

**The Delta-shaped Maltese Cross Cowry *Barycypraea fultoni deltoidea* n. ssp.,  
(Gastropoda: Cypraeidae) and a Further Discussion About Mozambican  
Populations and Observations of *Barycypraea* and Related Genera**

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**ABSTRACT** A new subspecies, *Barycypraea fultoni deltoidei* found at shallow depths in the northern Transkei, South Africa is described herein. It differs from the nominate *B. fultoni* by the deltoidal shape and also by stronger development of the margins. A further analysis and discussion about Mozambican populations and a comparison of all four *B. fultoni* taxa are included. Differences in size, ratios, shape, margins, and bases between the taxa are described. Further observations of *Barycypraea* and related genera are discussed.

**KEYWORDS** *Cypraeidae*, *Barycypraea*, *B. fultoni deltoidea*, South Africa, Mozambique, new subspecies

## INTRODUCTION

The Maltese cross Cowry *Barycypraea fultoni* (Sowerby III 1903) ranks among the most famous and sought-after species of the family Cypraeidae. Its unique color pattern, exquisite shape, rarity, and turbulent history which is described in the following sections, have all contributed to the mystery and fascination connected to this species.

*Cypraea fultoni* was described in 1903 by G.B. Sowerby III, in a book contribution entitled: Mollusca of South Africa, in Marine Investigations in South Africa, Volume II. The unique shell (See Figure 1) was apparently dredged, but damage to the parcel it was submitted in, caused the loss of exact locality data. Therefore, it was labeled; "from South Africa." The comprehensive description, beautiful illustrations, and the original specimen housed in the South African Museum (Registry number SAM A5053) allow a safe attribution of

the name to typical, pyriform specimens of the South African population.

Franz Alfred and Maria Schilder (1938) commented on *B. fultoni*: "The South African *fultoni* and the Arabian *teulerei* are relics of the genus *Bernaya*, which was abundant in Eocene times," and gave the information on *B. fultoni*



**Figure 1.** *Barycypraea fultoni fultoni* Sowerby III 1903, holotype (60 millimeters), collection of South African Museum. Photo courtesy William Liltved.

"mostly found in the stomachs of fishes." The fish is the musselcracker (*Cymatoceps nasutus* Castelnau, 1861).

A brief treatise of the species was given by C.M. Burgess (1970), who called it "one of the rarest species and one of the most unusual, since most specimens have been recovered from the stomachs of fish." <sup>1</sup> He illustrated an amazing shell, are described later in this article (See Type Locality, Distribution and Habitat section).

Before 1980, there were less than 40 specimens known from South Africa. Later on in the mid-1980s, Russian trawlers found thousands of specimens of *B. fultoni* around Mozambique. The following section will detail the populations found from Mozambique. One should realize that finding specimens around South Africa is still rare, with scattered findings made by dredging.

The Mozambican populations of *B. fultoni* were first discovered in early 1987, by Russian trawlers operating between Inhambane and Maputo in southern Mozambique. An American collector bought the then world record size of slightly less than 80 mm specimen for \$22,000 (Beautiful Cowries Magazine No. 2 (2012), page 6). Since then three of these specimens were purchased by Dr. Luigi Raybaudi Massilia, one of them, measuring over 80 millimeters, at \$25,000.00 US. This specimen was listed in the Guinness Book of World Records as the most expensive seashell ever sold. Another specimen was sold to the German collector Ludwig

Gabrielli in 1988, and several more made their way to Raybaudi and other top collectors at that time.

The first printed picture of a Mozambican *B. fultoni* *amorimi* *massieri* (Lorenz, 1991) was illustrated on the cover of the "Sea Gifts" Sales catalogue on September 5th, 1988, issued by Steven Whatmough, a shell dealer from Cape Town, South Africa. The shell, measuring 67 mm, was said to come from South Africa. The inflated shape, pattern, and size clearly reveal its Mozambican origin. Steven did not know the exact provenance and later stated that the shell (See Figure 2) was found by a commercial fish trawler somewhere north of Durban (personal communication with Felix Lorenz 1989).



**Figure 2.** The first illustrated specimen of a Mozambican *Barycypraea fultoni*. Explanation in the text.

<sup>1</sup> A student of biology reading about *fultoni* being recovered from the stomachs of fish questioned this information: "a seashell can impossibly live in the stomach of a fish"! (in a personal communication with Felix Lorenz, circa 2005).

In 1989, the discovery of the northern (Mozambican) population was announced by Raybaudi (in *The Connoisseur* No. 22). By that time, large numbers of Mozambican specimens had become available at relatively affordable

prices. In The Connoisseur magazine Number 23, Raybaudi subdivided the Mozambican shells into two groups: pyriform specimens, which he assigned to *B. fultoni fultoni*, with the taxonomically invalid name "*mozambicana*," (which was described as a variety rather than a taxa) and extremely calloused, deltoidal shells, for which he proposed the subspecies name *B. fultoni amorimi* Raybaudi 1990.

As described by Lorenz in his work in 1991, the "*mozambicana*" form should be given a taxonomically valid name, as it differed considerably from the nominate South African *B. fultoni fultoni*. (Lorenz, 1991) With the consent of Raybaudi, Lorenz formally described *B. fultoni massieri* in 1991, which differs from *B. fultoni amorimi* by the pyriform shape, a flat instead of convex base, and the lack of marginal callus protuberances. This publication also gave a comprehensive analysis of the conchological differences between the nominate *B. fultoni* and the Mozambican shells, and a general overview on the genus *Barycypraea*.



