

## **Introduction**

This dissertation evaluates the evolutionary history of the marine gastropod family Haliotidae, part of the clade Vetigastropoda. Abalone are important for commercial fisheries, hence are relatively well-known. However, it is surprising that the assessment of its species-level diversity has remained untouched since the beginning of this century. After one hundred years of neglect it seems appropriate to re-evaluate the alpha and beta taxonomy of the family and to provide a hypothesis of relationships.

At the beginning of any phylogenetic analysis, the ingroup taxa need to be evaluated, because any phylogenetic tree is only as good as the names on the terminal nodes. In chapter 1, I assess all the over 200 species-level and the 17 genus-level taxa. The evaluation is based on all the original descriptions as well as much secondary literature, both scientific as well as grey literature. Inspection of US and European museum collections adds to the in-depth study of the taxonomic issues.

The family has an evolutionary history reaching at least to the Upper Cretaceous, with some fossil representatives known from many regions of the world. Can the fossils contribute to the understanding of the evolution of the group leading to today's diversity? Chapter 2 investigates this question, which will also determine whether the fossil representatives can help to elucidate the phylogeny of Haliotidae.

The goal of this study is a “total evidence cladistic analysis”, which by definition utilizes multiple sources of information. The treatment of different kinds of data often gives rise to internal methodological conflicts. Some of the most severe conflicts arise in the treatment of DNA sequence data. In order to include DNA sequences in the analysis, the treatment of all observations is scrutinized, and a methodology that can accommodate all types of data is developed in Chapter 3. The new and rather unorthodox

coding strategies are based on a sound understanding of principle in philosophy of science. These strategies will be applied in the analyses presented in Chapters 4 and 5.

One of the basic biological parameters is the distribution of species. This information is mostly unavailable for members of the family Haliotidae. Chapter 4 presents distributional data for each species within the family, for the inference on distributional patterns will be based on actual localities, as opposed to vague intuitive indications. The distributional data are subjected to a rigorous analysis using Brooks parsimony, where taxa are used as characters, and the distributional areas are used as taxa. This will help to evaluate the possible evolutionary scenarios and their implication for the distribution of abalone world-wide.

Chapter 5 reviews published data and phylogenetic hypotheses, re-analyzes the data, and assesses the differences in the phylogenetic hypotheses due to altered character coding. The main re-coding strategies will convert allozyme frequencies to character state data and change the handling of questionably aligned sequences. Morphological characters from the radula, the epipodium, and the hypobranchial gland are added, and all data are analyzed using outgroups from all vetigastropod families. The effect of recoding strategies and missing data on the ensuing hypotheses are evaluated. Recommendations concerning the use of genus-level taxa within the family Haliotidae, based on recurring groupings from the phylogenetic analyses are given at the end of chapter 5, bringing to closure the circle started in chapter 1.

# **Chapter 1: Recent Genera and Species of the Family Haliotidae Rafinesque, 1815 (Gastropoda: Vetigastropoda)**

## **INTRODUCTION**

Members of the family Haliotidae occur in most tropical and temperate oceans, particularly in the shallow subtidal zone. The first mention of abalone in the literature was made in the 4<sup>th</sup> century B.C. by Aristotle. In the 1<sup>st</sup> century A.D. the name of *otia* (little ear) was used by Pliny. In Japan abalone were mentioned as early as the 4<sup>th</sup> century A.D. In the medieval literature of Europe they were noted for the first time by Gessner in 1553. The first good illustrations were provided by Buonanni, Lister, Gualtieri, and Rumphius between 1681 and 1741, which were later cited by Linnaeus (1758). The pre-Linnean descriptions of abalone have been dealt with more extensively in Crofts (1929), Cox (1962) and Muller (1984a).

Taxonomic publications on the family began with Linnaeus (1758), who described the first seven species of abalone using his system of binominal nomenclature. His work was continued and enlarged by Gmelin (1791), who added a further twelve taxa. Reeve (1846) described 43 new taxa in his monograph, which is one of the most important sources for the taxonomy of the family Haliotidae. In the late 19<sup>th</sup> century, three larger monographs were published by Sowerby (1882), Weinkauff (1883), and Pilsbry (1890), but only a few new taxa were introduced by these authors. Wagner & Abbott (1978) provided a list of taxa including tentative synonymies. Kaicher (1981) illustrated all the species and subspecies she considered valid, providing the most comprehensive means available to identify the Recent Haliotidae. Pickery (1991) listed most abalone taxa chronologically, including their references. Ubaldi (1993, 1995) has started to publish a

series intended to cover, in alphabetical order, all extant species of abalone; to date, four species have been treated.

The latest valid species described is *H. roberti* McLean, 1970. *Haliotis coccinea canariensis* Nordsieck, 1975, is the most recent taxon that has been described. All taxa have been based on shells; only the neotype of *H. unilateralis* Lamarck, 1822, and the types of *H. aurantium* Simon, 1998, from Brazil are complete specimens with the animal (Geiger, 1996; Simone, 1998).

The alpha taxonomy of the majority of species has been uncertain, except for most of the important commercial species. Between 30 (Dauphin *et al.*, 1989) and 130 (Cox, 1962) of the over 200 species-level taxa described have been considered valid species. Most authors have estimated the number of distinct species to be approximately 75 (Thiele, 1931; Pickery, 1980; Kaicher, 1981; Lindberg, 1992). The objective here is to re-evaluate this family, to critically review all the published information, and to include additional unpublished observations. This groundwork is necessary in the light of a forthcoming phylogenetic analysis of the entire family, because the working unit—the species—should be clearly understood so that the data matrix will not be obscured by unresolved taxonomic problems.

The conclusions that form the substance of this paper are presented in three lists: Index, Notes, and Valid Species by Faunal Regions. The alphabetical index and the valid species by faunal regions are both cross-referenced to the notes. Species illustrated are those that are infrequently shown in other publications.

## **MATERIALS AND METHODS**

This work is based on a number of visits to major museums in Europe and the United States, where the available type specimens were examined. Museum material was sup-

plemented with specimens from private collections, including those of Katharine Stewart (Carmel, California), Don Pisor (La Jolla, California), Roger Pickery (Wilrijk, Belgium), Mark Jones (Auckland, New Zealand), and Benjamin Singer (Rehovot, Israel). Every original description was carefully checked in the original language. An effort was made to track all relevant secondary literature through later citations and the *Zoological Record*. Some results from ongoing studies of the animals are mentioned where they help in the understanding of taxonomic questions; a detailed coverage of the characters of the animals is beyond the scope of the present chapter and will be provided elsewhere. The radular terminology of Geiger (1996) is used.

The statistical analysis of the shell morphometrical data was performed with STATISTICA™ Mac 4.1 (StatSoft, 1994). For the breakpoint regression, piecewise linear regression with Quasi-Newton estimation method and least-square loss function was employed. Linear regression on the data-sets on either side of the breakpoint yielded the slope statistics.

Abbreviations of collections. ANSP: Academy of Natural Sciences, Philadelphia; BMNH: The Natural History Museum, London; DMNH: Delaware Museum of Natural History, Wilmington, Delaware; HUI: Hebrew University, Jerusalem; KBIN: Koniglich Belgische Institut for Natuurwetenschappen, Brussels; LACM: Los Angeles County Museum of Natural History; LSL: Linnean Society London; MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MNHN: Muséum Nationale d'Histoire Naturelle, Paris; MHNG: Muséum d'Histoire Naturelle, Genève; NMW: National Museum Wales, Cardiff; SAM: South Australian Museum, Adelaide; SBMNH: Santa Barbara Museum of Natural History, California; USNM: United States National Museum of Natural History, Smithsonian Institution, Washington.

## SYSTEMATIC AFFINITIES AND CHARACTERISTICS OF THE FAMILY

Haliotidae are part of the prosobranch Vetigastropoda, having the nacreous shell, certain characters in the cleavage pattern (van den Biggelaar, 1996), a streptoneurous nervous system, two bipectinate ctenidia (gills) served by two heart atria (Diotocardia), and ctenidial bursicles (Hickman, 1988; Haszprunar, 1987; 1993 for review). The row of tremata in abalone and the slit of pleurotomariids (Pleurotomariidae) are homologous structures, but are not diagnostic characters (Delhaes, 1909; Haszprunar, 1993).

Historically, Haliotidae were considered to be closely related to Pleurotomariidae and Scissurellidae and were united with these families in the superfamily Pleurotomarioidea. The rhipidoglossan radula was thought to be a common character for Pleurotomariidae and Haliotidae. However, the radulae in the two families differs in many ways. The rows of the radular teeth are almost symmetrical in abalone, but in the pleurotomariids they are distinctly asymmetrical. The rachidian tooth is well-formed in Haliotidae, but reduced in Pleurotomariidae. The fine outer marginal teeth in Haliotidae show denticulate cusps (Wu & Huang; 1989; Herbert, 1990; Geiger, 1996; Stewart & Geiger, 1999); in Pleurotomariidae, however, a fan of articulated bristles is found (Hickman, 1984a; Harasewych & Askew, 1993; Anseeuw & Goto, 1996). A comparison of Pleurotomariidae and Haliotidae to Scissurellidae is not appropriate, because the latter are subjected to different evolutionary constraints due to their small size and their detrital diet (Fretter & Graham, 1976; Herbert, 1986), which is reflected in their radular structure. The radulae of juvenile abalone were treated by Tong (1985) and Garland *et al.* (1985) and are similar to those of small Trochidae (Hickman & McLean, 1990) and Scissurellidae (Marshall, 1993). The independence of radular morphology and feeding ecology has to be questioned due to the extensive morphological plasticity of the radula in response to the feeding ecology of the respective animals. The radula of Pleuro-

tomariidae and Haliotidae will not help to resolve their phylogenetic relationship, because the former is that of a specialized spongivore, the latter that of a strict macroalgal herbivore. The coding of paedo- and peramorphic structures adds further problems, as in the case of the radular characters of Scissurellidae and Haliotidae. Either stage-specific structures are considered for coding the character states, which overstate the degree of differentiation. The rachidian tooth in mature animals is coded as serrate in Scissurellidae, but bears a smooth cutting edge in Haliotidae. Alternatively, when heterochronic processes are taken into account, characters with inapplicable character states are created. In this case the serrate rachidian tooth of animals <5 mm unites Scissurellidae and Haliotidae, but the rachidian characters for animals > 10 mm are inapplicable to Scissurellidae. The use of the radula to resolve family-level relationships within Vetigastropoda is, therefore, questionable (see also Haszprunar, 1993).

The nearly symmetrical body plan of *Haliotis* has been cited as being plesiomorphic, which puts the abalone very close to the root of the flexoglossate prosobranchs (Fleure, 1904; Salvini-Plawen & Haszprunar, 1987). This view is supported by the primitive sperm ultrastructure (Lewis *et al.*, 1980; Healy, 1988; 1990; Healy & Harasewych, 1992). However, several left parts of the paired body structures, *e.g.*, the gonad and the kidney, are reduced or modified in abalone (Crofts, 1929; Haszprunar, 1988a). The nervous system is close to the primitive condition of *Pleurotomaria*, but in abalone the additional structures of the epipodium and the osphradium are innervated by pleural and visceral elements, respectively. Haliotidae and Trochidae have synapomorphic osphradial characters (Haszprunar, 1985; 1993), but the Trochidae are clearly separated from Scissurellidae, Pleurotomariidae, and Haliotidae by the lack of the right ctenidium and associated organs (Salvini-Plawen & Haszprunar, 1987).

The three families within the old Pleurotomarioidea are now placed in their nominal superfamilies, *i.e.*, Haliotidae are now in Haliotoidea, on the same level as Pleurotomarioidea, Scissurelloidea and the remaining Vetigastropoda (Haszprunar, 1988b; Healy & Harasewych, 1992).

## **PROBLEMS PERTAINING TO THE TAXONOMY OF ABALONE**

### **Tremata as a taxonomic character and teratological type specimens**

Abalone can be easily recognized by the depressed shell and the tremata, the row of holes used for respiration, release of gametes, and defecation (Ino, 1952; Tissot, 1992; Voltzow & Collin, 1995). One may potentially confuse them with some members of the Stomatellinae, a trochid subfamily (Hickman & McLean, 1990; Pickery, 1995). Some taxa with imperforate shells described in the genus *Haliotis* are actually Stomatellinae (*e.g.*, *H. impertusa* Burrow, 1815, and are not dealt with here. Stomatellids that resemble haliotids (*Gena*, *Stomatella* and *Microtis*) are rather small ( $\leq 40$  mm), have no right ctenidium, a flat shell, no tremata, and no spiral sculpture. They might suggest imperforate specimens of juvenile *H. asinina* Linnaeus, 1758, but the latter have several distinct spiral ridges (see Kaicher, 1981), which are no longer formed as the shell grows larger than 3.5 to 4 cm. Specimens of the trochid genus *Granata* have been erroneously identified as imperforate *H. cyclobates* Péron, 1816 (Geiger, pers. obs.).

In most descriptions of abalone the number of open tremata is indicated, erroneously suggesting that it is of value for the identification of a given species. However, the number of open tremata changes during the growth of the shell (Hemphill, 1907; Sinclair, 1963). The larval shell has no tremata at all; the first one is formed at a size of approximately 1-3 mm (Crofts, 1929; Murayama, 1935; Bonnot 1940; Ino, 1952; Shibui, 1971; Mu *et al.*, 1976; Bevelander, 1987). Figure 1-1 shows the size dependent change of the

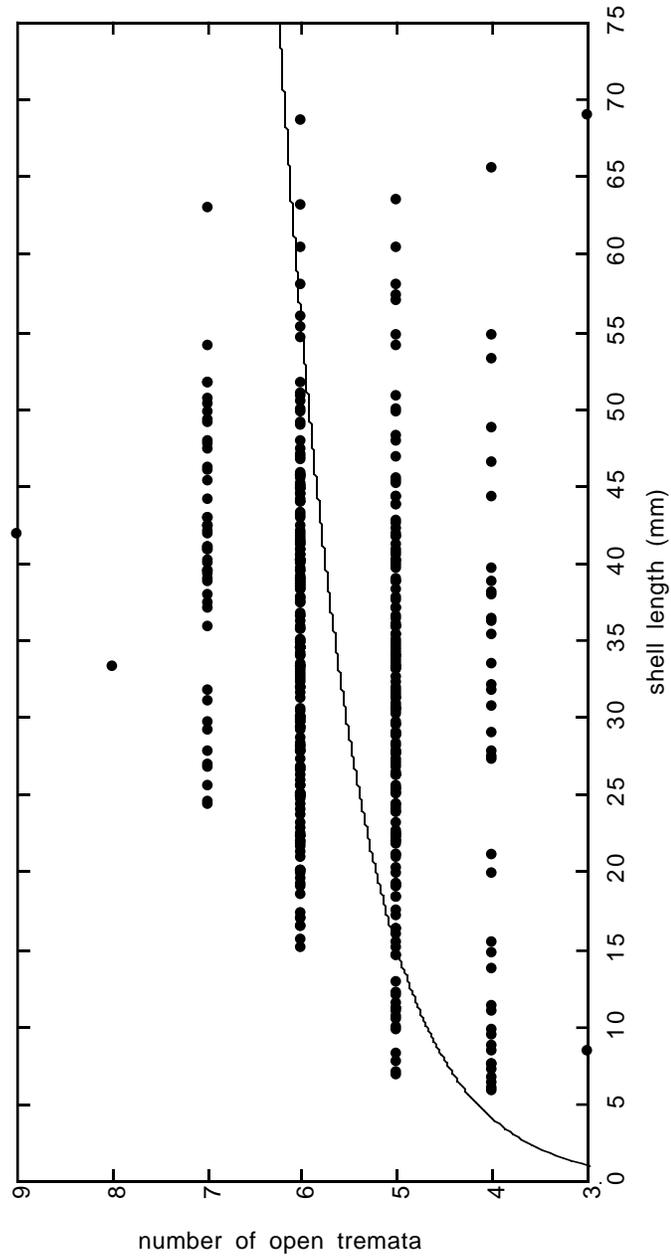
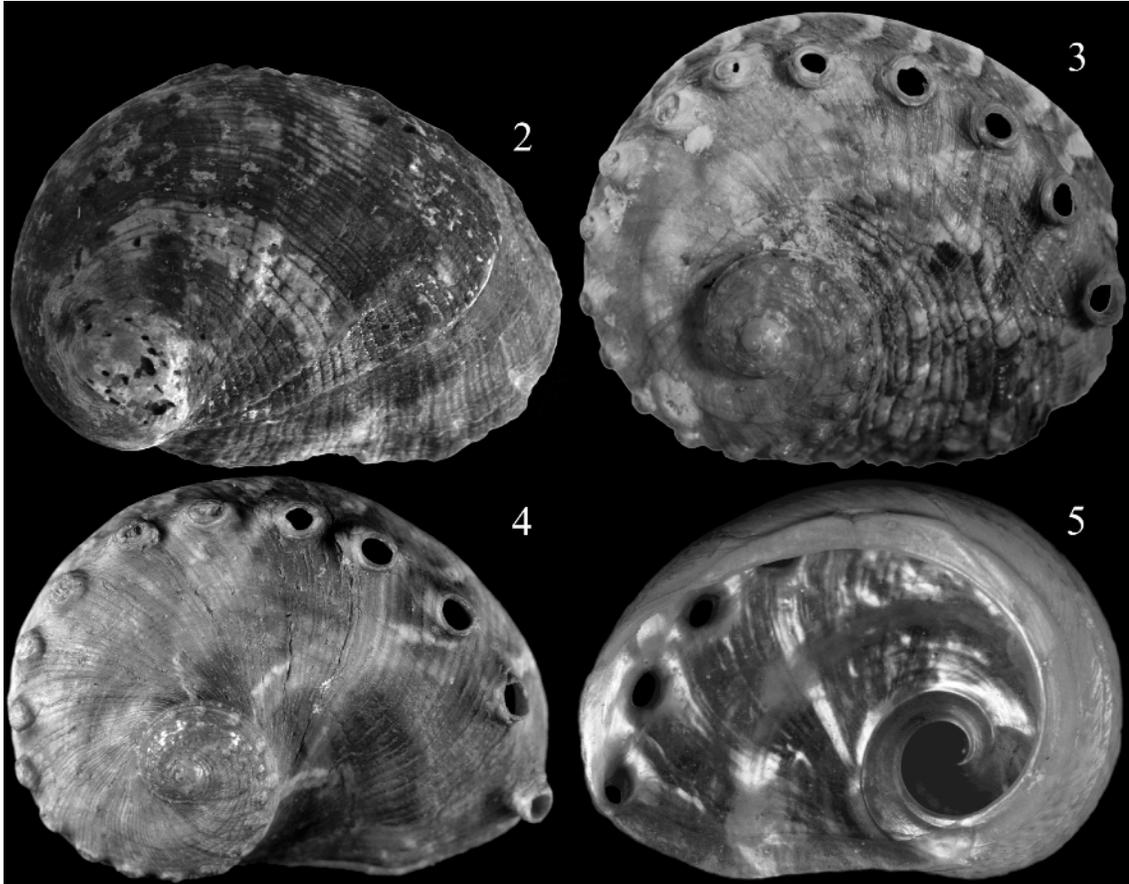


Figure 1-1. Plot of shell length versus number of open tremata in *H. tuberculata* from numerous Mediterranean populations (n = 433). Note the positive correlation between the two parameters, for which a logarithmic curve has been fitted. Note the intersection with the x-axis around 2 mm shell length, the size at which the first perforation is formed. The first specimens with five open tremata are found at 7 mm, those with six open tremata at 15 mm, and those with seven open tremata at 24 mm.

number of open holes for the European *H. tuberculata* Linnaeus, 1758. Linear breakpoint regression ( $r^2 = 0.69$ ) estimated the breakpoint at 5.5 open holes, corresponding to a size of approximately 33 mm, where the slope changes from 3.8 (SE = 0.53) to 0.0017 (SE = 0.56). The number of open tremata varies greatly within a species and between populations (Hemphill, 1907; Schepman, 1909; Sinclair, 1963; Talmadge, 1960; Geiger & Groves, 1999). Therefore, the notion that the number of open tremata or total number of tremata is fixed, is misleading. Taxa based solely on the number of open tremata have to be rejected as in the case of *H. multiperforata* Reeve, 1846 (note 32), or *H. cracherodii* Leach, 1814, with the subspecies *bonita* Orcutt, 1900, and *californiensis* Swainson, 1822. Specimens from some populations on Guadalupe Island off Baja California have the *H. cracherodii californiensis* morphology. These specimens have more and smaller tremata, which are also more closely spaced than in specimens from the mainland. Specimens with the *californiensis* morphology have been cultured on the mainland of central California and the size and spacing of the tremata changed to those of a typical *H. cracherodii cracherodii* (B. Owen, pers. comm.), indicating that these characters are under environmental control.

