

Haliotids in the Red Sea, with neotype designation for *Haliotis unilateralis* Lamarck, 1822 (Gastropoda: Prosobranchia)

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Haliotids in the Red Sea, with neotype designation for *Haliotis unilateralis* Lamarck, 1822 (Gastropoda: Prosobranchia). – Two species of *Haliotis* are known from the Red Sea: *H. pustulata cruenta* Reeve, 1846 and *H. unilateralis* Lamarck, 1822. A neotype is here designated for *Haliotis unilateralis* because the specimen in the Lamarck collection of the Muséum d'Histoire Naturelle de Genève (MHNG) is clearly not the original specimen described by Lamarck, which is not traceable in the MHNG collections. The neotype, a complete specimen, is deposited in the MHNG. The designated type locality is Gulf of Aqaba: Sinai: Elat. The shell is redescribed and radular and epipodial characters are compared to those of similar species.

Key-words: Gastropoda - Prosobranchia - *Haliotis unilateralis* - neotype - Red Sea

INTRODUCTION

Members of the family Haliotidae occur in all tropical and temperate oceans (e.g. COX 1962; LINDBERG 1992), mostly in the shallow subtidal. Approximately 200 species level taxa have been described, 55 of which are considered valid species (Geiger, in prep.). Although seven taxa have been mentioned from the Red Sea, most authors record one or two species, usually identified as *H. pustulata cruenta* Reeve, 1846 and *H. unilateralis* Lamarck, 1822 (TALMADGE 1971; YARON 1983).

Comparison of animal characters as well as those of the shell has resulted in a new assessment of the Red Sea species. The specimen of *H. unilateralis* held in the Lamarck collection of the Muséum d'Histoire Naturelle de Genève proved not to be the specimen described by Lamarck, and this led me to designate a neotype for *H. unilateralis*.

Although I will use only the single genus *Haliotis*, the taxa used by other authors are often mentioned. Some authors use several genera in the family Haliotidae. I consider the use of these genera as unjustified for the following reasons.

1) In the descriptions of the 17 supraspecific taxa (ranked either as subgenera or genera; see PICKERY 1991 for list and references) only the type species had been assigned, occasionally with selected species. Of the 200 species level taxa only approximately 65 have ever been assigned to any supraspecific taxon, and 16 of those to more than one group (GEIGER, unpublished) demonstrating the problematic supraspecific taxonomy of this group. The descriptions of these genus-group taxa are entirely typological and differential diagnoses between them do not exist. 2) Only a few studies have been using modern systematic methods to determine the relationship between 17 (enzyme electrophoresis) and 22 (cDNA sequencing) abalone species (BROWN 1993; LEE & VACQUIER, 1995). The results show that the supraspecific taxa and the limited number of associated species are not in accordance with the groups shown in the more modern approaches. However, the type species of *Haliotis sensu stricto*, *H. asinina* Linné, 1758 (by designation: MONTFORT 1810), had not been included in either study, making any sound taxonomic decisions impossible. 3) The only inferable consensus in the literature as well as in the abalone community (Workshop "Evolutionary Biology and Genetics of Abalone" during the Second International Symposium on Abalone Biology, Fisheries & Culture, February 1994, Hobart, Tasmania) is not to use any supraspecific taxa until these groupings are based on data.

ABBREVIATIONS

HUJ	Hebrew University Jerusalem
KBIN	Royal Belgian Institute for Natural Sciences (Brussel)
LACM	Los Angeles County Museum of Natural History
MHNG	Muséum d'Histoire Naturelle de Genève
MNHA	Museum of Natural History Amsterdam
MNHL	Museum of Natural History Leiden
NMC	Nature Museum Coburg
NHML	Natural History Museum London (formerly British Museum, Natural History)
NMW	National Museum of Wales, Cardiff
TAU	Tel Aviv University
USNM	United States National Museum of Natural History

SUPPOSED TYPE SPECIMEN

The text of the original description of LAMARCK (1822) is given here:

11. Haliotide unilatérale. *Haliotis unilateralis*.

H. testâ ovali, convexo-depressâ, rudi, subverrucosâ, albido-flavescente, maculis fuscis pictâ; labio elevato, anteriùs latere producto; spirâ prominulâ, obtusâ.

An Rumph. Mus. t.40. fig. G? H?

Habite les mers de Timor et de la Nouvelle-Hollande. Mon cabinet. Bord droit fort court; nacre peu brillante, Diam. longit., 16 lignes; transv., 11 et demie.

The supposed type specimen has been dealt with by MERMOD & BINDER (1963) who previously had cast doubts about its authenticity. I strongly support their suspicion, as it is clear from the description that LAMARCK (1822) described a shell with different characteristics. The specimen is olive green and white in colour whereas Lamarck described it as white-yellow. It has a rather thick shell for the genus (Figure 1), but Lamarck indicated it as being thin. The only quantitative indication in Lamarck's description is the length and width that he assigned to the shell (36 x 26 mm), which does not correspond exactly to its dimensions (35.5 x 24 mm) (see also MERMOD & BINDER 1963), but the discrepancy may also be due to the inaccurate conversion from lines to millimeters. The MHNG has the copy of Lamarck's "Histoire des animaux sans vertèbres", which had been annotated by Lamarck's daughter. The annotations consist of handwritten indications of number of specimens in Lamarck's collection. For *H. unilateralis* two specimens are noted, indicating that some changes occurred during the history of the collection. I identify the supposed type specimen as *H. varia* Linné, 1758 and it matches the potential syntypes of *H. varia* held in the Linnean Society in London (GEIGER, in prep.). It is now evident that the original type specimen of *H. unilateralis* has been replaced by another specimen, and as no other specimen has been traced in Lamarck's collection (MERMOD & BINDER 1963), the original type specimen is assumed to have been lost.

