

Resurrection of *Nucella ostrina* (Gould, 1852), Lectotype Designation for *N. emarginata* (Deshayes, 1839), and Molecular Genetic Evidence of Pleistocene Speciation

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Abstract. Previous work demonstrating concordant patterns of reproductive isolation, fixed genetic differences, and morphological differentiation indicates the existence of morphologically cryptic “northern” and “southern” species within the nominal taxon *Nucella emarginata*. The southern species, which retains the name *Nucella emarginata* (Deshayes, 1839), is characterized by four to five rows of spiral sculpture on the body whorl of the shell in the form of regularly spaced knobs plus an adapical tooth or callus on the columella. The type locality for *N. emarginata* is San Miguel Island, California. The northern species, *N. ostrina* (Gould, 1852) is characterized by five to six cords of continuous spiral sculpture, a taller and more slender spire, and usually a more flared aperture than *N. emarginata*. The type locality for *N. ostrina* is Tillamook Bay, Oregon. Because Deshayes’ original description of *N. emarginata* was based on four specimens (syntypes), we have re-figured and designated one of these syntypes as a lectotype. A lectotype for *N. ostrina* was assigned previously (Johnson, 1964). A new analysis of previously published mitochondrial DNA sequences and molecular clock calibration dates from the fossil record also indicates a late Pleistocene divergence for *N. ostrina* and *N. emarginata*. A late Pleistocene divergence time, and the subtle nature of morphological differentiation between these two species, together provide an important counter-example to the prevailing view that little speciation occurred during the Pleistocene along rocky Californian shores, a period characterized by rapid and frequent environmental change.

INTRODUCTION

Accurate discrimination of biological species is essential for describing patterns of organismal diversity, a fundamental first step toward understanding the processes that generate diversity at the species level (Knowlton, 1993; Thorpe & Sole-Cava, 1994; Klautau et al., 1999). In the ocenebrine gastropod genus *Nucella* Röding, 1798, pervasive geographic variation in shell form within nominal species has led to an extensive history of taxonomic confusion at the species level (see Palmer et al., 1990). Currently, four nominal species of *Nucella* on the west coast of North America are widely recognized in the literature.

Because patterns of geographic variation in shell form are particularly pronounced in *Nucella*, this genus provides an unusually challenging group for characterizing the relationship between morphological form and reproductive isolation.

A combination of data from genetic markers and morphological characters, as well as direct evidence of reproductive isolation, together indicate the existence of two biological species within the nominal taxon *N. emarginata* (Deshayes, 1839). First, Palmer et al. (1990) demonstrated a fixed genetic difference at an allozyme locus (Isocitrate dehydrogenase-2, EC 1.1.1.42) between “northern” and “southern” populations of *N. emarginata*. Second, this fixed allelic difference was also shown to be concordant with subtle morphological differences in both shell and egg capsule morphology (Palmer et al., 1990). Third, con-

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trolled laboratory crosses between northern and southern populations failed to produce any offspring (Palmer et al., 1990). Lastly, a geographically broader survey of both allozyme loci and mitochondrial DNA (mtDNA) sequences (cytochrome c oxidase I) further revealed that genetic and morphological differentiation between northern and southern morphological forms of *N. emarginata* are consistent throughout a broad region of sympatry in central California, between San Francisco and Point Conception (Marko, 1998). The combination of morphological, reproductive, and genetic differences now provides conclusive evidence of two biological species within *N. emarginata*: a northern species found between Yakutat, Alaska and Point Conception, California, and a southern species distributed from San Francisco, California to Punta Eugenia, Baja California Sur (see Palmer et al., 1990; Marko, 1998).

The northern species was provisionally recognized as *Nucella ostrina* (Gould, 1852) in an earlier paper (see Marko, 1998). Here, we present formal systematic descriptions for these two sibling species plus designate a lectotype for *N. emarginata* (a lectotype for *N. ostrina* was previously chosen by Johnson, 1964). Given only subtle morphological differences between these two species, we also investigate these species' time of divergence, based on analyses of previously published mitochondrial DNA sequences (from Marko, 1998). We then discuss the relevance of the timing of this speciation event toward understanding spatial and temporal patterns of morphological and species diversity in molluscan faunas of the cool-temperate Eastern Pacific.