Imperforate abalone shells have been found (Smith, 1893; Marquand, 1906; Hemphill, 1907; Dall, 1919; Leighton, 1960; Geiger, pers. obs.; Figure 1-2), but are rather rare. Even rarer are specimens with a double row of tremata (Smith, 1888; Hamada, 1982). A somewhat larger number of specimens with a continuous slit instead of the row of tremata are known (*H. laevigata*: Gray, 1856; *H. asinina*, *H. cracherodii*, *H. parva* Linnaeus, 1758, *H. planata* Sowerby, 1882, *H. rufescens* Swainson, 1822, *H. tuberculata*: Geiger, pers. obs.). New tremata are formed at the anterior margin of the shell, and posteriorly the mantle eventually seals them when they are no longer used. Occasionally one to several tremata are closed out of the sequence just described



Figures 1-2 - 1-5. Shells of imperforate specimen and potential hybrid of *Haliotis brazieri* x *hargravesi*. 1-2. *H. cf. diversicolor* Reeve, 1846. 28 mm. MNHN [not numbered]. No locality data. An imperforate specimen of *Haliotis*. 1-3. *H. brazieri* - *hargravesi*. 31 mm. K. A. Stewart collection. Solitary Island, Coffs Harbour, New South Wales, Australia. This specimen begins growth with the smooth morphology of *H. brazieri*, but midway develops to the spiral ridges typical of *H. hargravesi*. 1-4 - 1-5. *H. brazieri* Angas, 1869. 29 mm. MHNG [not numbered]. Australia.

(Geiger, 1991: fig. 8; *H. parva*, *H. pulcherrima* Gmelin, 1791: Geiger, pers. obs.). Only in *H. elegans* Philippi, 1844, is this phenomenon found regularly and becomes the rule in large specimens (see Wilson, 1993: pl. 3, figs. 2A, 2B).

*Haliotis imperforata* Dall, 1919, *H. lusus* Finlay, 1927, and *H. holzneri* Hemphill, 1907, are based on imperforate type specimens. It is clear that these are teratological shells not warranting taxonomic recognition (note 66).

Three type specimens show further deformities. *Haliotis sieboldii* Reeve, 1846 (note 64) has been described from a distorted shell, in which the row of tremata is located abnormally close to the periphery of the shell. The same applies also to *H. whitehousei* (Colman, 1959) (note 55), although the distortion is not as pronounced as in *H. sieboldii*. This type of a deformation is also known from some specimens of *H. cracherodii* (LACM 23452; SBMNH 13522; USNM 199890). *Haliotis diegoensis* Orcutt, 1900 (note 65) has an extremely thick and stout shell, a growth form that had been induced by boring organisms, most likely sabellid polychaetes.

## **Hybrids**

The occurrence of hybrids may be challenging to the biological species concept, but can be better understood from the standpoint of the evolutionary species concept. As long as the two species that hybridize keep their identity, they remain intact; otherwise a case of reticulate speciation is found (*cf.* Wiley, 1981). When discussing hybrids, it is assumed at the outset that the two parent specimens belong to two discrete species, which may not be the case. We may also have a case of unrealized intraspecific variability of a single species.

Hybridization among the Californian species is well established and has been studied on the basis of the shell, the epipodium, and by using immunological techniques.

The hybrid specimens with intermediate shell and epipodial characters occurred with a frequency of approximately 1:500 (Owen *et al.*, 1971). These authors also found evidence for back crosses of hybrids with some of the parental species, demonstrating that the F1 hybrids are fertile. These results were later corroborated by laboratory rearings (Leighton, 1988). The identity of the recognized species was confirmed with DNA sequence data (Lee & Vacquier, 1992; 1995). Although hybrids involving *H. cracherodii* were successfully reared in the laboratory (Leighton, 1988), they are markedly absent in the field, but this can be accounted for by two factors. First, *H. cracherodii* has an entirely smooth and uniformly black shell, whereas all the other California species show some sculpture and may have a color pattern in the shell. As it is much more difficult to generate a new character (sculpture, color pattern), than to modify an existing one, the simple condition in *H. cracherodii* prevails in hybrid specimens. This condition is termed ‘overshadowing effect.’ Second, *H. cracherodii* is the only Californian abalone found in the intertidal region. The species is ecologically separated from the remaining species. Within the remaining six Californian species, 13 of the 15 possible hybrid combinations have been documented (Talmadge, 1977b; Leighton, 1988). The two missing hybrids both involve *H. fulgens* Philippi, 1845, which has been shown in the phylogenetic analysis of DNA sequence data to be slightly more distantly related to the other California species (Lee & Vacquier, 1995). Pre-fertilizing barriers (analogous to pre-mating barriers in broadcast spawners), such as spawning season and vertical distribution of the species, have to be taken into account. Unfortunately, no information on the fertility of F2 and backcross specimens is available, although many profound changes affecting the fertility may take place after the F1 generation (see King, 1993 for review).

In a second case, two Australian species *H. laevigata* and *H. rubra* Leach, 1914, form hybrids that occur in nature (Anonymous, 1973; R. Fallu, pers. comm.). These

two species are well-known and have been shown to be distinct species (Brown, 1993; Lee & Vacquier, 1995). In this case, hybrids have been identified on the basis of enzyme electrophoresis data. The hybrids occur in varying frequency between 0% and 2% in several populations studied. Good evidence has been presented for the presence of backcrosses of hybrids with either parental species. The hybrids are not believed to represent a starting point of reticulate speciation because of the different habitat requirements of the two species, which is strongly reflected particularly in the thickness of the shell (Shepherd, 1973; Brown, 1995).

Hybrids are reported from two sympatric populations of the two subspecies of *H. discus* Reeve, 1846, *H. discus discus* and *H. discus hannai* Ino, 1952 (Fujino *et al.*, 1980; Sasaki *et al.*, 1980). Although a case of sympatric subspecies may seem a contradiction in terms, it can be seen as a necessary step of gradual, sympatric speciation (see Futuyma, 1986). As the two subspecies are very difficult to distinguish, enzyme electrophoresis was used to identify them with polymorphic loci of several enzymes. Later the same data and method were used to identify hybrids between these two taxa. It is not clear whether there was rather extensive variability in one biological species, or whether true hybrids were found; no data on the identification of the specimens studied using alternative methods had been mentioned.

Yet another case is the least clear and has not been discussed in the literature to date. It involves the following taxa from south eastern Australia: *H. brazieri* Angas, 1869, *H. ethologus* (Iredale, 1927), *H. hargravesi* Cox, 1869, and *H. melculus* (Iredale, 1927), all uncommon to rare. I regard *H. melculus* as a synonym of *H. brazieri*, and *H. ethologus* a synonym of *H. hargravesi* (notes 62, 66, and 72). Spiral ribs showing extensive intraspecific variation in respect to number and elevation are found on the dorsal side of the shell of *H. hargravesi*. *Haliotis brazieri* (Figures 1-4 - 1-5) has no spiral

sculpture at all, only an uneven but smooth surface. Intergrading specimens, *i.e.*, potential hybrids, show slight spiral grooves, which, however, are much less distinct than any form within the range of *H. hargravesi*. Some specimens are known in which the early whorls lack spiral cords, but on the body whorl such ridges appear abruptly (Figure 1-3). These patterns suggest a highly variable species with a few conchological forms, which would not warrant taxonomic separation.

M. Jones (pers. comm.) noted that *H. brazieri* and *H. hargravesi* are separated by their vertical distribution. *Haliotis brazieri* occurs from the lower reef surface to 40 m and *H. hargravesi* from 40 m downwards of the slope of the reef, where they can be found under coral heads and boulders. Coleman (1981:86) confirmed a deep water habitat (“15 to 40 m”) of *H. hargravesi* as compared to other abalone species, though the depth range indications of these two sources do not overlap. Hybrids are most often found around 40 m, the depth where the vertical ranges of the two species overlap. On one occasion a *H. brazieri* and a *H. hargravesi* were found under the same boulder. The epipodium of the hybrid specimens showed intermediate characteristics (M. Jones, pers. comm.), though my own investigations show very little difference in the two taxa.

It is well known that abalone show gregarious spawning behavior (Murayama, 1935; Shepherd, 1986) and it is, therefore, not too difficult to imagine hybrids being formed under the circumstances described above. Although Vacquier and co-workers (Vacquier *et al.*, 1990; Lee & Vacquier, 1992; 1995; Vacquier & Lee, 1993; Lee *et al.*, 1995) have demonstrated that the protein lysin in the head of the acrosomal vesicle in the head of the sperm strongly promotes species-specific fertilization, it does not fully prevent interspecific fertilization. Although no good data on the frequency of the Australian hybrids are available, it is evidently rather low. It is open to discussion whether we observe here a case of an erratic fertilization pattern of two distinct species, or whether two recently

diverged species still occasionally form hybrids, or whether we stand at the cradle of a reticulate speciation event.

## GENUS-LEVEL TAXA

A list of all supraspecific taxa of the family Haliotidae is given in Table 1-1. Some comments are warranted on a few taxa and are given here.

### *Haliotis, sensu stricto*

The subsequently designated type species (Montfort, 1810) of the genus *Haliotis*, *H. asinina*, has been accepted by the majority of authors (*e.g.*, Iredale, 1910; Kennard *et al.*, 1931; Wenz, 1938; Talmadge, 1963a; Ubaldi, 1985; 1993). Other species have been cited as type species, but these are erroneous (*e.g.*, Cossmann, 1918: *H. tuberculata*. Thiele, 1931; Cotton, 1943; Cox, 1962: *H. midae* Linnaeus, 1758. Children *vide* Kennard *et al.*, 1931: *H. iris* Gmelin, 1791). The type designation by Montfort (1810) was unfortunate, as the most atypical species within the family was chosen as the type species. The two presumed type specimens of *H. asinina* are held in the LS, and correspond with what is currently known as this species. The type locality has been designated as Amboina (= Ambon), Indonesia (Talmadge, 1963a). Cotton (1943:176) discussed the status of *H. asinina* as type species and following Adams & Adams (1853-1858) stated “that *asinina* is the genotype of the *Haliotis* of Montfort 1810 and not of the true *Haliotis* Linnaeus 1758,” a statement in contradiction with the original text. Montfort (1810:115) only introduced *Padollus* as a new genus: “... nous avons cru pouvoir en former un genre particulier” (... we have thought to be able to form from it a distinct genus). A similar statement cannot to be found with *H. asinina*, which is only designated as type of the genus *Haliotis* on page 120: “Sous la dénomination d’oreille

Taxon	Valid type species	Original type species (if different)
<i>Euhaliotis</i> Wenz, 1938	<i>midae</i> Linnaeus, 1758 [od]	
<i>Eurotis</i> Habe & Kosuge, 1964	<i>tuberculata</i> Linnaeus, 1758 [m]	
<i>Exohaliotis</i> Cotton & Godfrey, 1933	<i>cyclobates</i> Péron & Lesueur, 1816 [m]	
<i>Haliotis</i> Linnaeus, 1758	<i>asinina</i> Linnaeus, 1758 [sd: Montfort, 1810]	
<i>Marinauris</i> Iredale, 1927	<i>brazieri</i> Angas, 1869	<i>melculus</i> Iredale, 1927 [sd: Wenz, 1938]
<i>Miohaliotis</i> Itoigawa & Tomida, 1982	<i>amabilis</i> Itoigawa & Tomida, 1982 [m]	
<i>Neohaliotis</i> Cotton & Godfrey, 1933	<i>scalaris</i> Leach, 1814 [od]	
<i>Nordotis</i> Habe & Kosuge, 1964	<i>gigantea</i> Gmelin, 1791 [od]	
<i>Notohaliotis</i> Cotton & Godfrey, 1933	<i>rubra</i> Leach, 1814	<i>naevosa</i> Martyn, 1784 [od]
<i>Ovinotis</i> Cotton, 1943	<i>ovina</i> Gmelin, 1791 [od]	
<i>Padollus</i> Montfort, 1810	<i>parva</i> Linnaeus, 1758	<i>rubicundus</i> Montfort, 1810 [m]
<i>Paua</i> Fleming, 1952	<i>iris</i> Gmelin, 1791 [m]	
<i>Sanhaliotis</i> Iredale, 1929	<i>varia</i> Linnaeus, 1758 [od]	
<i>Schismotis</i> Gray, 1856	<i>laevigata</i> Donovan, 1808	<i>excisa</i> Gray, 1856 [not available]
<i>Sulculus</i> Adams, & Adams 1854	<i>tuberculata</i> Linnaeus, 1758	<i>incisa</i> Reeve, 1846 [sd: Cossmann, 1918]
<i>Teinotis</i> Adams & Adams, 1854	<i>asinina</i> Linnaeus, 1758 [m]	
<i>Tinotis</i> Fischer, 1885	<i>asinina</i> Linnaeus, 1758 [obj. syn. of <i>Haliotis</i> ]	
<i>Usahaliotis</i> Habe & Kosuge, 1964	<i>cracherodii</i> Leach, 1814 [m]	

Table 1-1. Genus-level taxa in the family Haliotidae. Abbreviations: od = original designation; m = monotypy; sd = subsequent designation.

de mer, tous les anciens conchyliologues avoient déjà reconnu ce genre ... . Nous avons choisi pour type, au lieu de l'haliotide commun (*haliotis vulgaris*, *haliotis tuberculata* [*sic*]), celui auquel on a donné le nom d'oreille d'âne" (Under the name of ear of the sea, all the old conchologists have already known this genus ... . We have chosen as type, instead of the common abalone (*Haliotis vulgaris*, *Haliotis tuberculata*), the one, for which one has given the name of donkey's ear [*H. asinina*]). Montfort clearly designated the type species of Linnaeus' *Haliotis*, and not a monospecific genus for *H. asinina* because two other taxa are included under *Haliotis*. The fact that a common name is used in the text of the designation (see ICZN Article 12c) does not invalidate it. Montfort (1810:119) used the following titles for the description of the species: "*Espèce servant de type au genre. Haliotide orielle d'ane. Haliotis asininus.*" (Species serving as type of the genus. Haliotid donkey's ear. *Haliotis asininus*). First, the type species is clearly designated, and second, the association between common name and scientific name is unequivocal.

The name *Haliotis* stems from the two Greek words *halios* (the sea) and *ous*, *otis* (the ear). The gender of the genus is feminine because Linnaeus used the feminine ending for the species-level taxa derived from an adjective, particularly for *H. asinina*, the type species of the genus by subsequent designation of Montfort (1810).

### **Other genus-level taxa, and their type species**

One objective synonym of *Haliotis* has been introduced, *i.e.*, a taxon that is based on the same type species, *H. asinina*: *Teinotis* Adams & Adams, 1854. Note that *The Genera of Recent Mollusca* by Adams & Adams (1853-1858) has as an inside cover publication date 1858, but in Vol. 2:661 the actual publication dates of the various parts

were indicated. For part 14 on Haliotidae, June 1854; therefore, this latter is the correct date for Adams & Adams' abalone taxon.

The genus *Padollus* Montfort, 1810, with the type species by monotypy, *P. rubicundus* Montfort, 1810 (*non H. rubicunda* Röding, 1798: see note 20), is problematic. *Haliotis scalaris* (Leach, 1814) has been listed as the type species of *Padollus* (e.g., Knight *et al.*, 1960; Wagner & Abbott, 1978; Lindberg, 1992:16), but *P. rubicundus* Montfort is a synonym of *H. parva* and not of *H. scalaris* (see note 20); therefore, the valid type species for *Padollus* is *H. parva*. The fact that the type species in the original description of *Padollus* is no longer invalid does not invalidate the description (ICZN Recommendation 67B). *Haliotis rubicunda* (Montfort) can be unequivocally identified and the senior synonym is the correct, valid type species.

*Neohaliotis* Cotton & Godfrey, 1933, has been synonymized with *Padollus* on the basis of having the same type species: *H. scalaris* (see above: Pickery, 1991). However, as I have shown that *H. rubicundus* Montfort is not a synonym of *H. scalaris* but of *H. parva*, the synonymy of *Neohaliotis* with *Padollus* has to be rejected.

The type species of *Sulculus* Adams & Adams, 1854, is *H. incisa* Reeve, 1846, which is a synonym of *H. tuberculata* (see also note 16). As *H. tuberculata* has also been chosen as the type species of *Eurotis* Habe & Kosuge, 1964, the latter is now a subjective, junior synonym of *Sulculus*.

Most genus-level taxa had their type species designated by the original author. Designations made in the 19<sup>th</sup> century may not meet modern conventions for designation of a type species in respect to the specificity of the language used. However, I (unlike Fleming, 1952) interpret “explicitly designated” (ICZN Article 67b) somewhat more generously.

Adams & Adams (1853-1858) gave the genus name, followed by its diagnosis and the mention of one particular species as “*Ex.*” (example = type species). This example cannot be confused with the species considered to belong in that genus, which were listed further below in smaller print and in two columns. This form had been utilized for all the genera (*Haliotis* Linnaeus, *Teinotis* H. & A. Adams, *Padollus* Montfort), but not for the subgenus *Sulculus*, for which no example was given. I consider this construction as an explicit designation (ICZN Article 67b), which cannot be confused with the exception mentioned under ICZN Article 67c1 (“mention of a species as an example of a genus or subgenus”) in conjunction with the example that follows in the Code. The narrow reading of the word “example” should not obscure the clear intentions of the authors. Fleming (1952) did not accept the designation for *Teinotis* and attributed the subsequent designation to Cossmann (1918).

*Marinauris* was described by Iredale (1927) without any perceptible intention to designate either *M. melculus* or *M. ethologus* as the type species; the genus was introduced in an extremely casual form. Fleming (1952:229) made claims for the designation (“Type (here designated)”), but had overlooked the clear designation by Wenz (1938:172).

*Schismotis* Gray, 1856, has been listed by some authors (Pickery, 1991; Ubaldi, 1993). Gray did not intend to introduce a new name for the specimens he discussed as monstrosities of *H. albicans* Quoy & Gaimard, 1834 (= *H. laevigata*), but only indicated a suitable, hypothetical name. The name is a *nomen nudum* and is not available (see also note 70).

*Haleotis* Binkhorst, 1861, has been cited as an objective synonym of *Haliotis*, *i.e.*, is treated as an available emendation of *Haliotis* (*e.g.*, Knight *et al.*, 1960). An emendation according to ICZN 33b(i) and 33b(iii) must be “demonstrably intentional,” other-

wise it is an incorrect subsequent spelling (ICZN 33c), which is not available. No intent by the author to change the original spelling can be found; the name is unavailable. *Tinotis* Fischer, 1885, however, is available as a clear intent to change the name is given (Fischer, 1885:845): “*Tinotis* H. et A. Adams, *em.* (*Teinotis*).” It is an objective synonym of *Haliotis*.