**Figure 3.** *Barycypraea fultoni deltoidea*, ex pisce, South Africa. From Burgess (1970) Plate 4 Figure A, A1 - the exact locality, size, and whereabouts of this specimen are unknown. First published record of the new subspecies (though not appreciated at the time as a new subspecies).

In World Shells No. 9 (1994), Raybaudi challenged the subspecific status of *B. massieri*

as he could assemble intermediate stages of *B. amorimi*, assuming that the heavily calloused shells are gerontic, adding the varietal name "*triangularis*." He illustrated several Mozambican shells as "*fultoni typica*" (See Figure 3 and Figure 5) as supposedly from Natal, and introduced the varietal name "*miniatra*" for the nominate South African population. In his Tables 1 and 2, he tried to demonstrate that *B. amorimi* and *B. massieri* were gradual forms. However, while Table 1 shows specimens clearly not showing marginal callus (= typical *B. massieri*), Table 2 shows a South African *B. fultoni fultoni* (top row left), an inflated, but otherwise typical *B. massieri* (top middle), and six specimens of *B. fultoni amorimi* with varying degree of marginal callus well-discernible on their dorsal views.

In the Beautiful Cowries Magazine No. 2 (2012), Bergonzoni gave a detailed report on the species, with a comparison with fossil taxa of the genus. This study is a highly recommended reference as it gives a lot of interesting extra information and anecdotes. He perpetuated the usage of the name "*miniatra*" as a variety of *B. fultoni fultoni* from South Africa, and gave preference to the name earlier, taxonomically invalid name *mozambicana* over the legitimately introduced *B. massieri*. In his richly illustrated article, Bergonzoni did not mix up Mozambican and South African shells, and on comparing the illustrations of the Mozambican specimens carefully, the differences between *B. amorimi* and *B. massieri* once again are quite obvious.

In Lorenz & Hubert's first two "Guides" (1993, 2000), the status of *B. massieri* was still kept on the subspecies level, but in the checklist of the book "New Worldwide Cowries" (2002) Lorenz reduced its status to that of a variety of *B. amorimi*. In the recent "Cowries" Volume 1, Lorenz described the differences between South African *B. fultoni fultoni* and Mozambican

populations: "In *fultoni fultoni*, the anterior extremity tapers gradually. The dorsal part of the anterior canal exceeds the pointed extremities in length, so that from dorsal view, the anterior tips are not visible. In all Mozambican shells (*amorimi* and its variation *massieri*), the tips on either side of the anterior extremity are swollen, forming ridges that are visible from dorsal view. Hence the anterior extremity is narrow below the dorsum and then widens slightly because of the produced tips" Page 318, paragraph 6) (...) (and on referring to the number of columellar teeth: "The most notable difference is the fewer, more widely spaced columellar teeth in *fultoni* (11-14 counted teeth in an average-sized shell of 60 mm), against the considerably denser and more numerous teeth in *amorimi* (16-20 in an average-sized shell of 70 mm)" (paragraph 9). Lorenz also mentioned that only in Mozambican populations, the dorsal nacre is usually granulose in fully adult specimens, whereas South African shells always have a smooth nacre.

The above published descriptions by Lorenz are different from his own study of 1991, in which he demonstrated the differences between *B. amorimi* and *B. massieri* in a convincing manner. (Lorenz, 1991) These features include the convexity of the base in *B. amorimi* as opposed to the flat base of *B. massieri*, apart from the obvious difference in the shells' outlines (as well as multiple other features). The published opinions by Lorenz that only one Mozambican population exists, is not shared herein. (Lorenz 2017, Volume 1) The reasons include the following:

a) There are conchological differences between *B. fultoni amorimi* and *B. massieri* characterizing what appear to be separate populations, with only a few specimens that are not clearly assignable to either one. Specimens

of *B. fultoni massieri* are more likely to be globular in shape than *B. amorimi*, and their extremities are quite rostrated. *B. fultoni amorimi* often have deltoidal appearances (See Table 1 and Plate 3).

b) There are also extremely heavy and calloused shells of *B. massieri* without the slightest indication of marginal protuberances characteristic in *B. amorimi*. At the same time, there are specimens of *B. amorimi* without dorsal granules characteristic of fully mature shells. Therefore, the extreme formation of callus is not an indication that *B. amorimi* is based on gerontic specimens as noted by Raybaudi.

c) The formulae (after Bridges & Lorenz 2013) indicate differences between *B. massieri* and *B. amorimi* (See Table 1).

d) It is not known where exactly the shells of *B. amorimi* as opposed to the vast amount of *B. massieri* were collected within the exact same range along the Mozambican coast. The two taxa might originate from geographically or bathymetrically-separated populations.

e) From all the information available, the population of deltoidal *B. amorimi* is from considerably deeper water than the comparatively abundant pyriform *B. massieri* from shallower water (*i.e.*, more than 250 meters as opposed to 75 to 125 meters, according to Raybaudi, 1990). There is a consensus that in direct developers such as the related Australian *Zoila*, bathymetric subspecies exist, whose conchological differences become more and more obvious with the different depths the shells originate from. (Lorenz, F.: Monograph of the Living *Zoila*, 2001, pages 13 to 14).