MATERIALS AND METHODS

Both Gould's and Deshayes' specimens were examined for comparison to the morphological differences that are associated with genetic differences and reproductive isolation between *Nucella emarginata* and *N. ostrina* (Palmer et al., 1990; Marko, 1998). Shells from PBM's personal collection were examined and photographed to present a sampling of geographic variation in shell form within both species. Rather than attempting to document the entire range of variation in both species, and considering that the basic morphological differences were recently figured elsewhere (Palmer et al., 1990), we instead focused on specimens that exhibit relatively subtle differences in shell morphology. Material from the Natural History Museum, London (NHM), Museum National d'Histoire Naturelle, Paris (MNHN), The United States National Museum of Natural History (USNM), the Natural History Museum of Los Angeles County (LACM), and the Zoological Institute of the Russian Academy of Sciences (ZIRAS) were also examined.

To determine whether limited morphological differentiation between these species reflects recent speciation, we inferred the time of divergence for *N. ostrina* and *N. emarginata* using previously published (Marko, 1998) cy-

tochrome c oxidase I (COI) sequences from 50 individuals (Genbank accession numbers for mtDNA haplotypes: AFO76536–AFO76560). We calculated maximum likelihood sequence divergences among all COI haplotypes with PAUP* 4.0 (Swofford, 2001) using the HKY model of nucleotide substitution (Hasegawa et al., 1985) coupled with gamma-distributed rate heterogeneity among nucleotide sites (Yang, 1994). Actual nucleotide frequencies were assumed to equal the observed frequencies, and the transition to transversion ratio (t) and the shape parameter (α) for rate heterogeneity among sites were each inferred using a Neighbor-joining tree topology based on Jukes-Cantor genetic distances (Jukes & Cantor, 1969). A log-likelihood ratio test (see Felsenstein, 1988; Huelsenbeck & Crandall, 1997) was used to determine if *Nucella* COI satisfied the criterion of substitution rate constancy, an assumption that must be valid in order to infer divergence times from molecular sequences. In all analyses, trees were rooted with haplotypes from the congeners *N. canaliculata* and *N. lima* (Genbank accession numbers AFO76561–AFO76565).

Using the procedure described by Nei & Li (1979), we calculated the net sequence divergence at third positions between species as $p_{AB(\text{net})} = p_{AB} - 0.5(p_A + p_B)$, where p_A and p_B are the mean sequence divergences among individuals within species A and B, respectively, and p_{AB} is the mean sequence divergence among individuals between species (also see Avise & Walker, 1998; Edwards & Beerli, 2000). Net nucleotide divergence more accurately estimates the time elapsed since population splitting because uncorrected gene divergences between species will always predate speciation (Nei & Li, 1979; Avise & Walker, 1998; Avise, 2000; Edwards & Beerli, 2000). To determine the rate at which COI diverges, we used the split between *N. canaliculata* and the *N. emarginata*/*N. ostrina* clade as a calibration point, which is known from the fossil record to have occurred between 5–10 Ma ago (Collins et al., 1996). The rates inferred from this fossil calibration were then applied to the net COI divergence between *N. ostrina* and *N. emarginata* to infer their time of separation.

SYSTEMATICS

Family MURICIDAE Rafinesque, 1815

Subfamily OCENEBRINAE Cossmann, 1903

Genus *Nucella* Röding, 1798

Nucella emarginata (Deshayes, 1839)

(Figures 1A–D, 2M–T)

Purpura emarginata Deshayes, 1839: 360.—Deshayes, 1841: pl. 25.—Reeve, 1845: 3, pl. 10, fig. 46.—Cooke, 1915: 203.

Thais emarginata Vanatta, 1910: 38.

