Chapter 2: Review of Fossil Abalone (Gastropoda: Vetigastropoda: Haliotidae) with Comparison to Recent Species.

INTRODUCTION

Recent members of the family Haliotidae, with “abalone” as their common name, are well-known. Due to their economic value, living species have received much scientific attention (e.g., Shepherd *et al.* [1992, 1995]; Fleming & Hone [1996]), for only relatively few and isolated accounts of fossil abalone are found in the literature, with Lindberg (1992) supplying a limited overview. A more extensive review on is presented what little is known about fossil abalone to stimulate further work.

DIAGNOSTIC CHARACTERS OF THE FAMILY

Shell morphological characters clearly separate abalone from any other family of fossil as well as extant gastropods (Figure 2-1). Abalone shells are easily recognized by their flat, limpetlike shape and row of tremata toward the left periphery. This row of tremata represents the subdivided selenizone found in Pleurotomaroidea, Scissurelloidea, and Fissurelloidea (Knight *et al.*, 1960; Bandel, 1998; Geiger, 1998a; McLean & Geiger, 1998). The extremely hypertrophied epipodium is diagnostic character for the anatomy of Haliotidae, but such characters do not apply to fossil representatives, and are not further discussed here (see Geiger, 1998a). Some Paleozoic Bellerophontoidea possessed shells somewhat resembling those of abalone. The former, however, are involute, have the row of tremata along the median of the shell, have cross lamellar aragonite, and have a muscle scar is more similar to that of Fissurelloidea than to Haliotidae (McLean, 1984a).

Figure 2-1: Specimens of fossil haliotids. 1, *Haliotis rufescens*, Pliocene, Saugus Formation. Simi Valley, Ventura County, California, LACMIP loc. 12660, internal mold showing muscle scar. 209 mm. 2, *Haliotis* sp., Miocene, Topanga Canyon Formation, Moorpark, Ventura County, California, LACMIP loc. 16896, internal mold, LACMIP 12659, 116 mm. 3, *Haliotis tuberculata volhynica*, "Post Pliocene? West Indies? Europe?", internal mold with dendrites, AMNH 45571, 62 mm. 4, *Haliotis walallensis*, Pliocene, San Diego Formation, hills south of Tijuana River, San Diego County CA, LACMIP loc. 16817 (ex LACMIP loc. 305c), specimen with shell preserved, 113 mm.

Several genera in the trochid subfamily Stomatellinae (Hickman & McLean, 1990; Pickery, 1995) have shells that loosely resemble abalone. Stomatellids are found in the late Triassic?, and from the Pliocene through Recent (Knight *et al.*, 1960). They have rather small (≤ 40 mm), flat, oblong shells that lack tremata or spiral sculpture, and may be mistaken for imperforate specimens of juvenile *Haliotis asinina* Linnaeus, 1758. The latter, however, have several distinct spiral ridges that become obsolete as the shell grows larger (> 35 mm). Specimens of the living genus *Granata* (Trochidae: Eucyclinae) have been erroneously identified as imperforate *H. cyclobates* Péron, 1816 (Geiger, 1991, 1998a). Imperforate specimens of abalone have been found in the Recent but are very rare (see Geiger, 1998 a, for review). For Recent as well as for fossil specimens, it is unlikely that an imperforate shell with a depressed, flaring shell is an imperforate abalone.

Although Trochotomidae (Pleurotomaroidea) are superficially similar to abalone, most trochotomid species have a distinctly trochiform shell and only one trema on the shoulder of the last third of the body whorl. In addition, their early Triassic to Late Jurassic geologic range does not overlap with the known range of Haliotidae (Knight *et al.*, 1960).

TAXONOMY

The shell as the basis of taxonomy

As with most fossils, discrimination of taxa in abalone is based on their hard parts. The shell of abalone, however, is extremely plastic in Recent species and, therefore, can be inferred to be plastic in fossil congeners by application of uniformitarian principles. Some examples of morphological plasticity in Recent taxa are discussed below to illustrate the problems using a limited number of specimens to define taxa.

The most striking example of variability is the number of open tremata, which has been considered a constant and diagnostic character by previous workers. The above is particularly true for Recent species (e.g., Kaicher, 1981; Abbott & Dance, 1983), but only to a lesser extent for fossil ones (but see e.g., Sohl, 1992), because the incomplete state of most specimens is recognized. In Figure 2-2, the number of open tremata is plotted for several Recent species for which sufficient data is available. The number of open tremata varies within species, and the range for each species overlaps to a great extent with ranges of the other species shown. Therefore, this character is not diagnostic (cf. Geiger 1998a).

Sculpture has been used to separate Recent "species". For example, the European "*H. lamellosa*" Lamarck, 1822, and "*H. tuberculata*" Linnaeus, 1758, which are now considered forms (Geiger, 1998a) of the single, variable species *H. tuberculata*, are distinguished by the presence or absence of obliquely radial lamellae. As with the number of open tremata, there is a great variability for this character. If a large number of specimens from any population is examined, entirely smooth to highly lamellar shells can be found (Geiger, unpublished data).

Shell outline, particularly roundness, is to some extent under environmental control as documented by transplant experiments of a Japanese species (Ino, 1952). Stewart & Geiger (1999) showed for the tropical *H. clathrata* Reeve, 1846, that shell roundness also changes through ontogeny. Therefore, this character is of limited use for species discrimination. Other variable shell characters include (a) the degree of coverage of the shell with a particular sculptural element (e. g., scales in *H. jacnensis* Reeve, 1846: Geiger, personal observation), (b) the stength of spiral cords for *H. rubra* Leach, 1814 (see Geiger, 1998a), and (c) shell flatness in *H. ovina* Gmelin, 1791, for which extremely