The subdivision of *B. massieri* versus the deeper water *B. amorimi* on the level of subspecies, therefore, is consistent with the taxonomic treatment of bathymetric populations in species of *Zoila*, as well as the South African

*Cypraeovula*, and the Caribbean *Muracypraea*. In these cases, Lorenz postulates that: "juvenile intracapsular developers can travel long distances on pieces of host sponge torn off from the sea floor (phoretic dispersal)." This may account for the relatively shallower-located *B. massieri* versus deep water *B. amorimi*. (Lorenz, 2001. Monograph of the Living *Zoila*).

Recently, a series of outstanding specimens of South African *B. fultoni* were brought to the author's attention. These shells originated from a confined area towards the southern border of the species' distribution. They present an interesting parallel to the conchological differences noted between *B. f. amorimi* and *B. f. massieri*.

*Barycypraea fultoni deltoidea*

M.A. Mont, n. ssp.

(Plate 1, Figures A-D)

**Description.** The shell is rather large for the genus and extremely heavy. The outline is deltoidal, due to marginal protuberances protruding on either side of the posterior end. The dorsal profile is evenly rounded, with its highest point in the midsection. The posterior canal is broad and deeply cut, bordered by callus dorsally. The shell is evenly tapering from the protuberances towards the anterior extremity. The tips are shorter than the dome of the anterior end, which is separated from the dorsum by a shallow indentation. The anterior tips are thick and pointing downwards. The aperture is evenly narrow and slightly curved to the left. The labral teeth are dense, well-produced along the aperture, becoming slightly denser and thinner anteriorly. They extend onto the labrum as shallow ribs. The columellar teeth are sparse and coarse, with side interstices. The fossula is concave, slightly projecting, and separated from a produced terminal pleat, which reaches far into the aperture. The base is

calloused and convex. The shell's ground color is grayish-white. The dorsum is framed by dark brown, leaving a cream-colored window, framed by darker brown-to-black irregular lines. These run parallel in some areas, and along a shallow longitudinal groove running from the anterior third to just above the extremity. The margins are grayish-cream and densely-spotted, with large, somewhat indistinct brown spots, which reach far onto the base and the labrum. These form depressions and indentations in the calloused areas and especially on the marginal protuberances. The teeth are orange along the aperture, enhanced by dark brown stripes labrally. The animal has a thin, transparent mantle with numerous fingerlike papillae, which may merge from the same spot on the mantle, forming structures resembling tiny bushes. The tips of the papillae are white. They extend onto the transparent siphon. The tentacles, eye stalks, and the foot are transparent grayish.

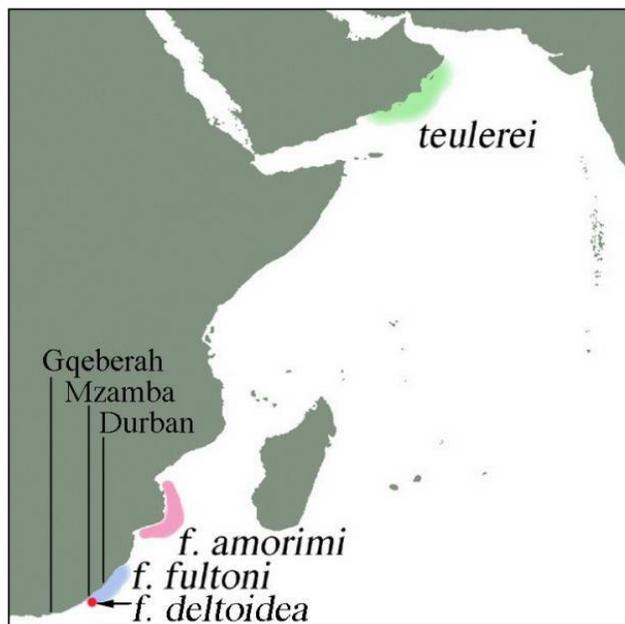
**Type Material.** Eleven live-collected and two dead specimens (one subfossil). All paratypes agree with the description of the holotype in a remarkably similar manner. Measurements enlisted length × width × height in millimeters (labral : columellar tooth count), [weight in grams].

Holotype:	62.6 × 45.3 × 31.3 (20:11) [59.6]
Paratype 1:	62.3 × 44.0 × 31.0 (19:11) [54.9]
Paratype 2:	65.5 × 44.5 × 31.6 (17:13) [56.9]
Paratype 3:	57.7 × 42.2 × 29.2 (18:11) [42.7]
Paratype 4:	64.5 × 44.1 × 31.6 (21:12) [57.1]
	fresh dead, not fully adult
Paratype 5:	62.3 × 42.2 × 31.2 (19:14) [50.9]
Paratype 6:	62.0 × 44.7 × 32.2 (19:10)
	subfossil
Paratype 7:	62.8 × 41.8 × 30.7 (19:12) [52.5]
Paratype 8:	66.6 × 45.2 × 31.8 (21:10) [57.9]
Paratype 9:	65.9 × 43.3 × 32.7 (21:14) [57.1]
Paratype 10:	62.0 × 41.8 × 31.2 (18:9) [49.7]
Paratype 11:	66.1 × 45.2 × 32.4 (20:12) [57.6]
Paratype 12:	68.5 × 46.3 × 34.9 (19:11) [66.6]

The types are placed in the Molluscan Science Foundation, Inc. ("MSF"), Baltimore, Maryland, USA. The Holotype bears MSF No. 11261, and Paratypes 1 to 6 bear MSF Nos. 11262-11267.