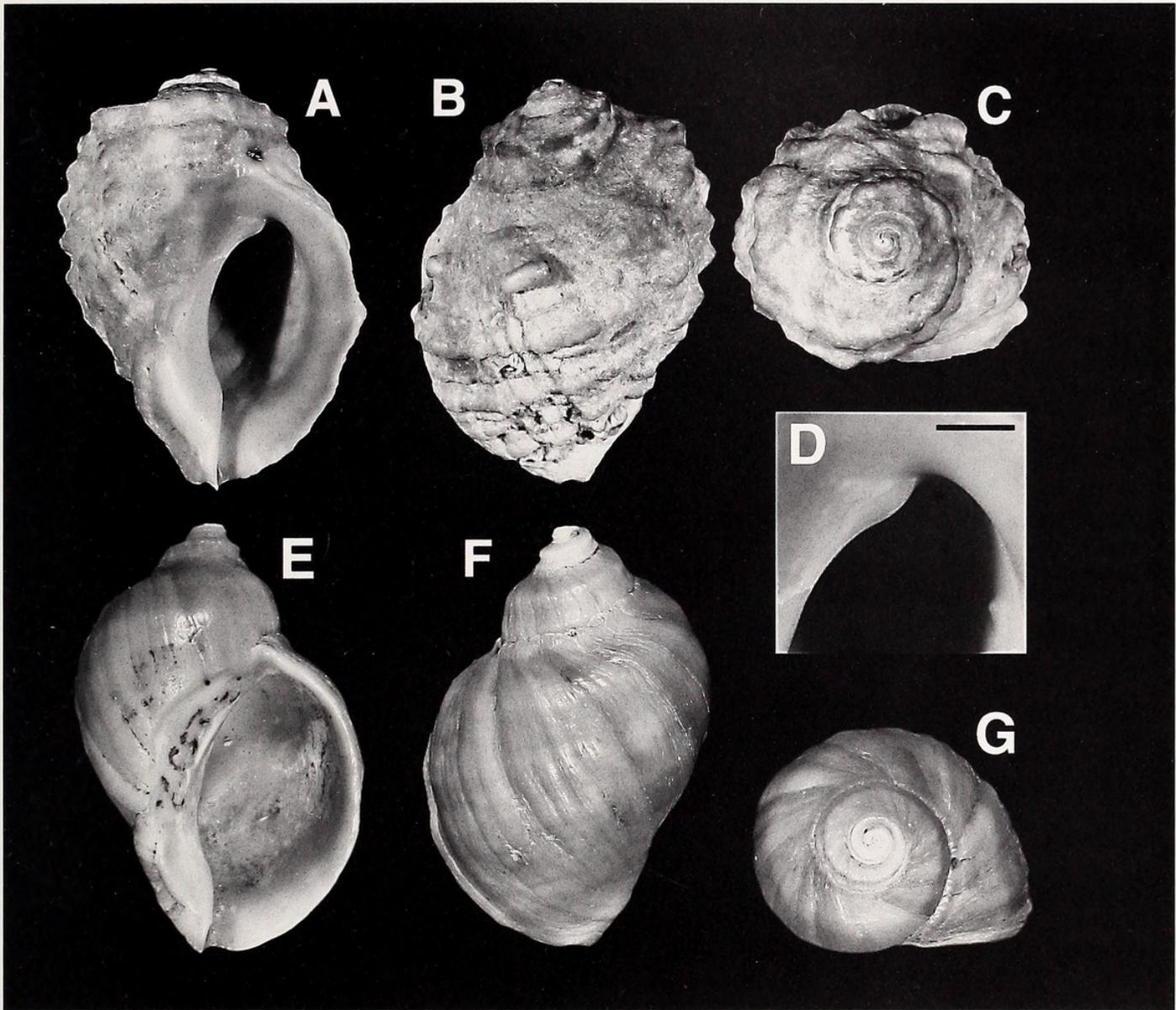


Figure 1. A–D. Lectotype of *Nucella emarginata* (Deshayes, 1839). Shell length: 25 mm. E–G. Lectotype of *N. ostrina* (Gould, 1852). Shell length: 20 mm. A and E. Apertural views; B and F. Abapertural views. C and G. Apical views. D. Callus or tooth on the adapical end of the aperture of *N. emarginata* lectotype. Scale bar = 2 mm (F only).

Thais (Nucella) emarginata Dall, 1915: 569, pl. 75, figs. 2–3.—Oldroyd, 1927: 44, pl. 36, figs. 2–3.

