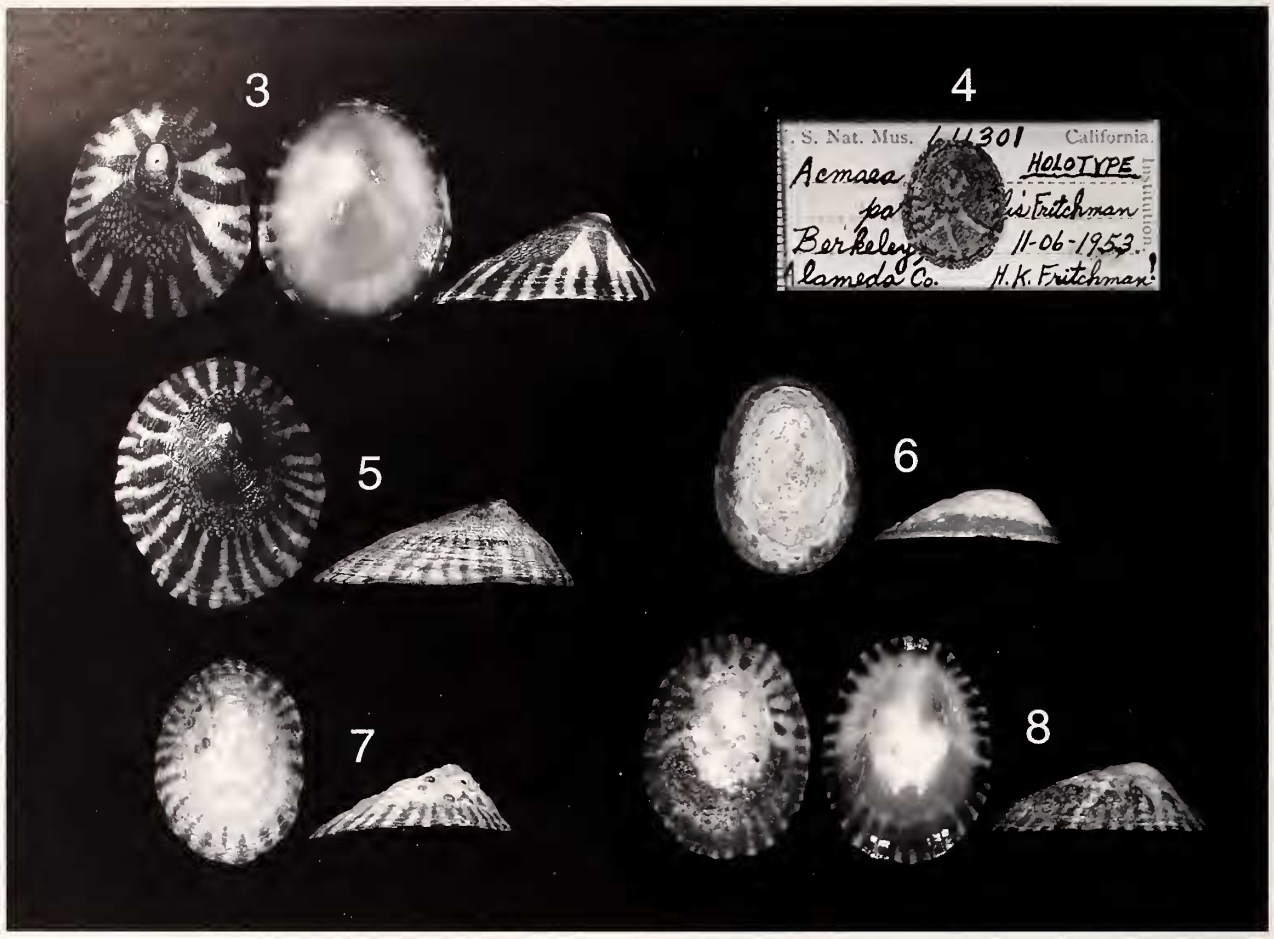
Acmaea paradigitalis Fritchman 1960:53.
Collisella borealis Lindberg, 1982:52.