#### Type Locality, Distribution and Habitat.

Most specimens of *B. fultoni deltoidea* n. ssp. were collected at 67 to 72 meters, on muddy sand with sparse sponge growth, offshore at the mouth of the Mzamba River, which is on the border between southern Kwa-Zulu-Natal and the northern Transkei (Type locality). A subfossil specimen (Paratype 6) with pronounced marginal protuberances was dredged in the same general area at 75 meters. A specimen conchologically identical to the recent findings was taken *ex pisces* in the 1960s and illustrated in Burgess (1970) (his Plate 4, A and A<sub>1</sub>). The exact provenance and depth of this shell are unknown (See Figure 3).



Map 1. Distributions of living *Barycypraea* (after Lorenz 2018, modified)

**Etymology.** *B. fultoni deltoidea* is named on account of its most outstanding feature; the deltoid shape.

#### DISCUSSION

*B. fultoni deltoidea* n. ssp. was collected at lower depths than the nominate *B. fultoni fultoni* found offshore in the northern Transkei to the north of Durban (See Map 1). Dead, subfossil specimens have been found as far south as East London. It lives at 67 to 72 meters on a similar sandy habitat and has repeatedly been found by dredging. Although variable in shape and coloration, no specimens with comparable marginal protuberances have ever been observed in the nominate *B. fultoni fultoni*. Specimens with an indication of such structures are known, and the holotype of *B. fultoni* is such a shell (See Figure 1). Further examples are shown on Plate 3. However, the deltoidal shape and the conspicuous marginal protuberances set all known specimens of *B. fultoni deltoidea* completely apart from its deeper water South African sister. This supports the subspecific (rather than the varietal) status. The indentation of the posterior canal on the dorsal view is shorter in *B. f. deltoidea*, and in *B. f. fultoni* the tips are more pointed and projecting. The specimens of *B. f. deltoidea* known to date are all quite large and exceptionally uniform, indicating that they belong to a confined genetically-isolated community.

Both South African taxa share the characteristics of the formation of the anterior extremity and the lesser number of columellar teeth, which separates these shells from the Mozambican *B. amorimi* and *massieri* among other less obvious features (See Table 1). The existence of a bathymetric-located subspecies with pronounced marginal callus accumulations in both areas inhabited by the species (Southern Africa and Mozambique) is an interesting parallel. However, one can ponder that the bathymetric occurrence of the "triangular" shape is the opposite.

	<i>fultoni fultoni</i>	<i>fultoni deltoidea</i>	<i>fultoni amorimi</i>	<i>fultoni massieri</i>
Distribution	Kwa-Zulu-Natal to Northern Transkei	Northern Transkei	Southern Mozambique	Southern Mozambique
Depth range (meters)	90-150	67-72	> 250	75-125
Length (mm)	56-64 (61)	58-69 (64)	66-78 (70)	54-84 (72)
Width/length in %	60-68 (64)	66-73 (69)	71-76 (74)	64-69 (67)
height/length %	47-52 (50)	48-52 (50)	53-58 (56)	54-57 (55)
Columellar teeth	9-15 nl: 10	9-14 nl: 10	17-19 nl: 13	16-21 nl: 13
Mass ratio	17-21 (18.5)	20-22 (21.3)	18-20 (18.9)	14-19 (16.0)
Shape	narrow, pyriform	<b>deltoidal</b>	rhomboidal	inflated pyriform
Dorsal profile	low, rounded	low, rounded	high, humped	high, humped
Margins	Rounded	<b>Rounded</b>	Bent up, rounded	Low, less rounded
Base	Convex	Convex	Convex	Flat
Posterior tips	Pronounced	<b>Shorter</b>	Pronounced	Pronounced
Anterior tips	narrow, pointed	narrow, pointed	broad, spatulate	broad, spatulate
Basal spots	large, dense, dark	large, dense, dark	less dense, paler	less dense, paler
Enamel (mostly)	smooth, glossy	smooth, glossy	granulose, silky	granulose, silky
Formulae	61 (64 - 50 - 79) 15 : 10 [18.5]	<b>64 (69 - 50 - 72)</b> <b>15 : 10 [21.3]</b>	70 (73 - 56 - 77) 17 : 13 [18.9]	72 (67 - 55 - 82) 15 : 13 [16.0]

**Table 1.** Comparison of the subspecies of *B. fultoni*. The number of specimens from which the measurements were derived are: *B. f. fultoni*: 17; *B. f. deltoidea*: 11; *B. f. amorimi*: 8; and *B. f. massieri*: 26. Formulae after Bridges & Lorenz 2013. Average values in brackets, nl: normalized average number of teeth.

While the subdivision of the species in South African (*B. fultoni*) versus a Mozambican (*B. amorimi*) subspecies is well-supported as well by molecular data, there remains an uncertainty concerning the two taxa from shallower water from the same general areas (*B. deltoidea* in South Africa and *B. massieri* in Mozambique). Their position either as bathymetric subspecies or bathymetric formae is an open question and for the time being, can remain as a matter of subjective interpretation.

### Observations on the genus *Barycypraea* and related genera

In 2016, Fehse described the genus *Afrozoila* for the Pliocene *Barycypraea zietsmani* (Liltved & Le Roux, 1988), the living *Barycypraea fultoni* (G.B. Sowerby III, 1903) from South Africa, the Arabian *B. teulerei* (Cazenavette 1846), and various species from the Miocene of India and Indonesia. These are supposedly distinct from *Barycypraea*, which was based on *B. caputviperae* (Martin 1899) from the Indonesian Miocene. Fehse (2016) makes statements which deserve some further discussion.