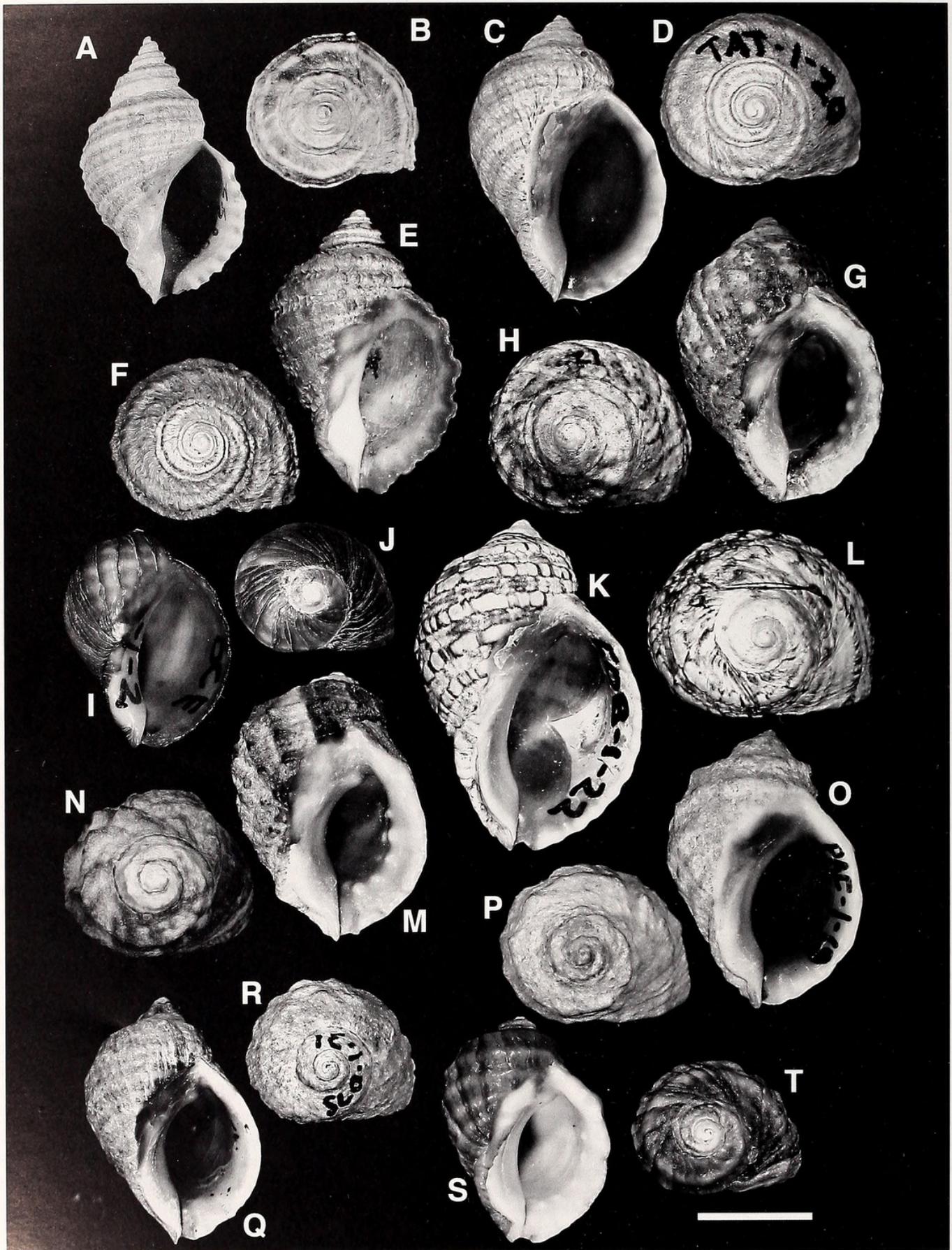
Nucella emarginata Abbott, 1974: 182, fig. 1909.—McLean, 1978: 46, fig. 24–4.—Palmer et al., 1990: 325, fig. 3.

Type material examined: *Purpura emarginata*, MNHN syntypes. *Purpura rupestris*, MNHN syntypes.

Designation of lectotype: Deshayes' descriptions were based on four different specimens. We have therefore designated the specimen in Figure 1 as the lectotype.

Type locality: *Purpura emarginata*, San Miguel Island, California, USA. *Purpura rupestris*, no type locality recorded.