THE IDENTITY of *H. unilateralis*

SYNONYMS / MISIDENTIFICATIONS:

H. unilateralis Lamarck, 1822: Vol. 6, part. 2, p. 217, no 11.— YARON 1983: 489-491.

"*Sanhaliotis* cf. *pustulata* (Reeve, 1846)".— SHARABATI 1984: Pl. 2, figs. 1, 1a, 1b.

H. varia Linné, 1758. *sensu* DRIVAS & JAY 1988: 32, fig. 17, not LINNÉ, 1758.

"*H. cf. ovina* Gmelin, 1791".— GEIGER 1991: 95-103, figs. 1a-d, 2a-d, 3a-d, 4a-d, x (lower specimen).

"*H. sp.*".— SINGER 1993: 15.

Non H. unilateralis of KAICHER 1981 [*H. varia* Linné, 1758].

AUTHORS UNCERTAIN AS TO THE IDENTITY OF *H. unilateralis*:

WEINKAUFF (1883: 55).— SOWERBY (1887: 37).— PILSBRY (1890: 97). — MERMOD & BINDER (1963: 148-149).

CHRONOLOGICAL TREATMENT:

REEVE (1846), in his extensive monograph of the genus, did not mention *H. unilateralis*, although he discussed other Lamarckian species.

WEINKAUFF (1883) called *H. unilateralis* a missing species ("verschollene Art"). His wording subtly alludes to the possible loss of the type specimen. His

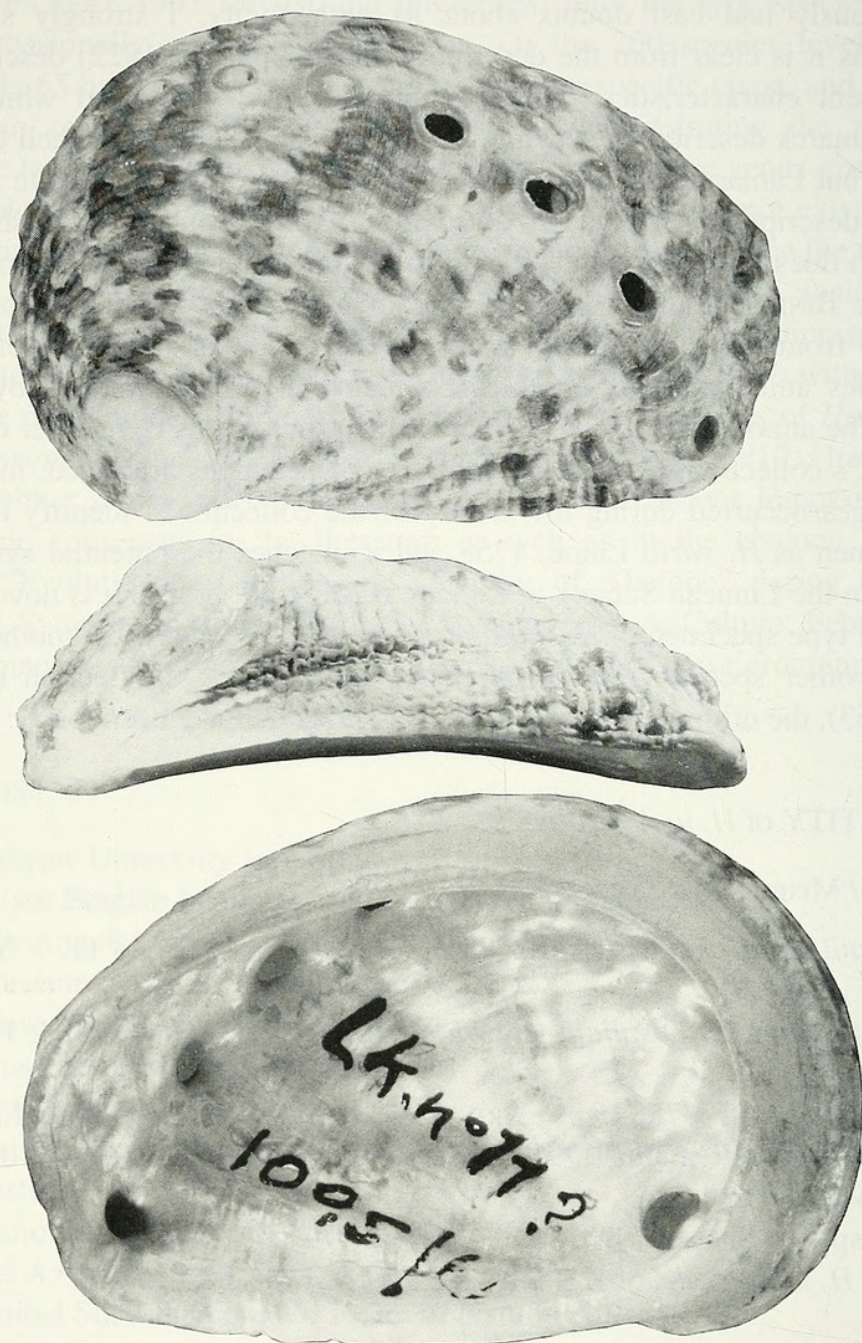


FIG. 1

Supposed type specimen of *H. unilateralis* held in the MHNG. 35.5 x 24 mm. The specimen is identified as *H. varia*. Photographs by C. Ratton, MHNG.

illustration (pl. 6: 4, 5) cannot be identified with certainty, but is closer to *H. pustulata cruenta* than *H. unilateralis* as defined here. He (p. 55-56, 66) synonymised *H. pustulata* and *H. cruenta* with *H. unilateralis*, and identified *H. concinna* as a juvenile *H. unilateralis* (p. 55, 75). WEINKAUFF (1883: 2) used informal groupings termed

“Formenkreis” or form groups, because he did not want to use the then described genera. He assigned *H. unilateralis* to the “Formenkreis” of *H. varia*, but did not synonymise *H. varia* with *H. unilateralis*. However, he mentioned that *H. varia* occurs in the Red Sea.