The shell is moderately thin with the apex positioned approximately ⅓ of the way from the anterior end. The apex is often eroded and rounded, but on less eroded specimens the apex comes to a strong point and slightly protrudes toward the anterior. Both the anterior and posterior slopes from the apex to the margin are slightly convex. Shell height is medium in profile and the shell typically lacks radial ribbing. Fine and regular concentric growth lines are the predominate form of shell sculpture. The shell apex is typically eroded to white with either brown radial markings at the margins or a dark band at the apex margin (e.g., Figures 7, 8). Less eroded specimens show a range of radial patterns that include tessellate green-brown apical areas with white radial lines leading to the shell margin (Figures 3, 5). Specimens appear to change substrates during their ontogeny and this is reflected in changes in the color and pattern of the shell (Figure 5). White radial markings often bifurcate at the shell margin creating numerous short radial parallel lines along the apertural margin. This pattern is often mirrored on the interior of the shell as well.

The interior surface of the shell typically has very little dark staining. Usually there is a translucent white coating over the entire inner surface except at the very margins. The exterior color patterns clearly show through to the interior surfaces, particularly at the shell margins where the white layer is lacking. Occasional specimens have darkly stained interiors overlaying the translucent white layers.

Radula (Figures 26–28): The first lateral teeth have pointed cusps, and the anteromedial edges of the ventral

[1] The trinomials used here should not be confused with the subgeneric rank of the Linnean classification scheme. Here they are clade names that provide additional hierarchical information regarding relationships (e.g., see Figure 2).



Figures 3–8. Shell morphology of *Lottia paraditigalis* (Fritchman, 1960). Figure 3. UCMP 157022: Bodega Bay, Sonoma County, California. Figure 4. USNM 611301 [Holotype]: Berkeley Marina, Alameda County, California. Figure 5. Transitional shell morphology. UCMP 157021: Bodega Bay, Sonoma County, California. Figure 6. UCMP 157020: San Francisco, San Francisco County, California. Figure 7. UCMP 157018: San Francisco, San Francisco County, California. Figure 8. UCMP 157019: San Francisco, San Francisco County, California.

attachment plates are roughly parallel. The second lateral teeth are also pointed, and the inner and outer tooth margins are convexed. The cusps lie lateral to the outer edges of the first lateral teeth. The third lateral teeth are reduced and pointed. They lie lateral and almost perpendicular to the bases of the second lateral teeth. The third lateral teeth are distinct from the second lateral teeth except at their bases. The third lateral cusps extend posterior to a position similar to that of the second lateral cusps. The uncini on the radular membrane are prominent and appear rounded.

Holotype dimensions: Length 16 mm, width 15 mm, height 5.5 mm.

Type locality: (Figure 1). UNITED STATES: California; Alameda County, Berkeley Marina (37°52′N, 122°18′W)

Type material: Holotype (USNM 611301), 5 paratypes (USNM 1611302). Although Fritchman (1960) extensively studied the radula of *Acmaea paradigitalis,* the type material consists entirely of shells; not a single radula associated with a type specimen was found.

Distribution: The recognition of synonymy between the taxa known as *L. borealis* and *L. paradigitalis* increases the range of this species into the northwestern Pacific. Based on morphological comparisons (Lindberg, 1982), *Lottia paradigitalis* likely ranges from De Kastri, Russia (51°28′N, 140°47′E) to Kalevala Bay, Russia (42°30′N, 130°50′W) through the Aleutians and down the North American coast to southern California. Based on molecular data, the most northwestern population is found at Gibson Island, Chichagoff Harbor, Attu Island (52°57′N, 173°16′W), Aleutian Islands, Alaska [type locality of *Collisella borealis*]. The southern limit appears to lie near Point Conception, California (34°27′N, 120°28′W), with

a small scattering of individuals occurring at mainland and island localities within the southern California bight. Such a range is comparable with those of other members of the *Collisella* clade such as *Lottia Collisella pelta* (Rathke, 1833) and *Lottia Collisella digitalis* (Rathke, 1833).

Discussion: Lindberg (1981) unexpectedly noticed radular differences in *Lottia paradigitalis* that distinguished it from *L. strigatella.* These differences included the shorter and more compact ventral plate length and the shorter and blunter second lateral teeth. However, it is doubtful that these characters would have held up in a larger and statistically valid study. Fritchman's (1960) original radular study of "*Acmaea paradigitalis*" included specimens of *L. paradigitalis* as well as *L. strigatella.* For example, Fritchman's figured specimens 8 and 9 (and possibly the top specimen in Figure 7) appear to be *L. strigatella* not *L. paradigitalis.* It is highly probable that his quantitative analysis of radular morphology confounds both *L. strigatella* and *L. paradigitalis,* especially in his "S of 34°" category.