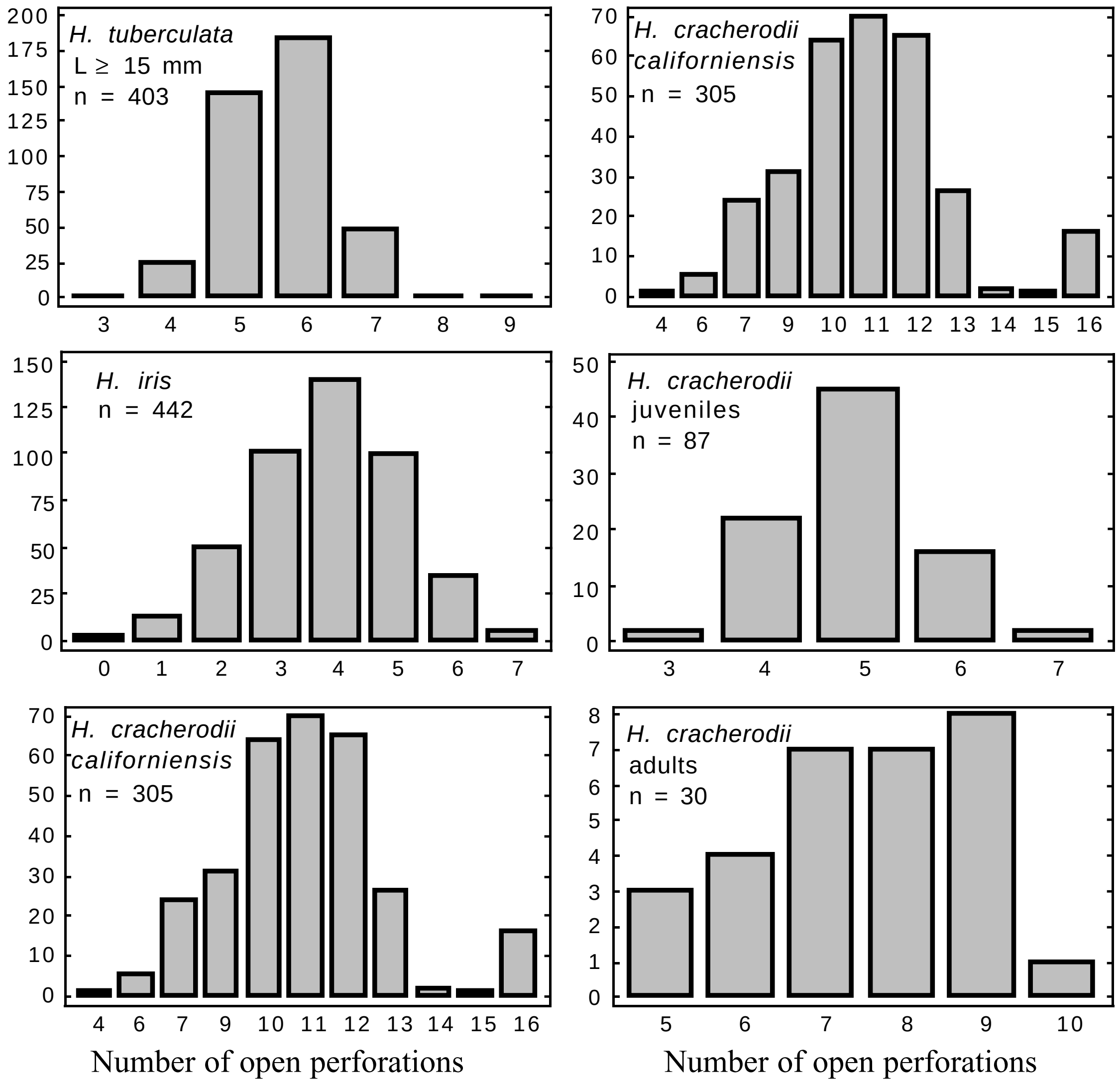


Figure 2-2: Histograms of number of open tremata for several species of *Haliotis*. n = sample size. Sources of data as follows. *Haliotis tuberculata*: only Mediterranean populations: Geiger (unpublished). *Haliotis coccoradiata*: Talmadge (1960); the number of half open tremata was split equally between the neighboring integers. *Haliotis iris*: Sinclair (1963). *Haliotis cracherodii* juvenile: Hemphill (1907). *Haliotis cracherodii californiensis*: Hemphill (1907). *Haliotis cracherodii* adult: Hemphill (1907). Note the bell-shaped distributions, with large differences in the modal class. Further note the shift of the modal class between juvenile and adult *H. cracherodii*. The large number of specimens with 16 open tremata in the plot of *H. cracherodii californiensis* stems from *a priori* selection from the original stock of shells.

flat, Vietnamese specimens contrast with towering forms from the Philippines (Geiger, personal observation).

Hence, sound taxonomic decisions are impossible on the basis of a limited number of shells. Usually for each fossil taxon few specimens are available, which in many instances show only slight differences between the nominal taxa. Nevertheless it would also be unwise to synonymize all fossil taxa, and the taxonomy of fossil abalone will probably remain highly typological. It is the intention of this contribution to demonstrate that character variability within living taxa must be considered when describing new fossil taxa. Multivariate statistical techniques might eventually help, but to date have not been used for fossil haliotids and only in a single study of a Recent species (McShane *et al.*, 1994).

Fossil abalone taxa

At least 35 fossil abalone species have been described, excluding reports of Recent taxa with a fossil record. It is unclear whether all these taxa are truly distinct species. A critical and comprehensive taxonomic revision of fossil abalone has not been attempted and is not feasible because of the limited material. Most fossil abalone have been described from single specimens (cf. Vokes, 1978), the exceptions being the two specimens of *H. kurosakiensis* Kotaka & Ogasasawara, 1974, from the Miocene of Japan, four specimens of *H. saldanhae* Kensley, 1972, from the Pliocene of South Africa, and ten specimens of *H. antillesensis* from the Maastrichian of Puerto Rico and Jamaica (Kensley, 1972; Kotaka & Ogasawara, 1974; Sohl, 1992). Several fossil species have shells similar to thoses of modern representatives within *Haliotis*. It is unknown whether these fossil forms are ancestors, conspecifics, or share similarities due to convergent evolution. A list of fossil taxa, expanded from Lindberg (1992), is contained in Table 2-

3, where all records are listed using the original taxa. Nevertheless, it was tried to shed some light on potential synonymies and similarities between certain taxa.

Haliotis lomaensis Anderson, 1902, from the Late Cretaceous (Maastrichian) of San Diego County, California, has been compared to the extant *H. iris* Gmelin, 1791, endemic to New Zealand. *Haliotis antillesensis* Sohl, 1992, from Upper Cretaceous (Maastrichian) rocks of Puerto Rico and Jamaica is similar to the extant Australian species *H. cyclobates* Péron, 1816 (Sohl, 1992). Due to the magnitude of the temporal hiatus and the large geographical distances involved in these two species pairs, a close relation is doubtful in either case. Additionally, the fossil *H. lomaensis* is only 13 mm in size, and is a juvenile specimen by the standard of all northern Pacific species as well as of *H. iris*. Identification of juveniles is extremely difficult. Juvenile *H. iris,* in particular, have a very distinct morphology and are often confused with adult *H. virginea* Gmelin, 1791, from New Zealand, a species readily distinguishable from *H. lomaensis* by its pronounced sculpture. The cited similarity between *H. lomaensis* and *H. iris*, therefore, must be viewed with much caution.

Shell morphological similarities between certain pairs of species from the upper Tertiary (Miocene and Pliocene) and the Quartenary (Pleistocene-Recent) from California and Japan have been noted (Hertlein, 1937; Talmadge, 1964; Hatai *et al.*, 1970; Mulliner, 1984) and are listed in Table 2-1. A close evolutionary affinity can be considered in each case because species are morphologically similar, are reported from the same area, and are separated by relatively small time spans.

Haliotis powelli Fleming, 1952, from the Miocene and Pliocene of New Zealand, was thought by Talmadge (1963) to belong to the group of *H. clathrata* Reeve, 1846, *H. rubiginosa* Reeve, 1846 [as *H. howensis* (Iredale, 1929)], and *H. coccoradiata* Reeve, 1846. *Haliotis clathrata* Reeve, 1846 (*non* Lichtenstein, 1794), has recently received

Miocene/Pliocene	Pleistocene-Recent	Region
Haliotis koticki Hertlein, 1937	*H. assimilis* Bartsch, 1940	California
H. lasia Woodring, 1932	*H. fulgens* Philippi, 1845	California
H. elsmerensis Vokes, 1935	*H. rufescens* Swainson, 1822	California
H. elsmerensis /*H. lasia*	*H. fulgens* / *H.walallensis* Stearns, 1898	California
H. kamtschatkana koyamai Makiyama, 1927	*H. discus hannai* Ino, 1952	Japan

Table 2-1: Comparison of upper Tertiary species with Pleistocene-Recent species from California according to Hertlein (1937), Talmadge (1964), Hatai *et al.* (1970), and Mulliner (1984).

further attention elsewhere (Geiger, 1998a, 1998b; Geiger & Stewart, 1998; Stewart & Geiger, 1999). *Haliotis clathrata* Reeve, 1846, *H. rubiginosa*, and *H. coccoradiata* do not occur on New Zealand, and none of the New Zealand species—Recent or fossil—has been recorded outside these islands. In addittion, Stewart & Geiger (1999) disagreed with Talmadge's (1963) opinion on the basis of discrete morphological differences and disjunct geographical distribution of these taxa.