Description: Shell ovate, body whorl typically large, and spire both short and broadly conical. Color yellowish to brown, some banded. Whorls convex. When shell sculpture is well developed, spiral sculpturing consists of regularly spaced knobs at the distal margins of the spiral cords (Palmer et al., 1990: fig. 3). Body whorl with four to five rows of major spiral cords; some specimens with minor cords between major cords. Penultimate whorl with two cords. Columella curved, flattened; color light brown to white. Aperture large, outer lip sometimes wavy (depending on extent of external sculpturing), five teeth recessed from margin. Typically with a tooth or callus on the adapical end of the aperture of the shell (Figures 1A,



D). Egg capsules cylindrical with relatively short necks, distal flared margin. Shells and egg capsules of *N. emarginata* are figured extensively elsewhere; for examples see Palmer et al. (1990).

Geographic range: On rocky shores in the middle to high intertidal between Punta Eugenia, Baja California, Mexico and Fort Point, near San Francisco, California, USA. Although a single specimen from Punta Eugenia, Baja California Sur has been collected (LACM 51-43.16), *N. emarginata* appears to be rare south of Punta Cabras, Baja California, Mexico. In 1993 and 1994, PBM found *N. emarginata* to be abundant (approximately five to 10 individuals/m²) at Punta Descanso, Punta Mesquite, Punta Banda, Punta Santo Tomas, and Punta Cabras. However, 7 km to the south of Punta Cabras, only eight individuals were found at Ejido Erendira; only four individuals were collected farther south at Punta Baja. These observations correspond to a pattern found in the collections housed at the LACM: only two of 13 Baja California lots are from south of Punta Cabras (including the Punta Eugenia individual), totaling eight specimens. *Nucella emarginata* is patchily distributed but abundant in southern California wherever suitable rocky substrate is found. Between Point Conception, California and San Francisco, California, *N. emarginata* is found only in embayments such as Monterey Bay, San Luis Bay, Morro Bay, Half Moon Bay, and at Fort Point, just inside San Francisco Bay (see Palmer et al., 1990; Marko, 1998). LACM material from Tomales Bay, just north of San Francisco, includes two individuals that possess spiral knobs and an apertural tooth, suggesting that the geographic range of *N. emarginata* extends beyond San Francisco. PBM collected extensively in Tomales Bay between 1991–1997, but found no individuals with the uniquely derived morphological features of *N. emarginata*.

Remarks: *Purpura emarginata* was first described by Deshayes (1839) but no figures were published in the original description. A drawing was published 2 years later (Deshayes 1841), but this figure captures little detail of the shell. We therefore re-examined Deshayes' syntypes (Figure 1) and found that they possess the characteristic knobby sculpture on the body whorl of the shells that is characteristic of the southern species described by Palmer et al. (1990). Vanatta (1910:38) remarked that the name *N. emarginata* Deshayes refers to a "short-spined rather rough surfaced form," likely referring to the typically short-spined shell and rough, knobby sculpture of

populations found from San Francisco south. In some populations where sculpture is weakly developed, such as in the vicinity of Point Conception, California (e.g., Figures 2R, T), the early (juvenile) whorls of the shell often exhibit the characteristic uniformly spaced knobs. One of us (GJV) noticed that a small tooth or callus on the adapical end of the columella also characterizes the southern species (Figure 1D). The presence of the adapical tooth can be subtle in thin-shelled specimens (e.g., Figure 2O), but is often well developed in shells from wave-protected environments (e.g., Figures 2M, Q). Due to its position on the inner surface of the columella, the presence of the adapical tooth is often readily diagnosed by sliding a blunt probe over the posterior end of the columella. Based on the correspondence between the morphological characters, the southern species recognized by Palmer et al. (1990) retains the name *N. emarginata*.

Deshayes' syntypes were said by their collector, M. Chiron, to have been collected in New Zealand (Deshayes, 1839). Dall (1915) later revised the type locality as San Miguel Island "where the typical form is abundant" (Dall, 1915:570). One of us (PBM) examined museum specimens from San Miguel Island (LACM 67–38.33, 60602, 60571, 60576) finding a mixture of both *N. emarginata* and *N. ostrina* morphologies. Although both species are likely present on San Miguel Island, we see no reason to change the type locality given the apparent abundance of snails at this location possessing the characteristic shell features of *N. emarginata*.

