

REVIEW OF FOSSIL ABALONE (GASTROPODA: VETIGASTROPODA: HALIOTIDAE) WITH COMPARISON TO RECENT SPECIES

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ABSTRACT—Compared to their Recent counterparts, fossil abalone are rare and poorly known. Their taxonomy is problematic, because most of the 35 fossil species have been described from single specimens and shell characteristics of Recent species are extremely plastic. Thus, the use of fossil species in phylogeny is questionable. Abalone first appear in the Upper Cretaceous (Maastrichtian) with one species each in California and the Caribbean, are unknown in the Paleocene, and appear again in the late Eocene and Oligocene of New Zealand and Europe. They are regularly found from the late Miocene to the Recent in tropical to temperate regions worldwide. Most records are from intensely studied areas: SW North America, Caribbean, Europe, South Africa, Japan, and Australia. Despite their highest present-day diversity being found in the Indo-Pacific, their scarcity in the fossil record in this region is remarkable. The family may have originated in the central Indo-Pacific, Pacific Rim, or Tethys. An extensive list of all known fossil records including new ones from Europe and western North America is given. Fossil and Recent abalone both apparently lived in the shallow, rocky sublittoral in tropical and temperate climates. No on-shore/off-shore pattern is detected.

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, 1995a) and Fleming and Hone (1996). However, only relatively few and isolated accounts of fossil abalone are found in the literature, with Lindberg (1992) supplying a limited overview. We present here a more extensive review on 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 gastropod (Fig. 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 and Geiger, 1998). The extremely hypertrophied epipodium is a key diagnostic character for the anatomy of the Haliotidae, but such characters do not apply to fossil representatives, and are not further discussed here (see Geiger, 1998a). Some Paleozoic Bellerophon-toidea possessed shells somewhat resembling those of abalone. The former, however, are involute, have the row of tremata along the median periphery of the shell, have cross lamellar aragonite, and have a muscle scar more comparable to that of the Fissurelloidea than to the Haliotidae (McLean, 1984).

Several genera in the trochid subfamily Stomatellinae (Hickman and 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, 1998a, for review). For Recent as well as for fossil specimens, it is

unlikely that an imperforate specimen with a depressed, flaring shell is an aberrant abalone.

Although the 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 the 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 variable in Recent species and, therefore, can be inferred to be plastic in fossil congeners by application of uniformitarian principles. We outline below some examples of morphological plasticity in Recent taxa 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 and Dance, 1983), but less for fossil ones (but see e.g., Sohl, 1992), because the incomplete state of most specimens is recognized. In Figure 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 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, 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 its roundness, is to some extent under environmental control as documented by transplant experiments of a Japanese species (Ino, 1952). Stewart and Geiger (1999) showed for the tropical *H. clathrata* Reeve, 1846, that shell roundness also changes through ontogeny. Therefore, this



FIGURE 1—Specimens of fossil haliotids. 1, *Haliotis rufescens*, Pliocene, Saugus Formation, Simi Valley, Ventura County, California, LACMIP no. 12660 from LACMIP loc. 29227, internal mold showing muscle scar, 209 mm. 2, *Haliotis* sp., Miocene, Topanga Canyon Formation, Moorpark, Ventura County, California, LACMIP no. 12659 from LACMIP loc. 16896, internal mold, 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 no. 12658 from LACMIP loc. 16817 (ex LACMIP loc 305c), specimen with shell preserved, 113 mm.

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 (scales in *H. jacnensis* Reeve, 1846: Geiger, personal observation), (b) the strength of spiral cords for *H. rubra* Leach, 1814 (see Geiger, 1998a), and (c) shell flatness in *H. ovina* Gmelin, 1791, for which extremely 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 few specimens are available for each fossil taxon, 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 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 on 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 would not be 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 and Ogasawara, 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 and Ogasawara, 1974; Sohl, 1992). Several fossil species have similar shells to 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,