SOWERBY (1887: 37) called *H. unilateralis* “not identified”, i.e. gave it the status of a *nomen dubium*. He compared *H. varia* with *H. concinna*, and called the differences between *H. pustulata* and *H. varia* “of questionable specific value” (p. 28).

PILSBRY (1890) corroborated the similarity between *H. concinna* and *H. varia*. He also cited Weinkauff (1883) on the synonymy between *H. concinna* and *H. unilateralis* although he had not seen any specimens of the latter. PILSBRY (1890: pl. 17: 97, 98) had based his somewhat cruder drawing on Weinkauff’s figure. He also indicated *H. varia* from the Red Sea.

TALMADGE (1971) first noted the confusion regarding the identity of *H. unilateralis* that culminated in PILSBRY (1890), but did not realize that WEINKAUFF (1883) as well as SOWERBY (1887) gave *H. unilateralis* the status of a *nomen dubium*. He assigned the mistake to Weinkauff “... who evidently failed to check on the type specimens ...”(p. 83). As an alternative the type specimens might have already been lost at this time, although only subtle supporting evidence can be found in the wording of Weinkauff (see above). TALMADGE (1971) recognized *H. unilateralis* according to the supposed type specimen in the MHNG, figured in MERMOD & BINDER (1963).

KAICHER (1981) gave the only modern illustration under the name of *H. unilateralis*, which clearly shows a specimen of *H. varia*.

Apparently only YARON (1983) has used *H. unilateralis* as defined here (see below: studied specimens), but he did not illustrate his work.

GEIGER (1991) mentioned a further species of abalone in the Red Sea, which was found, from the inspection of type material, neither to be *H. unilateralis* nor *H. pustulata cruenta*, and finally was identified as *H. cf. ovina* Gmelin, 1791. At that time the status of the supposed type specimen of *H. unilateralis* in the MHNG had not been clarified.

In summary, *H. unilateralis* was called a *nomen dubium* early on, was compared to *H. concinna*, which is a synonym of *H. varia*, and as the latter name was better known to the scientific community, *H. unilateralis* was taken as a synonym of *H. varia*. This error was compounded by erroneous citations of locations for *H. varia* including the Red Sea. In a further complication the supposed type specimen is a specimen of *H. varia*.

In modern collections specimens of *H. unilateralis* as defined here are very uncommon (TALMADGE 1971; this study). Equally, no old specimens of this species could be found in the European collections consulted: HUI, KBIN, MHNG, MNHA and MNHL (R. PICKERY, pers. comm.), NHML, NMC (W. KORN, pers. comm.) and NMW, supporting the possibility that the original type specimen had been lost not long after Lamarck described the taxon. Hence, the biological species may have become unknown to the scientific community again resulting in confusion about the identity of Lamarck’s taxon.

Is it possible to positively identify the species from LAMARCK's (1822) description? First, the origin of Lamarck's material has to be discussed. Lamarck indicated Timor and Australia (his Nouvelle-Hollande) for the origin of his material. As he did not collect the specimens himself, an error in these localities might have been easily, but inadvertently, committed. In a similar case, GRAY (1826) described *H. squamosa* from Australia; only recently that species has been relocated in a restricted area of southern Madagascar (STEWART 1984; pers. comm.; D. PISOR, pers. comm.). Therefore, an error concerning the geographical provenance of the original specimens of *H. unilateralis* should not present an *a priori* hindrance to the identification of the species, and biological species from outside the Australian region should not be excluded from possibly being Lamarck's *H. unilateralis*. The taxon has primarily been reported from the Red Sea (WEINKAUFF 1883; SOWERBY 1887; PILSBRY 1890; HALL & STANDEN 1907; TALMADGE 1971; MERGER & SCHUHMACHER 1974; YARON 1983; including three additional references; SINGER 1993), but at least some of these indications may not refer to *H. unilateralis* as defined here.

LAMARCK (1822) made reference to two figures of RUMPHIUS (1766), but as he marked them with question marks, these two illustrations are of no use for the correct identification of *H. unilateralis*. Unfortunately, Lamarck did not illustrate his work, and we are left with a short description. However, he mentioned that the form of species no 12 (*H. rugosa*) is somewhat similar to the preceding one, i.e. *H. unilateralis* ("Forme un peu rapprochée de celle de la précédente": p. 217). The type material of *H. rugosa* contains two separate species (three specimens). HERBERT (1990) designated a lectotype, and identified the other specimens as *H. pustulata*. These three specimens are highly similar in the outline of the shell; therefore, the fact that Lamarck mixed two species under one name does not impose any problem in respect of the indicated similarity of form between *H. rugosa* and *H. unilateralis*.