### **Use of genus-level taxa**

Some authors (*e.g.*, Talmadge, 1963a; Habe & Kosuge, 1964; Hara & Fujio, 1992) have used several genera in the family Haliotidae. Pickery (1991) provided a list and all references for the Recent taxa, which have been ranked as genera or subgenera (Table 1-1). As pointed out recently (Geiger, 1996), I consider the usage of these genera to be unjustified at this time for the following reasons:

1) In the descriptions of the one fossil (Itoigawa & Tomida, 1982) and the 17 Recent supraspecific taxa, only the type species had been assigned, occasionally with selected species. Of the 200 species-level taxa only approximately 83 have ever been assigned to any supraspecific taxon, and 22 of those to more than one group, demonstrating the problematic supraspecific taxonomy of haliotids. The descriptions of these genus-level taxa are entirely typological and no author has attempted to provide serious differential diagnoses.

2) Only two studies have utilized systematic methods other than shell morphology to determine the relationships of abalone species. Brown (1993) studied 17 species using enzyme electrophoresis and Lee & Vacquier (1995) used cDNA sequences of the sperm acrosomal protein lysin (see Vacquier & Lee, 1993 for review) of 22 haliotids. The nominal supraspecific taxa and the limited number of associated species are not in accordance with the groups hypothesized by these more recent studies. However, the

type species of *Haliotis*, *H. asinina* (see above for discussion), was not included in either study, making any sound taxonomic decisions impossible.

3) The only inferable consensus in the literature (McLean, 1966:151-153; Lindberg, 1992) as well among abalone researchers (Workshop “Evolutionary Biology and Genetics of Abalone” during the Second International Symposium on Abalone Biology, Fisheries and Culture, February 1994, Hobart, Tasmania) was not to use any genus-level taxa other than *Haliotis*. Yet there was an equally, strong consensus among the workshop participants that the diversity within the family may well justify the recognition of several genus-level taxa. However, monophyletic groups will have to be determined from a phylogenetic study treating the majority of all abalone species.

## **SPECIES-LEVEL TAXA**

### **Use of subspecies**

Subspecies are defined as allopatric populations with a fixed character (Futuyma, 1986). They do not yet represent discrete, evolutionary lineages. Interbreeding at the periphery of these populations is not necessarily a sign of the erroneous application of the subspecific classification, but may show that the populations are not yet independent species or discrete lineages. Only in very few shallow-water, broadcast-spawning gastropods have subspecies been described, but in *Haliotis* these have been invoked a number of times (Lindberg, 1992), *i.e.*, in the following groups: *H. discus*, *H. mariaae* Wood, 1828, *H. pustulata* Reeve, 1846, *H. rubra*, *H. scalaris*, *H. tuberculata*, *H. varia*, *H. virginea* Gmelin, 1791, and the populations of Californian abalone occurring on Guadalupe Island off Baja California, Mexico. In most cases the subspecific division is found along a temperature gradient; *i.e.*, subspecies are described from different latitudes and not from different longitudes. Most continental coast lines run in a north-

south direction, which may explain the above observation. The exceptions to the north-south pattern are two southern Australian species, *H. scalaris* and *H. rubra*. On the other hand, the Indo-Malayan Archipelago offers rich opportunities for the development of isolated populations, but no subspecies have been proposed for species with a wide east-west range such as *H. asinina* (Thailand - Fiji), *H. clathrata* Reeve (East Africa - Samoa), *H. ovina* (Maldives - Tonga), or *H. planata* (Thailand - Fiji).

In *H. discus*, the karyotypes differ between the two subspecies (Nakamura, 1985), although their populations interbreed at their common boundary (reviewed in Fujino, 1992). In this case the two taxa are more likely to represent subspecies than ecomorphs.

The two formerly recognized subspecies of *H. tuberculata*—*H. tuberculata tuberculata* and *H. tuberculata lamellosa* Lamarck, 1822—have identical caryotypes (Colombera & Tagliaferri, 1983) and have been recently shown to have identical sequences of the lysin protein (Lee & Vacquier, 1995; see also note 5).

In New Zealand, four geographically separated subspecies of *H. virginea* Gmelin are reported (note 60): *H. virginea virginea*, *H. virginea crispata* Gould, 1847, *H. virginea morioria* Powell, 1938, and *H. virginea huttoni* Filhol, 1880 (Kaicher, 1981; Ubaldi, 1986). These subspecies show gradual changes in several morphological characters used to distinguish them due to environmental parameters associated with geographical location based on field observations as well as collection records (Talmadge, 1957a). M. Jones (pers. comm.) has found some other forms on the very remote islands off New Zealand that seem to be more stable and distinct than the subspecies mentioned above. In these two cases the described subspecies seem to be ecomorphs not justifying taxonomic separation. However, as no hard data is available, and because they are widely used, the subspecies of *H. virginea* are conservatively retained.

None of the Californian subspecies is retained because those cases for which data is available (*H. cracherodii californiensis*, *H. corrugata diegoensis*: see above and note 65) have been shown to be mere ecomorphs or teratological specimens. One former species has been allocated at the subspecies rank (*H. kamtschatkana assimilis* Dall, 1878: see McLean, 1966; Owen *et al.*, 1971; note 67).

Two pairs of subspecies are found in southern Australia. These are separated along an east-west axis: the eastern *H. r. rubra* with the western *H. rubra conicopora* Péron, 1816 (see note 53), and the eastern *H. scalaris emmae* Reeve, 1846, with the western *H. s. scalaris* (see note 56). Information other than shell morphology (Shepherd, 1973; Brown, 1993) suggests one polymorphic species in both instances. However, the shells can be distinguished reasonably well and the geographic distribution of the morphs is more or less disjunct. The available data suggests subspecies status of the respective populations.

Due to the limited information currently available, the last three cases are provisionally studied as follows: *H. mariae dentata* Jonas, 1846, is easily recognized by the deep furrows resulting in the denticulated anterior margin of the shell, which are missing in the nominate subspecies. The biogeographical data on the species is scant. No assessment of geographic variation is possible. I retain the two subspecies of *H. mariae*.

*Haliotis pustulata cruenta* Reeve, 1846, has a reddish coloration, a very flat shell, and is found particularly in the Red Sea. *Haliotis pustulata pustulata* on the other hand is more sculptured, usually dark green to mud-colored, and is found along the east African mainland. There are no striking differences between the animals, and molecular data on the two morphs is not yet available. I retain the two subspecies tentatively. However, as their relation to *H. rugosa* Lamarck, 1822, is currently unresolved (see note

12), they may eventually be treated as subspecies of *H. rugosa* or may be united in a single species without further division into subspecies.

For *H. varia*, seven subspecies are regularly found in the literature, but none are recognized here. As the name suggests, this species is extremely variable. I have been unable to find any geographic pattern and intermediate specimens abound. These taxa are clear results of typological thinking of the 19<sup>th</sup> century.

## **Index**

In this section I give my opinion of the taxonomic status of every taxon of Recent abalone. Spelling mistakes, erroneous dates, and incorrect taxon-author combinations have not been included, unless widespread confusion exists. Controversial opinions and new assessments of the taxonomic status of various taxa are indicated in the “Notes” that follow. The notes are arranged according to their appearance in the section “Valid Species by Faunal Region” below, *i.e.*, they are grouped by valid species.

The two most recent, but brief, taxonomic assessments of the family Haliotidae were provided by Wagner & Abbott (1978) and Kaicher (1981). All differences between the present study and the opinion of these authors are listed in Table 1-2.

An analysis of all the species-level taxa reveals that only 27% of described taxa are still considered valid species. The status of the subspecies (5%) is very much debated, because the unit of a subspecies is somewhat vaguely defined as a geographically limited population with a certain character, raising the percentage of all valid taxa to slightly less than one third (see also discussion below). Taxa that had originally been described as either forms or varieties are excluded from modern taxonomy and represent what we generally call ecomorphs. I do not use Latin form names in an informal fashion (*contra* Reid, 1996), as all available evidence for abalone suggests that such taxa do not consti-

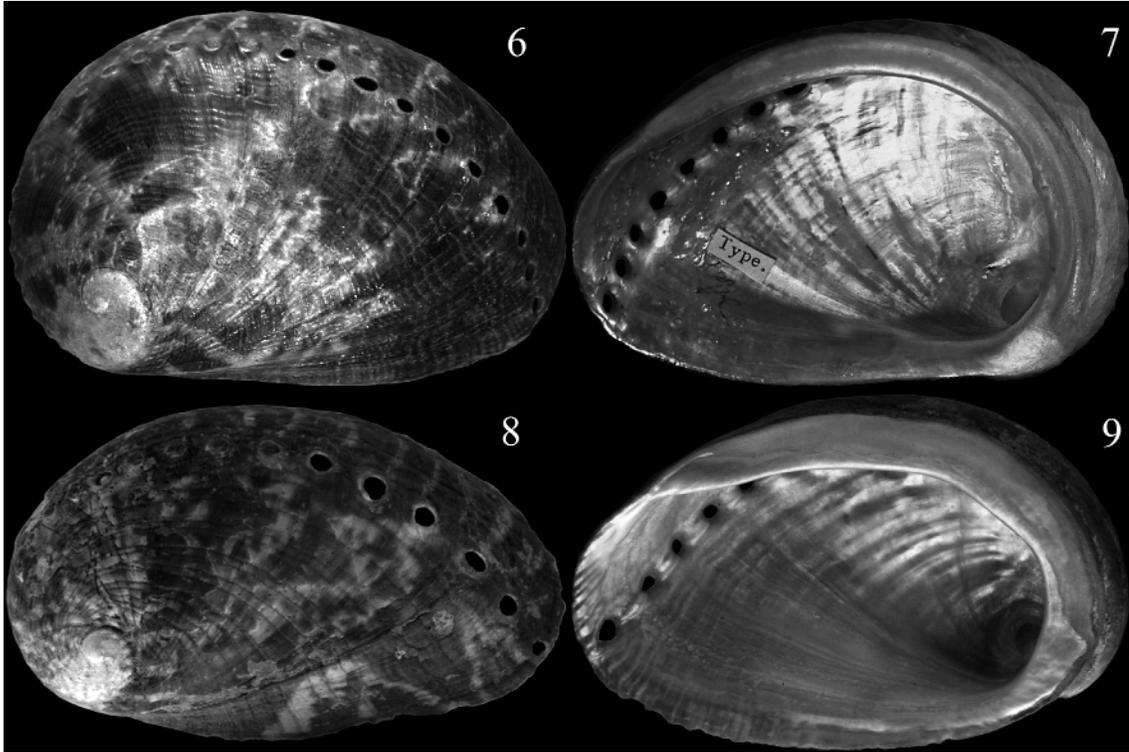
Table 2. Differences between the valid taxa of this study with their status in Wagner & Abbott (1978) and illustrations in Kaicher (1981). Subspecies rank is indicated by indentation under the respective species. The following epithets were regarded as valid by Wagner & Abbott (1978), but are here variously synonymized (see Index for details): *canariensis*, *dringii*, *gibba*, *hanleyi*, *howensis*, *japonica*, *kraussi*, *tuberculata lamellosa*, *melculus*, *multiperforata*, *sulcosa*, *vixlirata*, *whitehousei*. Forms listed by Kaicher (1981) have been ignored unless specifically indicated. The following epithets shown by Kaicher (1981) are either variously synonymized here, or were illustrated by specimens that cannot be identified (see Index for details): *bistriata*, *corrugata oweni*, *disona*, *elevata*, *gemma*, *multiperforata*, *sepiculata*, *whitehousei*.

This study	Wagner & Abbott (1978)	Kaicher (1981)
<i>brazieri</i> Angas, 1869	<i>brazieri</i>	also as <i>melculus</i>
<i>cracherodii</i> Leach, 1814	<i>cracherodii</i>	including all ssp.
<i>clathrata</i>	as <i>rubra clathrata</i>	also as <i>crebrisculpta</i> auct and <i>venusta</i>
<i>diversicolor</i> Reeve, 1846	not mentioned	also as <i>aquatilis</i> and all ssp
<i>dohrniana</i> Dunker, 1863	“no information”	<i>dohrniana</i>
<i>planata</i> Sowerby, 1882	<i>planata</i>	also as <i>grayana</i>
<i>hargravesi</i> Cox, 1869	<i>hargravesi</i>	also as <i>ethologus</i>
<i>jacnensis</i> Reeve, 1846	<i>jacnensis</i>	also as <i>hanleyi</i>
<i>kamtschatkana</i> Jonas, 1845	<i>kamtschatkana</i>	also as <i>aulaea</i>
<i>assimilis</i> Dall, 1878	<i>assimilis</i>	<i>assimilis</i>
<i>mariae dentata</i> Jonas, 1846	not mentioned	<i>mariae dentata</i>
<i>madaka</i> (Habe, 1977)	not mentioned	not mentioned
<i>marmorata</i> Linnaeus, 1758	undetermined species	as <i>guineensis</i>
<i>ovina</i> Gmelin, 1791	<i>ovina</i>	shows <i>cyclobates</i>
<i>pustulata</i> Reeve, 1846	<i>pustulata</i>	also as <i>revelata</i>
<i>cruenta</i> Reeve, 1846	not mentioned	<i>cruenta</i>
<i>roei</i> Gray, 1826	<i>roei</i>	also as <i>sulcosa</i>
<i>rubiginosa</i> Reeve, 1846	synonym of <i>varia</i>	as <i>varia rubiginosa</i> , <i>howensis</i>
<i>rubra</i> Leach, 1814	<i>rubra</i>	also as <i>ancile</i>
<i>conicopora</i> Péron, 1816	<i>conicopora</i>	<i>conicopora</i>
<i>rugosa</i> Lamarck, 1822	synonym of <i>tuberculata</i>	as <i>pustulata</i> form <i>alternata</i>
<i>scalaris emmae</i> Péron, 1816	<i>emmae</i>	<i>emmae</i>
<i>speciosa</i> Reeve, 1846	synonym of <i>fulgens</i>	<i>speciosa</i>
<i>squamosa</i> Gray, 1826	<i>squamosa</i>	<i>cf. diversicolor</i> shown
<i>stomatiaeformis</i>	<i>varia</i>	not mentioned
<i>tuberculata</i> Linnaeus, 1758	<i>tuberculata</i>	also as <i>lamellosa</i>
<i>coccinea</i> Reeve, 1846	<i>coccinea</i>	also as <i>zealandica</i>
<i>unilateralis</i> Lamarck, 1822	<i>unilateralis</i>	<i>varia</i> shown
<i>varia</i> Linnaeus, 1758	<i>varia</i>	also as <i>unilateralis</i> , <i>dringii</i> and ssp. <i>papulata</i> , <i>pustulifera</i> , <i>viridis</i>
<i>virginea</i> Gmelin, 1791	<i>virginea</i>	also as <i>gibba</i>
<i>crispata</i> Gould, 1847	as form of <i>virginea</i>	<i>crispata</i>
<i>huttoni</i> Filhol, 1880	as form of <i>virginea</i>	<i>huttoni</i>
<i>moria</i> Powell, 1938	as form of <i>virginea</i>	<i>moria</i>

tute discrete gene pools. The invalid taxa—synonyms (46%), homonyms (5%), *nomina dubia* (6%), *nomina nuda* (2%), ecomorphs (6%), unavailable names (3%)—account for over two thirds of all published species-level taxa.

The status of some taxa is still unclear; some may never be fully resolved due the loss of type material, or there is currently too little material available to make a definitive assessment. Unresolved cases are mentioned here. The type of *H. canaliculata* Fischer, 1907, was lost prior to 1872 (Ivanov & Kantor, 1991) and its synonymy with *H. parva* is uncertain (note 19). The following taxa can only be tentatively synonymized, because the type material remains to be located and the original description and/or illustration do not allow a clear assessment: *crenata* Swainson, 1822, *glabra* Swainson, 1822, *scutulium* Reeve, 1846 (notes 47, 48), *sepiculata* Reeve, 1846, and *sinuata* Perry, 1811 (note 22). Seven taxa cannot be identified and are treated as *nomina dubia*: *adriatica* Nardo, 1847, *bistriata* Gmelin, 1791 (notes 5, 14), *imperforata* Gmelin, 1791 (not Dall, 1919) (note 66), *interrupta* Valenciennes, 1831 (note 73), *parma* Valenciennes, 1831 (note 73), *plicata* Gmelin, 1791, and *rotundata* Perry, 1811 (note 22). The taxa *maculata* Küster, 1840 (note 18), *maculosa* Küster, 1840 (note 18), *modesta* auct. (note 75), *secernenda* Monterosato, and *schroeteri* Menke (note 76) are treated as *nomina nuda*, because they could not be traced to the original source. The deposited type specimen of *H. victoriae* Brazier is, in the absence of an original description, a *nomen nudum* (note 77). *Haliotis stomatiaiformis* Reeve, 1846 = *neglecta* Philippi, 1848 (Geiger & Owen, in prep.), is tentatively resurrected but the material available is very limited and restricted to a limited number of shells with some preserved animals (notes 5, 8, 9). *Haliotis exigua* Dunker, 1863, is tentatively retained as a valid species (note 63).

Lectotypes are here selected for two taxa: *H. multiperforata* Reeve, 1846 (note 32), and *H. revelata* Deshayes, 1863 (note 12). The figured type specimen of unknown prove-



Figures 1-6 - 1-9. Shells of designated lectotypes for *Haliotis multiperforata* and *H. revelata*. 1-6 - 1-7. *H. multiperforata* Reeve, 1846. 63 mm. BMNH. Mus. Cuming. Lectotype here selected. 1-8 - 1-9. *H. revelata* Deshayes, 1863. 58 mm. MNHN. Bourbon. Lectotype here selected.

nance of *H. multiperforata*, which is here designated as lectotype (Figures 1-6 - 1-7), is clearly a specimen of *H. rugosa* Lamarck (note 12), however, with rather weak spiral sculpture. The two other specimens in the lot are *H. tuberculata*. The number of open tremata of these specimens is somewhat higher than usual, but not beyond the expected and documented range of the latter species (data not shown). Consequently a taxonomic separation is not justified.

*Haliotis revelata* Deshayes, 1863, was described from Île de Bourbon (= Reunion Island). The MNHN holds three lots of type material of this species with a total of six specimens. One lot with a single specimen is labeled as “ex auteur,” another of three specimens is labeled as “syntypes,” and a third lot with two specimens is called “type.” From the labeling of the specimens, it is not clear which may be the holotype; therefore, all six specimens are presumed to be syntypes. Deshayes’ original illustrations (plate 36, figs. 1&2), were meticulously drawn, but cannot be matched to any of the shells in the MNHN. In fact, the illustrations do not resemble any of the species found on Reunion Island, which may be attributable to excessive artistic liberty. The rather long description lacks much necessary detail. Only two quantitative indications are of some help. The length of the largest specimen (61 mm) and the cited six open perforations are applicable to one specimen in the third lot, but this specimen has irregular growth on the columella that is clearly not illustrated or mentioned. The illustration shows only a weak growth line at the level of the penultimate hole, which is also found in the second specimens of the third lot. This specimen is here designated lectotype (Figures 1-8 - 1-9), and the remainder become paralectotypes. *Haliotis revelata* is identified as *H. rugosa* Lamarck, a species common at the type locality. The status of *H. rugosa* Lamarck itself is not resolved (see also note 12).

*Haliotis fatui* has only recently been validly described (Geiger, 1999a), based on an unpublished name of the late Dr. H. Rehder (USNM) given to specimens that somewhat resemble *H. varia* Linnaeus, 1758. Ubaldi (1993) listed *H. fatui* with the authority “Rheder [*sic*], 1981 ?”. This listing is a *nomen nudum* (see also note 71).