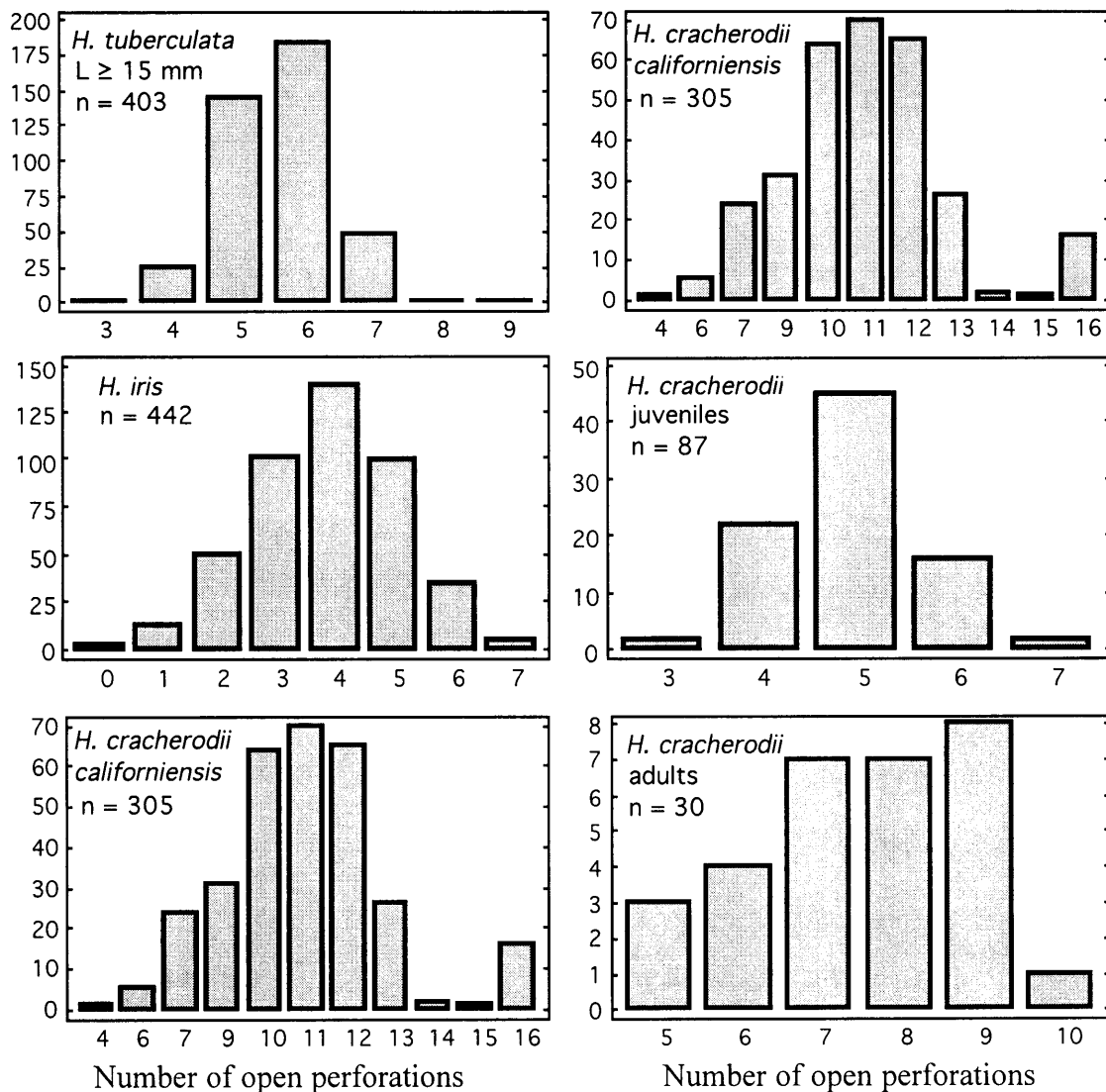


FIGURE 2—Histograms of number of open tremata for several species of *Haliotis*. n = sample size. Sources of data as follows. *Haliotis tuberculata*: only Mediterranean populations: Geiger (unpublished). *Haliotis coccoradiata*: Talmadge (1960); the number of half open tremata was split equally between the neighboring integers. *Haliotis iris*: Sinclair (1963). *Haliotis cracherodii* juvenile: Hemphill (1907). *Haliotis cracherodii californiensis*: Hemphill (1907). *Haliotis cracherodii* adult: Hemphill (1907). Note the approximately normal distribution, with large differences in the modal class. Further note the shift of 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.

expanded from Lindberg (1992), is contained in the Appendix, where we listed all records using the original taxa. Nevertheless, below we have tried to shed some light on potential synonymies and similarities between certain taxa.

Haliotis lomaensis Anderson, 1902, from the Late Cretaceous (Maastrichtian) of San Diego County, California, has been compared to the extant *H. iris* Gmelin, 1791, endemic to New Zealand (Durham, 1979b). *Haliotis antillesensis* Sohl, 1992, from Upper Cretaceous (Maastrichtian) 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, we doubt a close relation 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 *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, itself 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 Quaternary (Pleistocene-Recent) from California and Japan have been noted (Hertlein, 1937; Talmadge, 1964; Hatai et al., 1970; Mulliner, 1984) and are listed in Table 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 further attention elsewhere

TABLE 1—Comparison of upper Tertiary species with Pleistocene–Recent species according to Hertlein (1937), Talmadge (1964), Hatai et al. (1970), and Mulliner (1984).