Lorenz briefly commented on *Afrozoila* in his 2017 Cowries Volume 1: "As the shell morphology of the Indonesian *B. caputviperae* group also resembles members of *Muracypraea*, Fehse (2016a) suggested a phylogenetic relationship between these genera. He erected the genus *Afrozoila* to accommodate morphologically less extreme fossils and two living species (*Barycypraea fultoni* and *B. teulerei*) that are interpreted as ancestral to the genus *Zoila*. To me, the morphological ties between the Indonesian fossils and the South African *B. fultoni* and its fossil precursor *B. zietsmani* are too obvious to follow this interpretation. First of all, the dorsal tubercles forming a window with a Maltese cross pattern is a feature that the living *B. fultoni* and the Indonesian Miocene *B. caputviperae* (Martin, 1899) and related taxa have in common. Secondly, the formation of the tubercles is quite similar between the South African Pliocene *B. zietsmani* and the *B. caputviperae* group. The similarity to *Muracypraea* is remarkable but superficial, as the marginal stripes observed in some *B. caputviperae* are a structural color, not a color pattern that can be compared to the striped margins of many *Muracypraea*. Instead, the margins of the *B. caputviperae* group were spotted as in all other *Barycypraea*, as can be seen under UV light."

When *Barycypraea fultoni* and *B. teulerei* are superficially compared with the conchologically extreme *B. caputviperae*, on which the concept of the genus *Barycypraea* must be based, the relationship might not seem that obvious. However, there are numerous closely related fossil species described from the same general area and stratigraphy as *B. caputviperae* which show a very similar shape, and a Maltese cross pattern visible even with the bare eye. The South African *B. zietsmani* from the Pliocene conchologically connects *B. fultoni* with the Indonesian Miocene *B. caputviperae* and its

allies, as the Plates 5 and 6 herein demonstrate. Fehse related one of the less extreme relatives, *Barycypraea musissimilis* (Martin 1879) to *Muracypraea henekeni* (Gabb 1873) from the Caribbean Miocene.

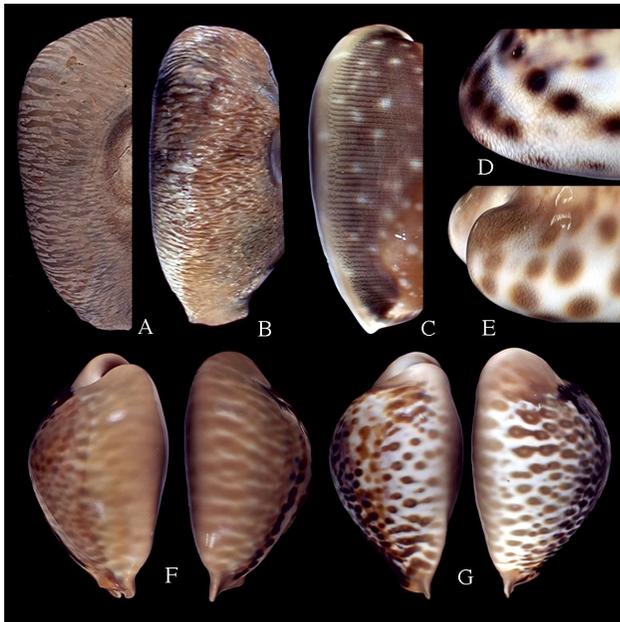
A depression on the base above the columellar teeth found in both of these specimens is supposed to support this. A similar depression is also discernible in *B. zietsmani*, and it is absent from other Indonesian species directly related to *B. caputviperae*, and also, from most other fossil *Muracypraea* from the Caribbean (See Figure 4).



**Figure 4.** The depression above the columellar peristome. Left: *Muracypraea* sp. Miocene, Panama. Middle: *Barycypraea* cf. *caputviperae* Miocene, Indonesia. Right: *Barycypraea zietsmani* Pliocene, South Africa.

The margins of *Barycypraea caputviperae* and its relative *B. murissimilis* show a brilliant iridescent striping, which is a phenomenon caused by the microstructure of the shell in combination with a process of fossilization that enhances this feature. In living cowries, such a structure is well-visible in *Cypraea tigris* Linnaeus 1758 and *Lyncina vitellus* (Linnaeus 1758). In other species of *Lyncina* (e.g. *L. lynx* Linnaeus 1758), this structure is absent and therefore does not aid in generic characterization. To a lesser extent, it is found in *B. teulerei* and quite obviously is a feature found mainly in strongly calloused shells (See Figure 5). This pattern is not homologous with the striped coloration margins in derived forms

of *Muracypraea*, in which the marginal pattern is primarily dark spotting, as can be seen in fossils as well as living specimens of the extant *Muracypraea mus tristensis* Petuch 1987. This dark spotting is also discernible in fossil and extant *Barycypraea*.