In the index that follows, the taxa with their status and/or the currently recognized valid species name are given. The taxa in bold are species currently recognized as valid species and subspecies with the original genus given if different from *Haliotis* s.s. The numbers in brackets refer to the notes that follow. Abbreviations: juv.: juvenile shell; *s.l.*: *sensu lato*; ssp.: subspecies; syn.: synonym; var.: variety, form; ?: uncertain statement (status, identification).

*adriatica* Nardo, 1847: *nomen dubium*

*albicans* Quoy & Gaimard, 1834: *laevigata* Donovan, 1808

*alfredensis* Bartsch, 1915: *speciosa* Reeve, 1846

*aliena* (Iredale, 1929) [in *Sanhaliotis*]: *varia* var. *papulata* Reeve, 1846

*aleata* Röding, 1798: *australis* Gmelin, 1791

*alternata* Sowerby, 1882: *rugosa* Lamarck, 1822 [31]

*ancile* Reeve, 1846: juv. *rubra* Leach, 1814 [52]

*aquatilis* Reeve, 1846: *diversicolor* Reeve, 1846

***asinina* Linnaeus, 1758: valid [4]**

*asinum* Donovan, 1808: *asinina* Linnaeus, 1758

***assimilis* Dall, 1878: ssp. of *kamtschatkana* Jonas, 1845 [67]**

*astricta* Reeve, 1846: var. of *varia* Linnaeus, 1758

*aulaea* Bartsch, 1940: *kamtschatkana assimilis* Dall, 1878 [67]

***aurantium* Simone, 1998 [1]**

***australis* Gmelin, 1791: valid**

*barbouri* Foster, 1946: *varia* Linnaeus, 1758 [1]

*bistriata* Gmelin, 1791: *nomen dubium*, *tuberculata* Linnaeus, 1758, *s.l.* [5, 14]

*bistriata* Costa, 1829: homonym, var., syn. of *tuberculata* var. *lamellosa* Lamarck,  
1822

*bisundata* Monterosato: *tuberculata* var. *lamellosa* Lamarck, 1822 [15]

*bonita* Orcutt, 1900: *cracherodii* var. *californiensis* Swainson, 1822

***brazieri* Angas, 1869: valid [34, 35]**

*caelata* Röding, 1798: *ovina* Gmelin, 1758

*californiana* Valenciennes, 1831: *rufescens* Swainson, 1822

*californiensis* Swainson, 1822: var., syn. of *cracherodii* Leach, 1814

*canaliculata* Fischer, 1807: *parva* Linnaeus, 1758 ? [19]

*canaliculata* Lamarck, 1822: homonym, *parva* Linnaeus, 1758

*canariensis* Nordsieck, 1975: *tuberculata coccinea* Reeve, 1846

*capensis* Dunker, 1844: *midiae* Linnaeus, 1758

*carinata* Swainson, 1822: *parva* Linnaeus, 1758

*cingulata* Röding, 1798: *parva* Linnaeus, 1758

*clathrata* Lichtenstein, 1794: *elegans* Philippi, 1844 [25]

***clathrata* Reeve, 1846: valid (homonym) [24, 25]**

***coccinea* Reeve, 1846: ssp. of *tuberculata* Linnaeus, 1758 [17, 18]**

***coccoradiata* Reeve, 1846: valid [49]**

*concinna* Reeve, 1846: *varia* Linnaeus, 1758

***conicopora* Péron, 1816: ssp. of *rubra* Leach, 1814 [53]**

*coreanica* Weinkauff, 1883: *nomen nudum* [68]

***corrugata* Wood, 1828: valid [26]**

*costata* Swainson, 1822: *australis* Gmelin, 1791  
***cracherodii* Leach, 1814: valid**  
***crebrisculpta* Sowerby, 1914: valid [25, 36]**  
*crenata* Swainson, 1822: *scalaris* Leach, 1814 ?  
***crispata* Gould, 1847: ssp. of *virginia* Gmelin, 1791 [60]**  
***cruenta* Reeve, 1846: ssp. of *pustulata* Reeve, 1846 [10]**  
*cunninghami* Gray, 1826: *rubra conicopora* Péron, 1816 [27, 53]  
***cyclobates* Péron, 1816: valid**  
***dalli* Henderson, 1915: valid [2]**  
*decussata* Philippi, 1850: *marmorata* Linnaeus, 1758 [7]  
***dentata* Jonas, 1846: ssp., var. of *mariae* Wood, 1828**  
*diegoensis* Orcutt, 1900: var. of *corrugata* Wood, 1828 [65]  
***discus* Reeve, 1846: valid [62]**  
***dissona* (Iredale, 1929) [in *Sanhaliotis*]: valid [36, 39]**  
***diversicolor* Reeve, 1846: valid [37]**  
***dohrniana* Dunker, 1863: valid [40]**  
*dringii* Reeve, 1846: *varia* Linnaeus, 1758 [45]  
*dubia* Lamarck, 1822: *nomen dubium* [69]  
*echinata* Sowerby, 1882: *jacnensis* Reeve, 1846 [31, 41]  
*elatior* Pilsbry, 1890: var. of *midiae* Linnaeus, 1758  
***elegans* Philippi, 1844: valid [23, 50]**  
*elevata* Sowerby, 1882: *squamata* Reeve, 1846 [31, 57]  
***emmae* Reeve, 1846: ssp. of *scalaris* Leach, 1814 [56]**  
*ethologus* (Iredale, 1927): *hargravesi* Cox, 1869 [34]  
*excavata* Lamarck, 1822: *cyclobates* Péron, 1816

*excisa* Gray, 1856: unavailable, *laevigata* Donovan, 1808 [70]

***exigua* Dunker, 1877: valid [63]**

*expansa* Talmadge, 1954: *cracherodii* Leach, 1814

***fatui* Geiger, 1999 valid [71]**

*ficiformis* Menke, 1844: *spadicea* Donovan, 1808

***fulgens* Philippi, 1845: valid**

*funbris* Reeve, 1846: *squamata* Reeve, 1846 [58]

*gemma* Reeve, 1846: *varia* Linnaeus, 1758 [46]

*gibba* Philippi, 1846: *virginea* Gmelin, 1791 [61]

*gigantea* Chemnitz, 1788: unavailable, *gigantea* Gmelin, 1791 [59, 64]

***gigantea* Gmelin, 1791: valid [64]**

*gigas* Röding, 1798: *gigantea* Gmelin, 1791

*glabra* Chemnitz, 1788: unavailable, *glabra* Gmelin, 1791 [59]

***glabra* Gmelin, 1791: valid**

*glabra* Swainson, 1822: homonym, *laevigata* Donovan, 1808 ?

*granti* Pritchard & Gatliff, 1902: *rubra conicopora* Péron, 1816 [53]

*granulata* Röding, 1798: *varia* Linnaeus, 1758

*grayana* Sowerby, 1882: *planata* Sowerby, 1882 [31]

*gruneri* Philippi, 1848: var., syn. of *diversicolor* Reeve, 1846

*guadalupensis* Talmadge, 1964: var. of *fulgens* Philippi, 1845

*guineensis* Gmelin, 1791: *marmorata* Linnaeus, 1758

*hanleyana* Sowerby, 1882: *nomen dubium* [31, 72]

*hanleyi* Ancey, 1881: *jacnensis* Reeve, 1846 [41]

***hannai* Ino, 1953: ssp. of *discus* Gmelin, 1791**

***hargravesi* Cox, 1869: valid [34, 35]**

*hattorii* Bartsch, 1940: var. of *rufescens* Swainson, 1822  
*holzneri* Hemphill, 1907: var. of *cracherodii* Leach, 1814 [66]  
*howensis* (Iredale, 1929) [in *Sanhaliotis*]: *rubiginosa* Reeve, 1846 [43]  
***huttoni* Filhol, 1880: ssp. of *virginea* Gmelin, 1791 [60]**  
*imperforata* Gmelin, 1791: *nomen dubium* [66]  
*imperforata* Dall, 1919: homonym, *cracherodii* Leach, 1814 [66]  
*improbula* Iredale, 1924: syn., var. of *rubra* Leach, 1814  
*incisa* Reeve, 1846: *tuberculata* Linnaeus, 1758 [16]  
*interrupta* Valenciennes, 1831: *nomen dubium* [73]  
*iridis* Karsten, 1789: unavailable, *iris* Gmelin, 1791 [74]  
***iris* Gmelin, 1791: valid [54]**  
***jacnensis* Reeve, 1846: valid [41]**  
*janus* Reeve, 1846: *tuberculata coccinea* Reeve, 1846 [17]  
*japonica* Reeve, 1846: *tuberculata* Linnaeus, 1758 [16]  
*jousseaumi* Mabille, 1888: *pustulata* Reeve, 1846 [11]  
***kamtschatkana* Jonas, 1845: valid [62, 67]**  
*kraussi* Turton, 1932: *parva* Linnaeus, 1758  
***laevigata* Donovan, 1808: valid**  
*lamellosa* Lamarck, 1822: var. of *tuberculata* Linnaeus, 1758 [5, 13]  
*latilabris* Philippi, 1848: *ovina* Gmelin, 1791 [8]  
*lauta* Reeve, 1846: *semiplicata* Menke, 1843 [49]  
*lucida* Requien, 1848: *tuberculata* var. *lamellosa* Lamarck, 1822  
*lusus* Finlay, 1927: var. of *cracherodii* Leach, 1814 [66]  
*maculata* Küster, 1840: *nomen dubium* [18]  
*maculosa* Küster, 1840: *nomen dubium* [18]

***madaka* (Habe, 1977) [in *Nordotis*]: valid [64]**

***mariae* Wood, 1828: valid [26]**

***marmorata* Linnaeus, 1758: valid [4, 5, 6]**

*marmorata* Reeve, 1846: homonym, *virginea* Gmelin, 1791

*melculus* (Iredale, 1927) [in *Marinauris*]: *brazieri* Angas, 1869 [35]

***midae* Linnaeus, 1758: valid [04]**

*modesta* auct.: *nomen nudum* ?, *midae* Linnaeus, 1758 [75]

***morioria* Powell, 1938: ssp. of *virginea* Gmelin, 1791 [60]**

*multiperforata* Reeve, 1846: *rugosa* Lamarck, 1822 [32]

*naevosa* Philippi, 1844: *rubra* Leach, 1814 [54]

*nebulata* Reeve, 1846: *rugosa* Lamarck, 1822 [33]

*neglecta* Philippi, 1848: *stomatiaeformis* Reeve, 1846 [5, 8, 9]

*nodosa* Philippi, 1845: *corrugata* Wood, 1828

***ovina* Gmelin, 1791: valid**

*oweni* Talmadge, 1966: var. of *corrugata* Wood, 1828

*papulata* Reeve, 1846: var. of *varia* Linnaeus, 1758

*parma* Valenciennes, 1831: *nomen dubium* [73]

***parva* Linnaeus, 1758: valid [4]**

*parva* Risso, 1826: homonym, *tuberculata* var. *lamellosa* Lamarck, 1822

*pellucida* von Salis, 1793: *tuberculata* var. *lamellosa* Lamarck, 1822

*pertusa* Reeve, 1846: *rugosa* Lamarck, 1822 [33]

*picta* Röding, 1798: *glabra* Gmelin, 1791

***planata* Sowerby, 1882: valid [42]**

*planilirata* Reeve, 1846: *fulgens* Philippi, 1845 [47]

*plicata* Karsten, 1789: unavailable, *australis* Gmelin, 1791 [74]

*plicata* Gmelin, 1791: *nomen dubium*

*ponderosa* Adams, 1848: *rufescens* Swainson, 1822

***pourtalesii* Dall, 1881: valid [1, 2, 3]**

***pulcherrima* Gmelin, 1791: valid**

***pustulata* Reeve, 1846: valid [12]**

*pustulifera* Pillsbry, 1890: *varia* Linnaeus, 1758

***queketti* Smith, 1910: valid**

*reticulata* Reeve, 1846: *tuberculata* Linnaeus, 1758 [16]

*revea* Bartsch, 1940: *fulgens*, *nomen nudum*

*revelata* Deshayes, 1863: *rugosa* Reeve, 1846 [12]

***roberti* McLean, 1970: valid [2]**

*roedingi* Menke, 1844: *squamosa* Gray, 1826 [29]

***roei* Gray, 1826: valid [27]**

*rosacea* Reeve, 1846: *marmorata* Linnaeus, 1758

*rosea* Orcutt, 1900: *cracherodii* Leach, 1814

*rotundata* Perry, 1811: *nomen dubium* [22]

*rubicunda* Röding, 1798: *parva* Linnaeus, 1758 [20]

*rubicunda* (Montfort, 1810) [in *Padollus*]: homonym, *parva* Linnaeus, 1758 [20]

***rubiginosa* Reeve, 1846: valid [43]**

***rubra* Leach, 1814: valid [25, 51]**

***rufescens* Swainson, 1822: valid**

***rugosa* Lamarck, 1822: valid [12]**

*rugosa* Reeve, 1846: homonym, *tuberculata* Linnaeus, 1758

*rugosoplicata* Chemnitz, 1788: unavailable, *australis* Gmelin, 1791 [59]

*rugosoplicata* Reeve, 1846: *australis* Gmelin, 1791 [59]

*sanguinea* Hanley, 1840: *spadicea* Donovan, 1808 [21]  
***scalaris* (Leach, 1814) [in *Padollus*]: valid [56]**  
*scabricostata* Menke, 1843: *roei* Gray, 1826  
*schroeteri* Menke: *nomen dubium* [76]  
*scutulum* Reeve, 1846: *varia* Linnaeus, 1758 ? [47, 48]  
*secernenda* Monterosato: *tuberculata* var. *lamellosa* Lamarck, 1822  
***semiplicata* Menke, 1843: valid**  
*semistriata* Reeve, 1846: *varia* Linnaeus, 1758  
*sepiculata* Reeve, 1846: *diversicolor* Reeve, 1846 ?, *tuberculata* Linnaeus, 1758 ?  
*sieboldii* Reeve, 1846: *gigantea* Gmelin, 1791 [64]  
*sinuata* Perry, 1811: *spadicea* Donovan, 1808 ? [22]  
*smithsoni* Bartsch, 1940: *kamtschatkana assimilis* Dall, 1878  
***sorenseni* Bartsch, 1940: valid**  
***spadicea* Donovan, 1808: valid [21]**  
***speciosa* Reeve, 1846: valid**  
*splendens* Reeve, 1846: *fulgens* Philippi, 1845  
*splendidula* Williamson, 1893: *cracherodii* Leach, 1814  
***squamata* Reeve, 1846: valid**  
***squamosa* Gray, 1826: valid [27, 28]**  
***stomatiaeformis* Reeve, 1846: valid [39]**  
*striata* Linnaeus, 1758: *tuberculata* var. *lamellosa* Lamarck, 1822 [4, 13]  
*strigata* Weinkauff, 1883: *marmorata* Linnaeus, 1758  
*subvirginea* Weinkauff, 1883: *virginea* Gmelin, 1791  
*sulcosa* Philippi, 1845: *roei* Gray, 1826  
*supertexta* Lischke, 1870: var., syn. of *diversicolor* Reeve, 1846 [38]

*tayloriana* Reeve, 1846: var., syn. of *diversicolor* Reeve, 1846  
*tricostalis* Lamarck, 1822 : *scalaris* Leach, 1814  
*tricostata* Wood, 1828: *scalaris* Leach, 1814  
***tuberculata* Linnaeus, 1758: valid [4, 5, 13]**  
*tubifera* Lamarck, 1822: *gigantea* Gmelin, 1791  
*turveri* Bartsch, 1940: var. of *fulgens* Philippi, 1845  
***unilateralis* Lamarck, 1822: valid [30]**  
***varia* Linnaeus, 1758: valid [4]**  
*varia* Risso: homonym, *tuberculata* var. *lamellosa* Lamarck, 1822 [4, 44]  
*venusta* Adams & Reeve, 1848: *clathrata* Reeve, 1846 [24]  
*victoriae* Brazier: *nomen nudum* ?, *rubra* Leach, 1814 [77]  
***virginea* Gmelin, 1791: valid [60]**  
*virginea* Reeve, 1846: homonym, *marmorata* Linnaeus, 1758  
*viridis* Reeve, 1846: *varia* Linnaeus, 1758  
*vixirata* (Cotton, 1943): *rubra conicopora* Péron, 1816 [53]  
*vulgaris* da Costa, 1778: *tuberculata* Linnaeus, 1758  
***walallensis* Stearns, 1898: valid**  
*whitehousei* (Colman, 1959) [in *Sanhaliotis*]: *rubra* Leach, 1814 [55]  
*zealandica* Reeve, 1846: *coccinea* Reeve, 1846 [17]  
*ziczac* Reeve, 1846: *glabra* Gmelin, 1791

## Notes

01. *Haliotis barbouri* Foster, 1945, has been a very controversial species. It was described from a single beach shell from the coast of Brazil. It has been hypothesized that it is either a distinct species or a mislocated specimen of either *H. pour-*

*talesii* Dall, 1881, from the Caribbean (Rios, 1975) or the only Polynesian species *H. pulcherrima* Gmelin, 1791 (Cox, 1962; Rios, 1985, 1994). *Haliotis barbouri* has not been treated in the discussion of Brazilian abalone by Simone (1998). Klappenbach (1968) mentioned a living specimen taken off Brazil, refuting the claim the species represents specimens left by tourists (*cf.* Cox, 1962). Specimens of *H. pourtalesii* have been indicated from the Gulf of Mexico to as far south as Venezuela and Brazil (Henderson, 1915; Foster, 1946; Aguayo & Jaume, 1947; Harry, 1966; Guice, 1968; Klappenbach, 1968; Sarasúa, 1968; Nijssen-Meyer, 1969; Titgen & Bright, 1985; Odé, 1986; Martinez & Ruiz, 1994). The more southern reports of *H. pourtalesii* including Klappenbach's (1968) live specimens can be attributed to confusion with *H. aurantium* (Simone, 1998).

Inspection of the type of *H. barbouri* (MCZ 152469) revealed its true identity as a somewhat aberrant form of *H. varia* Linnaeus, 1758. At a size of 22 mm it is a rather small specimen for the species. In general, small specimens of abalone tend to be rounder than larger ones (*cf.* Stewart & Geiger, 1999: fig. 4). Hence, based on the overall shape of the shell one may be led to place the type of *H. barbouri* in the vicinity of *H. pulcherrima*. However, the sculpture differs greatly. Most significantly, in *H. pulcherrima* a narrow spiral band adjacent to the row of tremata and towards the suture is found, which is devoid of oblique radial folds or other elevated shell structures. A similar structural element is present in *H. jacnensis* Reeve, 1846 (*cf.* Figure 1-16, note 41). In *H. varia* and the type of *H. barbouri* this bare space is not seen. The type of *H. barbouri* reminds one somewhat of the type specimens of *H. gemma* Reeve, 1846 (= *H. varia*: see note 46) in terms of size, rotundity and sculptural elements.