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

(Geiger, 1998a, 1998b; Geiger and Stewart, 1998; Stewart and 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 addition, Stewart and Geiger (1999) disagreed with Talmadge's (1963) opinion due to discrete morphological differences and disjunct geographical distribution of these taxa.

Haliotis clathrata Reeve, 1846, is mentioned from Fiji (as *H. tuvuthaensis* Ladd in Ladd and Hoffmeister, 1945) and Guam (Ladd and Hoffmeister, 1945; Ladd, 1966). Stewart and 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 been designated (Stewart and Geiger, 1999).

The taxonomic state 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. roberti*, *H. dalli*). The living species are found at a depth of 60–400 m (Henderson, 1915; Bartsch, 1940; Foster, 1946; Aguayo and Jaume, 1947; Harry, 1966; Jung, 1968; Klappenbach, 1968; Sarsua, 1968; Nijssen-Meyer, 1969; McLean, 1970; Kaicher, 1981; Titgen and Bright, 1985; Odé, 1986; Finet, 1993; Martinez and Ruiz, 1994; Simone, 1998). Using the species concept of interbreeding populations, the Recent *H. roberti* and *H. dalli* are distinct from *H. pourtalesii* because they occur on opposite sides of Central America. However, the geological closure of the Isthmus of Panama in the middle Pliocene (Coates and Obando, 1996) complicates the situation for the fossil species considered here. The open waterway could have provided a means for gene flow in a single amphipannamic 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 the 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, we consider them distinct.

We agree with Strausz (1966) and refer 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) to *H. tuberculata volhynica* because the Recent species (*H. t. tuberculata*) with its Atlantic and Mediterranean populations is known to be extremely plastic in its

shell morphology. Most illustrations and material of European fossil specimens (e.g., Fig. 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 six of the European taxa he mentioned to *H. tuberculata*; four further species were compared to the Indo-Pacific *H. pustulata*. 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, 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 separation of those specimens from *H. tuberculata* s.l. (Geiger, personal observation). The remaining European taxa have not received any attention beyond a simple mention in the sources cited in the Appendix.

Fossil abalone in the phylogenetic context.—A phylogenetic study of fossil abalone alone, or integrated in the framework of Recent taxa (cf. Smith, 1994 for review of conceptual approaches), unfortunately is 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 in three fundamentally different mineralogical types (calcitic, aragonitic, admixed calcitic and aragonitic: Mutvei et al., 1985; Dauphin et al., 1989; Dauphin and Denis, 1995; Shepherd et al., 1995b), and may be taxonomically informative. These authors used Feigl's stain to identify aragonite, although this stain will also show high-magnesium calcite (C. Hedegaard, personal communication). Therefore, the mineralogical composition of abalone shells needs reexamination. However, the phylogenetic character states "Feigl-staining" and "non-Feigl-staining" may also be useful without the 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 and 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 throughout the Cenozoic (Johnson, 1987). However, rock-inhabiting organisms are rarely preserved (Carter, 1972), because the habitat is destructive to the shells (Woodring, 1931; Kotaka and Ogasawara, 1974; Parsons and 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 and Standen, 1907)].

A major constituent of abalone shells is aragonitic platelets in the nacreous layer. This type of microstructure are 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 (Fig. 1.1–1.3), 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. 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 other morphologically similar groups such as limpets. Not surprisingly fossil Haliotidae inhabited comparable habitats. Below we present supporting evidence.

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 and Sohl, 1974; Sohl, 1987). Associated species include 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 and 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) interpreted 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 elsmersensis* 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 (Ad-dicott and 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 *Petalococonchus anellum* (Mörch, 1861), which is attached to a shell of an unspecified abalone (Grant and Gale, 1931). Vermetids are common in shallow, rocky habitats.

In Japan, *H. kurosakiensis* Kotaka and Ogasawara, 1974 (upper Miocene); *H. fujiokai* Hatai, Kotaka, and Noda, 1937 (middle Miocene); and *H. kochibei* Hatai and 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 and Ogasawara, 1974; Noda et al., 1995). As with *H. elsmersensis*, 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 change in the depth distribution (=on-shore/off-shore pattern) can be detected, which has been documented during the geological history of a number of invertebrate taxa (Hickman, 1984; Bottjer and 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: Maastrichtian) 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 and 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 Maastrichtian of Puerto Rico and Jamaica, *H. antillesensis*. We consider only *H. lomaensis* and *H. antillesensis* to be Cretaceous abalone, both from Maastrichtian rocks.