Although Lindberg (1982) noted similarities in the color patterns of *L. borealis* and *L. paradigitalis* (as *Collisella strigatella*), there was little subsequent discussion of possible relationships. This was due in part to the color variation present in *L. borealis* (Figures 29–34). Although the tessellate and rayed color patterns are common in *L. paradigitalis,* the solid and white color patterns of the nominal taxon *L. borealis* have not been previously recognized in *L. paradigitalis.* At Attu, specimens with the solid color patterns are often associated with *Mytilus* aggregations, while the white form occurs in a wide variety of habitats and in aggregations that include specimens with other color patterns (Lindberg, 1982). Based on the color patterns seen in specimens of *L. paradigitalis* in Alaska it is likely that similar variation is present in the southern part of the range as well, but it has been confused with other taxa in this more speciose section of its range.

Lottia strigatella (Carpenter, 1864)

(Figures 9–15, 20–22)

Acmaea strigatella Carpenter 1864b:474; *Acamaea patina* var. *strigillata* Carpenter, 1866:334.

The shell is moderately thin with the apex positioned in the anterior third of the shell. The apex is often eroded and rounded, but on less eroded specimens the apex is anteriorly directed. Both the anterior and posterior slopes from the apex to the margin are slightly convex; the anterior slope may be straight in some specimens. Shell height is medium in profile. The shell exterior surface of the shell lacks prominent radial ribbing although evenly spaced, microscopic radial treads are often present. These threads are substantially weaker than the concentric growth lines that sculpted the exterior shell surface. Specimens of *L. strigatella* likely change substrates during their ontogeny, and this is reflected in changes in the color and pattern of the shell (Figure 11). Initially the protoconch is brown in color, but it is often eroded and the apex is white; sometimes with a small, darker spot at its center. In the northern part of its range (southern California and Baja California Norte) most specimens are olivaceous green with grayish white markings (Figure 12). The markings surrounding the apex may radiate outward as evenly spaced stripes, but they soon deteriorate into offset blotches of lighter shell material that maintain the radial pattern. This pattern may be maintained to the shell margin or the blotches may elongate into stripes that then continue to the shell edge. It is not unusual for specimens to exhibit all three color patterns; however, the regular, radial white markings surrounding the aperture are the most distinctive. While the markings nearer the apex are more gray- or blue-white, the markings closer to the margin are whiter. In the southern part of its range, and into the Gulf, variegated patterns are more common (Figures 9–13). In central Baja California, a solid yellow-tan forma has also been found (Figure 14), and juveniles may be dark with two lateral white flashes (Figure 15).

The central area of the shell inside of the muscle scar is typically marked with a brown stain. In some specimens the coloration does not extend into the actual apical area which remains white. The intermediate area between the muscle scar and the shell margin ranges from blue to white. In darker specimens this may be suffused with brown. The interior margin is narrow and dark and reflects the exterior shell markings.