02. *Haliotis dalli* Henderson, 1915, and *H. roberti* McLean, 1970, are two small, insular species found offshore from Central America at the Galapagos Islands (*H. dalli*) and Cocos Island (*H. roberti*). The two species are fairly similar, but can be distinguished as indicated by McLean (1970). Radulae of both species share a very narrow lateral tooth 1 and concentric rings on the cephalic tentacles. These characters are shared only with *H. pourtalesii* Dall, 1881, and *H. aurantium* from Brazil (Simone, 1998), but are not seen in any of the other 30 abalone species studied so far (Geiger, pers. obs.).
03. The neotype of *H. pourtalesii* Dall, 1881, is now broken in many pieces. The original illustration of the neotype (Henderson, 1915: pls. 45-46) showed an intact shell.
04. At the time when Linnaeus (1758) introduced the first seven haliotids (*H. asinina*, *H. marmorata*, *H. midae*, *H. parva*, *H. striata*, *H. tuberculata*, *H. varia*), the concept of type specimens was not yet established. The LSL holds specimens in the collection, and I agree with Talmadge (1977a) that most correspond well with the current concept of the respective species; Talmadge (1977a) noted a single specimen of *H. tuberculata*, whereas I found six specimens with a note by S. P. Dance from 1963 also referring to six specimens. No specimens are currently designated as types. As indicated by Talmadge (1977a) there is no specimen of *H. parva* in the LSL. As it is a unproblematic species, a designation of a neotype is not necessary (ICZN Article 75b).
05. The *H. tuberculata*-group contains the following main taxa: *H. tuberculata* Linnaeus, 1758, *lamellosa* Lamarck, 1822, *coccinea* Reeve, 1846, *bistriata* Gmelin, 1791; this group may additionally contain *H. marmorata* Linnaeus, 1758 (*cf.* Talmadge, 1963a) (Figures 1-18 - 1-19) and *H. stomatiaformis* Reeve, 1846 (Figures 1-20 - 1-21). *Haliotis tuberculata* was the earliest to be named of the well-known taxa

in the group, hence the group name is attributed to this species. All the species are found in Europe and northwest Africa (Mediterranean, Brittany to São Tomé and Gabon, Canary Islands, Azores). cDNA analysis of the protein lysin (Lee & Vacquier, 1995) has shown, that *tuberculata* and *lamellosa* from the Mediterranean are the same species. The *tuberculata* and the *lamellosa* forms are usually found within one population (Geiger, pers. obs.). The taxon *lamellosa*, therefore, refers to a variety or ecomorph of *H. tuberculata*. The taxon *coccinea* was shown to be closely related to *H. tuberculata* (Lee & Vacquier, 1995). It differs from *H. tuberculata* in only four positions of the 132 amino acid sequence of lysin whereas most species differ in approximately 15-20 amino acid positions. Despite the small difference in amino acid sequence, the shells are readily distinguishable and *coccinea* is found only at the Canary Islands. The two conditions for a subspecific status for *H. tuberculata coccinea* are found: distinct character and specific geographic location. *Haliotis bistriata* seems to be a variation of *H. tuberculata*, *sensu lato*, based upon shell morphological observations (see note 14). *Haliotis marmorata* Linnaeus, however, seems to be distinct in terms of shell morphology (Figures 1-18 - 1-19), but neither anatomical characters nor biochemical data are available. Its status in relation to *H. tuberculata* remains unresolved.

06. The specimens labeled *H. marmorata* Linnaeus, 1758, are conspecific with what is best known as *H. rosacea* Reeve, 1846, which has been synonymized with *H. guineensis* Gmelin, 1791 (Talmadge, 1963b; Ubaldi, 1987) (Figures 1-18 - 1-19). Despite the possibility of exchange of material (K. Way, pers. comm.), three lines of evidence suggest that the specimens are likely to represent the species as described by Linnaeus: 1) Sowerby (1882) already indicated the synonymy between *H. marmorata* Linnaeus, *H. rosacea*, and *H. guineensis* (explanation to plate 11, figs. 88,

89); 2) some old specimens of this species labeled *H. marmorata* Linnaeus have been found in collections (e.g., DMNH 011036); 3) S. P. Dance stated on a label from 1963 that “from several undocumented shells I have selected one that matches specimens in Brit. Mus. (Nat. Hist.) labeled ‘*H. rosacea* Reeve.’ This is almost certainly the example mentioned by Hanley as present.” Therefore, the correct name for the continental west African species is *H. marmorata* Linnaeus. Talmadge (1977a), in his discussion of Linnean haliotids, erroneously synonymized *H. marmorata* Reeve (*non* Linnaeus) with *H. virginea* Reeve (*non* Gmelin). *Haliotis marmorata* Reeve is clearly *H. virginea* Gmelin from New Zealand and not *H. marmorata* Linnaeus (= *H. virginea* Reeve) from west Africa.

07. *Haliotis decussata* Philippi, 1850, was described in Philippi’s (1847-1851) third volume, with the date of the volume given as 1851. However, the pages with the description of *Haliotis* are dated April 1850, which is the correct date.
08. Philippi referred to figure 4 for his *H. latilabris* Philippi, 1848, and figure 5 for *H. neglecta* Philippi, 1848; this is obviously an error and one should consult figures 5 and 4 for these species, respectively. Pickery (1991) indicated 1851 as publication date, but the species were already described by Philippi (1848:16).
09. Philippi’s (1847-1851) *H. neglecta* Philippi, 1848, is a junior synonym of *H. stomatiaeformis* Reeve, 1846, as recognized by Sowerby (1882:27): “... *H. neglecta* of Philippi ... is undoubtedly identical with our present species [*H. stomatiaeformis*]” (see also note 39). Ubaldi (1987) indicated this species [as *H. neglecta*] as being distinct, occurring on islands close to Sicily, Malta and Lampedusa, but without illustrating any specimens. Some specimens, which correspond very well to the figured specimen have been located: one in MNHN (Sicily and Palermo), four in HUJ (6313a, b: Lampedusa and Giardini), one in DMNH (097371: near Malta Island),

and one in my personal collection (Malta: Figures 1-20 - 1-21); additional specimens were obtained by Buzz Owen (pers. comm.) and were made available for examination. *Haliotis tuberculata* Linnaeus, 1758, with the form *lamellosa* Lamarck, 1822, is the only native, well known, and highly variable species in the Mediterranean. *Haliotis stomatiaeformis* might just represent aberrant specimens of *H. tuberculata* (cf. Weber, 1928). However, the specimens I have seen, including two preserved animals, are very distinct and unlikely to be only a variation of *H. tuberculata*. I consider *H. stomatiaeformis* to be a valid species. Geiger & Owen (in prep.) will discuss this taxon in more detail. Geiger (1998a) erroneously synonymized *H. stomatiaeformis* with *H. squamata* Reeve, 1846.

Interestingly, a similar case is found in the Conidae. *Conus ventricosus* Gmelin, 1791, is the species predominantly living throughout the Mediterranean. In the Sicily Channel area *C. vayssieri* Pallary, 1906, is found (Villa, 1985), but this species has also been regarded as a mere form of *C. ventricosus* (Poppe & Goto, 1991).

10. *Haliotis pustulata* Reeve, 1846, migrated from the Red Sea into the Mediterranean Sea through the Suez Canal. It has been found along the Israeli coast (Talmadge, 1971; Fainzilber, 1984) and in Lybia (Giannuzzi-Savelli *et al.*, 1994). One alcohol-preserved specimen without the shell from Greece has an epipodium more or less identical to that of *H. pustulata* from the Red Sea. The epipodia of *H. pustulata* and *H. tuberculata* differ markedly. It is, therefore, possible that *H. pustulata* has advanced further into the eastern Mediterranean. The few reports in the literature of *H. pustulata* in contrast to other species—*e.g.*, *Strombus decorus* (Röding, 1798) (see *e.g.*, Fischer, 1993; Lindner, 1993)—may be due to the fact that the shells of *H. pustulata* often are not strikingly different from the native *H. tuberculata*.

11. The geographic provenance of *H. jousseaumi* Mabille, 1888, was not given in the original description (Mabille, 1888), but the label of the specimen held in the MNHN cites the Red Sea (“Mer Rouge”). The name has only been used once thereafter by Talmadge (1956), who correctly synonymized it with *H. pustulata* Reeve, 1846.
12. A lectotype for *H. revelata* Deshayes, 1863, is here selected (see main body of text, Figures 1-8, 1-9). The specimens are conspecific with what is better known as *H. rugosa* Lamarck, 1822. Herbert (1990) speculated about the synonymy between *H. pustulata* Reeve, 1846, and *H. rugosa*, which had already been indicated indirectly by Wagner & Abbott (1978) by the synonymization of *H. alternata* Sowerby, 1882, with *H. pustulata*. I have not seen any material that has intermediate characters and question the synonymy between the two taxa. The taxa *cruenta* Reeve, 1846, and *pustulata* may eventually be treated as subspecies of *H. rugosa*, pending further clarification based on animals of the these taxa, but I tentatively consider them as distinct species (*cf.* Herbert, 1990; Geiger, 1996).
13. *Haliotis striata* Linnaeus, 1758, belongs in the *H. tuberculata* Linnaeus, 1758 group (see note 5). I agree with Talmadge (1977a) that it corresponds with what is well known as *H. tuberculata* var. *lamellosa* Lamarck, 1822 (Figures 1-28 - 1-29). If *H. tuberculata* is a synonym of *H. lamellosa*, then *H. striata* is also a synonym of *H. tuberculata*. *Haliotis tuberculata* is preferred over *H. striata* as the valid name for the species because it is the established name. However, if a taxonomic distinction between *tuberculata* and *lamellosa* is desired, then *striata* has priority over *lamellosa*. Potentially, a suppression of *striata* would be advisable as already suggested by Pilsbry (1890:87).
14. Weber (1928) mentioned the extensive variability of *H. bistriata* Gmelin, 1791, from Tenerife, Canary Islands; some specimens correspond with its original descrip-

tion of *H. bistrinata*, some are typical *H. tuberculata* Linnaeus, 1758, and concluded that the two taxa are most likely conspecific. He did not mention *H. coccinea* Reeve, 1846, and possibly was synonymizing too much under one taxon (see also note 9). The taxon *bistrinata* is mostly encountered in the old literature, and a few specimens from old collections labeled *H. bistrinata* were be found in the BMNH and ANSP. Most of the specimens that show some resemblance to old illustrations (*e.g.*, Reeve, 1846: pl. 11, fig. 33) originated from the Canary Islands and the Azores. The specimens are characterized by strong radial groves and a flared aperture. A separation of *H. bistrinata* from other members of the *H. tuberculata* group (see note 5) cannot be accepted. The localities, illustrations, and specimens labeled as *H. bistrinata* do not show any coherent pattern. *Haliotis bistrinata* should be regarded as a growth form of either *H. tuberculata coccinea* for specimens from the Canary Islands and the Azores, or of *H. tuberculata* or *H. marmorata* in the case of specimens from the East Atlantic mainland. As *bistrinata* most likely refers to three different species-level taxa, I prefer to treat it as a *nomen dubium*, which further provides stability to nomenclature, because the populations from the Canary Islands are well known under the epithet *coccinea*.

15. *Haliotis bisundata* Monterosato is listed as a variety of *H. tuberculata* Linnaeus, 1758, in Priolo (1948) and Ghisotti (1964), but cannot be traced.
16. *Haliotis incisa* Reeve, 1846, *H. japonica* Reeve, 1846, and *H. reticulata* Reeve, 1846, are all reported from Japan. This type locality is doubtful and the type specimens look exactly like the Mediterranean *H. tuberculata* Linnaeus, 1758, as also indicated by Reeve (1846) and discussed in Dunker (1882), Weinkauff (1883), McLean (1966), and Kaicher (1981: card no. 2882). Weinkauff (1883:59) nevertheless reported for *H. japonica* similar specimens “without any doubt” from Japan,

but not giving the locality more credibility. In modern times no similar specimens have been mentioned from the well studied area of Japan. *Haliotis japonica* and *H. tuberculata* var. *lamellosa* Lamarck, 1822, have also been synonymized erroneously (Pilsbry, 1890:87) with *H. aquatilis* Reeve, 1846, this latter a synonym of *H. diversicolor* Reeve, 1846.

17. The epithet *coccinea* Reeve, 1846, is assigned as a subspecies of *H. tuberculata* Linnaeus, 1758. This is here established on the basis of cDNA sequencing data (Lee & Vacquier, 1995), distinct shell characters, and its isolated geographic occurrence on the Canary Islands (see also note 5). *Haliotis janus* Reeve, 1846, is a color form of *H. tuberculata coccinea* (Talmadge, 1958a).
18. *Haliotis maculata* Küster, 1840, and *H. maculosa* Küster, 1840 (spelling variations ?) are mentioned by Sowerby (1882:36, pl. 9) and Weinkauff (1883:83) as senior synonyms of *H. coccinea* Reeve, 1846. The name is based on figure 137 in Martini & Chemnitz (1769) (non-binominal), which shows very clearly an *H. tuberculata coccinea* (see note 17). The original source could not be traced, and Küster's taxa were not listed in Sherborn (1922; 1932). According to Weinkauff, Küster's name has priority over Reeve's, an opinion not followed here, because the citation of Küster's work cannot be located.
19. The type specimen of *H. canaliculata* Fischer, 1807, was lost prior to 1872 (Ivanov & Kantor, 1991). Fischer (1807) indicated the presence of a deep, spiral canal and a brownish shell with many spiral cords in this small species. These characters point toward *H. parva* Linnaeus, 1758, a species to which he did not refer. The synonymy is tentative.
20. *Haliotis rubicunda* (Montfort, 1810) has also been attributed erroneously to Gray (1826) (see also note 27). Gray clearly referred to Montfort. Montfort used this

species as type species for his genus *Padollus* and did not refer to any other author, which makes it likely to be a new taxon introduced by him and not *H. rubicunda* Röding, 1798 (synonym of *H. parva* Linnaeus, 1758). *Haliotis rubicunda* (Montfort) was inflected to the masculine by Montfort for his new genus *Padollus* (see Knight *et al.*, 1960; Pickery, 1991; also Schremp, 1981:1125). The type locality is the “African coasts.” The key feature of the species is the spiral ridge on the shell; a character seen only in *H. parva* among the African species (Iredale, 1927:334). *Padollus rubicundus* Montfort has also been put into synonymy with *H. scalaris* (Leach, 1814) (see also note 56), a species that, however, occurs only in Australian waters. Because *H. rubicunda* Röding and *P. rubicundus* Montfort refer to the same species, they must belong to the same genus, for which the species have to take the correct generic ending of the adjectival species name, causing *P. rubicundus* Montfort either way to become a secondary homonym. Note, that although *Padollus* is based on an invalid name, it does not make *Padollus* itself invalid.

21. *Haliotis sanguinea* Hanley, 1840, was reported to have been described in 1808 (cf. Muller, 1986), in the same year as the senior synonym *H. spadicea* Donovan, 1808. Muller (1986) discussed the date of publication of *H. sanguinea* at length and concluded it was actually described in 1840.
22. The descriptions of *H. rotundata* Perry, 1811, and *H. sinuata* Perry, 1811, given by Perry (1811: pl. 52) are very brief and general, and his figures are rather stylistic. Pilsbry (1890) listed both as unidentified species. The undulation of the apertural margin as well as the general shape of the shell of *H. sinuata* is reminiscent of *H. spadicea* Donovan, 1808.
23. *Haliotis clathrata* Lichtenstein, 1794, which has so far been considered a *nomen dubium* (Wagner & Abbott, 1978), would cause *H. clathrata* Reeve, 1846 to be an

invalid, junior, primary homonym. *Haliotis clathrata* Lichtenstein is discussed by Geiger (1998b) and identified as *H. elegans* Philippi, 1844. Geiger & Stewart (1998) have petitioned the International Commission on Zoological Nomenclature to suppress *H. clathrata* Lichtenstein so as to preserve *H. elegans* and *H. clathrata* Reeve. This position, pending decision by the Commission, is adopted here (ICZN Article 80).

24. *H. venusta* Adams & Reeve, 1848, has so far been considered distinct from *H. clathrata* Reeve, 1846, due to the absence of radial lamellae on the type specimens. Several characters can be observed on both series of type specimens of *H. clathrata* Reeve and *H. venusta* (1 holotype, 2 paratypes each in BMNH): 1) a pattern of approximately 4 of 5 faint growth lines followed by one stronger one; 2) tremata only slightly oval, but rather large in proportion to the shell; 3) all shells of orange and white color, despite some fading; 4) in both series, some specimens with spire fully visible in ventral position, some only partially; 5) numerous spiral cords; 6) usually three or four of these cords stronger than others; stronger cords regularly spaced between suture and row of tremata; 7) the Indo-Pacific type localities for both taxa: Baclayon, Island of Bohol, Philippines for *H. clathrata* Reeve, and Eastern Seas for *H. venusta*. The holotypes of *H. clathrata* Reeve is distinguished from *H. venusta* by the discrete, numerous radial lamellae. The lamellae of *H. clathrata* Reeve are formed along the stronger growth lines, *i.e.*, every four or five faint growth lines. The lamellae of *H. clathrata* Reeve represent elevated, strong growth lines in *H. venusta*, hence the two structures are homologous. Radial lamellae are known to appear randomly in populations of a single species of *Haliotis*. The best documented case is that of *H. tuberculata* Linnaeus, 1758, from the Mediterranean, where the lamellate form is well-known as *H. lamellosa* Lamarck, 1822, *H. tuberculata lamel-*

*losa*, or *H. tuberculata* form *lamellosa* (Ubaldi, 1987; Poppe & Goto, 1991). In a large series of over 400 specimens, all intermediate forms could be found within any given population (Geiger, unpubl. data). The two taxa have been shown to have an identical karyotype (Colombera & Tagliaferri, 1983) and an identical cDNA sequence of the acrosomal sperm protein lysin (Lee & Vacquier, 1995). Although not as much material is available for *H. clathrata* Reeve and *H. venusta* as for the Mediterranean *H. tuberculata*, I am convinced that a similar range of variation can be expected for the Indo-Pacific *H. clathrata* and *H. venusta*. I, therefore, synonymize *H. venusta* under *H. clathrata* Reeve.

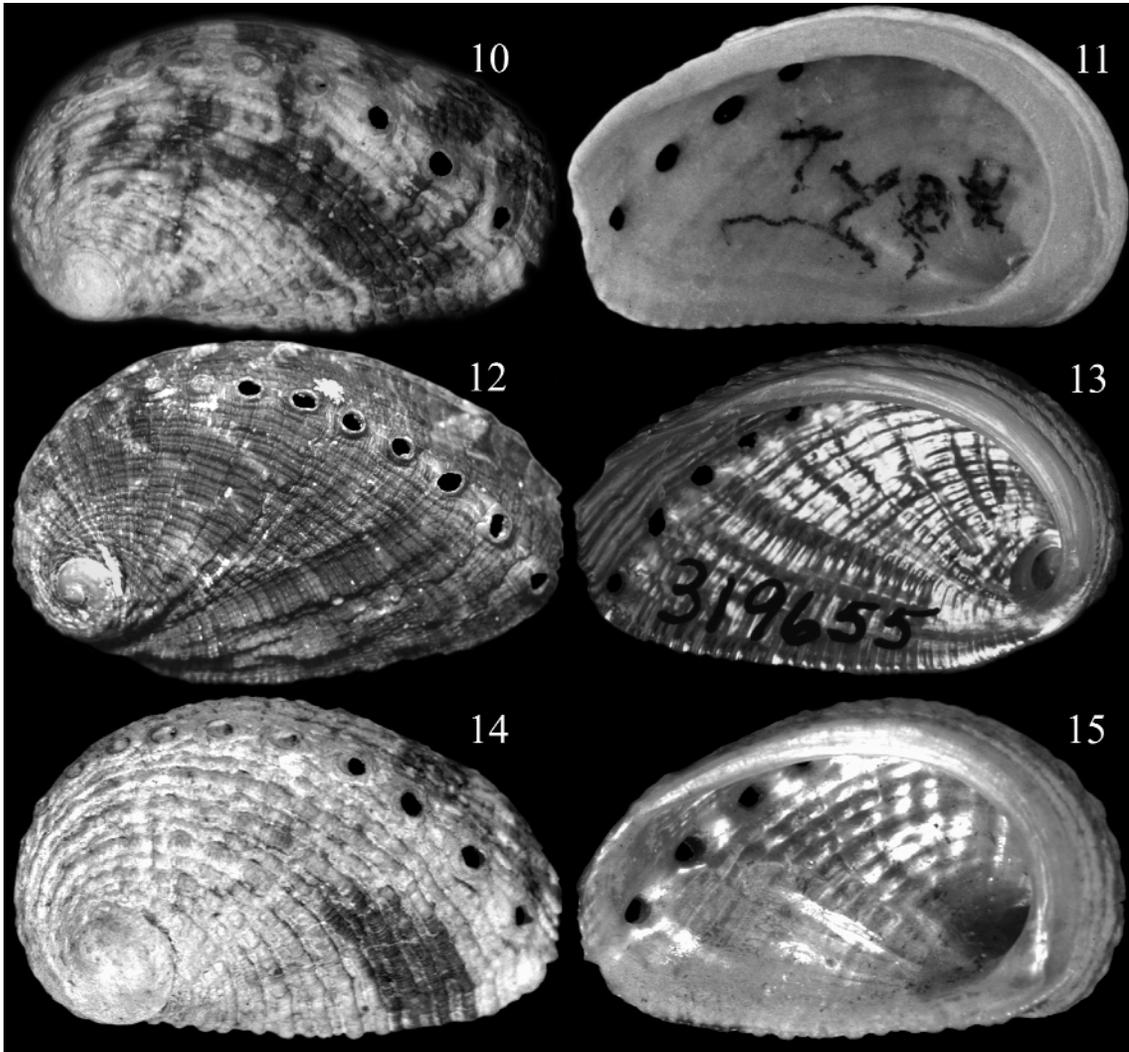
25. *Haliotis crebrisculpta* Sowerby, 1914, has been synonymized with *H. clathrata* Reeve, 1846 (Kuroda & Habe, 1952). It has also been listed as a subspecies of *H. rubra* Leach, 1814 (Talmadge, 1957b). Both opinions are rejected; the validity of the species is discussed in Stewart & Geiger (1999) and the reader is referred to this work for an in-depth treatment (see also note 36).