Within the Tertiary, Delhaes (1909) and Beu and 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 be considered to explain the hiatus in the fossil record between the Maastrichtian and the Miocene. First, Paleogene rocky-shore habitats are hardly preserved (Lindberg and Squires, 1990). Second, in general there is a taphonomic bias against rock-clinging mollusks (Sohl, 1992). Third,

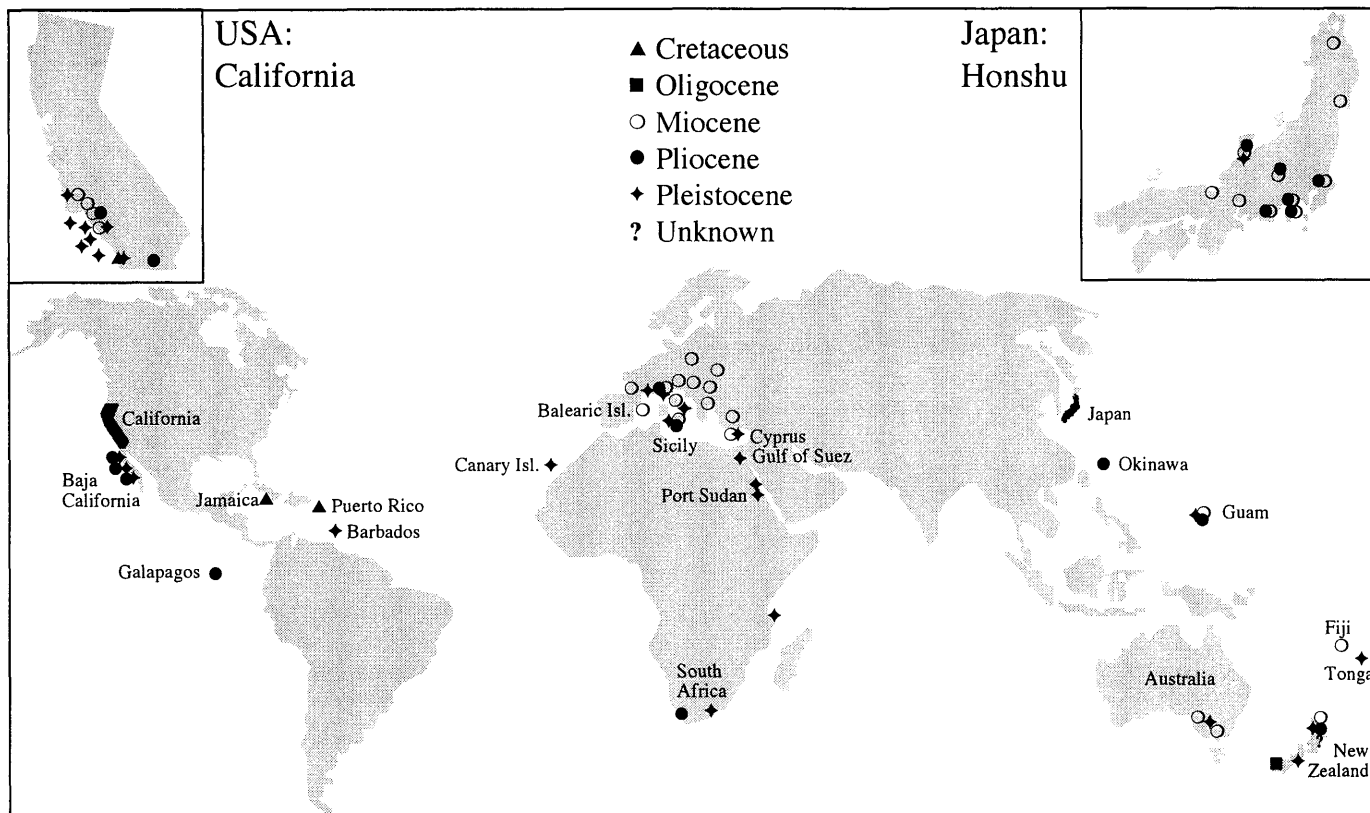


FIGURE 3—Localities of fossil abalone listed in Appendix. The two inserts provide details for California, and Honshu, Japan; the location of each area on the larger map is shaded. Overlapping symbols indicate different geological times being represented at the same locality.