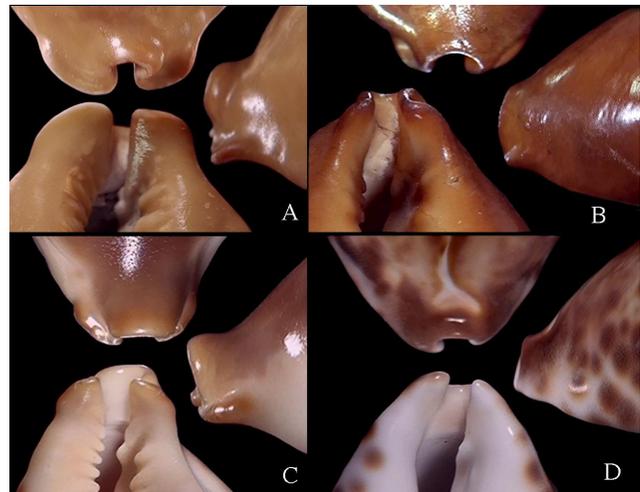


**Figure 5.** Top: Iridescent microstructure in **A, B**= *Barycypraea caputviperae*, **C**= *Lyncinia vitellus*, **D**= *Cypraea tigris*, and **E**= *B. teulerei*. Bottom: Marginal pigmentation in **F**= *Muracypraea mus mus*, and **G**= *M. mus tristensis*. Not to scale. Explanations in the text.

Aspects of the anterior extremity shown in Figure 3 show that this feature can not be used to distinguish between *Barycypraea* and the "*Afrocypraea*" group, and the spatulate anterior extremity of most *Muracypraea* does not resemble that of *B. caputviperae* at all. Instead, the peculiar split callus-ridge on the center of the dorsum (See Plate 5: L, M) is only found in the *B. caputviperae* group and *B. zietsmani*, which indicates a close relationship between them.

Fehse's statement that "*mus* and *fultoni* are not related" is in my opinion a misinterpretation of the molecular data. The phylogram (See Figure

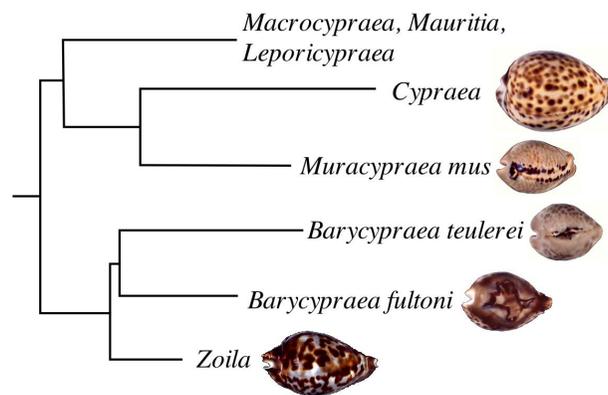
7) merely shows that the relationship between *Barycypraea* and *Zoila* is closer than to *Muracypraea*, but all three genera merge from an ancient lineage which also gave rise to *Cypraea* and the group of *Mauritia*, *Leporicypraea*, and *Macrocypraea*. What can be said is that the Caribbean *Muracypraea* split off that lineage at an earlier date than *Barycypraea* and *Zoila*, but this does not denote that it is "not related" to *B. fultoni* and *B. teulerei*. Given the fossil record, we can assume that the separation between these groups could have happened in the Oligocene, and *Muracypraea* has always been restricted to Central and Northern America. An interesting observation on the side is that the animals of *Cypraea tigris*, *Muracypraea mus*, and *Barycypraea fultoni* have in common is that their papillae are finger-like, with a conspicuous white tip (See Figure 14).



**Figure 6.** Different aspects of the anterior extremity. **A**= *Muracypraea* sp., Miocene, Dominican Republic; **B**= *Barycypraea caputviperae*, Miocene, Indonesia; **C**= *Barycypraea fultoni amorimi*, recent, Mozambique. **D**= *Barycypraea teulerei*, recent, Oman.

The supposed generic division of the Indonesian Miocene fossils related to *B. caputviperae* (*Barycypraea sensu stricto*) from certain Miocene fossils and the extant *B. fultoni* and *B. teulerei* (*Afrozoila* according to Fehse, 2016) is

based on conchological features. The dilemma is only that the differences between *B. teulerei* and *B. fultoni* are certainly greater than between *B. fultoni*, the ancestral *B. zietsmani*, and the *B. caputviperae* group. In *B. teulerei*, there is no distinct dentition, the fossula region differs from all other taxa (except the Pliocene *B. zietsmani* to a certain extent), and the dorsal pattern shows no indication of an exposed median area or a Maltese cross pattern (See Plate 9).



**Figure 7.** Molecular phylogram of *Barycypraea* and related genera, after Meyer (2004, modified).

The recently described *Barycypraea iungo* Aiken & Seccombe, 2022 from Richards Bay is clearly linked to *B. zietsmani* from further south. Its exact stratigraphy is unknown, but assumed to be of similar age (Pleistocene of the Alexandria formation). The remarkable, well-preserved shell resembles an inflated *B. zietsmani*, but shows distinct columellar dentition, and its position as a conchological link between the fossil South African lineage and the living *B. fultoni* is obvious and its name well-chosen (See Figure 17). The authors also note a similarity to the Indonesian *B. murissimilis*. In concluding, if a distinction of *Afrozoila* from *Barycypraea* was pursued, then *B. teulerei* would require a separate genus, based on the aberrant conchology of that species. The molecular data, on the other hand, shows *B. fultoni* and *B. teulerei* to be sisters. What can be

said is that none of the conchological features we can derive from the fossil and the living record is suitable for a distinction of the Miocene Indonesian and the Pliocene to recent Western species complexes.



**Figure 8.** *Barycypraea iungo* Aiken & Seccombe 2022. (60 mm) Richardsbay, Kwa-Zulu Natal, South Africa, Pleistocene. MSA-Mol 0P2009/T4560.