The description of *H. unilateralis* is fairly general, potentially fitting several species. However, a set of three characters - thin, warty, white yellow - is found in only two species: the little known *H. barbouri* Foster, 1946 from Brazil, and the species known from the Red Sea area as *H. unilateralis* (YARON 1983; SINGER 1993). Of the latter, the shape of a typical shell is very similar to that of the type specimens of *H. rugosa* in the sense of Lamarck (see above for discussion of this taxon), for which Lamarck indicated to have a similar shape of the shell to *H. unilateralis*. The shell is very thin for the genus, mostly as thin as or even thinner than *H. brazieri* Angas, 1869. The shell most often is found in red and orange tones with some markings in a darker colour: brown and green. The indication of colour is slightly in contrast with "white and yellow" and "dark spots" by Lamarck. He also describes the shell as "dull" and having "little shiny nacre", and, therefore, I agree with WEINKAUFF (1883), that he described the species from a beach or slightly worn shell. It is well established that such shells lose the bright colouration and tend to fade to a certain extent, i.e. a fading from orange to yellow is easily conceivable. One of the most prominent features of the shell is the elevation and folding near the columella, a feature not clearly addressed by Lamarck.

In a statistical analysis, the length and width of the shell indicated in LAMARCK (1822) lie near the regression line of the same data for all the available specimens from the Red Sea species, which supports its identification as *H. unilateralis* (graph not shown).

I have shown above that the species from the Red Sea is quite likely the same species on which LAMARCK (1822) had based his description of *H. unilateralis*. For the sake of stability of nomenclature (ICZN Article 75(b)) I shall maintain the rather well established name. However such a decision necessitates the designation of a neotype, as the original type must be assumed to be lost and the identity of the species is highly controversial (ICZN Article 75(b)(ii)). The alternative is to designate *H. unilateralis* a *nomen dubium* and to describe the species from the Red Sea as a new species. However, for the following reasons the designation of a neotype is preferred: No new taxon is introduced; the already used association of the taxon with a biological species is retained; and, in contrast to the designation of a neotype, the declaration of *H. unilateralis* as a *nomen dubium* could eventually be overturned, causing further disruption of taxonomic stability.

The complete specimen designated here as the neotype represents the specimen that best fits the description of Lamarck, although it is not a perfect match (cf. ICZN Article 75(d)(4); MAYR & ASHLOCK 1991).

DESIGNATION OF NEOTYPE of *H. unilateralis* Lamarck, 1822

NEOTYPE: *Haliotis unilateralis* Lamarck, 1822. MHNG no. 18020. The complete specimen is stored together with Lamarck's collection. It comprises the dry shell, the animal in alcohol, and the mounted radula.

TYPE LOCALITY: Red Sea: Gulf of Aqaba: Sinai: Elat. 40 m depth, under backward slope of reef. Collected by M. Fainzilber, D. Korkos and B. Singer.

DESCRIPTION: Shell of neotype 33.8 mm long and 23.15 mm broad (Figure 2). Dorsal side bears three spiral rows of bumps, corresponding to depressions in the nacre. Tremata raised considerably. Last four tremata fully open, fifth partially closed. Dorsal surface only slightly convex and forms an angle of approximately 70° with lateral margin of shell. Most distinct character is the plicate margin which itself bears blunt lamellae. Between fold and columella three spiral ridges. Suture pronounced and spire distinctly elevated. No scar of hypertrophied adductor muscle.

Colour (based on wet shell; in dry condition colour dulled by periostracum): Overall bright reddish orange with some light green spots on dorsal side in posterior part, and at very margin (aperture) near last respiratory hole formed. Several fine, lighter spiral lines. Red margin intersected from columella up to fold by pairs of vertical, white bands. Length of intersection between pair of bands 1-2 times as wide as pair of bands themselves. Nacre uniform and shiny.

Radula: see figure 3 for terminology used. On rachidian tooth, basally, posterior end of basis bears vertical groove and not horizontal one. On lateral tooth 1, cutting edge has distinct ridge, bent to the posterior. Primary ridge forms an angle of