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 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 (Fig. 3; Appendix) is surprising, because it houses the highest diversity of Recent Haliotidae (Delhaes, 1909; Lindberg, 1992). This discrepancy may be associated with the greater paleontological 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 and Standen, 1907 (Red Sea); Ladd and 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 able to evaluate 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 and Vacquier (1995).

3) A third scenario is based on chromosomal data, which have been documented for 10 species (Table 2). Because basal gastropods have a very low diploid number of 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). Note the marked contrast to the westward dispersal of other mollusks (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 rather limited dispersal capability, the precise extent of which is currently debated (Tegner and Butler, 1985; Prince et al., 1987; McShane et al.,

TABLE 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.

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

¹ *Haliotis lamellosa* has been shown to be a synonym/ecomoroph of *Haliotis tuberculata* (Lee and Vacquier, 1995).

² As *Haliotis japonica*.

³ As *Haliotis diversicolor aquatilis* in Nakamura (1985), but as *H. aquatilis* in Nakamura (1986).

⁴ As *Haliotis planata*.

⁵ As *Haliotis varia*.

⁶ As *Haliotis gigantea*.

1988; Wells and Keesing, 1990; Shepherd et al., 1992). Under the Tethyan origin model, the Upper Cretaceous abalone from California and the Caribbean would not be early representatives of the family and the origin of the family would have to be much earlier. A similar model has been proposed by Lee and Vacquier (1995) and is preferred by Eagle (1996).

None of these three biogeographic models has more than anecdotal evidence. The phylogenetic trees published to date (Brown and Murray, 1992; Brown, 1993; Lee and Vacquier, 1995) are all unrooted, and species 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 and Gale, 1931, p. 96). Biochemical data support this hypothesis. In a tree based on the cDNA sequences of the fertilization protein lysin (Vacquier and 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 and 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 and 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 latitudes 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. kamtschaticana*).

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APPENDIX

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).

Taxon	Geologic time interval	Locality	Literature source and museum specimens
CRETACEOUS			
<i>antillesensis</i>	Maastrichian	Puerto Rico and Jamaica	Sohl, 1992
<i>lomaensis</i>	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. <i>waitemataensis</i>	Oligocene/Miocene	Cookson Volcanics, NZ	Beu and Maxwell, 1990 ¹
<i>benoisti</i>	Oligocene, u; Chattien Adour	St.-Paul-Lès-Dax, France	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-Lès-Dax, France	MNHN no #
	Miocene, l	Meilhan, Landes, France	MNHN no #
	Miocene, l	Larrey, 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, France	MNHN no #
Miocene			
<i>amabilis</i>	Miocene, m	Gifu Pref., Japan	Itoigawa and Tomida, 1982
<i>kurosakiensis</i>	Miocene, u	Aomori Pref., Japan	Kotaka and Ogasawara, 1974; Itoigawa and Tomida, 1982; Lindberg, 1992