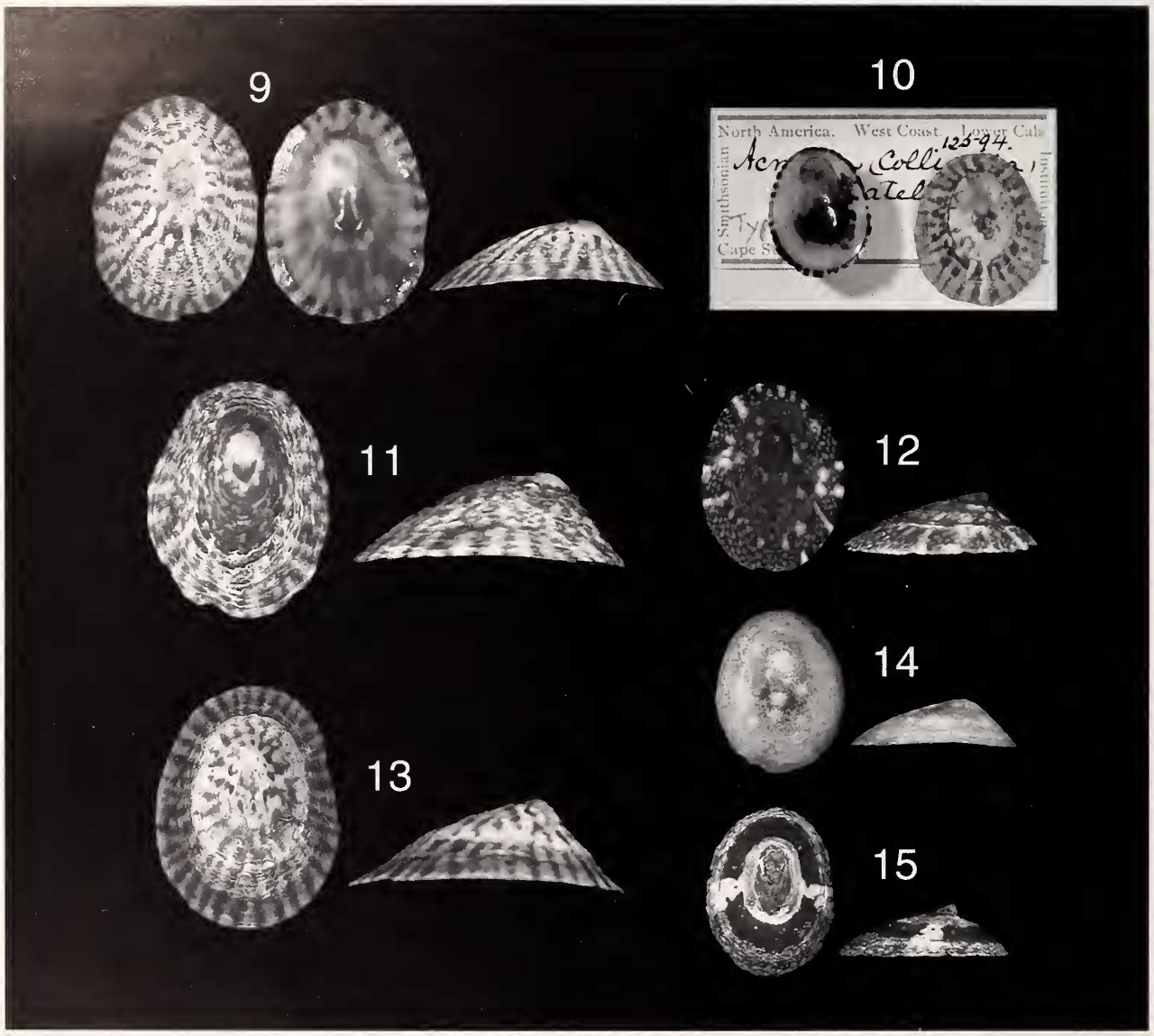
Radula (Figures 20–22): The first lateral teeth have sharply pointed cusps that flare out laterally. The second lateral teeth are also pointed, and the inner and outer margins convexed. The cusps lie lateral of the cusps of the first lateral teeth in the adjacent row. The third lateral teeth are reduced and also sharply pointed. They lie lateral and almost perpendicular to the bases of the second lateral teeth. The third lateral teeth are distinct from the second lateral teeth except at their bases. The third lateral cusps extend posterior to a position slightly behind that of the second lateral cusps. The uncini on the radular membrane are prominent and appear rounded.

Type locality (Figure 1): MEXICO: Sonora; Guaymas (28°N, 111°W).

Type material: Six syntypes (USNM 12594).