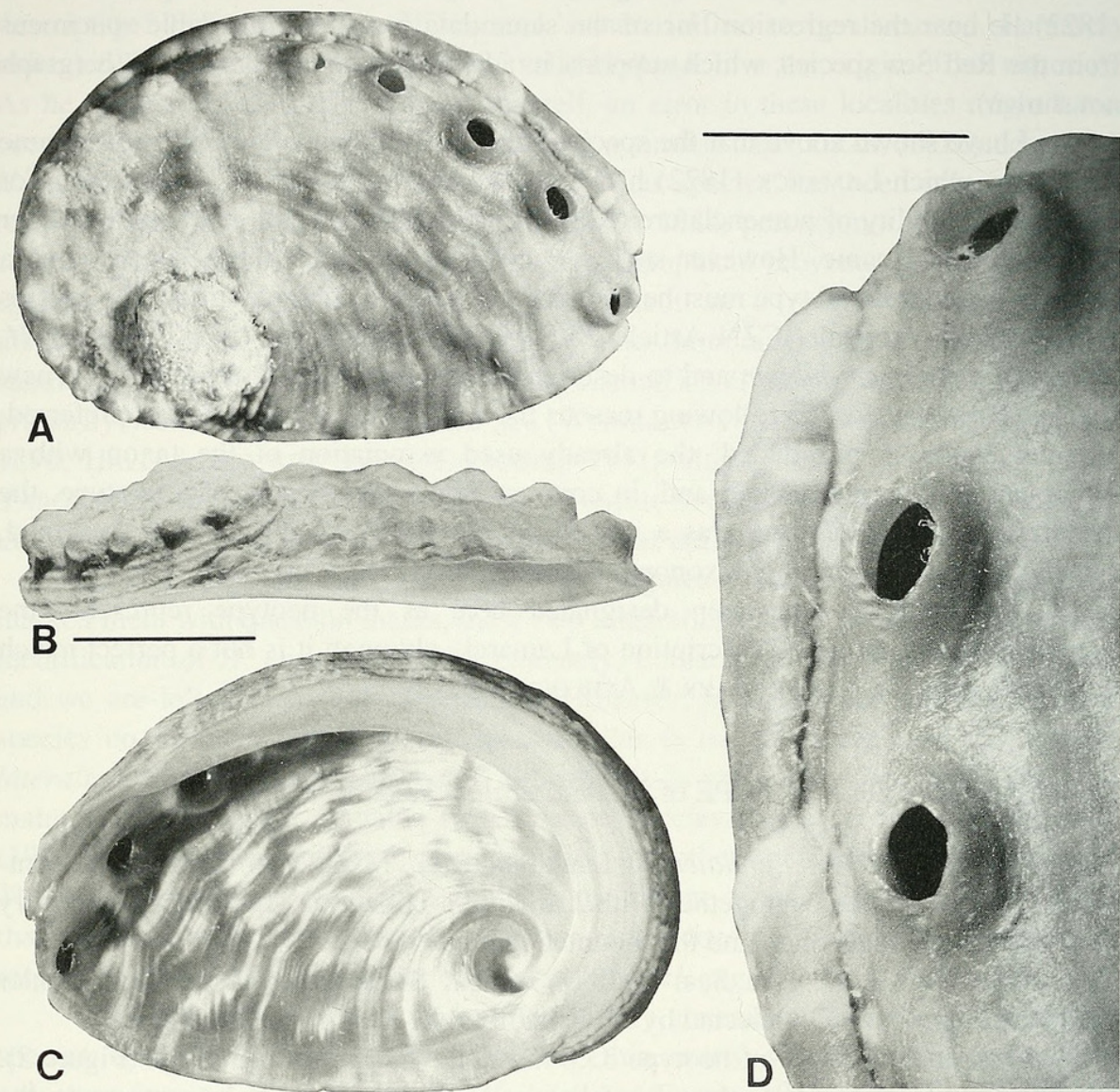


FIG. 2

Neotype of *Haliotis unilateralis*. A) Dorsal. B) Apertural. C) Ventral. D) Anterior part of row of tremata with folded margin on the left side. A-C: Bar = 10 mm, D: Bar = 5 mm.

approximately 45° to cutting edge. Primary ridge approximately as long as cutting edge. Secondary ridge separates from main part of tooth in its top third, only slightly shorter than primary ridge, and very pointed. Cusps of lateral teeth 3-5 have no denticles. Cusps of inner and middle marginal teeth slightly asymmetrically denticulated, with denticles on inner margin closer to tip than those of outer margin. Outermost marginal teeth with far less denticles on outer margin and close to tip (Figure 4).

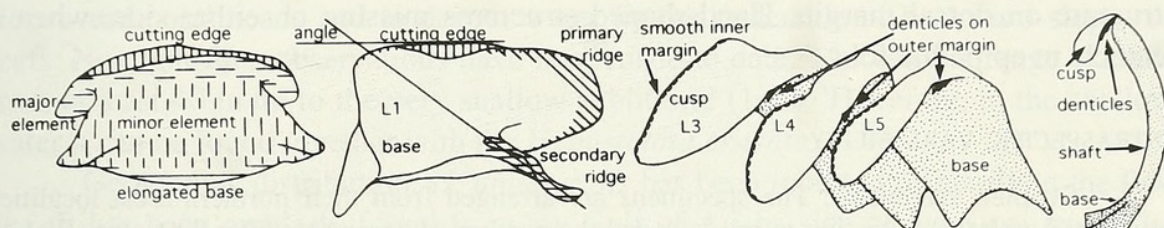


FIG. 3

Illustration of the terminology for the teeth of the radula of abalone.