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Taxon	Geologic time interval	Locality	Literature source and museum specimens
<i>kochibei</i>	Miocene, l	Kanagawa Pref., Japan	Hatai and Nisiyama, 1952; Hatai et al., 1970
	Miocene, m	Ibaraki Pref., Japan	Kotaka and Ogasawara, 1974; Itoigawa and Tomida, 1982
<i>koikei</i>	Miocene, m-u	Ibaraki Pref., Japan	Hatai and Nisiyama, 1952
	Pliocene	Ishikawa Pref., Japan	Lindberg, 1992
	Pliocene	Ibaraki Pref., Japan	Shibata, 1957; Noda et al., 1995
<i>glabrosa</i>	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	South Fossa-Magna, Japan	Tomida, 1996
<i>koyamai</i>	Miocene, l-m	Shizuoka Pref., Japan	Nomura and Niino, 1932; Hanzawa et al., 1961; Hatai et al., 1970; Kotaka and Ogasawara, 1974; Itoigawa and Tomida, 1982
	Pliocene, l	Shizuoka Pref., Japan	Itoigawa and Tomida, 1982
	Pliocene, l-m	South Fossa-Magna, Japan	Tomida, 1996
<i>notoensis</i>	Miocene, l	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
	Miocene, m	Ishikawa Pref., Japan	Masuda, 1966; Kotaka and Ogasawara, 1974; Itoigawa and Tomida, 1982
<i>moniwaensis</i>	Miocene, m	Fukui Pref., Japan	Ozawa et al., 1986
	Miocene	Miyagi Pref., Japan	Kotaka and Ogasawara, 1974; Itoigawa and Tomida, 1982
<i>fujiokai</i>	Miocene, m	Miyagi Pref., Japan	Hatai et al., 1970; Kotaka and Ogasawara, 1974; Itoigawa and Tomida, 1982
<i>*japonica koticki</i>	Miocene, l	Miyagi Pref., Japan	Hatai and Nisiyama, 1952; Lindberg, 1992
	Miocene, l	Santa Barbara County, CA	Hertlein, 1937; Bartsch, 1940; Keen and Benton, 1944
<i>lasia</i>	Miocene, u	San Luis Obispo County, CA	Woodring, 1932; Bartsch, 1940; Keen and Benton, 1944
<i>palaea</i>	Miocene	Los Angeles County, CA	Woodring, 1931; Bartsch, 1940; Keen and Benton, 1944
<i>flemingi</i>	Miocene, l	Kawau Isl, NZ	Powell, 1938; Eagle, 1996
<i>*iris</i>	Pleistocene	Whakatane, NZ	Beu and Maxwell, 1990; Lindberg, 1992
	Miocene	Cape Rodney, NZ	Harris, 1897
	Miocene	NZ	Suter, 1913 ¹⁰
<i>mathesonensis powelli</i>	Pliocene, u-Recent	NZ	Beu and Maxwell, 1990
	Pleistocene	Lyttleton, NZ	BMNH 98048
	Miocene, l	Leigh, Rodney District, NZ	Eagle, 1996
	Miocene, l	Mt. Luxmore, Fiordland, NZ	Fleming, 1952; Lee, et al., 1983 ^{3,4}
<i>waitematensis moorabolensis</i>	Pliocene	Komako, NZ	Carter, 1972 ⁴ ; Beu and Maxwell, 1990; Eagle, 1996
	Pleistocene	Bay of Plenty, NZ	Fleming, 1952
<i>naevosoides</i>	Miocene, l	Kawau Isl., NZ	Powell, 1938 ³ ; Eagle, 1996
	Miocene	Moorabool River, Australia	McCoy, 1876 ⁵
	Miocene	Victoria, Australia	Harris, 1897
<i>ovinoides</i> sp.	Miocene, u	Flemington, Australia	BMNH G1934
	Miocene	Flemington, Victoria, Australia	Lindberg, 1992 ⁵
	Miocene, u	Flemington, Australia	BMNH G1935
	Pliocene	Adelaide, Australia	Cotton, 1952; Ludbrook, 1954
	Pliocene	Adelaide and Melbourne, Australia	Ludbrook, 1956
	Pliocene	Royal Park, Melbourne, Australia	BMNH GG2373
<i>neuvillei monilifera</i>	Pliocene	Flemington, Australia	McCoy, 1876; Harris, 1897
	Miocene, u	Victoria, Australia	McCoy, 1876
<i>anomiaeformis tuberculata</i> var.	Miocene, l	New Caledonia	Eagle, 1996
	Miocene, l: f	Fiji	Ladd and Hoffmeister, 1945; Ladd, 1966
<i>tuberculata lamellosoides</i>	Miocene, l: f	Fiji	Ladd and Hoffmeister, 1945 ⁵ ; Ladd, 1966
	Miocene, u: g	Tinian	Ladd, 1966 ⁷
<i>ovata</i> sp.	Plio-, Pleistocene	Guam	Ladd, 1966 ⁷
	Miocene, lowest: Aquitanian	Gironde, France	Delhaes, 1909
	Miocene, l: Elveziano	Turin, Italy	Delhaes, 1909
<i>tuberculata volhynica</i>	Miocene	Turin, Italy	Glibert, 1962
	Miocene, l: Elveziano	Turin, Italy	Delhaes, 1909
	Miocene, l: Elveziano	Turin, Italy	Delhaes, 1909
<i>tuberculata lamellosoides</i>	Miocene	Miodoborow, W. Ukraine	Davidaschvili, 1937; Krach, 1981
	Miocene	Cserhát Mountains, Hungary	<i>vide</i> Strausz, 1966
	Pliocene	Piemont, Italy	Delhaes, 1909
	Miocene	Italy	Delhaes, 1909; Ruggieri, 1990
<i>tuberculata lamellosoides</i> sp.	Miocene	Tétényer Plateau, Hungary	Strausz, 1966
	Miocene	Vienna Bassin, Austria	H. D. Laatsch, personal commun.
	Miocene	Roztocze Lubelskie, Poland	Krach, 1981
	Miocene	Poland and Italy	Ghisotti, 1964; Ruggieri, 1990
<i>tuberculata lamellosoides</i> sp.	Miocene	Austria, Romania, Bulgaria, West Ukraine	Krach, 1981
	Miocene	Ukraine	Krach, 1981