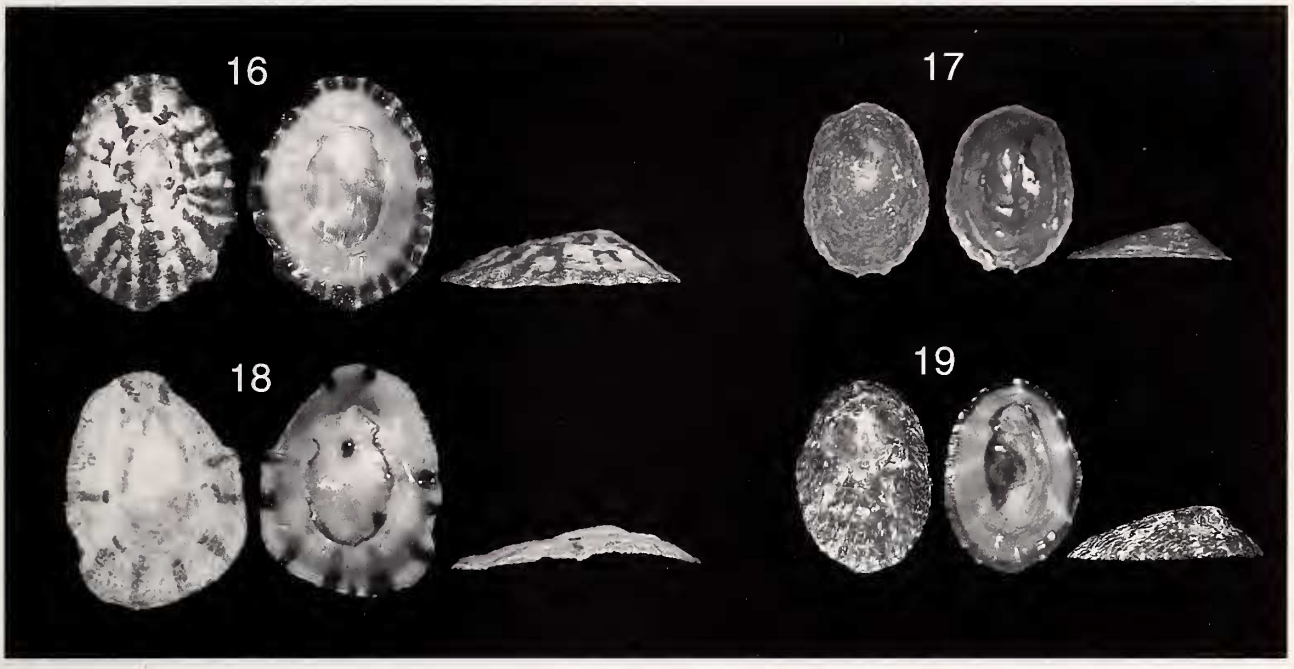
Distribution: MEXICO: Sonora; Guaymas (28°N, 111°W) to UNITED STATES: California; southern California bight region (Figure 1).

Discussion: Phenotypic variation present in *Lottia strigatella* has previously led to its being confused with other taxa, most notably *L. paradigitalis, L. persona,* and *L.*



Figures 9–15. Shell morphology of *Lottia strigatella* (Carpenter, 1846). Figure 9. UCMP 157011: Cabo San Lucas, Baja California Sur, Mexico. Figure 10. USNM 12584 [Lecotype on right]: Cabo San Lucas, Baja California Sur, Mexico. Figure 11. Transitional shell morphology. UCMP 157012: Cabo San Lucas, Baja California Sur, Mexico. Figure 12. UCMP 157001: Guaymas, Sonora, Mexico. Figure 13. UCMP 157013: Cabo San Lucas, Baja California Sur, Mexico. Figure 14. UCMP 157015: Bahía Tortugas, Baja California Norte, Mexico. Figure 15. UCMP 157002: Guaymas, Sonora, Mexico.

fenestrata (Reeve, 1855). It is possible that over 140 years ago P. P. Carpenter saw through this variation and distinguished both *L. strigatella* and *L. paradigitalis* only to have "modern" systematists confound his distinction because of the overall similarity shared by these taxa. However, Carpenter did not localize his nominal taxon *Acmaea patina* var. *strigillata,* but only stated that it was found in the Vancouver-Californian provinces. Jay (1852) indicated the locality as "Upper California," but this does not distinguish between the *L. strigatella* and *L. paradigitalis* in modern day central and southern California. Burch's Solomon-like division of *L. strigatella* for the southern taxon and *L. strigillata* for the northern one may have been correct. However, the fact that he thought both of these only to be forms of *Lottia persona* suggests even further nomenclatural confusion. Because of the lack of a locality or type specimens associated with the name *strigillata,* we chose to use the name *paradigitalis* for this taxon. This nominal taxon was well described, localized, and can be unequivocally associated with a genotype.



Figures 16–19. Shell morphology of *Lottia* ***argrantesta*** Simison & Lindberg, sp. nov. Figure 16. UCMP 157007 [Holotype]: Bahía de San Francisquito, Baja California Sur, Mexico. Figure 17. UCMP 157003 [Paratype]: Califin, La Paz, Baja California Sur, Mexico. Figure 18. UCMP 157008 [Paratype]: Bahía de San Francisquito, Baja California Sur, Mexico. Figure 19. UCMP 157006 [Paratype]: Tecolate, Baja California Sur, Mexico.