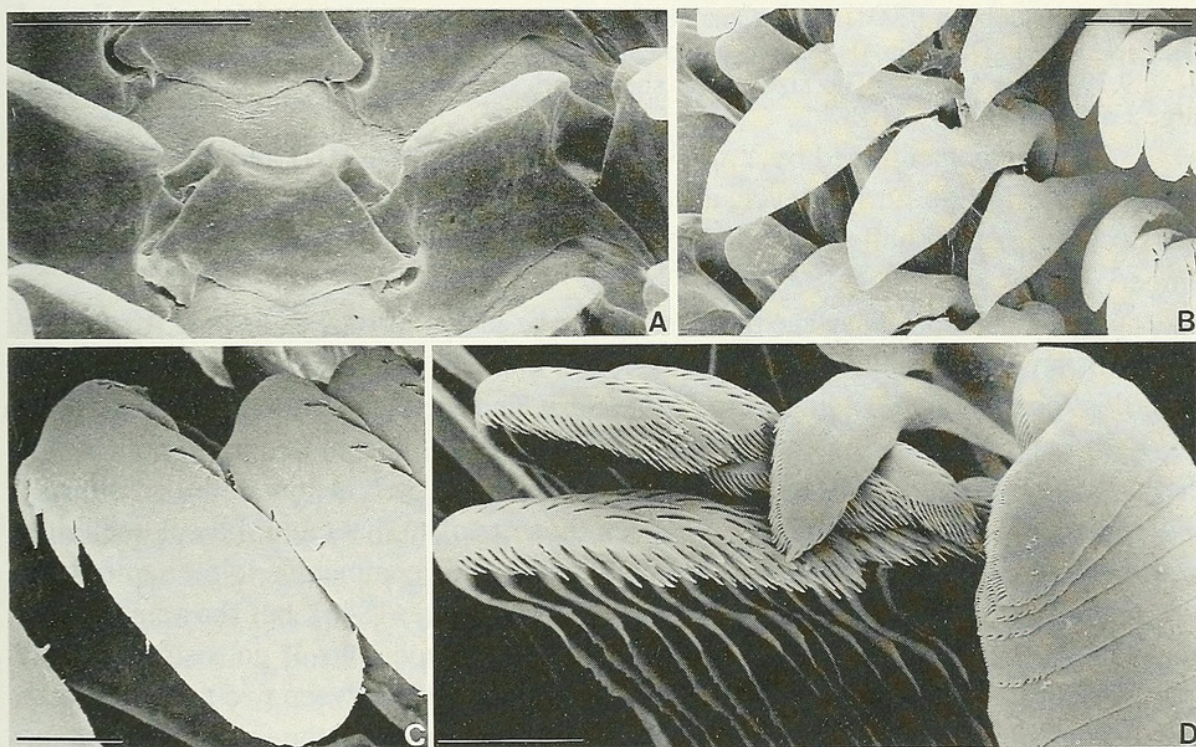


FIG. 4

SEM photographs of radular teeth of *H. unilateralis*. A: Rachidian tooth and lateral tooth 1. Scale bar = 100 μ m. B: Lateral teeth 3-5. Scale bar = 100 μ m. C: Inner marginal teeth. Scale bar = 25 μ m. D: Middle and outer marginal teeth. Scale bar = 25 μ m.

Epipodium: Very elaborate, despite rather narrow for genus. Dorsal margin bears hand-shaped leaflets, several times fingered. On inside of epipodium, palm gives rise to smaller, less fingered, hand-shaped projections. Longer dorsal tentacles sparse. Ventral margin instead bears numerous long tentacles and palms of hands longer than those on dorsal margin, but with fewer secondary hand-shaped leaflets. In

epipodial fold large tentacles at greater intervals, i.e. at intervals of 3-5 hand-shaped structure on dorsal margin. Hand-shaped structures missing on either side, when a tentacle in epipodial fold.

INTRASPECIFIC VARIABILITY

STUDIED SPECIMENS: The specimens are arranged from their northern-most localities southward with the collection in brackets and the number of specimens after the colon. Elat 40 m under backward slope of reef (Neotype MHNG no. 18020: 1); Elat, 3. 1994, at foot of reef, dead, 20 m (Singer: 1); Elat, 30.8. 1988, 10-30 m (Geiger: 1); off Elat: 2 m, on shell, 1972 (Stewart: 6); Elat (Stewart: 1); Elat 30 m (Stewart: 1); 30 km South of Elat, 8. 1993, beach, dead (Singer: 2); Lagoon of Dahab, 6. 1991, dead on sand (Singer: 1); Dahab, 8. 1993, amongst corals, 2m, dead (Singer:1); Gulf of Aqaba, approx. 1991, dead, shallow water (Singer: 2); Na'ama Bay, Sinai (Singer: 1); Gulf of Aqaba, approx. 1988 (Singer: 6); Sinai (Jones: 1); Sinai, 1 m under stone (Geiger: 1); Tiran, Jackson Reef, corals, 30-40 m (Singer: 1); Woody's Wreck, 2.9.1983 (NHML: 1); 5 mile reef, 8.1.1982 (NHML: 1); Safaga, Egypt (Pickery: 1); Djibouti: Ile des 7 frères (Stewart: 1); Djibouti, Ouaramous Island, 6 m rock (Stewart: 1); Aldabra: Ile Picard, Passé Dubois, 07.04. 1983, Channel margin 3-10 ft (USNM 836532: 1); Mozambique Channel: Bassas Da India, 04.90 live-taken (Stewart: 1); Djibouti: Ile des 7 frères (Stewart: 1); ---, 2.9.1982 (NHML: 1). The size of the shells varies between 12.75 and 33.8 mm for their largest dimension.

The shells mentioned by YARON (1983), housed in the HUJ and the TAU, were not available for study. However, according to the curator of the HUJ, H.K. Mienis (pers. comm.), the shells are "identical with the material you received from Solly Singer".

Shell: The dorsal surface of the shell can be planar or convex as in *H. varia*. The flat shells are so far only known from the Sinai coast of the Gulf of Aqaba. The shells from this locality are also similar to *H. brazieri*. The tremata are moderately to highly elevated, i.e. to a similar extent as in *H. parva* Linné, 1758 or more, but in none of the shells seen they are raised as much as in *H. brazieri*. The shell is thinner or occasionally as thin as *H. brazieri* or *H. parva*. Between the row of tremata and the columella the folded margin is one of the most noticeable features. It is comparable to the same structure found in *H. scalaris* Leach, 1814 [= *H. emmae* Reeve, 1846], but shows a reduced range in the extent it is formed. In the most pronounced state it consists of tightly spaced, delicate but short lamellae, approximately up to 15 between two tremata. These may become fewer and sturdier and possibly may form nodes on the folded margin.

Colour: The whole range of light rose to orange and red leading occasionally even to brown tones are found. Some green specimens are known. Most frequently fine white mottling covers the shell, with larger spots in white or a second colour being rather rarely encountered. Only two specimens show radial flammae, a pattern often seen in *H. ovina*. The nacre is rather of a light colouration for the genus.

Radula and epipodium: The radula (GEIGER, unpublished) and the epipodium (OWEN *et al.* 1971; GEIGER, pers. obs.) of abalones shows characters which vary between species. In the description, only the features different from other species investigated so far are indicated. Two radulae were investigated with a SEM, and four alcohol specimens were available. The characters indicated in the description of the neotype adequately indicate the intraspecific variability.

Habitat: From all present information the species occurs during day time under stones and coral heads and in deeper water on the underside of backward slopes of reefs. No night time observations have been made to date. The vertical range extends from at least 40 m up to the very shallow sublittoral (1 m). Therefore, in the shallow water it can be found together with the *H. pustulata cruenta*.