The protoconch of *Barycypraea zietsmani* indicates intracapsular development, but morphologically, it is quite different from that of *B. fultoni*, being pointed instead of sunken, and much smaller (*i.e.*, 0.15 versus 0.25 millimeters in *B. fultoni*). But although more similar in size, it does not resemble the protoconch of *B. teulerei* in shape (See Figure 9). A scenario where *Muracypraea* is basically synonymous with *Barycypraea* would presuppose a westward migration from Central America across the Pacific. For cowries, only few species have migrated eastward across the Pacific to the Panamic province (*e.g.*, *Luria isabella*, *L. isabellamexicana*, *Talostolida pellucens*, and *T. p. panamensis*). However, this happened approximately five million years later, when prevailing ocean currents had changed after the closure of the isthmus of Panama.

Also, all cowry species that reached to the western coast of America from the Central Pacific are known to have a long planktonic phase, allowing the eastward travel during phases of exceptional surface currents from their western distributions, and only after geographically, "stepping stones" such as the

Hawaiian and Galapagos Islands and Clipperton Atoll had formed. The same could not have happened during the Miocene, in the opposite direction, and not within groups that had by then given up planktonic development.



**Figure 9.** Protoconchs of *B. fultoni fultoni* (top left and middle), *B. teulerei* (bottom left), and *B. zietsmani* (top and bottom right). Scale = 1 centimeter.



**Figure 10.** Cowries of the Eocene that might be forefathers of *Muracypraea* and *Barycypraea*. Are the similarities to *Barycypraea* (i.e., tubercles and callousities, reduced dentition), convergent developments, or an indication for relationship? Left: *Gisortia tuberculosa* (Duclos 1825), (117 mm) Ypresian Eocene,

Gan, France. Right: *Vicetia roncana* (De Gregorio 1896), (106 mm), Lutetian Eocene, Dudar, Hungary.

The conchological similarities between the fossil *Barycypraea*, *Muracypraea*, and the once widespread Eocene *Gisortia* and *Vicetia* suggest that there could be a common ancestry that lies much further back (See Figure 9). A problem in this hypothesis arises from the lack of sufficient fossil records dating from the Oligocene epoch (a gap of approximately 10 million years), or perhaps, we do not recognize them as what they might have been, as the state of preservation of the few candidates for continuing the lineages is too poor to allow exact generic assignments. Apart from fossil and living species of *Muracypraea* and *Barycypraea* (See Figure 7), and the "monsters of the Eocene of the genera *Gisortia* (see Figure 11 and *Vicetia*), there have been very few examples of cowries with prominent tubercles (with the popular exception of *Monetaria moneta*).

The features of marginal and dorsal tubercles framing a window (often decorated by a Maltese-cross pattern) could be a convergent development inherent to all cowries, which may be switched on and off within genera or even species. An example is *Monetaria moneta* (Linnaeus 1758), of which there are smooth and



**Figure 11.** A= *Muracypraea* cf. *henekeni* (52 mm) Miocene, Dominican Republic; B= *Barycypraea zietsmani* (51 mm) Pliocene, South Africa; C= *Barycypraea* cf. *caputviperae* (45 mm) Miocene, Java, Indonesia; D= *Barycypraea fultoni deltoidea* (62 mm) Recent, South Africa; E= *Barycypraea teulerei* (50 mm) Recent, Oman.

heavily tuberculose forms, and forms in which a distinct orange ring visually enhances the dorsal window encircled by callus and tubercles. Such forms do not occur throughout the range of the species, but predominantly in the Central Pacific and on isolated Atolls (See Figure 12).



**Figure 12.** *Gisoritia megaloptera*, 160 mm (Miocene)

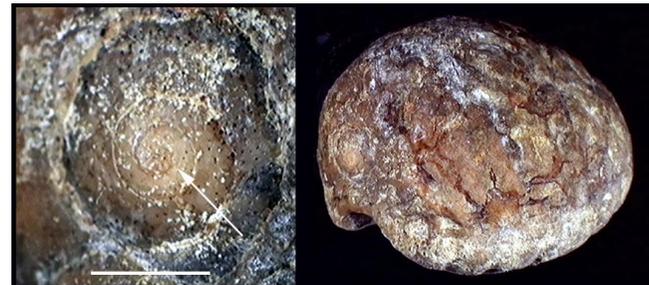


**Figure 13.** Convergent development of tubercles. Left: *Monetaria moneta* (14 mm) Tahiti, right: *Barycypraea cf. caputviperae* (48 mm) Java, Indonesia, Miocene.

Is intracapsular development an evolutionary cul-de-sac and not reversible within a lineage? Lorenz (2017) stated "the morphological modifications required from planktonic to intracapsular development are minimal (...) with few or no phylogenetic implications" to which he recently added "and is most probably reversible" (Lorenz, personal communication 2018). The dynamics by which cowries distribute, also over long distances, might include the capacity of switching back and forth between developmental modes to adapt to local conditions within a relatively short period of evolution: to low water temperature, or to strong prevailing ocean currents. In the intracapsular developers, the vertical dispersal of populations seems dependent on ocean currents, whereas, the horizontal dispersal over different bathymetric levels may require additional factors.

In planktonic developers, bathymetric boundaries do not exist as larvae may drop to deep water from the sea surface, the chances of survival are just much lower than in intracapsular developers. In this regard, they "play it safe."

An interesting observation, independent from the above, relates to one of the oldest known true cowries, *Afrocypraea chubbi* (Rennie 1930). This fascinating and mysterious cowry, completely covered with prominent pustules, had a large paucispiral protoconch suggesting an intracapsular developer (See Figure 13). It was discovered in the Campanian Cretaceous deposits along the beach of the Mzamba River, near the type locality of *B. fultoni deltoidea*.