Test (1946:11) suggested that "*Acmaea fenestrata*" represented one of "two polytypic species of the genus *Acmaea* known at the present time in North American waters . . ." While the northern form had a subcircular aperture with the interior of the shell suffused with brown, the southern form had an oviform aperture with a blue interior, and little if any brown coloring.

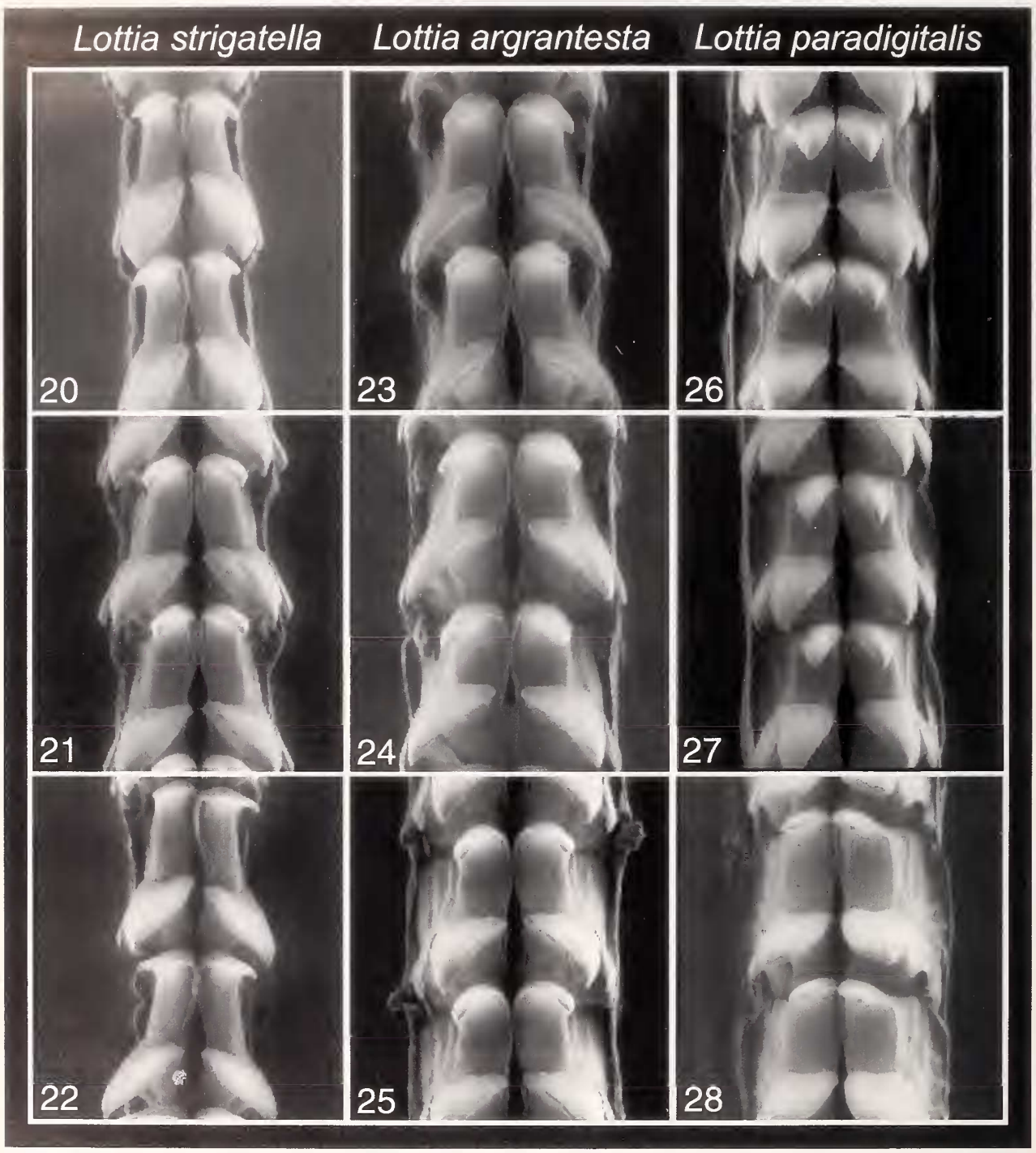
McLean (1966:105) also recognized this distinction between northern and southern specimens of *Lottia fenestrata*, but considered the differences to result from their occurrence in different habitats rather than geographical variation. McLean noted that both northern and southern forms were present at some localities albeit in different habitats (i.e., sandstone reefs near sand vs. rubble-reefs, respectively). McLean (1966:81) also noted, "Color patterns of the rubble-reef living form of *C. strigatella* are closely approximated by those of *C. fenestrata* (with which it is always in association), but the interior lacks the brown suffusion of *C. fenestrata.*"