Dall (1915) suggested that *Purpura lagenaria* Duclos, 1832 (not of Lamarck, 1822) and *Purpura rupestris* Valenciennes, 1846, might be junior synonyms of *Purpura emarginata*. The syntypes of *P. rupestris* (MNHN) were recently identified as *Lepsithais lacunosus* (Bruguère, 1789), from New Zealand (B. Marshall, personal communication). However, the whereabouts of *Purpura lagenaria* Lamarck, 1822, figured by Duclos 1832, is unknown. This specimen may be in the Natural History Museum of Clermont-Ferrand (France), which houses the Duclos collection, but this collection is currently unavailable for study (P. Bouchet, personal communication). Nevertheless, the specimen figured by Duclos (Duclos, 1832: pl. 11, fig. 11) clearly possesses a curved siphonal canal. Therefore, if from the eastern Pacific, *P. lagenaria* is most likely not a member of the genus *Nucella*, and may instead be a specimen of *Acanthinucella* Cooke, 1918.

Several authors (Reeve, 1845; Tryon, 1880; Vanatta,

←

Figure 2. Morphological geographic variation (apertural and apical views, respectively) among *Nucella ostrina* (A–N) and *N. emarginata* (M–T). A, B. Sitka, Alaska (USNM 88842). C, D. Tatoosh Island, Washington. E, F. Cape Arago, Oregon. G, H. Shelter Cove, California. I, J. Ocean Beach, San Francisco, California. K, L. Soberanes Point, California. M, N. Half Moon Bay, California. O, P. Pacific Grove, California. Q, R. San Luis Obispo, California. S, T. Laguna Beach, California. Scale bar = 10 mm.

Table 1

Comparison of morphological differences between *Nucella ostrina* and *N. emarginata*.

Shell character	<i>N. ostrina</i>	<i>N. emarginata</i>
Spire	Taller and more slender	Shorter and broader
Aperture	Typically flared	Narrow, with a callus or tooth on the abapical surface
External sculpture	Typically 5–6 continuous spiral cords	Evenly spaced spiral knobs
Egg capsules	Vase-shaped, with a longer neck	Cylindrical, with a shorter neck, flared distally

1910; Dall, 1915) regarded *Purpura conradi* Nuttall as a junior synonym of *N. emarginata*. *Purpura conradi*, however, was never described, known only from an unpublished manuscript plus several specimens deposited in the NHM by Nuttall (see Reeve, 1845; Tryon, 1880). Therefore, it is not an available name and we do not include it in our synonymy. Reeve, Vanatta, and Tryon all remarked that the spiral cords of the *P. conradi* specimens are discontinuous, giving the shell a rough, knobby exterior. Two of us (PBM and GJV) have also examined the same shells (NHM 1855.3.14.34) and concur that they are specimens of *N. emarginata*.

Nucella ostrina (Gould, 1852)

(Figures 1E–G, 2A–L)

Purpura ostrina Gould, 1852: 244.—Gould, 1857: pl. 18, figs. 310a, b.—Johnson, 1964: 120, pl. 9, fig. 12.

Thais emarginata variety *projecta* Dall, 1915: 571.—Dall, 1921: 112 (refers to a figure in Dall, 1915, that is not *T. emarginata* var. *projecta*).

Nucella ostrina Abbott, 1974: 182, fig. 1910 (in synonymy with *N. emarginata*).

Type material examined: *Purpura ostrina* Gould 1852, lectotype, Museum of Comparative Zoology, Harvard University (MCZ 19275). *Thais emarginata* variety *projecta* Dall 1915, holotype, United States National Museum of Natural History (USNM 88842). *Purpura lapillus* variety *anomala* Middendorff 1849, holotype, Zoological Institute of the Russian Academy of Sciences (ZIRAS 20633).

Type locality: *Purpura ostrina*, Killimook [Tillamook Bay], Oregon, USA. *Thais emarginata* variety *projecta*, Sitka, Alaska, USA. *Purpura lapillus* variety *anomala*, Lapland Russia (Barents Sea).