Haliotis clathrata Reeve, 1846, is mentioned from Fiji (as *H. tuvuthaensis* Ladd *in* Ladd & Hoffmeister, 1945) and Guam (Ladd & Hoffmeister, 1945; Ladd, 1966). Stewart & Geiger (1999) have synonymized the Fiji record listed as *H. tuvuthaensis* under *H. clathrata* Reeve, 1846, because the type of *H. tuvuthaensis* can not be distinguished from *H. clathrata* Reeve, 1846. Talmadge (1963) listed *H. clathrata* Reeve, 1846, as *H. crebrisculpta* Sowerby, 1914, a highly controversial but distinct species for which a lectotype has since been designated (Stewart & Geiger, 1999).

The taxonomic states of *H. barbadensis* Trechmann, 1937, from the Pleistocene of Barbados, and the Recent *H. pourtalesii* Dall, 1881; *Haliotis aurantium* Simone, 1998; *H. dalli* Henderson, 1915; and *H. roberti* McLean, 1970, bears mentioning. These are small species for the genus with a maximum size of approximately 2 cm. They live in the Caribbean (*H. barbadensis*, *H. pourtalesii*), on the Atlantic coast of Venezuela and Brazil (*H. aurantium*), and in the eastern Pacific outliers of Isla del Coco and Islas Galápagos (*H. dalli, H. roberti*). The living species are found at a depth of 60 - 400 m (Henderson, 1915; Bartsch, 1940; Foster, 1946; Aguayo & Jaume, 1947; Harry, 1966; Jung, 1968; Klappenbach, 1968; Sarsua, 1968; Nijssen-Meyer, 1969; McLean, 1970; Kaicher, 1981; Titgen & Bright, 1985; Odé, 1986; Finet, 1993; Martinez & Ruiz, 1994; Simone, 1998). Using the species concept of interbreeding populations, the Recent *H. roberti* and *H. dalli* versus *H. pourtalesii* are clearly distinct species because they occur on opposite sides of Central America. However, the geological closure of the Isthmus of Panama in the middle Pliocene (Coates & Obando, 1996) complicates the situation for the fossil species considered here. The open waterway could have provided a means for gene flow within a single amphipanamic species. The question arises, when the modern species became distinct, and where to draw the line between the fossil species. Conflicting opinions are expressed by authors cited above as to whether *H. barbadensis* and *H. pourtalesii* are endpoints of a morphological range within a single species or are two valid species. Due to the scarcity of material for both species and the fairly extended time period separating these taxa, are considered them distinct.

Strausz (1966) is followed here and all fossil European taxa (*H. anomiaeformis* Sacco, 1896; *H. benoisti* Cossmann, 1895; *H. lamellosa* Lamarck, 1822; *H. lamellosoides* Sacco, 1896; *H. monilifera* Bonelli, 1827; *H. neuvillei* Bial de Bell, 1909; *H. ovata* Bonelli, 1827; *H. tauroplanata* Sacco, 1897; *H. torrei* Ruggieri, 1989; *H. tuberculata* Linnaeus, 1758; *H. volhynica* Eichwald, 1853) are referred to *H. tuberculata volhynica* because the Atlantic and Mediterranean populations of the Recent species (*H. t. tuberculata*) are known to be extremely plastic in its shell morphology. Most illustrations and material of European fossil specimens (e.g., Figure 2-1.3) fall within the range of variation within the Recent species. The time lapse may justify a separation on the subspecies level. All fossil taxa are of Miocene or younger age, with the exception of the Oligocene records (Lozouet, 1986) of the nominal taxon *H. benoisti*. The following differing opinions on the taxonomic states of these taxa have been offered. Hörnes (1856) synonymized *H. volhynica* with *H. ovata*. Delhaes (1909) referred all six of the European taxa he mentioned to *H. tuberculata*. Krach (1981) discussed the European taxa and retained two subspecies of *H. tuberculata*. Specimens rounder than any Recent *H. tuberculata*, *sensu lato*, were considered *H. tuberculata volhynica* (Krach, 1981: particularly figs. 2 and 3). Krach (1981: figs. 4-7) also figured *H. tuberculata tauroplanata*, which showed a typical representative of the Recent *H. tuberculata*. Lozouet (1986) separated *H. benoisti* from the French Oligocene from *H. tuberculata*. However, the material in the Muséum Nationale d'Histoire Naturelle in Paris does not justify a separatation of those specimens from *H. tuberculata*, *sensu lato* (Geiger, personal observation). The remaining European taxa have not received any attention beyond a simple mention in the sources cited in Table 2-3.

Fossil abalone in the phylogenetic context

A phylogenetic study of fossil abalone either alone or integrated in the framework of Recent taxa (cf. Smith, 1994 for review of conceptual approaches), is unfortunately fraught with problems. As with most fossil material, fossil abalone with soft-part preservation are unknown. The morphological plasticity in shell characters, outlined above, also makes phylogenetic analysis problematic. In addition, most fossils are preserved as internal and/or external molds, which limits the suite of potential characters to the shell sculpture characters. The predominance of moldic preservation is unfortunate. The prismatic layer of abalone shells has been reported to exist in three fundamentally different mineralogical types (calcitic, aragonitic, admixed calcitic and aragonitic: Mutvei *et al.*, 1985; Dauphin *et al.*, 1989; Dauphin & Denis, 1995; Shepherd *et al.,* 1995), and may be taxonomically informative. These authors used Feigel's stain to identify aragonite, although this stain also shows high-magnesium calcite (C. Hedegaard, personal commun.). Therefore, mineralogical composition of abalone shells needs reexamination. However, the phylogenetic character states "Feigl-staining" and "non-Feigl-staining" may also be useful without an explicit assumption of stain mineralogical specificity. The spatial sampling scale in X-ray diffraction studies is limited by the beam size to 1-

2 mm (e.g., Hedegaard & Wenk, 1998), which is too coarse to reveal mineralogical patterns, particularly admixed aragonitic elements of 2-5 µm width and 5-10 µm length in the calcitic external shell layer (Dauphin *et al.*, 1989). Additionally, it would only be possible to investigate rarely preserved shell material.

PRESERVATION

Abalone are rarely encountered as fossils, although rocky shores, which abalone inhabit, particularly in temperate regions, are thought to have occurred widely along the west coast of North and South America. However, rock-inhabiting organisms are rarely preserved (Carter, 1972), because the habitat is destructive to the shells (Woodring, 1931; Kotaka & Ogasawara, 1974; Parsons & Brett, 1991).

Many tropical abalone species occur in reef environments and tend to hide in cracks or underneath boulders. Upon death, the shells are likely to remain in the cryptic habitat and will eventually be incorporated into the biogenic limestone of the reef. Tectonic uplift or eustatic sea level change may expose these reefs above sea level, making them accessible (e.g., the Pleistocene record of *H. pustulata cruenta* Reeve, 1846, from the Red Sea [Hall & Standen, 1907]).

A major constituent of abalone shells is aragonitic platelets in the nacreous layer. This type of microstructure is very prone to disintegration, dissolution, and diagenetic change (Dodd, 1966). Disintegration accounts for the general scarcity of complete abalone specimens in the fossil record. The most frequent mode of abalone preservation is as internal and/or external molds (Figures 2-1.1 - 2-1.3), occasionally with some attached shelly remains. Preserved shell fragments are all calcitic, indicating some diagenetic effects (cf. Dodd, 1966), because the inner nacreous layer of the shell is always composed of aragonite (cf. Dodd, 1966). In addition, Durham (1979b) observed recrystallization in *H. lomaensis*. The effects of diagenesis make the wide application of shell mineralogy in the taxonomy of fossil abalone doubtful, although results on the mineralogy of shells from Recent abalone are promising (see also previous section on phylogeny).