The presence of brown interiors in specimens from Bahía Tortugas, Baja California Norte, Mexico that are molecularly identical to specimens of *Lottia strigatella* from the type locality of Guymas, suggests to us that the specimens of southern California rubble-reefs represent ecophenotypes of *L. strigatella* rather than *L. fenestrata.* As pointed out by McLean, rubble-reefs are rare north of Point Conception, California as are specimens of *L. strigatella.* In contrast, *Lottia fenestrata* is a northern taxon that is rare south of Point Conception and differs little throughout its northern range.

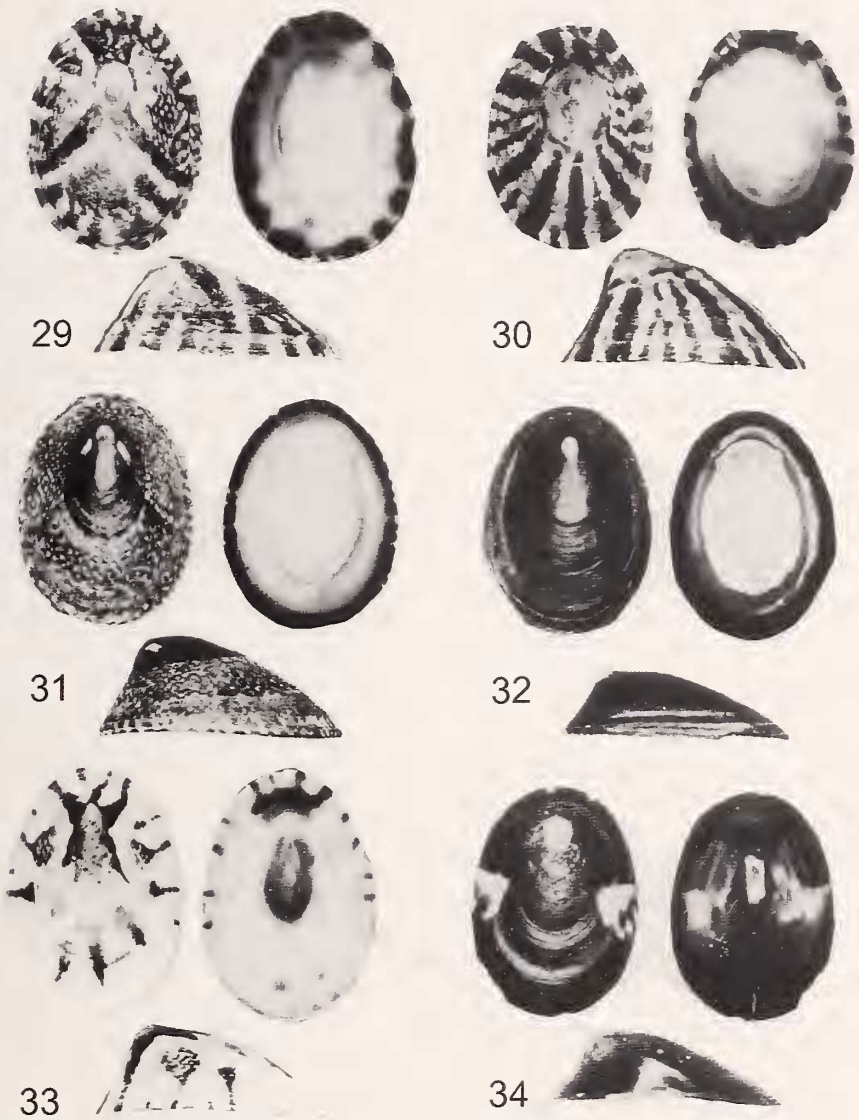
Lottia ***argrantesta*** Simison & Lindberg, sp. nov.