Description: Very similar to *N. emarginata*. Shell ovate, body whorl large, and spire both short and broadly conical. Color white to dark purple, some banded. Base color and banding variation extensive, greater than in *N. emarginata*. Whorls convex. When shell sculpture is well developed, spiral sculpturing consists of continuous spiral cords (Palmer et al., 1990:fig. 3). Body whorl with five to six rows of major spiral cords; most specimens with

minor cords between major cords. Penultimate whorl with two cords. Columella curved, flattened; color dark purple to white. Apertural teeth not common. Egg capsules vase-shaped, generally more slender than in *N. emarginata*.

Comparison: See Table 1.

Geographic range: From Yakutat, Alaska, (Vermeij et al., 1990) to Point Conception, California (Marko, 1998), but specimens also known from San Miguel Island, California (see above). Between San Francisco and Point Conception, *N. ostrina* is found predominantly on wave-exposed shores and seldom occurs in calm water environments.

Remarks: *Nucella ostrina* Gould (1852) is the oldest available name that has been applied to populations corresponding to the northern species. Although the *N. ostrina* lectotype has weak external shell sculpture, the spiral cords on the apex of this relatively tall shell are clearly continuous, the aperture is large, and the specimen lacks an adapical tooth on the columella. The only other taxon that potentially has priority over *N. ostrina* is *Purpura lapillus* var. *anomala* Middendorff, 1849, a species that resembles *N. ostrina* but which was synonymized with *N. emarginata* by Dall (1915). However, one of us (ARP) recently examined the *anomala* holotype, recognizing it as simply a highly aberrant specimen of *N. lapillus* collected in the North Atlantic.

Dall (1915) also published a detailed drawing of a single specimen from Lituya Bay, Alaska (USNM 220975) that possesses spiral knobs and an adapical apertural tooth. We have collected extensively throughout southeast Alaska and have found no specimens that remotely resemble the southern species in these respects. In fact, Alaskan specimens are typically unusually high spired and very thin shelled, such as Dall's (1915) *T. emarginata* var. *projecta* (Figures 2A, B, USNM 88842) from nearby Sitka, Alaska. Collections of *N. ostrina* (LACM 75–77.4 and 75–77.5) from the vicinity of Lituya Bay all lack an adapical tooth and are also high-spined shells with well developed spiral cords, similar to *T. emarginata* var. *projecta* (Figures 2A, B). Although some specimens of *N. ostrina* do exhibit weakly nodulose or bumpy sculpture, the specimen figured by Dall from Lituya Bay is unlike

any specimen we know of from north of San Francisco. We therefore believe that the southeastern Alaska locality assigned to the single specimen from Lituya Bay is also in error.

RESULTS

A likelihood ratio test indicates that a constant rate of nucleotide substitution can be rejected across all CO1 nucleotide sites for *Nucella emarginata* and *N. ostrina* ($2\Delta\ln = 48.0$, $df = 28$, $P < 0.025$). However, third position substitutions, most of which do not result in amino acid changes, satisfy the rate constancy assumption ($2\Delta\ln = 24.8$, $df = 28$, $P > 0.5$). Therefore, we restricted our estimates of divergence times to third codon positions. Using a divergence of 5–10 Ma for *Nucella canaliculata* and the *N. emarginata/N. ostrina* clade, we obtained a rate of third position divergence of 3.1–6.6% per 1 Ma for CO1 third positions. Given that *Nucella ostrina* and *N. emarginata* differ by 1.1% at third positions, we infer *N. emarginata* and *N. ostrina* diverged 167,000–355,000 years.

DISCUSSION

The existence and identification of cryptic species has important implications for characterizing spatial and temporal patterns of species diversity and therefore for developing hypotheses about the relative timing of environmental changes and speciation (Mayr, 1942; Levinton & Simon, 1980; Michaux, 1989; Jackson & Cheetham, 1990; Knowlton, 1993; Budd et al., 1994; Klautau et al., 1999; Marko & Jackson, 2001). For example, because of the high frequency and relatively rapid pace of changes in climate, sea level, and coastal geomorphology along the Californian coast during the Pleistocene, rates of speciation have been hypothesized to be relatively high during this period of time because such environmental changes are believed to cause disruptions in gene flow between populations of intertidal marine organisms (Golikov, 1973; Valentine & Jablonski, 1983; Vermeij, 1989; Reid, 1990; Collins et al., 1996).