Geographic distribution: *H. unilateralis* has been reported primarily in the Red Sea. It has been regularly found from the Gulf of Aqaba side of the Sinai from Elat down to Sharm el Sheik (Singer, pers. comm.; this study). In the southern Red Sea, SHARABATI (1984) has found the species at the locations called "Woody's Wreck" and "5 mile reef"; I was unable to find the precise location of these places. An underwater photograph of the species was taken at Hurghada (Egypt) by U. Wüest, but the specimen had not been preserved. Additionally, several specimen from Djibouti, one specimen from Aldabra (USNM), one from Msibati, Tanzania (K. Stewart, pers. comm.), one from Mozambique, and at least two specimens from Pointe du sel, St. Leu, Reunion (M. JAY, pers. comm.: see DRIVAS & JAY 1988) are known. YARON (1983: 491) indicates without references its occurrence in East Africa. Despite the more frequent findings of the species in the Red Sea area, the abundance of *H. unilateralis* must still be termed infrequent to rare.

COMPARISONS

– *H. brazieri*: For illustrations see KAICHER (1981), ABBOTT & DANCE (1983: 20), WILSON (1993: pl. 5 fig. 1). The flat form of *H. unilateralis* from around Elat somewhat resembles *H. brazieri*. However, *H. brazieri* is found only in southeast Australia from southern Queensland to Jeffries Bay, New South Wales (WILSON 1993). The tremata of *H. brazieri* are more raised than in *H. unilateralis*, and the shell is usually heavier, the spire is much more elevated, the colour pattern usually involves red oblique flammae, and no spiral row of depressions in the nacre can be observed. The soft parts of this species are unknown to me.

– *H. ovina*: For illustrations see SPRINGSTEEN & LEOBRERA (1986: pl. 2 fig. 3), ABBOTT & DANCE (1983: 22), DHARMA (1988: pl. 1 fig. 4), WILSON (1993: pl. 3 fig. 5). Whereas *H. ovina* extends as far west as the Gulf of Siam, Andaman Sea (TALMADGE 1974) and the Maldives (BAER 1989), *H. unilateralis* has only been found as far east as Reunion (M. Jay, pers. comm.). The shell of *H. ovina* is always much heavier, and the margin between the tremata and the columella does not form a fold as in *H. unilateralis*. *H. unilateralis* can also be distinguished easily from *H. ovina* on the basis of the epipodium. The latter species has warty triangles whose broad bases form the dorsal and ventral margin, and the tips point towards the epipodial fold. The dorsal and ventral triangles are shifted by half their widths, which causes the tips of the triangles of one side to point into the gap between the two triangles on the opposite side. This arrangement forms an undulating epipodial fold. The dorsal and ventral margin bear many small projections, arranged in a single line. Dorsal to the dorsal epipodial margin large tentacles are found.

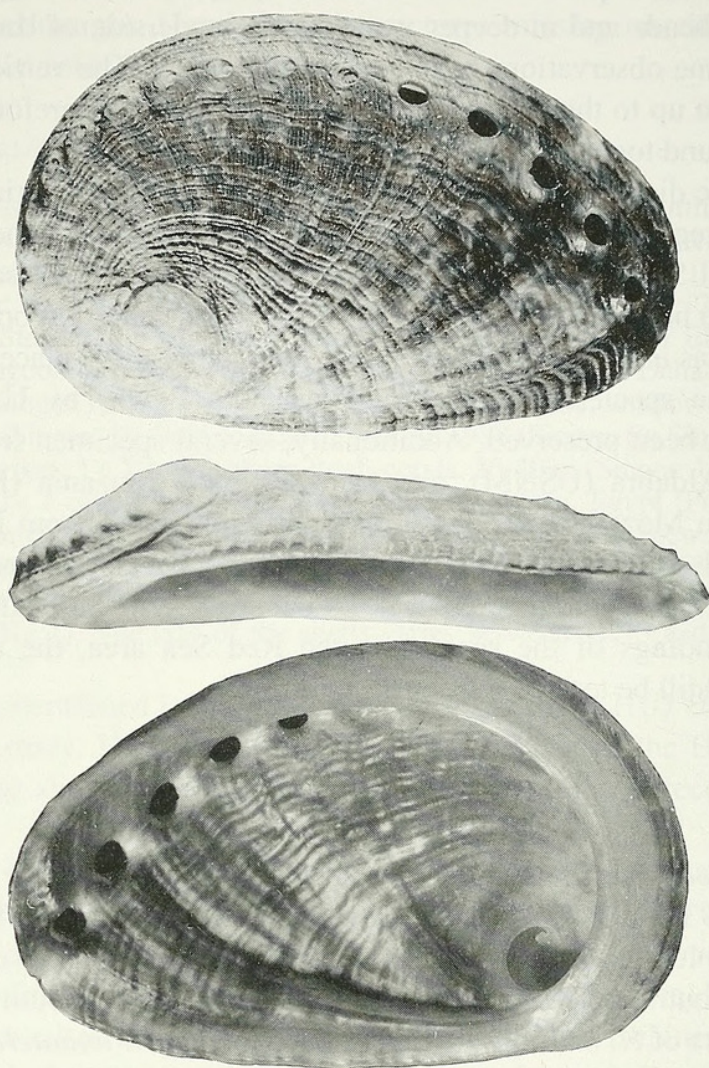


FIG. 5

Shell of *H. pustulata cruenta* in dorsal, apertural and ventral view. Sinai, Gulf of Aqaba. 34 x 21.5 mm. Collection Geiger.