(Figures 16–19, 23–25)

Shell height ranges from relatively low to medium profiles. Shell ribbing typically consists of irregular ribs, and shells less than 10 mm in length tend to be smoother, but still have a knobby texture. The aperture and growth lines are irregular. The apical area erodes to white and the initial shell is dark with approximately six to eight white rays radiating from the apex. Subsequent shell color varies from predominately black with radially drawn out white markings (Figure 17) or predominately white with black radial markings corresponding to coarse irregular ribs (Figure 14). In most cases, the markings on both the white and black ground colors do not extend from the apex to the margin, but rather stop and restart in different positions. In the lighter shells the white areas are marked with brown markings; in darker specimens the brown markings are more sparse, but are often visible at the margins associated with the white markings. Occasional small specimens (less than 10 mm in length) are found that are completely brown in color (Figure 15). The ribs are not regular but instead often form knuckles or knobs at irregular intervals from the apex to the margin, and do



Figures 20–28. Radular morphology. Figures 20–22. *Lottia strigatella* (Carpenter, 1846). Figure 20. Chileno, Cabo San Lucas, Baja California Sur, Mexico (UCMP 157014). Figure 21. Cabo San Lucas, Baja California Sur, Mexico (UCMP 157010). Figure 22. Guaymas, Sonora, Mexico (UCMP 1570009). Figures 23–25. *Lottia* ***argrantesta*** Simison & Lindberg, sp. nov. Figure 23. Califin, La Paz, Baja California Sur, Mexico (UCMP 157003). Figures 24, 25. Bahía de San Francisquito, Baja California Sur, Mexico (UCMP 157008, 157007, respectively). Figures 26–28. *Lottia paradigitalis* (Fritchman, 1960). San Francisco Bay, San Francisco County, California (UCMP 157020, 157018, 157019, respectively).



Figures 29–34. *Collisella borealis* Lindberg, 1982 = [Lottia paradigitalis (Fritchman, 1960)]. Figure 29. Holotype, CAS 024715. Figure 30. Rayed color pattern (Paratype, CAS 024716). Figure 31. Tesselate color pattern (Paratype, CAS 024717). Figure 32. Solid color pattern (Paratype, CAS 024718). Figure 33. White color pattern (Paratype, CAS 024719). Figure 34. Juvenile color pattern (CAS 024720). All specimens from Gibson Island, Attu Island, Aleutian Islands, Alaska.

not protrude to form a crenulated margin; in smaller specimens the shells are typically smoother.

The inner surface of the shell is typically marked with a brown or yellow-brown apical stain that clearly delineates the interior boundary of the shell attachment muscle scar. Sporadic darker markings may also be present in the central area. The intermediate area ranges from blue to white and is often overlain by a yellow-brown stain as well. The interior margin is broad and dark, reflecting the outer white markings. In the small brown shells the entire interior surface is brown with the central area being slightly darker than the intermediate area and margin. The edge of the aperture is slightly reflected back.

Radula (Figures 23–25): The first lateral teeth have sharply pointed cusps that flare out laterally. The second lateral teeth are also pointed, the inner tooth margins are concaved, and the outer margins slightly convexed. The cusps lie close to the edge of the radular ribbon. The third lateral teeth are reduced and also sharply pointed. They lie lateral and almost perpendicular to the bases of the second lateral teeth. The third lateral teeth are distinct from the second lateral teeth except at their bases. The

third lateral cusps extend posterior to a position similar to that of the second lateral cusps. The uncini on the radular membrane are prominent and appear rounded.

Holotype dimensions: Length 20 mm, width 16.5 mm, height 4.2 mm.

Type locality (Figure 1): MEXICO: Baja California Sur; Bahía de San Francisquito [Holotype]. MEXICO: Baja California Sur: La Paz and Tecolate [Paratypes].

Type material: Holotype UCMP No. 157007, Paratypes UCMP Nos. 157003, 157006–157008. Paratypes have also been deposited in LACM and USNM.

Distribution: MEXICO: Baja California Sur; Bahía de San Francisquito (28°30′N, 112°40′W) to La Paz (24°10′, 110°21′) and MEXICO: Sonora; Guaymas (27°56′, 110°54′).

Material examined: Nine specimen lots, 33 specimens three radula preparations.

Etymology: It is an honor for us to name this species for the first limpet systematist of the University of California at Berkeley, the late Dr. Avery Ransome Grant Test, in recognition of her contributions to our knowledge of the Lottiidae.

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