26. *Haliotis corrugata* Wood, 1828, has also been attributed to Gray. However, Wood (1828) published a figure with the name of *H. corrugata* in the supplement to his *Index Testaceologicus*. Gray apparently supplied some of the material, on which the figures were based (p. iiv of Supplement), but Wood actually published the figure; hence, he is the author of the taxon.

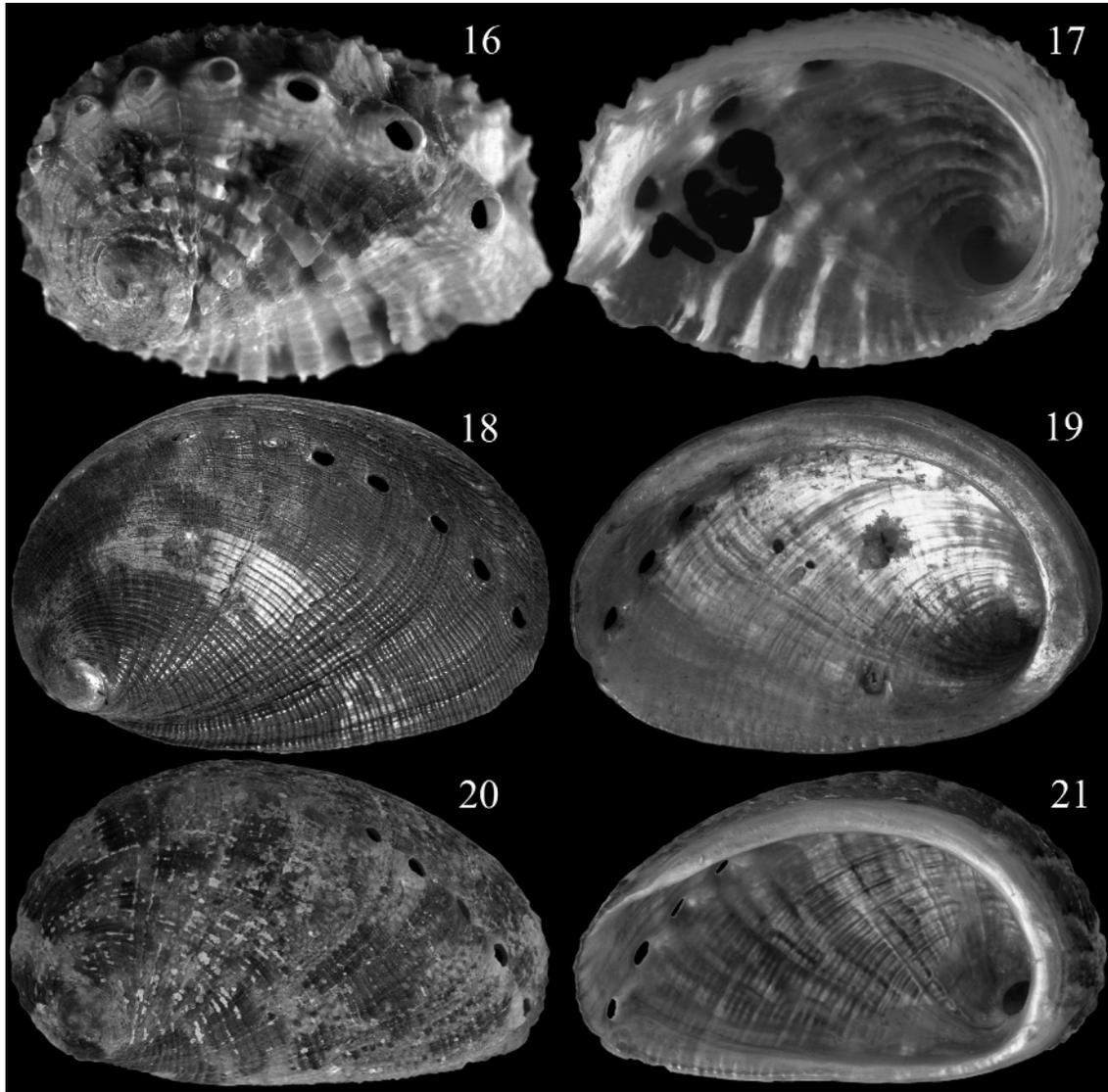
27. Serious confusion about the date of publication of Gray's (1826) work is found in the literature. The publication dates indicated are 1826 and 1827. The work was edited in two volumes, of which volume 1 is dated 1827, but one copy of volume 2 that I have seen is dated 1826 and another copy is dated 1827. Generally, 1826 is accepted as the correct date, because it is the earliest credibly supported date of publication.

28. *Haliotis squamosa* Gray, 1826, was erroneously described from Australia, but actually occurs in a restricted area in southern Madagascar. The species was rediscovered in Madagascar by Dautzenberg (1932) and again by Stewart (1984).
29. *Haliotis roedingi* Menke, 1844, was described by Menke (1844:97) in “2 neue *Haliotis* Arten, beschrieben vom Herausgeber” (2 new species of *Haliotis*, described by the editor). According to Menke, the species was already known and named by Chemnitz; Menke gave the name “*Haliotis Roedingi*, Chemn.” It is clear that the species was known to Chemnitz, but was described by Menke. I agree with Stewart (1984) that Menke, 1844, is the author, and that *H. roedingi* is a synonym of *H. squamosa* Gray, 1826, based on the description as well as the locality (*cf.* Pilsbry, 1890:112, note 28).
30. *Haliotis unilateralis* Lamarck, 1822, has been much disputed (Figures 1-32 - 1-33). Geiger (1996) designated a neotype and discussed the taxon in detail. Menke (1830:88) listed this species. The credibility of the mention in Casto de Elera (1896) in his catalog of shells from the Philippines is very low. He also mentioned species known at the time not to be found on the Philippine Islands. The best example is *H. mariae* Wood, 1828, an endemic species to Oman.
31. Sowerby’s abalone taxa from the *Thesaurus Conchyliorum* have been dated 1883 (Abbott & Dance, 1983) or 1887 (Pickery, 1991). The individual volumes were issued in a number of parts (*cf.* British Museum (Natural History), 1915). Volume 5 was published between 1882 and 1887. Haliotids appeared in the first part of Volume 5 in 1882, which is the correct date for these taxa. It is not a printing date as opposed to a publication date, as most taxa are listed in the Zoological Record of 1882 (Martens, 1882).

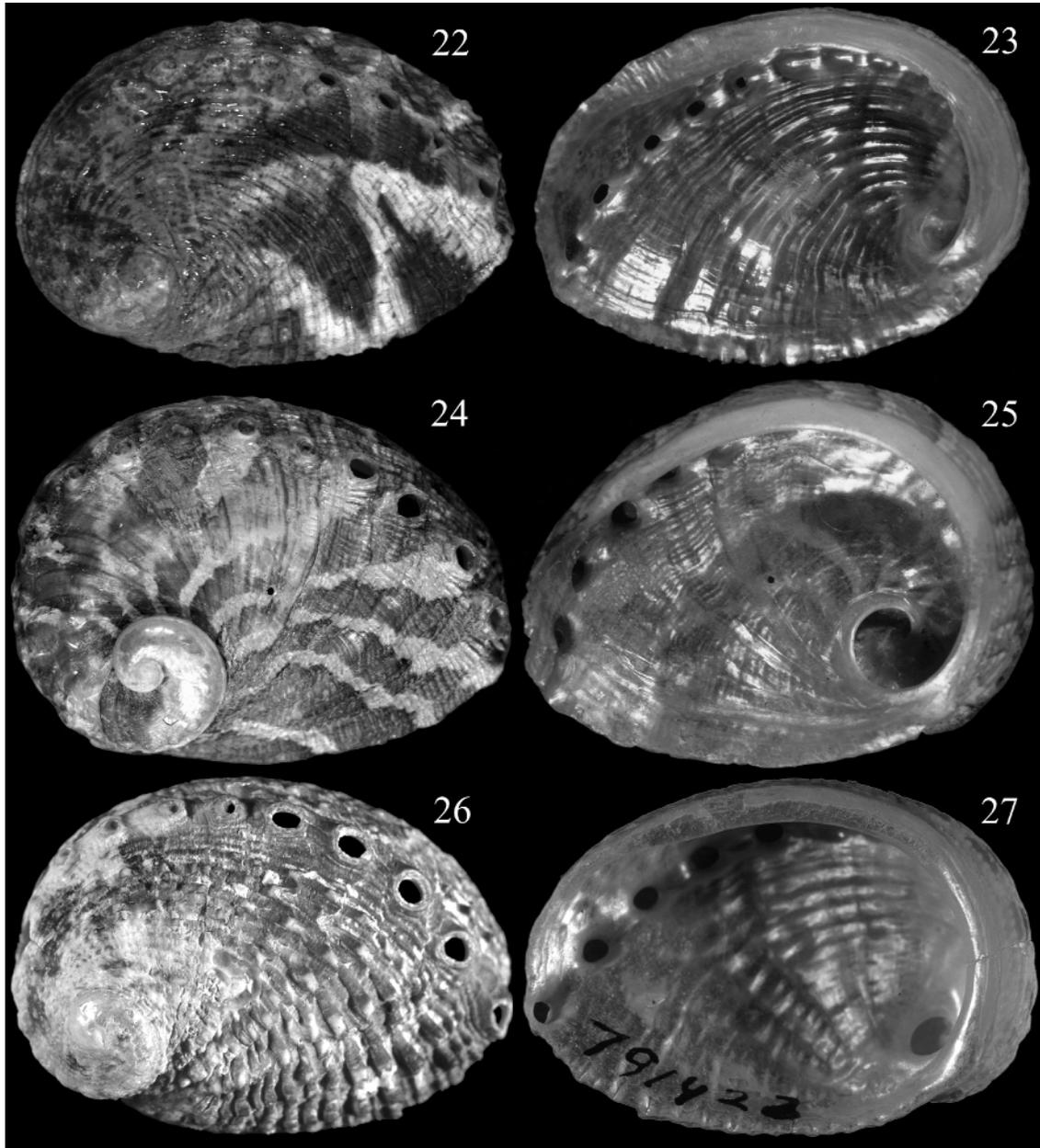
32. A lectotype for *H. multiperforata* Reeve, 1846, is here selected (see main body of text, Figures 1-6 - 1-7). The synonymy with *H. spadicea* Donovan, 1808, (Wagner & Abbott, 1978), is certainly wrong.
33. *Haliotis pertusa* Bartsch, 1915, and *H. nebulata* Turton, 1932, are indicated in Barnard (1963) as synonyms of *H. spadicea* Donovan, 1808. I assume that Barnard intended to indicate *H. pertusa* Reeve, 1846, *sensu* Bartsch (1915) and *H. nebulata* Reeve, 1846, *sensu* Turton (1932). The types of *H. pertusa* and *H. nebulata* are clearly referable to *H. rugosa* Lamarck, 1822 (see also note 12).
34. *Haliotis hargravesi* Cox, 1869, and *H. ethologus* (Iredale, 1927) are uncommon to rare in southern Queensland and northern New South Wales. Whitehead (1981:5) specifically noted for *H. hargravesi* that “known localities are as for *H. ethologus*.” The only characters distinguishing these two taxa are the numbers of spiral ribs and their elevations. However, these characters seem to be rather variable, pointing to extensive intraspecific variability and indicating presence of a single polymorphic species. The two taxa represent slight variations within the morphological range when a large enough sample is examined.
35. The type of *H. melculus* (Iredale, 1927) is severely chipped, has very elevated tremata and hardly any spiral ribs: is reminiscent of *H. brazieri* Angas, 1869. Wilson (1993) figured a specimen with many thin spiral threads as *H. melculus*. I regard it as a specimen in the *H. hargravesi* Cox, 1869—*brazieri* continuum (see also note 34 and Hybrids section above).
36. For *H. crebrisculpta* Sowerby, 1914, three syntypes are known in the BMNH, the NMW, and the USNM. The specimen in the BMNH is very similar to that figured in Sowerby (1914) and has been designated as the lectotype (Stewart & Geiger, 1999). The specimens in the NMW and the USNM represent *H. clathrata*



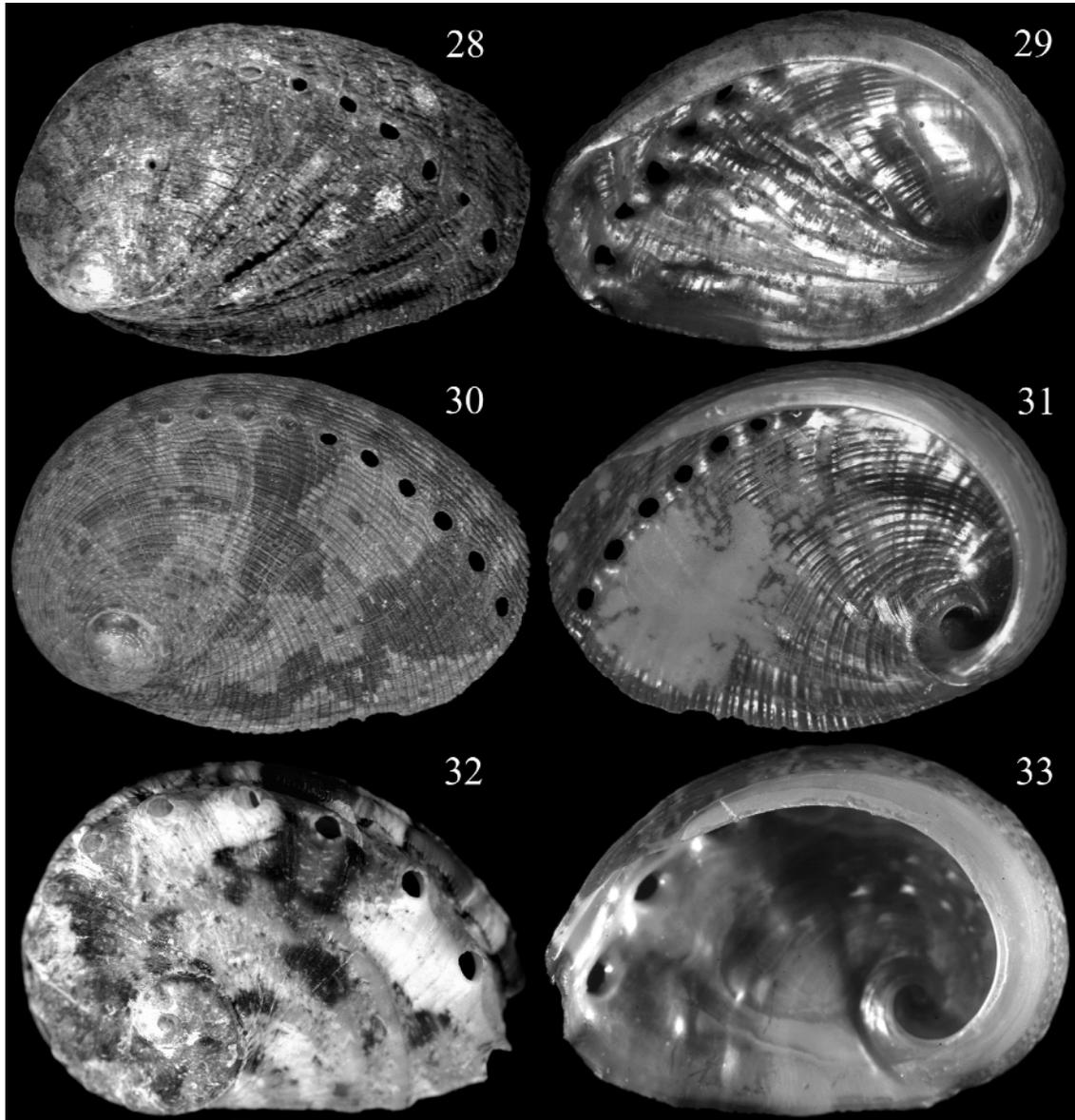
Figures 1-10 - 1-15. Shells of uncommonly illustrated abalone I. *H. dissona* (Iredale, 1929). 33 mm. R. Pickery collection. New Caledonia. 1-12 - 1-13. *H. diversicolor* Reeve, 1846. 30 mm. ANSP 319655. Bali Beach Hotel. 1-14 - 1-15. *H. exigua* Dunker, 1877. 21 mm. NMW 1955.158.2133. Japan.



Figures 1-16 - 1-21. Shells of uncommonly illustrated abalone II. 1-16 - 1-17. *H. jacnensis* Reeve, 1846. 12 mm. R. Pickery collection. No location data. 1-18 - 1-19. *H. marmorata* Linnaeus, 1758. 63 mm. LSL. *Mare africanus*. 1-20 - 1-21. *H. stomatiaeformis* Reeve, 1846. 29 mm. Collection Geiger AAB 51a. Malta Island.



Figures 1-22 - 1-27. Shells of uncommonly illustrated abalone III. 1-22 - 1-23. *H. planata* Sowerby, 1882. 1-22. 39 mm. NMW 1955.158.2124. Philippines. 1-23. 33 mm. NMW 1955.158.2125. Guadalcanal. 1-24 - 1-25. *H. queketti* Smith, 1910. 33 mm. NMW 1955.158.2129. Pondoland. 1-26 - 1-27. *H. rubiginosa* Reeve, 1846. 25 mm. USNM 791422. Lord Howe Island.



Figures 1-28 - 1-33. Shells of uncommonly illustrated abalone IV. 1-28 - 1-29. *H. striata* Linnaeus, 1758. 56 mm. One of the six specimens in LSL. *Mare europaeus*. 1-30 - 1-31. *H. speciosa* Reeve, 1846. 31 mm. NMW 1955.158.2126. Algoa Bay. 1-32 - 1-33. *H. unilateralis* Lamarck, 1822. 1-32. 23 mm. Collection S. Singer. Red Sea, Gulf of Aquaba. 1-33. 24 mm. Collection Geiger AAB 48a. Elat, Red Sea.