PALEOENVIRONMENTS

The habitat of abalone, with their large aperture, is the rocky shores, as is the case for morphologically similar groups such as limpets. Not surprisingly, fossil Haliotidae inhabited comparable habitats . Below supporting evidence is presented.

Reef paleoenvironments

Both fossil and Recent abalone are found in similar microhabitats within tropical reefs. *Haliotis antillesensis* has been found in a rudist-framework bioherm in the Upper Cretaceous of Puerto Rico (Sohl, 1992), part of the shallow tropical Tethys Sea (Kauffman & Sohl, 1974; Sohl, 1987). Associated species included abundant neritid gastropods, indicators for an intertidal to shallow subtidal hard substrate in the tropics. *Haliotis pustulata cruenta* has been found in a Pleistocene raised coral reef of the Red Sea area [Newton, 1900; Hall & Standen, 1907 (as *H. unilateralis* Lamarck, 1822); Brauwer *et al.* cited in Yaron, 1983] in association with the typical, molluscan reef fauna found in the Red Sea. The reconstructed paleoenvironment is fully congruent with the modern habitat of this species (Yaron, 1983; Geiger, 1996). For European sites, Davidaschvili (1937) and Krach (1981) proposed a nearshore shallow-water reef environment for their *H. volhynica* based on a community analysis.

Shallow-water rocky paleoenvironments

Fossil abalone also are reported from deposits associated with rocky shorelines, a common habitat for Recent members of the family. In the Cretaceous of California, *H. lomaensis* was found with an oyster, a serpulid worm, and encrusting calcareous algae, which together indicate a shallow-water, rocky environment (Durham, 1979b). In the Miocene of California, *H. palaea* Woodring, 1931, was discovered with other molluscan genera indicative of rocky substrate, i.e., *Tegula, Arca, Crassadoma* [as *Hinnites*], *Lima,* and *Mytilus* (Woodring, 1931). Only the limids may be freely mobile as adults and associated with sandy substrates. *Haliotis elsmerensis* Vokes, 1935, from the Pliocene of California, however, was found admixed with infaunal bivalves (*Chione*) as well as with rocky shore bivalves (*Arca*). This mixed fauna indicates some transport (Vokes, 1935). Similarly, *H. cracherodii* Leach, 1814, from the Pleistocene of northwestern Baja California (Addicott & Emerson, 1959). *Haliotis rufescens* Swainson, 1822, has been found in a Pliocene shallow-water channel deposit with rock-dwelling species, as well as infaunal species (Groves, 1991). Additional, indirect evidence of California abalone paleohabitat stems from the type specimen of the Late Pleistocene vermetid gastropod *Petaloconchus anellum* (Mörch, 1861), which is attached to a shell of an unspecified abalone (Grant & Gale, 1931). Vermetids are common in shallow, rocky habitats.

In Japan, *H. kurosakiensis* Kotaka & Ogasawara, 1974 (upper Miocene); *H. fujiokai* Hatai, Kotaka, & Noda, 1937 (middle Miocene); and *H. kochibei* Hatai & Nisiyama, 1952 (Pliocene), have been found in strata containing typical rock-inhabiting molluscan genera such as *Ostrea, Arca*, and *Acmaea* admixed with sand-dwellers, such as *Macoma* and *Lucinoma* (Hatai *et al.*, 1970; Kotaka & Ogasawara, 1974; Noda *et al.*, 1995). As with *H. elsmerensis,* some transport of the original fauna must be assumed, but a rocky shore habitat for abalone is indicated.

In summary, available evidence indicates that the ecology of the fossil abalone is comparable to that of Recent species (see e.g., Crofts, 1929, Cox, 1962, Shepherd, 1973). Particularly, no difference in the depth distribution (= on-shore/off-shore pattern) can be detected. This pattern has been documented during the geological history of a number of invertebrate taxa (Hickman, 1984; Bottjer & Jablonski, 1988). It may seem farfetched to consider an on-shore/off-shore pattern in a largely herbivorous organism, however, one abalone species (*H. cracherodii*) is known to feed on bacterial mats as adults (Stein, 1984). Juvenile abalone feed on diatoms and the associated biofilms (Kawamura *et al*., 1998, for review). Accordingly, the potential to exploit deep water habitats directly or by neoteny is present in abalone.

TIME RANGE

Fossil abalone have been found from the Late Cretaceous through the late Pleistocene, with a conspicuous hiatus in the early Paleogene (see Appendix for details). A controversy has long existed regarding the true identity and systematic affinities of some of the earliest records (Late Cretaceous: Maastrichian) in this family: *H. antiqua* Binkhorst, 1861, from the Netherlands; *H. cretacea* Lundgren, 1894, from Sweden, and *H. lomaensis* from San Diego County, California (Binkhorst, 1861; Lundgren, 1894; Anderson, 1902). Davies & Eames (1971) considered none of these records to represent abalone. Woodring (1931) doubted that *H. lomaensis* is an abalone, because of poor preservation; the only diagnostic characteristic preserved was the flat shell. In addition, Knight et al. (1960: 221) cited the Cretaceous record of *Haliotis* with a query. Vokes (1935) considered *H. lomaensis* to be an abalone, but most likely a young specimen.

Equally, Sohl (1992) discussed these three Cretaceous taxa and concluded that only *H. lomaensis* is an abalone, as did Durham (1979b) and Lindberg (1992). More recently, Sohl (1992) described a second Late Cretaceous abalone from the Maastrichian of Puerto Rico and Jamaica, *H. antillesensis*. Only *H. lomaensis* and *H. antillesensis* are considered here to be Cretaceous abalone, both from Maastrichian rocks.

Within the Tertiary, Delhaes (1909) and Beu & Maxwell (1990) reported abalone from the Eocene. However, the Standard European Stages in Delhaes (1909) are Miocene (Lindberg, 1992), and consequently only one record, from New Zealand, is of Eocene age. Three factors may explain the hiatus in the fossil record between the Maastrichian and the Miocene. First, Paleogene rocky-shore habitats are hardly preserved (Lindberg & Squires, 1990). Second, in general there is a taphonomic bias against rock-clinging mollusks (Sohl, 1992). Third, by comparison to ecologically similar taxa such certain limpets (Acmaeidae), which are known from the Triassic through the Recent (Knight *et al*., 1960), Cretaceous abalone can be inferred as rare with just two localities. K-T extinction may have reduced the abundance of abalone to such low densities that they do not show up in the fossil record of the Paleocene. However, complete extinction at the K-T boundary with convergent evolution of the same shell morphology by another gastropod group in the Eocene-Oligocene is unlikely. Cretaceous and Tertiary/Recent specimens share many similarities, such as the row of tremata, the flattening of the shell, and the high translation value of the spire. This combination of structural elements is not known from any other gastropod, living or extinct. These similarities are best explained by common descent, rather than two separate radiations.

GEOGRAPHIC DISTRIBUTION

In general, one might expect the Neogene distribution of taxa to be fairly congruent with its present-day distribution. However, the very few recorded fossil abalone specimens from the central Indo-Pacific (Figure 2-3, Appendix) is surprising, because this region houses the highest diversity of Recent Haliotidae (Delhaes, 1909; Lindberg, 1992). This discrepancy may be associated with the greater paleotological effort being carried out in the United States and Europe as compared to the Indo-Pacific. In the few, more extensive studies in tropical settings [Hall & Standen, 1907 (Red Sea); Ladd & Hofmeister, 1945; Ladd, 1966 (Indo-Pacific)] abalone specimens have been recovered. Therefore, more extensive searches for fossil abalone in the Indo-Pacific, as well as in the Australian region, might close both this noticeable geographical gap for fossil abalone, as well as narrow the Cretaceous to late Eocene hiatus in the abalone record.

