

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

DANIEL L. GEIGER AND LINDSEY T. GROVES

Department of Biological Sciences, University of Southern California, Los Angeles, 90089-0371, <dgeiger@usc.edu>, and Natural History Museum of Los Angeles County, Sections of Malacology and Invertebrate Paleontology, 900 Exposition Boulevard, Los Angeles, CA 90007, <lgroves@nhm.org>

**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

**R**ECENT 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 ( $\leq 40$  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,

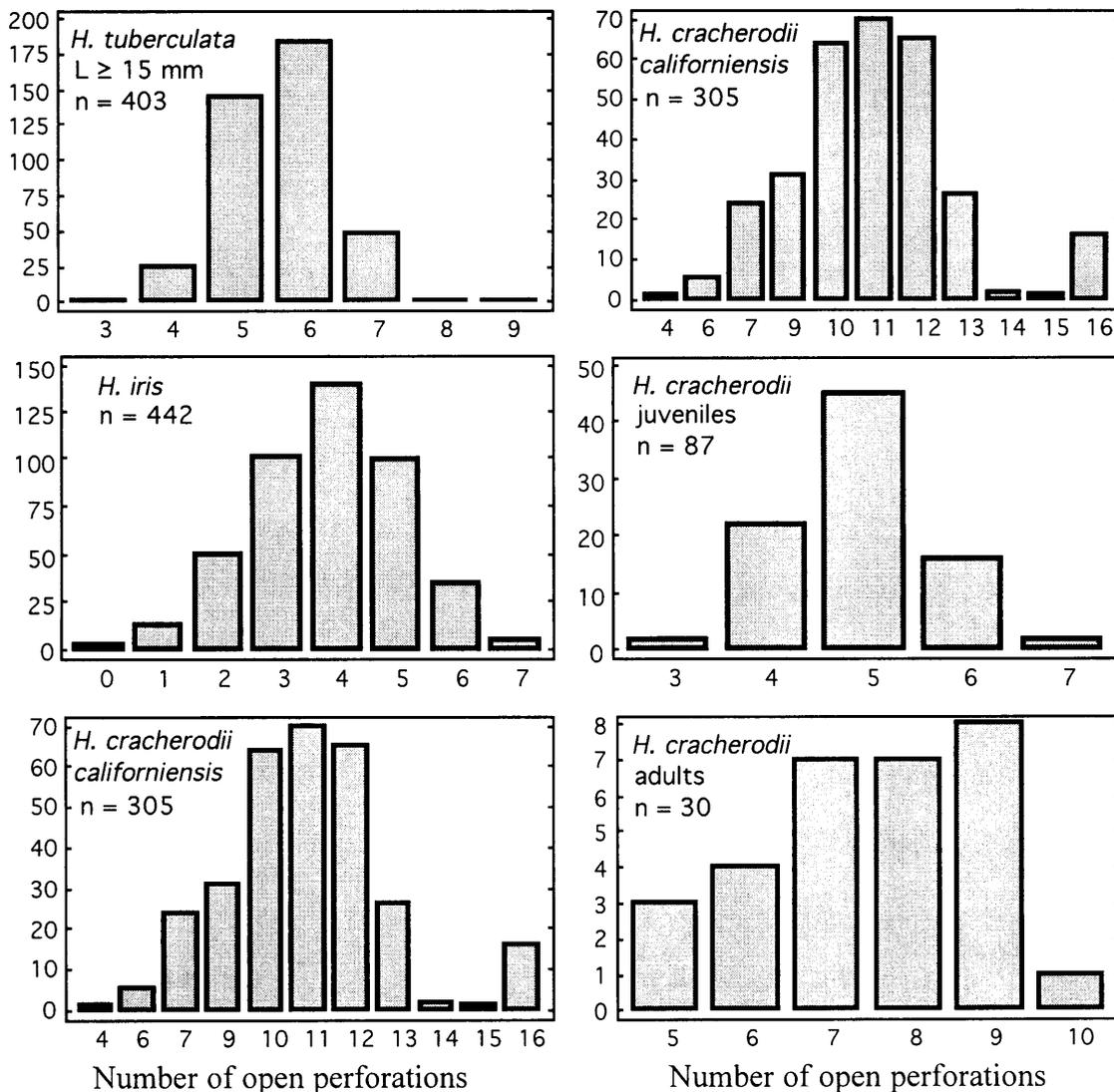


FIGURE 2—Histograms of number of open tremata for several species of *Haliotis*.  $n$  = sample size. Sources of data as follows. *Haliotis tuberculata*: only Mediterranean populations: Geiger (unpublished). *Haliotis coccoradiata*: Talmadge (1960); the number of half open tremata was split equally between 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  $\mu\text{m}$  width and 5–10  $\mu\text{m}$  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