Reeve, 1846 (see notes 24, 25). *Haliotis dissona* (Iredale, 1929) is here considered a valid species (*cf.* note 39; Figures 1-10 - 1-11) although Whitehead (1981) listed it as a synonym of *H. crebrisculpta*. *Haliotis dissona* has also been synonymized by Wagner & Abbott (1978) with *H. diversicolor* Reeve, 1846, and its forms (Figures 1-12 - 1-13), an opinion I strongly oppose. The characters common to *H. dissona* and *H. diversicolor* (more or less smooth shell with spiral ridges) are due to the type specimen of *H. dissona* being badly worn and rather small. The distinct elongated shape of the shell of *H. dissona* with rather deep spiral ridges and grooves in fresh specimens sets it apart from *H. diversicolor*. The illustration of Iredale (1929) exaggerated the sculpture of the shell to a great extent; it may be considered a reconstructive drawing of a fresh shell from a worn specimen.

37. *Haliotis diversicolor* Reeve, 1846, is well known from the temperate northwestern Pacific, from central to southern Japan (Lindberg, 1992) and somewhat further south. The species has now been found in a small number of independent lots from Bali and New Caledonia, but only from localized upwelling areas (Figures 1-12 - 1-13). Upwelling areas are thought to exist on many of the surrounding islands that may provide habitat for this temperate species (S. A. Shepherd, pers. comm.). The shells are more elongated in general shape than typical ones and are as highly arched as shells of *H. squamata*. Additionally, they are mostly of uniform, dark sepia coloration, which may be interpreted as a case of melanism. Melanistic shells are well known in some gastropods such as in the Cypraeidae, and New Caledonia is known for a higher frequency of such dark-colored specimens. Whether these tropical populations of *H. diversicolor* represent refugia or have only been colonized in geologically recent time is not known. A taxonomic separation seems inappropriate.

38. Two spelling variations are found in the literature: *H. supertexta* Lischke, 1870, and *H. supratexta*. The original spelling was *H. supertexta*.
39. Talmadge (1962) treated *H. stomatiaeformis* Reeve, 1846, as a subspecies of *H. varia* Linnaeus, 1758. I disagree with his conclusion after inspection of the type material: *H. stomatiaeformis* is the valid name for one Mediterranean species (see note 9). Specimens normally identified as *H. stomatiaeformis* are usually referable to *H. dissona* (Iredale, 1929) (*cf.* note 36).
40. *Haliotis dohrniana* Dunker, 1863, is a little known species with distinct affinities to *H. varia* Linnaeus, 1758, as already indicated by Dunker (1870:7). The epipodium has distinct characteristics (Geiger, pers. obs.).
41. *Haliotis hanleyi* Ancey, 1881, and *H. jacnensis* Reeve, 1846, have been considered to be distinct species (*e.g.*, Talmadge, 1963a; Kaicher, 1981). The distinguishing characters were thought to be the general shape of the shell and the extent to which the shell is corded. These characters are highly variable and the two taxa represent slight variations within the morphological spectrum of one biological species. The geographical distribution of the two taxa is congruent. The smooth, dorsal part of the shell proximal to the row of tremata is a synapomorphy with *H. pulcherrima* Gmelin, 1791 (see note 1) and a diagnostic character of the species (Figures 1-16, 1-17).
42. Sowerby indicated Carpenter as authority for *H. planata* Sowerby, 1882. Weinkauff (1883:76) could not find the source; he indicated “*ubi?*” (Latin for ‘where?’). Today Sowerby is usually credited with the authorship of the taxon. *Haliotis planata* is occasionally confused with *H. varia* Linnaeus, 1758. I agree on the basis of the epipodia with Talmadge (1963a) that the two species can be separated.

43. *Haliotis rubiginosa* Reeve, 1846, has most often been used as a synonym, form, or subspecies of *H. varia* Linnaeus, 1758 (e.g., Kaicher, 1981). *Haliotis howensis* (Iredale, 1929) was described from and is endemic to Lord Howe Island. Old specimens labeled as *H. rubiginosa* from Lord Howe Island were located in the BMNH (K. Stewart, pers. comm.) and in the HUU (12557). The types of the two species are highly similar, and I agree with K. Stewart that the two names refer to the same species. *Haliotis rubiginosa* has priority over *H. howensis*, despite the latter being better known (Figures 1-26 - 1-27).
44. The type locality of *H. varia* Linnaeus, 1758, is Philippine Islands as designated by Iredale (1910).
45. It is unclear whether *H. dringii* Reeve, 1846, represents a distinct species or a form of *H. varia* Linnaeus, 1758. As *H. varia* is such a variable species, I am inclined to synonymize *H. dringii* under *H. varia*. Many specimens in collections identified as *H. dringii* are actually *H. jacnensis* Reeve, 1846 (Figures 1-16 - 1-17).
46. *Haliotis gemma* Reeve, 1846, is quite certainly a color form of *H. varia* Linnaeus, 1758, as seen from the series of four type specimens in the BMNH, of which one specimen is marked "type." The synonymization is not entirely certain as the shells are rather small; juvenile abalone are notoriously difficult to identify, and *H. varia* is an extremely variable species. The selection of the specimen labeled "type" is somewhat doubtful because the measurements of the shells and the indications in the description of the species do not match. The illustration of *H. gemma* is "magnified double" and the illustration is 19.5 mm long; hence, the corresponding specimen should be a little less than 10 mm long. The specimen labeled "type" measures 20.5 mm, which is twice the size of the original specimen. It is believed that the ref-

- erence to “magnified double” in the original description was incorrect. Kaicher (1981) illustrated another, unidentifiable specimen as *H. gemma*.
47. I found no type specimens for *H. planilirata* Reeve, 1846, or *H. scutulium* Reeve, 1846, in the BMNH. Talmadge (1964) indicated a type of *H. planilirata* was in the BMNH.
48. From the description “waved, here and there larger,” the coloration “olive brown ... dotted and spotted with green,” and the irregular spiral ridges with occasional thickenings to be seen in the figure 64 of Reeve (1846), I tentatively identify *H. scutulium* Reeve, 1846, as *H. varia* Linnaeus, 1758 (*cf.* note 47).
49. *Haliotis lauta* Reeve, 1846, was tentatively placed in the synonymy of *H. coccordiata* Reeve, 1846, by Talmadge (1960). After inspection of the type specimens of both species in the BMNH, it is clear that the two taxa are not synonymous. I agree with other authors that *H. lauta* represents *H. semiplicata* Menke, 1843.
50. The authorship of *H. elegans* has also been indicated as “Koch *in* Philippi” (*e.g.*, Wells & Bryce, 1985:34). The date printed on the description page of *H. elegans* is June 1844. This is the correct date. Philippi (1842-1845) indicated Koch as a reference; however, it is apparent that Philippi actually wrote the description and that only a short note was taken directly from Koch. Accordingly, I consider Philippi, 1844, the author.
51. The taxon as described by Leach (1814: pl. 23) is *H. ruber*. The correct inflected spelling for this adjectival species epithet, however, is *H. rubra*. Both spellings are found in the literature.
52. *Haliotis ancile* Reeve, 1846, has been shown to be a juvenile *H. rubra* Leach, 1814 (Geiger, 1996; Stewart & Geiger, 1999), and not a green form of *H. pustulata* Reeve,

1846 (*cf.* Talmadge, 1956), or *H. japonica* Reeve, 1846 (*cf.* Wagner & Abbott, 1978) (note 16).

53. *Haliotis conicopora* Péron, 1816, and *H. rubra* Leach, 1814, have been shown to be closely related on the basis of allozyme frequency data (Brown, 1993: 430): “*Haliotis conicopora* clustered with the three populations of *H. rubra*, with a maximum D of 0.018. Similar genetic distances were found between all conspecific populations studied (0.003 in *H. roei* and 0.014 in *H. laevigata*).” Further on pages 430-431: “*Haliotis conicopora* appears to represent an allopatric population (Western Australian) of *H. rubra*, as originally suggested by Shepherd (1975) and noted by Brown & Murray (1992a).” However, the two taxa can readily be distinguished by the shell thickness (dependent upon wave energy of the habitat), coloration (a potential function of food availability), and the presence of strong spiral cords (somewhat variable in both taxa) on a bumpy dorsal shell surface in *H. rubra*. Additionally, *H. rubra* is found in southeastern Australia, whereas *H. conicopora* occurs in southwestern Australia. The genetic data suggest conspecificity, but the shell and the disjunct geographical distribution indicate distinct taxa. Thus, there is some justification for subspecies recognition of *conicopora* under *H. rubra*, although this remains to be resolved.

54. *Haliotis iris* is credited either to Martyn (1784: *cf.* Sinclair, 1963) or to Gmelin (1791: *cf.* Pickery, 1991; Lindberg, 1992). *Haliotis pulcherrima* has mostly been attributed to Gmelin except by Cotton (1943), but *H. naevosa* exclusively to Martyn. All three taxa are figured and named in Linnean binominal nomenclature by Martyn. However, the work of Martyn has been invalidated by ICZN opinion 456 (ICZN, 1957). Martyn’s taxa are, therefore, not available and are now credited to the author who thereafter mentioned the species for the first time, which is Gmelin

(1791) for *H. iris*, and Philippi (1842-1845:147) for *H. naevosa*. Philippi's Volume I is dated 1845, but the page with the description of *H. naevosa* is dated "Juli 1844;" therefore, the latter is the correct date for *H. naevosa*.

55. Only a single specimen, *i.e.*, the holotype, of *H. whitehousei* (Colman, 1959) is known. It is considered by P. Colman (pers. comm.), who described the taxon, as a teratological specimen of *H. rubra* Leach, 1814. Despite regular collecting at the type locality, no second specimen has ever been found (P. Colman, pers. comm.).
56. Intermediate specimens of *H. scalaris* (Leach, 1814) and *H. emmae* Reeve, 1846, are well known from western South Australia, indicating a close relationship between the two taxa (Shepherd, 1973; Wilson, 1993). The variation in the specimens seems to be caused by the interplay of environmental factors such as wave energy, depth, and temperature (S. A. Shepherd, pers. comm). As the morphological gradient between the two taxa occurs only in a small geographical area, with the majority of the distribution showing only one of the morphologies, subspecific status of the taxon *emmae* under *H. scalaris* is indicated.
57. The type specimen of *H. elevata* Sowerby, 1882, has not been found. The specimen was not figured in the standard dorsal and ventral positions, but was tilted. However, it is evident from the dorsal sculpture and the excentric spire that a small specimen of *H. squamata* Reeve, 1846, was illustrated. According to Sowerby (1882:27), *H. elevata* differs from *H. stomatiaeformis* Reeve, 1846 (see note 9), by having strong, scaly ridges, a character rather typical for juvenile specimens of *H. squamata* (Talmadge, 1955).
58. *Haliotis funebris* Reeve, 1846, was synonymized by Hedley (1914) with *H. diversicolor* Reeve, 1846, and *H. tayloriana* Reeve, 1846. My inspection of the type mate-

- rial in the BMNH shows that *H. funebris* is clearly a synonym of *H. squamata* Reeve, 1846 (see Pilsbry, 1890:92).
59. *Haliotis gigantea* Chemnitz, 1788, *H. glabra* Chemnitz, 1788, and *H. rugosoplicata* Chemnitz, 1788, are names that stand only from the two first words of the descriptions and, therefore, cannot be interpreted as binominal names: the work and the taxa therein are not available (ICZN, 1954). The names were validated by Gmelin (1791: *H. gigantea*, *H. glabra*) and Reeve (1846: *H. rugosoplicata*).
60. *Haliotis virginea* Gmelin, 1791, has been divided into four, geographically separated subspecies: *H. virginea virginea*, *H. virginea crispata* Gould, 1847, *H. virginea huttoni* Filhol, 1880, and *H. virginea morioria* Powell, 1938 (Kaicher, 1981; Ubaldi, 1986). Conflicting opinions are expressed as to whether these are valid subspecies (Powell, 1979; Ubaldi, 1986), or represent variations caused by differences in water temperature (Talmadge, 1957a). No good data are available to support either of the hypotheses; I retain usage of subspecific taxa.
61. *H. gibba* Philippi, 1846, is given as a synonym of *H. virginea* Gmelin, 1791, by Suter (1913), supported by the figures in Reeve (1846) and Weinkauff (1883).
62. Old specimens of *H. discus hannai* Ino, 1952, from Japan are usually identified on the original label as the North American *H. kamtschatkana* Jonas, 1845, to which it is strikingly similar. *Haliotis discus hannai* and *H. k. kamtschatkana* differ at the species level (Owen *et al.*, 1971; Brown, 1993; Lee & Vacquier, 1995).
63. *Haliotis exigua* Dunker, 1863, is usually encountered in material from the Ryukyu Archipelago (Figures 1-14 - 1-15). It has morphological affinities to both *H. varia* Linnaeus, 1758, and *H. diversicolor* Reeve, 1846. Pilsbry (1895) regarded *H. exigua* as a juvenile of *H. diversicolor*. The flat shells are rather nondescript, have an irregular sculpture, and are usually of a dark, muddy coloration. Whether these speci-

mens deserve recognition at the species level is unclear. Inspection of preserved material would certainly help to resolve the status of this species.

64. The type specimen of *H. sieboldii* Reeve, 1846, is an aberrant specimen, as indicated *e.g.*, by Dunker (1882:148): “Haec species mihi est valde dubia, ... credam eam nil representare nisi conformationem *Haliotis giganteae* monstruosam.” (This species is very doubtful to me, ... I believe it does represent nothing but a grotesque form of *Haliotis gigantea*). The types of *H. sieboldii* and *H. gigantea* Gmelin, 1791, refer to the same species (Habe, 1983). The taxon *sieboldii* had long been used for a further species eventually named *H. madaka* (Habe, 1977). The two species can be distinguished as follows. In *H. gigantea* a line drawn through the apex of the shell and the last perforation results in very unequal areas of the shell, whereas such a line drawn in *H. madaka* divides the surface area of the shell approximately in half.

*Haliotis gigantea* Menke was mentioned in Weinkauff (1883:25) as published in Menke (1843), but Sherborn (1922) considered 1830 to be the year of publication of this taxon. Menke (1830:87; 1843:31) referred to *H. gigantea* Chemnitz, 1788, an unavailable name first mentioned thereafter by Gmelin (1791:3691), who listed this species from Australia (“*Habitat rarissima ad novam Hollandiam*” [lives very rarely in Australia]). However, the type specimen of *H. gigantea* Gmelin, 1791, figured in Habe (1983) clearly shows the well-known northwest Pacific species. Due to the erroneous type locality, *H. gigantea* has been incorrectly synonymized with the common, commercially exploited *H. rubra* Leach, 1814, from southern Australia (*e.g.*, Menke, 1843).

65. The type specimen of *H. diegoensis* Orcutt, 1900, is a monstrosity induced by boring organisms, most likely sabellid polychaetes (see also Oakes & Fields, 1993).

66. Adult specimens with missing tremata have been reported occasionally in the literature. These represent deformations (see Leighton, 1960), rather than valid taxa. *Haliotis imperforata* Gmelin, 1791, may belong in this category or may be a misidentified, non-haliotid species. In the case of *H. imperforata* Dall, 1919 (*non* Gmelin, 1791), *H. lusus* Finlay, 1927, was proposed as a *nomen novum*. Finlay (1927), however, had overlooked *H. cracherodii holzneri* Hemphill, 1907, which has priority and precludes the establishment of an *nomen novum*.
67. *Haliotis assimilis* Dall, 1878, is a subspecies of *H. kamtschatkana* Jonas, 1845, as discussed by McLean (1966).
68. *Haliotis coreanica* Weinkauff, 1883, is mentioned in Habe & Kosuge (1964) and Habe (1983) as a synonym of *H. gigantea* Gmelin, 1791. This synonymy is based, however, on a misunderstanding of the German text of Weinkauff by these two authors. Weinkauff (1883:27-28) wrote (translated from German): “From Mr. Paetel I received on a loan basis a species, which was labeled *H. coreanica* A. Adams, which, however, could not be separated from *H. discus*, which would be considered a further variety. However, I cannot find where this species is described.” Although the second and the third statements contradict one another to a certain extent, my interpretation of the text is that Weinkauff considered the specimen labeled *H. coreanica* A. Adams to be the same as his *H. gigantea* Var. 1 = *H. discus* Reeve, 1846. This particular specimen was not figured by Weinkauff, ruling out the possibility that an illustration could serve the purpose of a valid description. The name is a *nomen nudum*.
69. The type specimen of *H. dubia* Lamarck, 1822, is not in MHNG or the MNHN. Most of Lamarck’s types are otherwise deposited in the MHNG (*cf.* Mermod & Binder, 1963).

70. *Haliotis excisa* Gray, 1856, is not listed in Sowerby (1882) or Weinkauff (1883), but is indicated in Abbott & Dance (1983) and in Pickery (1991) without indication of page number under Gray (1826) and not Gray (1856). *Schismotis excisa* was mentioned in Gray (1856:148), but as a hypothetical name for the teratological specimens with slit tremata he had at hand: “When I first saw the shell, I was inclined to regard it as a monstrosity; but when I considered the uniformity ... in the specimens ..., I thought that it might be the type of a new form, for which *Schismotis excisa* would be a good name. ... I am inclined to believe that the slit in the specimens is ... caused by the eroded and evidently diseased state of the specimens.” Clearly, no new taxa had been described and the genus and species are unavailable.
71. *Haliotis fatui* Rheder [*sic*], 1981, is mentioned in Ubaldi (1993:II 3-1). The date is most likely based on Kaicher’s (1981: card no. 2902) statement: “This subspecies [of *H. varia* Linnaeus, 1758] is currently under study by Dr. Harald Rehder (USNM) and will probably be described in detail before the end of the year (1981).” The name was mentioned a second time in the same year (Anon., 1981). *Haliotis fatui* has been validly described by Geiger (1999a).
72. *Haliotis hanleyana* Ancey, 1881, has some affinities with *H. clathrata* Reeve, 1846 (see also notes 24, 25). However, this identification is highly tentative.
73. *Haliotis californiana* Valenciennes, 1831, *H. interrupta* Valenciennes, 1831, and *H. parma* Valenciennes, 1831, were described from “America.” The author stated that it was unknown whether the specimens were obtained from the east or west coast. The specimens were 36 mm and larger, making it unlikely that they could have been the small *H. pourtalesii* Dall, 1881, *H. dalli* Henderson, 1915, or *H. roberti* McLean, 1970. *Haliotis parma* has markings from the shell muscle in the shell (Valenciennes, 1831), which additionally suggests that it represents one of the large California

species. If *H. californiana*, *H. interrupta*, or *H. parma* should be synonyms of either *H. fulgens* Philippi, 1845, *H. kamtschakana assimilis* Dall 1878, *H. walallensis* Stearns, 1898, or *H. sorenseni* Barsch, 1940, then Valenciennes' name would have priority; the other Californian species (*H. cracherodii*, Leach, 1814, *H. corrugata*, Wood, 1828, *H. rufescens* Swainson, 1822) were described before 1831. *Haliotis interrupta* has been synonymized with *H. cracherodii*, and *H. californiana* with *H. rufescens* (Carpenter, 1864:521 *vide* McLean, 1966:156, 159); the synonymy of *H. parma* is unresolved and the taxon is treated here as a *nomen dubium*. If any of Valenciennes' taxa should eventually be shown to be senior synonyms, then an application to the ICZN for the suppression of Valenciennes' taxa would be advisable.