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Taxon	Geologic time interval	Locality	Literature source and museum specimens
	Tortonian/Sarmatian	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
<i>torrei</i>	Miocene, u	Sicily, Italy	Fuggieri, 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	
<i>*gigantea</i>	Pliocene	Ishikawa Pref., Japan	Hatai et al., 1970
	Pleistocene, l	Ishikawa Pref., Japan	Itoigawa and Tomida, 1982
<i>gigantoides</i>	Pliocene	Okinawa Pref., Japan	Yabe and Hatai, 1941; Hanzawa et al., 1961; Hatai et al., 1970; Kotaka and Ogasawara, 1974
<i>*discus</i>	Pliocene, u	Ishikawa Pref., Japan	Itoigawa and Tomida, 1982
<i>*diversicolor</i>	Pliocene, u	Okinawa Pref., Japan	Itoigawa and Tomida, 1982
	Plio-, Pleistocene	Okinawa Pref., Japan	MacNeil, 1960
<i>*sieboldii</i>	Pliocene, u	Japan	Itoigawa and Tomida, 1982
<i>*pourtalesi</i>	Pliocene, early	Riverside County, CA	Schremp, 1981
<i>elsmerensis</i>	Pliocene, early	Los Angeles County, CA	Vokes, 1935; Bartsch, 1940; Keen and Bentson, 1944
<i>*fulgens</i>	Pliocene, l	Los Angeles County, CA	Woodring, 1931; Grant and Gale, 1931; Vokes, 1935
	Pliocene	NW BC, Mexico	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, Mexico	Hertlein, 1937
	Pleistocene	BC Sur, Mexico	Jordan and Hertlein, 1926; Emerson, 1980; Emerson et al., 1981
<i>*cracherodii</i>	Pliocene	CA	Lindberg, 1992
	Pliocene/Pleistocene	Punta China, BC, Mexico	ANSP 31487
	Pleistocene	San Diego County, CA	Webb, 1937; Glibert, 1962; this study: LACMIP loc. 12015; AMNH 12409
	Pleistocene	Santa Barbara Island, CA	this study; LACMIP locs. 326, 329, 5068
	Pleistocene	Santa Rosa Island, CA	Orr, 1960
	Pleistocene	San Nicolas Island, CA	Vedder and Norris, 1963
	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; Hertline, 1934; Valentine, 1957; this study: LACMIP locs. 23161, 22715-22718, 8220-8224; 10131, 23162
<i>*rufescens</i>	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
	Pleistocene	Orange County, CA	Kanakoff and Emerson, 1959
	Pleistocene	San Diego County, CA	Webb, 1937; this study: LACMIP loc. 11701
	Pleistocene	NW BC, Mexico	Valentine, 1957
	Pleistocene	BC, Mexico	this study: LACMIP loc. 22723, 22717