Direct comparisons of molluscan diversity between the Pleistocene and Recent, however, do not support the hypothesis that speciation and extinction rates were elevated during the last 1–2 million years: the strong similarity between Recent and Pleistocene faunas (e.g., Vedder & Norris, 1963; Marinovich, 1976; Valentine, 1989) is interpreted as evidence that the effects of speciation and extinction were likely negligible along rocky shores of the Californian coast during the last 1–2 Ma (Valentine & Jablonski, 1993; Lindberg & Lipps, 1996; Roy et al., 1996). However, if many evolutionarily distinct species, such as *N. emarginata* and *N. ostrina*, have been lumped into artificially cosmopolitan nominal species, rates of speciation and extinction in the fossil record are likely underestimated. A late Pleistocene separation for *N.*

emarginata and *N. ostrina* therefore provides an important counter-example to the conclusion that little speciation occurred during the Pleistocene along rocky Californian shores. Instead, for *Nucella*, the Pleistocene may have been a period of limited morphological differentiation between species.

Inferred divergence times based on molecular sequence data have important caveats, even if sequences evolve at a constant rate. Poor calibrations, due to inconsistencies in the fossil record, often introduce the greatest source of error in molecular clock analyses (Lee, 1999; Yoder & Yang, 2000). For example, *Nucella canaliculata* and the *N. emarginata/N. ostrina* clade likely diverged earlier than the fossil record indicates because actual splits always predate the appearance of new taxa in the fossil record. An earlier divergence of the calibration taxa would result in a smaller inferred rate of CO1 divergence, which in turn would yield an earlier time of separation for *N. emarginata* and *N. ostrina*. However, a pre-Pleistocene divergence for *N. ostrina* and *N. emarginata* would entail a time of divergence for the calibration in excess of 40 Ma. Although we cannot reject an earlier time of divergence for our calibration taxa, an Eocene divergence for *N. canaliculata* and the *N. ostrina/N. emarginata* lineage (a crown clade within *Nucella* see Collins et al., 1996) is highly improbable given that the genus *Nucella* only first appears in the fossil record during the latest Oligocene or earliest Miocene (Collins et al., 1996).

A second source of error we consider is that the amount of sequence divergence between our calibration lineages may be significantly underestimated. Although assuming an explicit model of nucleotide substitution takes multiple substitutions at single nucleotide sites into account, error in the estimates of molecular divergence (i.e., branch lengths between taxa) may also result in poor estimates of divergence rates. Because the divergences of interest here are relatively recent (5 to 10 Ma), the problem of saturation of nucleotide positions with multiple substitutions is probably not an important factor: uncorrected mitochondrial third positions only begin to approach saturation in *Nucella* after 5 to 10 million years (Collins et al., 1996; Marko & Vermeij, 1999). Nevertheless, even if our estimates of sequence divergence are biased because of saturation, this bias is conservative with respect to our conclusions: larger sequence divergences between the taxa used to calibrate our molecular clock would result in larger rates of sequence divergence, which in turn would yield an even more recent range of divergence times for *N. emarginata* and *N. ostrina*.

The inherent difficulty in distinguishing biological species based on morphology alone in *Nucella* suggests that the process of speciation (i.e., the evolution of reproductive isolation) is not necessarily accompanied by dramatic morphological differentiation when compared to patterns of geographic variation within species (also see Palmer,

1985b). Therefore, interpretations of the fossil record of *Nucella* that employ the assumption that speciation may be recognized by significant morphological changes (e.g., Kerr, 1995) must be considered in light of the subtle differences in shell form between the two most recently diverged species, *N. emarginata* and *N. ostrina*. Although the extent of intraspecific variation in shell morphology in *Nucella* is somewhat unusual, making the recognition of biological species particularly difficult, the existence of cryptic species in rocky shore gastropods is not an uncommon phenomenon. For example, other prominent fossilizable taxa such as *Littorina*, *Lottia*, and *Mexacanthina* (formerly assigned to *Acanthina*, see Marko & Vermeij, 1999) all harbor morphologically similar but genetically distinct species on the Pacific coast of North America (Murphy, 1978; Mastro et al., 1982; Marko & Vermeij, 1999). As a consequence, species identifications based purely on morphological grounds must always be assessed in this context.

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