74. Karsten (1789) published two names for *Haliotis*, *H. iridis* Karsten, 1789, and *H. plicata* Karsten, 1789. These two taxa are synonyms of *H. iris* Gmelin, 1791, and *H. australis* Gmelin, 1791, respectively. Karsten's taxa would be the senior synonyms, but Rosenberg (1996) has formulated a case to suppress Karsten's work that is currently pending with the ICZN. His argument, based on ICZN Article 80, is accepted here.

75. *Haliotis modesta* auct. was mentioned by Menke (1845:194) as a juvenile specimen of *H. capensis* Dunker, 1844 (= *H. midae* Linnaeus, 1758). The original source of *H. modesta* is unknown to me. Menke (1845), as the only author, also put *H. semiplicata* Menke, 1843, into synonymy with *H. capensis*. I do not accept his opinion for the following reasons. *H. semiplicata* occurs exclusively in Australian waters, whereas *H. midae* is endemic to South Africa. Comparisons of the shells of adult *H. semiplicata* and juvenile *H. midae*, which are of the same size, reveal the following characters. *Haliotis semiplicata* has distinct spiral cords, whereas in *H. midae* they are only weakly developed. Spiral undulations form nodes in the middle of the shell

of *H. semiplicata*, which give rise to a slight, but fairly distinct, spiral ridge, whereas *H. midae* tends to have a spiral depression approximately one third from the suture towards the row of holes. The shape of *H. semiplicata* is much more elongated than the rotund shell of *H. midae* from a size of approximately 2-3 cm onwards.

76. *Haliotis schroeteri* Menke was mentioned by Weinkauff (1883:83) as a taxon of doubtful status. Weinkauff indicated a potential synonymy with *H. scutulium* Reeve, 1846 (= *H. varia* Linnaeus, 1758 ?, cf. note 48). Weinkauff did not know of the original publication, and it is not listed in Sherborn (1922; 1932). I regard it as a *nomen dubium*.

77. A specimen labeled as type of *H. victoriae* Brazier is known from the SAM (R. Pickery, pers. comm.); however, no formal description has been located so far, which renders the name unavailable (ICZN Article 12c). The specimen can be identified as a *H. rubra* Leach, 1814. Any description of *H. victoriae* is very likely to have been published after 1814, as the only abalone species had been described by Brazier in 1878. In case a published description of *H. victoriae* should be found, the taxon would then only become a further junior synonym of *H. rubra*.

### **Valid species by faunal regions**

For each taxon considered valid here the broad zoogeographical distribution is indicated below. In the case of a minor overlap the species is listed only in the major province. The format of the entries is as follows: taxon. + synonyms. (Figures herein). Geographic distribution (illustrations) [Notes]. *Nomina dubia*, *nomina nuda* and unavailable names are not included under the synonymies. Tentative synonyms are indicated by a question mark after the taxon, and the author of a synonym is only indicated in case of homonymy (see Index to Species-Level Taxa for details).

The distributions of the species are mainly according to Macnae & Kalk (1958), Kira (1962), Habe (1964), McLean (1978), Muller (1984b), Ubaldi (1986), Dharma (1988), Herbert (1990), Wilson (1993), Geiger (1996), Stewart & Geiger (1999), and various collection records in museums and private collections. Species occurring in more than one province are marked with an asterix and are cross-referenced; their distribution is indicated for the area within the respective province.

The list of illustrations is not exhaustive, but focuses on the more recent publications. The following numerical code has been used: 1, Abbott (1954); 2, Kira (1962); 3, Habe (1964); 4, Keen (1971); 5, Hinton (1972); 6, Dance (1974); 7, Hinton (1978); 8, Powell (1979); 9, Eisenberg (1981); 10, Kaicher (1981); 11, Bosch & Bosch (1982); 12, Kilburn & Rippey (1982); 13, Abbott & Dance (1983); 14, Sharabati (1984); 15, Stewart (1984); 16, Wells & Bryce (1985); 17, Springsteen & Leobrera (1986); 18, Richards (1987); 19, Dharma (1988); 20, Drivas & Jay (1988); 21, Salvat *et al.* (1988); 22, Poppe & Goto (1991); 23, Barash & Danin (1992); 24, Wilson (1993); 25, Giannuzzi-Savelli *et al.* (1994); 26, Geiger (1996); 27, Stewart & Geiger (1999); 28, Simone (1998); 29, Geiger (1999a).

Species that have seldom been figured (*H. dissona* (Iredale, 1927), *H. exigua*, *H. jacnensis* Reeve, 1846, *H. marmorata* Linnaeus, 1758, *H. planata*, *H. queketti* Smith, 1914, *H. rubiginosa* Reeve, 1846, *H. speciosa* Reeve, 1846, *H. stomatiaeformis*, *H. unilateralis*) are here illustrated in Figures 1-10 - 1-33 along with some noteworthy specimens (*H. diversicolor* Reeve, 1846, from Bali, *H. striata* Linnaeus, 1758). All species are illustrated in Chapter 4 (= Geiger, in press).

## **Caribbean**

*aurantium* Simone, 1998. Venezuela to central Brazil (28) [note 1].

*pourtalesii* Dall, 1881. S Florida to Surinam (10, 13) [notes 1, 2, 3].

### **European and Senegalese**

*marmorata* Linnaeus, 1758. + *decussata*, *guineensis*, *rosacea*, *strigata*, *virginea* Reeve (*non* Gmelin). (Figures 1-18 - 1-19). Central W Africa (10 [as *H. guineensis*], 13 [as *H. rosacea*]) [notes 4, 5, 6, 7].

\* *pustulata cruenta* Reeve, 1846. Israel and Lybia; see also east African province (10 [as *H. cruenta*], 14, 23, 25) [notes 10, 11, 12].

*stomatiaeformis* Philippi, 1848 (Figures 1-20 - 1-21). Isl. S of Italy [notes 5, 8, 9].

*tuberculata tuberculata* Linnaeus, 1758. + *bistriata* Gmelin, *bistriata* Costa, *bisundata*, *incisa*, *janus*, *japonica*, *lamellosa*, *lucida*, *parva* Risso (*non* Linnaeus), *pellucida*, *reticulata*, *rugosa* Reeve (*non* Lamarck), *secernenda*, *striata*, *varia* Risso (*non* Linnaeus), *vulgaris*. Mediterranean, Brittany to Morocco (10 [as *H. lamellosa*], 13, 22) [notes 4, 5, 13, 14 15, 16].

*tuberculata coccinea* Reeve, 1846. + *canariensis*, *zealandica*. Canary Isl., Azores (10, 22 [both as *H. coccinea*]) [notes 5, 13, 17, 18].

### **South African**

*midae* Linnaeus, 1758. + *capensis*, *elator*. St. Helena Bay to W Transkei (6, 10, 12, 13, 18) [note 4].

*parva* Linnaeus, 1758. + *canaliculata* Fischer ?, *canaliculata* Lamarck, *carinata*, *cingulata*, *kraussi*, *rubicunda* Röding, *rubicunda* (Montfort). False Bay to East London (10, 12, 13, 18) [notes 4, 19, 20].

*queketti* Smith, 1910 (Figures 1-24 - 1-25). Transkei to S Mozambique (10).

*spadicea* Donovan, 1808. + *ficiformis*, *sanguinea*, *sinuata* ? Partridge Point, Cape Peninsula to N Natal (9, 10, 12, 13, 18) [notes 21, 22].

*speciosa* Reeve, 1846. + *alfredensis*. (Figures 1-30 - 1-31). Port Alfred to W Transkei (10 [also as *H. speciosa* form *alfredensis*], 13, 18).

### **Eastern African, Red Sea and Persian Gulf**

\* *clathrata* Reeve, 1846. + *venusta*. Kenya, Madagascar, Mascarene Isl., Rodrigues Isl., Aldabra, Seychelles, Chagos Arch., Maldives; see also tropical Pacific province (5 & 19 [both as *H. crebrisculpta*], 10 & 27 [also as *H. venusta*]) [note 24, 25].

*mariae mariae* Wood, 1828. Oman (10, 11) [note 26].

*mariae dentata* Jonas, 1846. Oman (10 [as *H. mariae* form *dentata*]) [note 26].

*pustulata pustulata* Reeve, 1846. + *jousseaumi*. N South Africa to Persian Gulf (10) [notes 10, 11, 12].

\* *pustulata cruenta* Reeve, 1846. Particularly Red Sea; see also European and Senegalese province (10 [as *H. cruenta*], 14, 23, 25) [notes 10, 12].

*squamosa* Gray, 1826. + *roedingi*. S Madagascar (15, 27) [notes 27, 28, 29].

*unilateralis* Lamarck, 1822 (Figures 1-32 - 1-33). Central E Africa to Red Sea, Aldabra, Madagascar, Mascarene Isl. (14 [as *Sanhaliotis pustulata*], 20 [as *H. varia*], 26) [note 30].

*rugosa* Lamarck, 1822. + *alternata*, *multiperforata*, *nebulata*, *pertusa*, *revelata*. Mascarene Isl., Madagascar, central E Africa (6 & 20 [both as *H. pustulata*], 10 [as *H. pustulata* form *alternata*]) [notes 11, 31, 32, 33].

## Indian Ocean and Tropical West Pacific

*asinina* Linnaeus, 1758. + *asinum*. S-most Japan to Sydney, Andaman Isl. to New Caledonia (2, 5, 6, 7, 10 [juvenile and adult], 13, 16, 17, 19, 24) [note 4].

*brazieri* Angas, 1869. + *melculus*. (Figures 1-4 - 1-5). S Queensland to Jervis Bay, New South Wales (7, 10, 13, 24) [notes 34, 35].

\* *clathrata* Reeve, 1846. + *venusta*. Andamans to American Samoa, S Japan to Sydney; see also east African province (5 & 19 [both as *H. crebrisculpta*], 10 & 27 [also as *H. venusta*]) [note 24, 25].

*crebrisculpta* Sowerby, 1914. New Caledonia (10, 27) [notes 25, 36].

\* *diversicolor* Reeve, 1846. + *aquatilis*, *gruneri*, *supertexta*, *tayloriana*. (Figures 1-12 - 1-13). China, Taiwan, Bali; see also northwestern Pacific province (2 [as *H. super-texta*], 3, 10 [also as forms *gruneri*, *tayloriana*, *supertexta*, and *H. aquatilis*]) [notes 37, 38].

*dissona* (Iredale, 1929). (Figures 1-10 - 1-11). Queensland, New Caledonia, Tonga (10) [note 36, 39].

*dohrniana* Dunker, 1863. New Caledonia, Tonga (10, 21, 27) [note 40].

*fatui* Geiger, 1999. Tonga, Marianas (29) [note 71].

*glabra* Gmelin, 1791. + *picta*, *ziczac*. Philippines, Maluku, Lesser Sunda Isl. (9, 10, 13, 17, 19 [as *H. planata*]).

*hargravesi* Cox, 1869. + *ethologus*. S Queensland to N New South Wales (7, 13, 10 & 24 [both also as *H. ethologus*]) [notes 34, 35].

*jacnensis* Reeve, 1846. + *echinata*, *hanleyi*. (Figures 1-16 - 1-17). S-most Japan (S of Amami Isl.), Philippines, New Caledonia, Marianas, Micronesia (3, 10 [also as *H. hanleyi*]) [notes 31, 41].

*ovina* Gmelin, 1791. + *caelata*, *latilabris*. Maldives to Tuamotus, SW Japan, Philippines, Vietnam, Queensland to Western Australia (2, 5, 7, 9, 13, 16, 17, 19, 21, 24) [note 8].

\* *planata* Sowerby, 1882. + *grayana*. (Figures 1-22 - 1-23). Philippines to Fiji, Northern Territories; see also northwestern Pacific province (10 [also as *H. grayana*]) [notes 31, 42].

*pulcherrima* Gmelin, 1791: Tuamotus, Henderson Isl. (9, 10, 13).

*rubiginosa* Reeve, 1846. + *howensis*. (Figures 1-26 - 1-27). Lord Howe Isl. (10 [as *H. varia rubiginosa* and *H. howensis*], 7 & 13 [both as *H. howensis*]) [note 43].

*varia* Linnaeus, 1758. + *aliena*, *astricta*, *barbouri*, *concinna*, *dringii*, *gemma*, *granulata*, *papulata*, *pustulifera*, *scutulum*, *semistriata*, *viridis*. Sri Lanka to Tonga, S Japan, Philippines, central W Western Australia to Sydney (2, 5, 7, 9, 10 [also as ssp. *astricta*, *papulata*, *pustulifera*, *viridis*, and *H. unilateralis*], 13, 16, 19) [notes 1, 4, 44, 45, 46, 47, 48].

### **Temperate Australian**

*coccoradiata* Reeve, 1846. New South Wales to E Victoria (7, 9, 10, 24) [note 49].

*cyclobates* Péron, 1816. + *excavata*. South Australia to central S Western Australia (9, 10 [also as *H. ovina*], 13, 16, 24).

*elegans* Philippi, 1844. + *clathrata* Lichtenstein (*non* Reeve). Western Australia (7, 9, 10, 13, 16, 24) [notes 23, 50].

*laevigata* Donovan, 1808. + *albicans*, *glabra* Swainson? (*non* Gmelin). Victoria to SW Western Australia (6, 7, 10, 13, 16, 24).

*roei* Gray, 1826. + *scabricostata*, *sulcosa*. Victoria to central W Western Australia (6, 7, 10 [also as *H. sulcosa*], 13, 16, 24) [note 27].

*rubra rubra* Leach, 1814. + *ancile*, *improbula*, *naevosa*, *whitehousei*. New South Wales to South Australia, Tasmania (7 & 13 [both as *H. ruber*], 10 [also as *ruber*, *r. improbulum*, *ancile*]) [notes 25, 27, 51, 52, 53, 54, 55].

*rubra conicopora* Péron, 1816. + *cunninghami*, *granti*, *vixlirata*. Victoria to Freemantle SW Western Australia. 7, 16, 24 [all as *H. conicopora*], 10 (also as *H. c. vixlirata*) [note 53].

*scalaris scalaris* (Leach, 1814). + *crenata*?, *tricostalis*, *tricostata*. W South Australia to central W Western Australia (7, 9, 10, 13, 16, 24) [notes 24, 56].

*scalaris emmae* Reeve, 1846. Victoria to W South Australia (7, 10, 13, 24 [all as *emmae*]) [note 56].

*semiplicata* Menke, 1843. + *lauta*. SW Western Australia (7, 13, 24) [note 49].

*squamata* Reeve, 1846. + *elevata*, *funbris*. Central W Western Australia to Northern Territories, Bali (7, 9, 10, 16, 19, 24) [notes 31, 39, 57, 58].

## **New Zealand**

*australis* Gmelin, 1791. + *aleata*, *costata*, *rugosoplicata*. New Zealand (8, 10, 13) [note 59].

*iris* Gmelin, 1791. New Zealand (6, 8, 10, 13) [note 54].

*virginea virginea* Gmelin, 1791. + *gibba*, *marmorata* Reeve (*non* Linnaeus), *subvirginea*. S South Isl. & Stewart Isl., N South Isl. to S North Isl. (6, 8, 10) [notes 60, 61].

*virginea crispata* Gould, 1847. NE North Isl. (8, 10) [note 60].

*virginea huttoni* Filhol, 1880. Auckland Isl., Chapman Isl. (8, 10) [note 60].

*virginea morioria* Powell, 1938. Chatham Isl. (8, 10) [note 60].

### Northwestern Pacific

- \* *diversicolor* Reeve, 1846. + *aquatilis*, *gruneri*, *supertexta*, *tayloriana*. (Figures 1-12 - 1-13). S Hokkaido; see also tropical Pacific province (2 [as *H. supertexta*], 3, 10 [also as forms *gruneri*, *tayloriana*, *supertexta*, and *H. aquatilis*]) [notes 37, 38].
- discus discus* Reeve, 1846. Honshu, Kyushu, Shikoku (10) [note 62].
- discus hannai* Ino, 1953. Korea, Hokkaido, NE Honshu (2, 10, 13) [note 62].
- exigua* Dunker, 1877 (Figures 1-14 - 1-15). S Japan (Okinawa) (10) [note 63].
- gigantea* Gmelin, 1791. + *gigas*, *sieboldii*, *tubifera*. Honshu (2, 10) [note 64].
- madaka* (Habe, 1977). S and central Honshu, Kyushu (2, 10 [both as *sieboldii*]) [note 64].
- \* *planata* Sowerby, 1882. + *grayana*. (Figures 1-22 - 1-23). S of Yakushima; see also tropical Pacific province (10 [also as *H. grayana*]) [notes 31, 42].

### Northeastern Pacific

- corrugata* Wood, 1828. + *diegoensis*, *nodosa*, *oweni*. Central to central Baja California (1, 6, 9, 10 [also as ssp. *oweni*], 13) [notes 26, 65, 66].
- cracherodii* Leach, 1814. + *bonita*, *californiensis*, *expansa*, *holzneri*, *imperforata* Dall (*non* Gmelin), *lusus*, *rosea*, *splendidula*. N California to central Baja California (1, 6, 9, 10 [as *H. cracherodii californiensis* and *H. c. cracherodii*], 13) [note 66].
- fulgens* Philippi, 1845. + *guadalupensis*, *planilirata*, *splendens*, *turveri*. Central California to central Baja California (1, 6, 10 [also as ssp. *guadalupensis*], 13) [note 47].
- kamtschatkana kamtschatkana* Jonas, 1845. Alaska to Point Conception, S California (1, 10, 13) [notes 62, 67].
- kamtschatkana assimilis* Dall, 1878. + *aulaea*, *smithsoni*. Central to S California (1, 9, 10, 13 [all as *H. assimilis*]) [notes 62, 67].

*rufescens* Swainson, 1822. + *californiana*, *hattorii*, *ponderosa*. N California - Central Baja California (1, 6, 13).

*sorenseni* Bartsch, 1940. Point Conception to central Baja California (10).

*walallensis* Stearns, 1898. S Washington to S California (10, 13).

### **Tropical Eastern Pacific**

*dalli* Henderson, 1915. Galapagos Isl., Gorgona Isl. (4, 10, 13) [note 2].

*roberti* McLean, 1970. Cocos Isl. (4, 10) [note 2].

### **Zoogeography**

The species from South Africa, New Zealand and the northeastern Pacific are all endemic, and with the exception of one questionable report (Macpherson, 1953: the South African *H. spadicea* Donovan, 1808, in Australia) no wide spread species have been found in these areas. The East African and the Indo-Pacific provinces are also more or less isolated from each other; Geiger (1996) discussed the apparent faunal barrier around India. Only *H. clathrata* Reeve, 1846, occurs in both areas (Stewart & Geiger, 1999). Indications particularly of *H. varia* in the East African province, and *H. pustulata* in the central Indo-Pacific are erroneous (Geiger, 1996; pers. obs.). In the Australian province the separation of tropical and temperate species is not very sharp; considerable overlap has to be noted for a few species. Only a limited number of species are widespread over several faunal provinces, *i.e.*, *H. asinina*, *H. clathrata* Reeve, *H. ovina* and *H. varia*. A much more detailed, specimen based account of the distribution of all abalone species will be provided elsewhere (see Chapter 4).

Three biogeographical models have been introduced and are reviewed in Geiger & Groves (1999 = Chapter 2). Talmadge (1963a) proposed the Pacific Rim hypothesis

with multiple centers of radiations along the Pacific islands from Japan to Australia and New Zealand. Lindberg (1992) pointed to the highest diversity of abalones being found in the central Indo-Pacific, which may (or may not) indicate the origin of the group there. Based on published chromosomal data Geiger & Groves (1999) suggested a potential origin of abalone in the Tethys Sea, which is also discussed by Lee & Vacquier (1995).