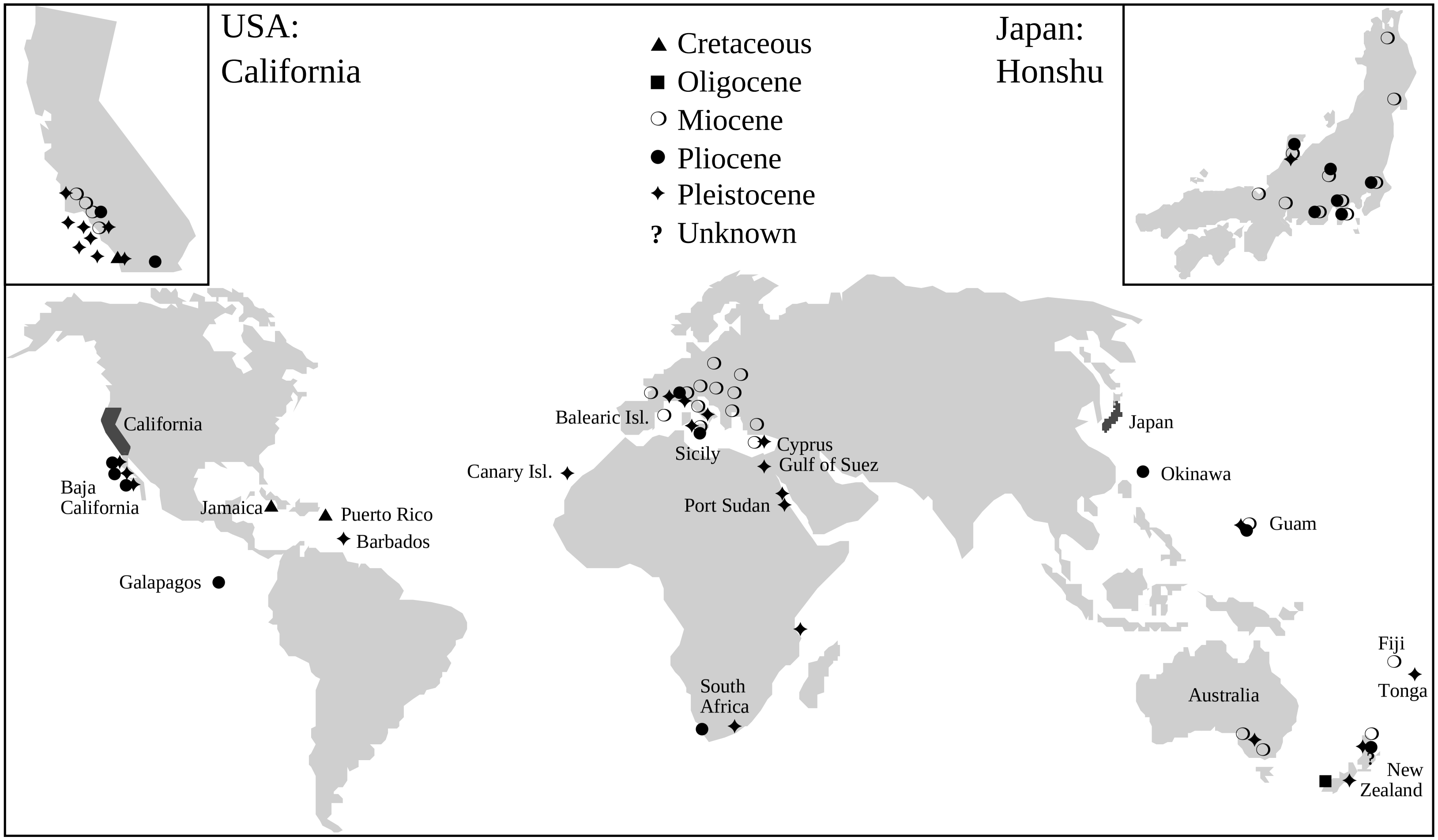
Geiger is currently preparing a phylogenetic analysis of the Recent species of the family, and the biogeographical investigation will be useful in evaluating the proposed models of radiation, summarized below:

1) Living abalone are most diverse in the Indo-Pacific, which may indicate that this is their center of radiation. However, this is certainly not a safe conclusion, as discussed by Lindberg (1992). It is unclear whether several small radiations or a single large-scale radiation took place within this family.

2) Talmadge (1963) proposed a “Pacific Rim” model, in which he postulated that abalone were originally found on an island arc from Japan to northern Australia and radiated from this area to California, southern Australia, and the Indo-Pacific. This proposal is similar to one of the two models in Lee & Vacquier (1995).

3) A third scenario is based on chromosomal data, which have been documented for 10 species (Table 2-2). Because the basal gastropods have a very low diploid number of

Figure 2-3. Localities of fossil abalone listed in Appendix. The two inserts provide details for California, and Honshu, Japan; the location of each area on the larger map is shaded. Overlapping symbols indicate different geological times are represented at the same locality..


USA:
California
▲ Cretaceous
■ Oligocene
○ Miocene
● Pliocene
✦ Pleistocene
? Unknown
Japan:
Honshu
California
Baja
California
Jamaica
Puerto Rico
Barbados
Galapagos
Canary Isl.
Balearic Isl.
Sicily
Cyprus
Gulf of Suez
Port Sudan
South
Africa
Japan
Okinawa
Guam
Australia
Fiji
Tonga
New
Zealand
?

Taxon	H	D	O	Source
Haliotis tuberculata	14	28	EM	Colombera and Tagliaferri, 1983
		28	EM	Arai and Wilkins, 1986
H. lamellosa[1]	14		EM	Colombera and Tagliaferri, 1983
H. aquatilis[2]	17	34	IP	Nakamura, 1985
H. diversicolor aquatilis[3]	16	32	IP	Nakamura, 1985, 1986
H. diversicolor		32	IP	Arai *et al.,* 1988, Yang et al., 1998
H. exigua[4]		32	IP	Arai *et al.,* 1988
H. planata[5]		32	IP	Arai *et al.,* 1988
H. asinina		32	IP	Jarayanbhand *et al*., 1998
H. ovina		32	IP	Jarayanbhand *et al*., 1998
H. asinina		32	IP	Jarayanbhand *et al*., 1998
H. varia	16	32	IP	Nakamura, 1986
H. cracherodii		36	NP	Minkler, 1977
H. discus discus		36	NP	Arai *et al.,* 1982
H. discus hannai		36	NP	Arai *et al.,* 1982
H. madaka[6]		36	NP	Nakamura, 1986

Table 2-2: Chromosome number in Recent *Haliotis* spp. as indicated in the respective source. H, Haploid number; D, Diploid number; O, Geographic occurrence; EM, European-Mediterranean; IP, Indo-Pacific; NP, North Pacific.

[1]*Haliotis lamellosa* has been shown to be a synonym/ecomoroph of *H.. tuberculata* (Lee and Vacquier, 1995). [2]As *H. diversicolor aquatilis* in Nakamura (1985), but as *H. aquatilis* in Nakamura (1986). [3]As *H. japonica*. [4]As *H. planata*. [5]As *H. varia*. [6]As *H. gigantea*.

chromosomes (18-20: Patterson, 1967; Haszprunar, 1988), a model of progressive increase in chromosome number can be postulated, from a low of diploid number of 28 in *H. tuberculata* from the Mediterranean, to 32 in Indo-Pacific species, to 36 in North Pacific species. This would suggest that *H. tuberculata* is a relict species from the ancient Tethys Sea, and that abalone dispersed eastward, which is in agreement with the eastward dispersal pattern in the Pacific (Briggs, 1995). This is in marked contrast to the westward dispersal of other molluscs (Squires, 1987). In westward dispersing families molluscan families such as Cypraeidae, Volutidae, and Ranellidae, however, larvae are teleplanktic. Abalone, on the other hand, have a limited dispersal capability, the precise extent of which is currently debated (Tegner & Butler, 1985; Prince *et al.*, 1987; McShane *et al.*, 1988; Wells & Keesing, 1990; Shepherd *et. al.*, 1992). Note that, under this model, the Upper Cretaceous abalone from California and the Caribbean would not be early representatives of the family and that the root of the family would have to be placed at a much earlier time. A similar model has been proposed by Lee & Vacquier (1995) and is preferred by Eagle (1996).