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Taxon	Geologic time interval	Locality	Literature source and museum specimens
*cf. <i>rufescens</i>	Pliocene Pleistocene	Isla Cedros, BC, Mexico Isla Cedros, BC, Mexico	Jordan and Hertlein, 1926; Woodring, 1931 Jordan and Hertlein, 1926; Grant and Gale, 1931
* <i>corrugata</i>	Pleistocene Pliocene Pliocene, m Pleistocene, m Pleistocene, m	Los Angeles County, CA Ventura County, CA Ventura County, CA Orange County, CA San Diego County, CA	Woodring, 1931 Woodring, 1931 Grant and Gale, 1931 Kanakoff and Emerson, 1959 Webb, 1937
* <i>assimilis</i>	Pliocene	CA	Lindberg, 1992
* <i>walallensis</i>	Pliocene	San Diego County, CA	Hertlein and Grant, MS
sp.	Pliocene	Los Angeles County, CA	Woodring, 1931; Kern, 1973
sp.	Pliocene	Ventura County, CA	Woodring, 1931
sp.	Pliocene	San Diego County, CA	Woodring, 1931
<i>santacruzensis</i>	Pliocene, u	Santa Cruz, Isla Galápagos	Durham, 1979a ⁸
* <i>ovina</i>	Pliocene, Pleistocene Pliocene Pleistocene	Guam — Tongatapu, Tonga	Ladd, 1966 Talmadge, 1974 Ostergaard, 1935
*cf. <i>varia</i>	Pliocene	Kankasanturai, Sri Lanka	BMNH G51083
* <i>tuberculata</i>	Pliocene Pliocene Pliocene Pleistocene Pleistocene Pleistocene Pleistocene Pleistocene ?	Piemont, Italy Palermo, Italy Cyprus Sicily, Italy Ravagnee, Calabria, Italy Panchia di Livorno, Italy Malta Favignana IIs. and Taranto, Italy Sicily, Italy	Delhaes, 1909; BMNH G32151 BMNH 31287 Fischer, 1993 Glibert, 1962 BMNH G31514 BMNH G11529 BMNH no # Philippi, 1844 Philippi, 1844; Weinkauff, 1868
*cf. <i>tuberculata</i>	Miocene, m	Loire Bassin, France	Glibert, 1962
sp.	1 Pliocene/u Miocene	Milazzo, Sicily, Italy	H. D. Laatsch, personal commun.
<i>saldanhae</i>	Pliocene	Langebaanweg, South Africa	Kensley, 1972
		Pleistocene	
* <i>australis</i>	Pleistocene, u-Recent ?	NZ Gisborne, North Island, NZ	Beu and Maxwell, 1990 Smith, 1977
* <i>virginea</i>	Pleistocene, u-Recent	NZ	Beu and Maxwell, 1990
* <i>cyclobates</i>	Pleistocene	Fleurieu Peninsula, Australia	Lindberg, 1992
* <i>emmae</i>	Pleistocene	Victoria, Australia	Lindberg, 1992
* <i>laevigata</i>	Pleistocene	Victoria, Australia	Lindberg, 1992
* <i>rubra</i>	Pleistocene	Victoria, Australia	Lindberg, 1992
* <i>kantschatkana</i>	Pleistocene	San Nicolas Island, CA	Vedder and Norris, 1963
*cf. <i>sorenseni</i>	Pleistocene	San Nicolas Island, CA	Vedder and Norris, 1963
*cf. <i>cracherodii</i>	Pleistocene	San Luis Obispo County, CA	Valentine, 1962
sp.	Pleistocene Pleistocene Pleistocene Pleistocene Pleistocene	Ventura County, CA Santa Barbara County, CA NW BC, Mexico Isla Guadalupe, Mexico	Woodring, 1931 this study: LACMIP loc. 12477 Valentine, 1957 Lindberg et al., 1980
* <i>fulgens guadalupensis</i>	Pleistocene	Whitehaven, Rugged Point and Spring Hall, Barbados	Trechmann, 1937; Jung, 1968; Durham, 1979a; BMNH GG4018-26; BMNH GG1913; BMNH GG4001-6; BMNH GG3977; BMNH GG9012-16 ⁹
<i>barbadensis</i>	Pleistocene		
<i>lamellosa</i>	Pleistocene Pleistocene Pleistocene	Camargue, France Monte Pellegrino, Italy Sicily, Italy	Paulus, 1949 Ghisotti, 1964 Malatesta, 1960; Glibert, 1962
sp.	Pleistocene/subfossil	Lanarca, Cyprus	H. D. Laatsch, personal commun.
* <i>tuberculata</i>	Pleistocene	Lanzarote, Canary Isl.	Lecointre et al., 1967
* <i>tuberculata coccinea</i>	Pleistocene	Tenerife, Canary Isl.	Talavera et al., 1978
* <i>midiae</i>	Pleistocene	Algoa Bay, South Africa	Barnard, 1963
* <i>unilateralis</i>	Pleistocene and Recent Pleistocene Pleistocene	Port Sudan, Sudan Zanzibar, Tanzania Gulf of Suez, Egypt	Hall and Standen, 1907 BMNH G41536 Newton, 1900
* <i>pustulata cruenta</i>	Pleistocene Pleistocene Pleistocene Pleistocene	Gharib Lighthouse, Red Sea Mugarsim Isl., Sudan Zanzibar, Tanzania	BMNH G24386 BMNH G35528 BMNH G41537

¹ *Haliotis* sp. is similar to *H. waitemataensis* (Beu and 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 and Maxwell (1990:8-9).

⁴ Originally reported as *Haliotis* sp. but corresponds exactly to the type of *H. powelli* illustrated in Beu and Maxwell (1990).

⁵ Delhaes (1909) interpreted these finds as Eocene.

⁶ *Haliotis tuvuthaensis* has been synonymized with *H. clathrata* Reeve, 1846 (Stewart and Geiger, 1999).

⁷ Plate 2, figure 5 illustrates a fairly round specimen superficially rather looking like *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 and 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* is rejected by Eagle (1996).