– *H. p. pustulata* and *H. pustulata cruenta*: For illustrations see KAICHER (1981), BARASH & DANIN (1992: fig. 9), GIANUZZI-SAVELLI *et al.* (1994: figs. 105 a-c), this study (fig. 5). *H. pustulata* is the only species to occur sympatrically with *H. unilateralis* in the Red Sea. Its distribution in the Indopacific extends from the Persian Gulf (TALMADGE 1974) to northeastern South Africa (JACKS 1983). The two subspecies can be distinguished from *H. unilateralis* by having a thicker shell, no elevated tremata, no folded margin and they usually have a dark brown to sepia colouration with off-white mottling (Figure 5). The relation between *H. pustulata* and *H. rugosa* Lamarck, 1822 (*non* Reeve, 1846) is currently debated (cf. HERBERT 1990).

The epipodium has dorsally and ventrally closely packed fingered structures, with thick fingers. These bundles are separated by spaces bare of any such structures.

From within these dense bundles a few longer tentacles emerge. Large, isolated tentacles appear in the middle of the epipodium, which, however, are not surrounded by hand-shaped projections. No clear epipodial fold can be identified.

Occasionally *H. unilateralis* and *H. pustulata* have been confused, as in the compilation by VINE (1986). There *Sanhaliotis pustulata* was described as having raised tremata, a feature of *H. unilateralis* and not of *H. pustulata cruenta*; the second species discussed is *S. varia*, which most likely represents *H. pustulata cruenta*. Note that VINE (1986: 126) used the genus *Sanhaliotis* in the description of shells, but *Haliotis* in the list on page 172 including the species mentioned in the text.

– *H. varia*: For illustrations see KAICHER (1981), ABBOTT & DANCE (1983: 22), SPRINGSTEEN & LEOBRERA (1986: pl. 2 fig. 2), DHARMA (1988: pl. 1 fig. 6), this study (fig. 1). *H. varia* seems to have its western distributional limit around Sri Lanka (TALMADGE 1974; NHML) and Cape Comorin, India (Geiger, unpublished); occasional specimens are found on the Maldives (NHML). One specimen has allegedly been collected from Muscat, Oman in 1838 (NHML). Therefore, the western distributional limit of the species seems to be very similar to that of *H. ovina*.

The shell is much heavier, the columella much narrower, and no fold between the row of tremata and the columella is present. Numerous, narrow, spiral cords are found on the dorsal surface and show in the nacre; the cords often bear scales. In some specimens oblique lamellae can be found. The colours are only rarely bright; muddy green and brown prevails (Caution: do not confuse with *H. dohrniana* Dunker, 1863).

The epipodium is rather narrow for the genus and is composed of distinct triangular units. Each unit bears a large tentacle on the margin which is bordered on either side by finer projections, which are often fingered and form small hand shaped structures, which, however, are less elaborate than in *H. unilateralis*. In addition, the secondary palmate structures of *H. unilateralis* are not found in *H. varia*. Towards the distinct undulating epipodial fold, which is formed as in *H. ovina*, no further structures can be found; the epipodium is smooth there.

SPECIES OF *Haliotis* IN THE RED SEA

Seven taxa have been indicated from the Red Sea: *H. ancile* Reeve, 1846, *H. dringii* Reeve 1846, *H. pustulata cruenta* Reeve, 1846, *H. cf. ovina* Gmelin, 1791, *H. scutulum* Reeve, 1846, *H. unilateralis* Lamarck, 1822 and *H. varia* Linné, 1758 (ABBOTT & DANCE 1983; YARON 1983; SHARABATI 1984; GEIGER 1991). YARON (1983) discusses in detail the various taxa reported from the Red Sea. *H. scutulum* is a little known taxon. No specimen labeled with this name could be found in the NHML (GEIGER, pers. obs. 1993). From the description “waved, here and there larger”, the colouration “olive brown ... dotted and spotted with green”, and the irregular spiral ridges with occasional thickenings to be seen in the figure 63 of REEVE (1846), I tentatively identify *H. scutulum* as *H. varia*. It is mentioned a few times in the literature from the Red Sea (cf. YARON, 1983), possibly stemming from a confusion of *H.*

pustulata with *H. varia*. Some additional indications on the remaining taxa are worth mention. *H. ancile* is noted by ABBOTT & DANCE (1983) to occur in the Gulf of Suez and the north western Indian Ocean. The figured specimen looks rather like a colour form of *H. pustulata* and bears only limited resemblance to the type of *H. ancile* (GEIGER, pers. obs. in NHML), which actually is a juvenile *H. rubra* Leach, 1814 (K. STEWART, pers. comm.). In his compilation, VINE (1986) includes *H. dringii* which is reported so far only from the Australian region (WHITEHEAD 1990). Despite mention of the seven taxa listed above, only *H. pustulata cruenta* and *H. unilateralis* are known to occur in the Red Sea. The more common *H. pustulata cruenta* has most likely been involved if only one species of abalone had been identified, particularly in the non-taxonomic literature.

In conclusion, only the well known *H. pustulata cruenta* and *H. unilateralis* are known from the Red Sea area. The confusion about the latter biological species has ceased to exist due to the present designation of a neotype, which does not disrupt the usage of the taxon, hence provides taxonomic stability.

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Note added in proof.

The shells shown by Pickery & Steppe (1995: *Gloria Maris* 34: pl. 5, fig. 7) as *H. unilateralis* are *H. pustulata cruenta*. Four additional specimens of *H. unilateralis* were located in the California Academy of Sciences in San Francisco (CASIZ). Zanzibar: Pinna (CASIZ 1594: 1); Mauritius, leg. Boswell (CASIZ 1532: 3).



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