None of these models has more than anecdotal evidence. The phylogenetic trees published to date (Brown & Murray, 1992; Brown, 1993; Lee & Vacquier, 1995) are all unrooted, and species suggested to be in a basal position may not be truly basal.

It is possible that in the Pleistocene, species of *Haliotis* migrated between Asia and North America (Grant & Gale, 1931, p. 96). Biochemical data support this hypothesis. In a tree based on the cDNA sequences of the fertilization protein lysin (see Vacquier & Lee, 1993, for review) of 22 abalone species, all California species cluster closely together with the west Pacific species *H. discus* Reeve, 1846, and *H. gigantea* Gmelin, 1791, whereas another species of the latter region (*H. diversicolor* Reeve, 1846) is far removed from the western Pacific species group (Lee & Vacquier, 1992, 1995). This pattern has been corroborated with allozyme frequency data from 17 abalone taxa (Brown, 1993). The California species have the most derived character states, which suggests an east-to-west progression. All three of the above models imply favorable conditions for dispersal of abalone between the east and west coasts of the north Pacific, with subsequent reproductive isolation of the amphipacific populations. Glaciation events could facilitate dispersal across the Pacific as sea level dropped, because the distance between the two shores at any latitude would be somewhat shortened (see also Lee & Vacquier, 1995). On the other hand, the distance across the Pacific is extensive, hence, dispersal across the Pacific must be termed a rare chance event. Accordingly, one may debate the possible contribution of glaciation to dispersal. Migration at northern latitiudes along the Bering Bridge seems unlikely due to the absence of any Recent species generally beyond 50° north or south (60° N for *H. k. kamtschtkana*).

Table 2-3: List of fossil abalone taxa, as indicated in the original source, by first occurrence in the fossil record and locality compiled from the literature and museum specimens. General locations such as 'California' have been omitted if more precise information is available for the same age. Taxa preceded by an asterisk (*) are living species. u: upper. m: middle. l: lower. BC: Baja California, Mexico. CA: State of California, USA. NZ: New Zealand. Pref.: Prefecture. AMNH: American Museum of Natural History, New York. ANSP: Academy of Natural Sciences Philadelphia. BMNH: The Natural History Museum, London. LACMIP: Natural History Museum of Los Angeles County, Invertebrate Paleontology. MNHN: Muséum National d'Histoire Naturelle, Paris. Circumpacific geologic time intervals have been correlated with European ones according to Kennett, and Srinivasan (1983).

[1]*Haliotis* sp. is similar to *H. waitemataensis* (Beu & Maxwell, 1990) and the illustration strongly resembles *H. emmae*. [2]The Shigarami Formation is interpreted as two different ages by the four publications cited. 3: Correlation of stages according to Beu & Maxwell (1990: 8-9). [4]Originally reported as *Haliotis* sp. but corresponds exactly to the type of *H. powelli* illustrated in Beu & Maxwell (1990). [5]Delhaes (1909) interpreted these finds as Eocene. [6]*Haliotis tuvuthaensis* has been synonymized with *H. clathrata* Reeve, 1846 (Stewart & Geiger, 1999). [7]Plate 2, figure 5 illustrated a fairly round specimen superficially more similar to *Haliotis ovina* than *H. clathrata* Reeve, 1846. However, this specimen is only 15.9 mm long. Small specimens of *H. clathrata* Reeve, 1846, are much more round than adult ones, which makes the identification of Ladd (1966) valid. [8]The Miocene of Durham (1979a) has been revised to late Pliocene by Hickman & Lipps (1985). [9]Durham re-dated the coral rock in which the abalone was found from Jung's Pliocene to Pleistocene. [10]The identification of the specimen by Suter (1913) as *Haliotis iris* was rejected by Eagle (1996).

Table 2-3

Taxon	Geologic Time Interval	Locality	Literature Source and Museum Specimens
		CRETACEOUS	
antillesensis	Maastrichian	Puerto Rico and Jamaica	Sohl, 1992
lomaensis	Maastrichian	San Diego County, CA	Anderson, 1902; Woodring, 1931, 1932; Bartsch, 1940; Cox, 1962; Durham, 1979b
		TERTIARY: Eocene	
sp.	Eocene, l	NZ	Beu and Maxwell, 1990; Eagle, 1996
		Oligocene	
sp. aff. *waitemataenis*	Oligocene/Miocene	Cookson Volcanics, NZ	Beu and Maxwell, 1990[1]
benoisti	Oligocene, u: Chattien Adour	St.-Paul-Lès-Dax, France	Cossmann, 1895; Delhaes, 1909; Lozouet, 1986
	Oligocene, u: Chattien Adour	Belus “Marcon”, Landes, France	MNHN no #
	Miocene, l	St.-Martin-de-Hinx, France	MNHN no #
	Miocene, l	Cabanes, St.-Paul-Les-Dax, France	MNHN no #
	Miocene, l	Meilhan, Landes, France	MNHN no #
	Miocene, l	Lariey, Saucats, Gironde, France	MNHN no #
	Miocene, l	Merignac, France	Cossmann, 1918
	Miocene	Gironde, France	Delhaes, 1909
sp	Miocene, m	Mirebeau, Indre and Loire, France	MNHN no #
sp	Miocene, u	Beugnon	MNHN no #
		Miocene	
amabilis	Miocene, m	Gifu Pref., Japan	Itoigawa and Tomida, 1982
kurosakiensis	Miocene, u	Aomori Pref. ,Japan	Kotaka and Ogasawara, 1974; Itoigawa and Tomida, 1982; Lindberg, 1992

Table 2-3, continued

kochibei	Miocene, l	Kanagawa Pref., Japan	Hatai and Nisiyama, 1952; Hatai *et al.*, 1970
	Miocene, m	Ibaragi Pref., Japan	Kotaka and Ogasawara, 1974; Itoigawa and Tomida, 1982
	Miocene, m - u	Ibarabi Pref. Japan	Hatai and Nisiyama, 1952
	Pliocene	Ishikawa Pref., Japan	Lindberg, 1992
	Pliocene	Ibaraki Pref., Japan	Shibata, 1957; Noda *et al.*, 1995
koikei	Miocene, l	Kanagawa Pref., Japan	Hanzawa *et al.*, 1961; Hatai *et al.*, 1970; Itoigawa and Tomida, 1982
	Pliocene	Kanagawa Pref., Japan	Kotaka and Ogasawara,1974
	Pliocene, l	S Fossa Magna, Japan	Tomida, 1996
glabrosa	Miocene, l - m	Shizuoka Pref., Japan	Nomura and Niino, 1932; Hanzawa *et al.*, 1961; Hatai and Nisiyama, 1952; Hatai *et al.*, 1970; Kotaka and Ogasawara, 1974
	Pliocene, l	Shizuoka, Pref. Japan	Itoigawa and Tomida, 1982
	Pliocene, l - m	South Fossa Magna, Japan	Tomida, 1996
koyamai	Miocene; Pliocene, u[2]	Nagano Pref., Japan	Makiyama, 1927; Hatai and Nisiyama, 1952; Hanzawa *et al.*, 1961; Hatai *et al.*, 1970; Kotaka and Ogasawara, 1974; Itoigawa and Tomida, 1982
notoensis	Miocene, m	Ishikawa Pref., Japan	Masuda, 1966; Kotaka and Ogasawara, 1974; Itoigawa and Tomida, 1982
	Miocene, m	Fukui Pref., Japan	Ozawa *et al.*, 1986

Table 2-3, continued

moniwaensis	Miocene	Miyagi Pref., Japan	Kotaka and Ogasawara, 1974; Itoigawa and Tomida, 1982
fuijokai	Miocene, m	Miyagi Pref., Japan	Hatai *et al.*, 1970; Kotaka and Ogasawara, 1974; Itoigawa and Tomida, 1982
**japonica*	Miocene, l	Miyagi Pref., Japan	Hatai and Nisiyama, 1952; Lindberg, 1992
koticki	Miocene, l	Santa Barbara County, CA	Hertlein, 1937; Bartsch, 1940; Keen and Bentson, 1944;
lasia	Miocene, u	San Luis Obispo County, CA	Woodring, 1932; Bartsch, 1940; Keen and Bentson, 1944
palaea	Miocene	Los Angeles County, CA	Woodring, 1931; Bartsch, 1940; Keen and Bentson, 1944
flemingi	Miocene, l	Kawau Isl., NZ	Powell, 1938; Eagle, 1996
	Pleistocene	Whakatane, NZ	Beu and Maxwell, 1990; Lindberg, 1992
**iris*	Miocene	Cape Rodney, NZ	Harris, 1897
	Miocene	NZ	Suter, 1913[10]
	Pliocene, u - Recent	NZ	Beu and Maxwell, 1990
	Pleistocene	Lyttleton, NZ	BMNH 98048
mathesonensis	Miocene, l	Leigh, Rodney District, NZ	Eagle, 1996
powelli	Miocene, l	Mt Luxmore, Fiordland, NZ	Fleming, 1952; Lee *et al.* 1983[3, 4]
	Pliocene	Komako, NZ	Carter, 1972[4], Beu and Maxwell, 1990; Eagle, 1996
	Pleistocene	Bay of Plenty, NZ	Fleming, 1952
waitematensis	Miocene, l	Kawau Isl., NZ	Powell, 1938[1]; Eagle, 1996
moorabolensis	Miocene	Moorabool River, Australia	McCoy, 1876[5]
	Miocene	Victoria, Australia	Harris, 1897

Table 2-3, continued

	Miocene, u	Flemington, Australia	BMNH G1934
naevosoides	Miocene	Flemington, Victoria, Australia	Lindberg, 1992[5]
	Miocene, u	Flemington, Australia	BMNH G1935
	Pliocene	Adelaide, Australia	Cotton, 1952; Ludbrook, 1954
	Pliocene	Adlaide and Melbourne, Australia	Ludbrook, 1956
	Pliocene	Royal Park, Melbourne, Australia	BMNH GG2373
	Pliocene	Flemington, Australia	McCoy, 1876; Harris, 1897
ovinoides	Miocene, u	Victoria, Australia	McCoy, 1876
sp.	Miocene, l	New Caledonia	Eagle, 1996
sp.	Miocene, l: f	Fiji	Ladd and Hoffmeister, 1945; Ladd, 1966
tuvuthaensis	Miocene, l: f	Fiji	Ladd and Hoffmeister, 1945 [5] Ladd, 1966
* *clathrata* Reeve, 1846		Miocene, u: g	Tinian Ladd, 1966[7]
	Plio-, Pleistocene	Guam	Ladd, 1966[7]
neuvillei	Miocene, lowest: Aquitan	Gironde, France	Delhaes, 1909
monilifera	Miocene, l: Elveziano	Turin, Italy	Delhaes, 1909
	Miocene	Turin, Italy	Glibert, 1962
anomiaeformis	Miocene, l: Elveziano	Turin, Italy	Delhaes, 1909
tuberculata var.	Miocene, l: Elveziano	Turin, Italy	Delhaes, 1909
	Miocene	Miodoborow, W. Ukraine	Davidaschvili, 1937; Krach, 1981
tuberculata lamellosoides		Miocene	Cserhát Mountains, Hungary *fide* Strausz, 1966
	Pliocene	Piemont, Italy	Delhaes, 1909
ovata	Miocene	Italy	Delhaes, 1909 ; Ruggieri, 1990
	Miocene	Tétényer Plateau, Hungary	Strausz, 1966
sp.	Miocene	Vienna Bassin, Austria	H. D. Laatsch, personal commun.

Table 2-3, continued

tuberculata volhynica	Miocene	Roztocze Lubelskie, Poland	Krach, 1981
	Miocene	Poland and Italy	Ghisotti, 1964; Ruggieri, 1990
	Miocene	Austria, Romania, Bulgaria, West Ukraine	Krach, 1981
	Torton/Saratian	Buituri, Romania	Moisescu, 1955
	Miocene, l	Austria and Hungary	Delhaes, 1909
	Miocene	Cserhát Mountains, Hungary	Strausz, 1966
	Tertiary	Gauderndorf, Austria	Hörnes, 1856
	Miocene	Malta	BMNH 27501
	Miocene, u	Phoukasa, Cyprus	BMNH GH3252-5
	Tertiary	Lebanon	BMNH no #
	?	Asti and Turin, Italy	Hörnes, 1856
torrei	Miocene, u	Sicily, Italy	Ruggieri, 1990
sp.	Miocene	Mallorca, Balearic Islands, Spain	H. D. Laatsch, personal commun.
sp.	Miocene	Cyprus	Hertlein, 1937
sp.	Miocene, u (?)	Cyprus	H. D. Laatsch, personal commun.
sp.	Miocene	Turkey (Asia minor)	Hertlein, 1937
		Pliocene	
* *gigantea*	Pliocene	Ishikawa Pref. Japan	Hatai *et al.*, 1970
	Pleistocene, l	Ishikawa Pref., Japan	Itoigawa and Tomida, 1982
gigantoides	Pliocene	Okinawa Pref. Japan	Yabe and Hatai, 1941; Hanzawa *et al.*, 1961; Hatai *et al.*, 1970; Kotaka and Ogasawara, 1974
* *discus*	Pliocene, u	Ishikawa Pref., Japan	Itoigawa and Tomida, 1982
* *diversicolor*	Pliocene, u	Okinawa Pref., Japan	Itoigawa and Tomida, 1982

Table 2-3, continued

	Plio- , Pleistocene	Okinawa Pref., Japan	MacNeil, 1960
* *sieboldii*	Pliocene, u	Japan	Itoigawa and Tomida, 1982
* *pourtalesi*	Pliocene, early	Riverside County, CA	Schremp, 1981
elsmerensis	Pliocene, early	Los Angeles County, CA	Vokes, 1935; Bartsch, 1940; Keen and Bentson, 1944
* *fulgens*	Pliocene, l	Los Angeles County, CA	Woodring, 1931; Grant and Gale, 1931; Vokes, 1935
	Pliocene	NW BC	Rowland, 1968, 1972
	Pleistocene	Los Angeles County, CA	Arnold, 1903; Grant and Gale, 1931; Woodring, 1931; Woodring *et al.*, 1946
	Pleistocene	San Diego County, CA	Arnold, 1903, Grant and Gale, 1931; Woodring, 1931; AMNH 12409; AMNH 12411
	Pleistocene	San Clemente Island, CA	Lipps, 1967
	Pleistocene	Orange County, CA	Kanakoff and Emerson, 1959
	Pleistocene	BC	Hertlein, 1937
	Pleistocene	BC Sur	Jordan and Hertlein, 1936; Emerson, 1980; Emerson *et al.*, 1981
* *cracherodii*	Pliocene	CA	Lindberg, 1992
	Pliocene/Pleistocene	Punta China, BC	ANSP 31487
	Pleistocene	San Diego County, CA	Webb, 1937; Glibert, 1962; this study: LACMIP loc. 12015; AMNH 12409
	Pleistocene	Santa Barbara Islands, CA	this study: LACMIP locs. 326, 329, 5068
	Pleistocene	Santa Rosa Island, CA	Orr, 1960
	Pleistocene	San Nicolas Island, CA	Vedder and Norris, 1963

Table 2-3, continued

	Pleistocene, u	San Clemente Island, CA	Susuki and Stadum, 1978
	Pleistocene	Los Angeles County, CA	Chace and Chace, 1919; Willett, 1937; Woodring *et al.*, 1946; Marincovich, 1976; this study: LACMIP loc. 10439
	Pleistocene	Orange County, CA	Kanakoff and Emerson, 1959
	Pleistocene	San Luis Obispo County, CA	Valentine, 1962
	Pleistocene	NW BC, Mexico	Addicott and Emerson, 1959; Herlein, 1934; Valentine, 1957; this study: LACMIP locs. 23161, 22715-22718, 8220-8224, 10131, 23162,
* *rufescens*	Pliocene	Humboldt County, CA	Woodring, 1931
	Pliocene	Ventura County, CA	Woodring, 1931; Grant and Gale, 1931; Groves, 1991
	Pliocene	Los Angeles County, CA	Vokes, 1978
	Pleistocene	San Quintin, BC, Mexico	AMNH 12410
	Pleistocene	Monterey County, CA	Glibert, 1962
	Pleistocene	Santa Barbara Island, CA	this study: LACMIP locs. 5066-5067
	Pleistocene	Santa Rosa Island, CA	Orr, 1960
	Pleistocene	Santa Clemente Island, CA	Lipps, 1967
	Pleistocene	San Nicolas Island, CA	Vedder and Norris, 1963
	Pleistocene	Anacapa Island, CA	this study: LACMIP locs. 24381, 24383
	Pleistocene	San Luis Obispo County, CA	Valentine, 1958
	Pleistocene	Los Angeles County, CA	Chace and Chace, 1919; Grant and Gale, 1931; Woodring *et al.*, 1946; Valentine, 1962; Marincovich, 1976

Table 2-3, continued

	Pleistocene	Orange County, CA	Kanakoff and Emerson, 1959
	Pleistocene	San Diego County, CA	Webb, 1937; this study: LACMIP loc. 11701
	Pleistocene	NW BC	Valentine, 1957
	Pleistocene	BC, Mexico	this study: LACMIP loc. 22723, 22717
* cf *rufescens*	Pliocene	Isla Cedros, BC	Jordan and Hertlein, 1926; Woodring, 1931
	Pleistocene	Isla Cedros, BC	Jordan and Hertlein, 1926; Grant and Gale, 1931
	Pleistocene	Los Angeles County, CA	Woodring, 1931
* *corrugata*	Pliocene	Ventura County, CA	Woodring, 1931
	Pliocene, m	Ventura County, CA	Grant and Gale, 1931
	Pleistocene	Orange County, CA	Kanakoff and Emerson, 1959
	Pleistocene	San Diego County, CA	Webb, 1937
* *assimilis*	Pliocene	CA	Lindberg, 1992
* *walallensis*	Pliocene	San Diego County, CA	Hertlein and Grant, MS
sp.	Pliocene	Los Angeles County, CA	Woodring, 1931
sp.	Pliocene	Ventura County, CA	Woodring, 1931; Kern, 1973
sp.	Pliocene	San Diego County, CA	Woodring, 1931
santacruzensis	Pliocene, u	Santa Cruz, Islas Galápagos	Durham, 1979[8]
**ovina*	Pliocene, Pleistocene	Guam	Ladd, 1966
	Pliocene	—	Talmadge, 1974
	Pleistocene	Tonga: Tongatapu	Ostergaard, 1935
* cf. *varia*	Pliocene	Kankasanturai, Sri Lanka	BMNH G51083
* *tuberculata*	Pliocene	Piemont, Italy	Delhaes, 1909; BMNH G32151
	Pliocene	Palermo, Italy	BMNH 31287

Table 2-3, continued

	Pleistocene	Cyprus	Fischer, 1993
	Pleistocene	Sicily, Italy	Glibert, 1962
	Pleistocene	Ravagnee, Calabria, Italy	BMNH G31514
	Pleistocene	Panchia di Livorno, Italy	BMNH G11529
	Pleistocene	Malta	BMNH no #
	?	Favignana Isl. and Taranto, Italy	Philippi, 1844
	?	Sicily, Italy	Philippi, 1844; Weinkauff, 1868
* cf. *tuberculata*	Miocene, m	Loire Bassin, France	Glibert, 1962
sp.	l Pliocene / u Miocene	Milazzo, Sicily, Italy	H. D. Laatsch, personal commun.
saldanhae	Pliocene	Langebaanweg, South Africa	Kensley, 1972
		Pleistocene	
* *australis*	Pleistocene, u - Recent	NZ	Beu and Maxwell, 1990
	?	Gisborne, North Island, NZ	Smith, 1977
* *virginea*	Pleistocene, u - Recent	NZ	Beu and Maxwell, 1990
* *cyclobates*	Pleistocene	Fleurieu Peninsula, Australia	Lindberg, 1992
* *emmae*	Pleistocene	Victoria, Australia	Lindberg, 1992
* *laevigata*	Pleistocene	Victoria, Australia	Lindberg, 1992
* *rubra*	Pleistocene	Victoria, Australia	Lindberg, 1992
* *kamtschatkana*	Pleistocene	San Nicolas Island, CA	Vedder and Norris, 1963
* cf. *sorenseni*	Pleistocene	San Nicolas Island, CA	Vedder and Norris, 1963
* cf. *cracherodii*	Pleistocene	San Luis Obispo County, CA	Valentine, 1962
sp.	Pleistocene	Ventura County, CA	Woodring, 1931
	Pleistocene	Santa Barbara County, CA	this study
	Pleistocene	NW BC, Mexico	Valentine, 1957
* *fulgens guadalupensis*	Pleistocene	Isla Guadalupe, Mexico	Lindberg *et al.*, 1980

Table 2-3, continued

barbadensis	Pleistocene	Whitehaven, Rugged Point and Spring Hall, Barbados	Trechman, 1937; Jung, 1968; Durham, 1979a; BMNH GG4018-26; BMNH GG1913; BMNH GG4001-6; BMNH GG3977; BMNH GG9012-16 [9]
lamellosa	Pleistocene	Camargue, France	Paulus, 1949
	Pleistocene	Monte Pellegrino, Italy	Ghisotti, 1964
	Pleistocene	Sicily, Italy	Malatesta, 1960; Glibert, 1962
sp.	Pleistocene /subfossil	Lanarca, Cyprus	H. D. Laatsch, personal commun.
**tuberculata*	Pleistocene	Lanzarote, Canary Isl.	Lecointre *et al.*, 1967
* *tuberculata coccinea*	Pleistocene	Tenerife, Canary Isl.	Talavera *et al.*, 1978
* *midae*	Pleistocene	Algoa Bay, South Africa	Barnard, 1963
* *unilateralis*	Pleistocene and Recent	Port Sudan, Sudan	Hall and Standen, 1907
	Pleistocene	Zanzibar, Tanzania	BMNH G41536
* *pustulata cruenta*	Pleistocene	Gulf of Suez, Egypt	Newton, 1900
	Pleistocene	Gharib Lighthouse, Red Sea	BMNH G24386
	Pleistocene	Mugarsim Isl., Sudan	BMNH G35528
	Pleistocene	Zanzibar, Tanzania	BMNH G41537