**Figure 14.** *Afrocypraea chubbi* (80 mm), Mzamba, Northern Transkei, Cretaceous (Campanian, approximately 72 million years old). Left: detail of the spire, arrow pointing at the paucispiral protoconch indicating intracapsular development. Scale = 1 centimeter.



**Figure 15.** Similar papillae in the animals of *Cypraea tigris* (left), *Muracypraea mus* (middle, photo Gary Schmeltz), and *Barycypraea fultoni*. Courtesy Felix Lorenz. Explanations in the text.

**Conclusion.** The delta-shaped *Barycypraea fultoni deltoidea*, was described as a new subspecies. The separation of the two distinct Mozambican *B. fultoni* populations has been

clarified. A further description of the four *B. fultoni* taxa have been compared and contrasted. Various observations about *Barycypraea* and related genera have been described in detail. *Afrocypraea chubbi*, found in Cretaceous deposits near locality of *B. fultoni deltoidea*, was described.

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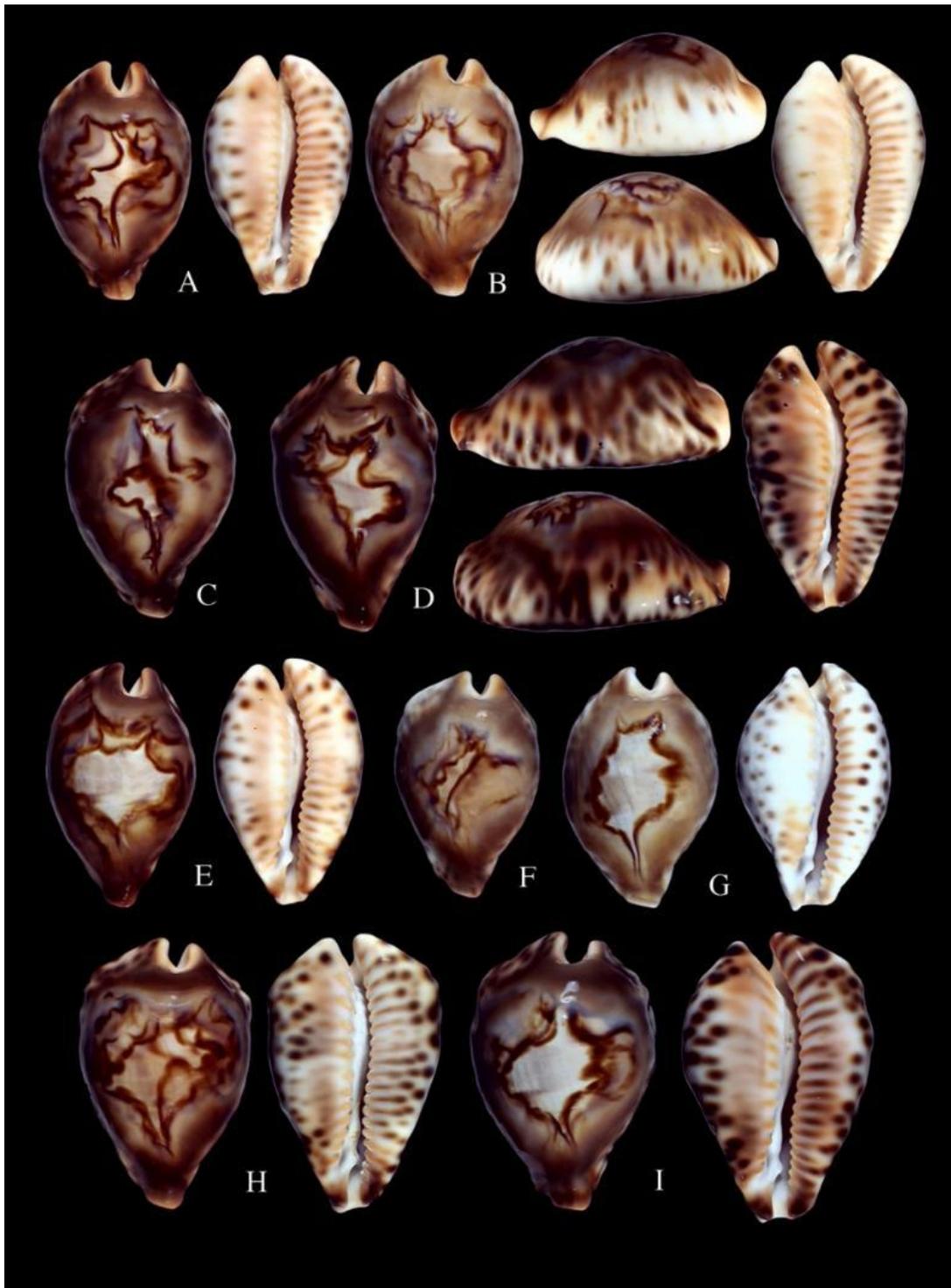
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**Plate 1.** *Barycypraea fultoni deltoidea* n. ssp. All from Mzamba, Northern Transkei, at 67-72 meters. **A**= Holotype (62.6 mm) (MSF No. 11261; **B**= Paratype 1 (62.3 mm) (MSF No. 11262); **C**= Paratype 3 (57.7 mm) (MSF Np. 11263); **D**= Paratype 2 (65.5 mm) (MSF No. 11264).



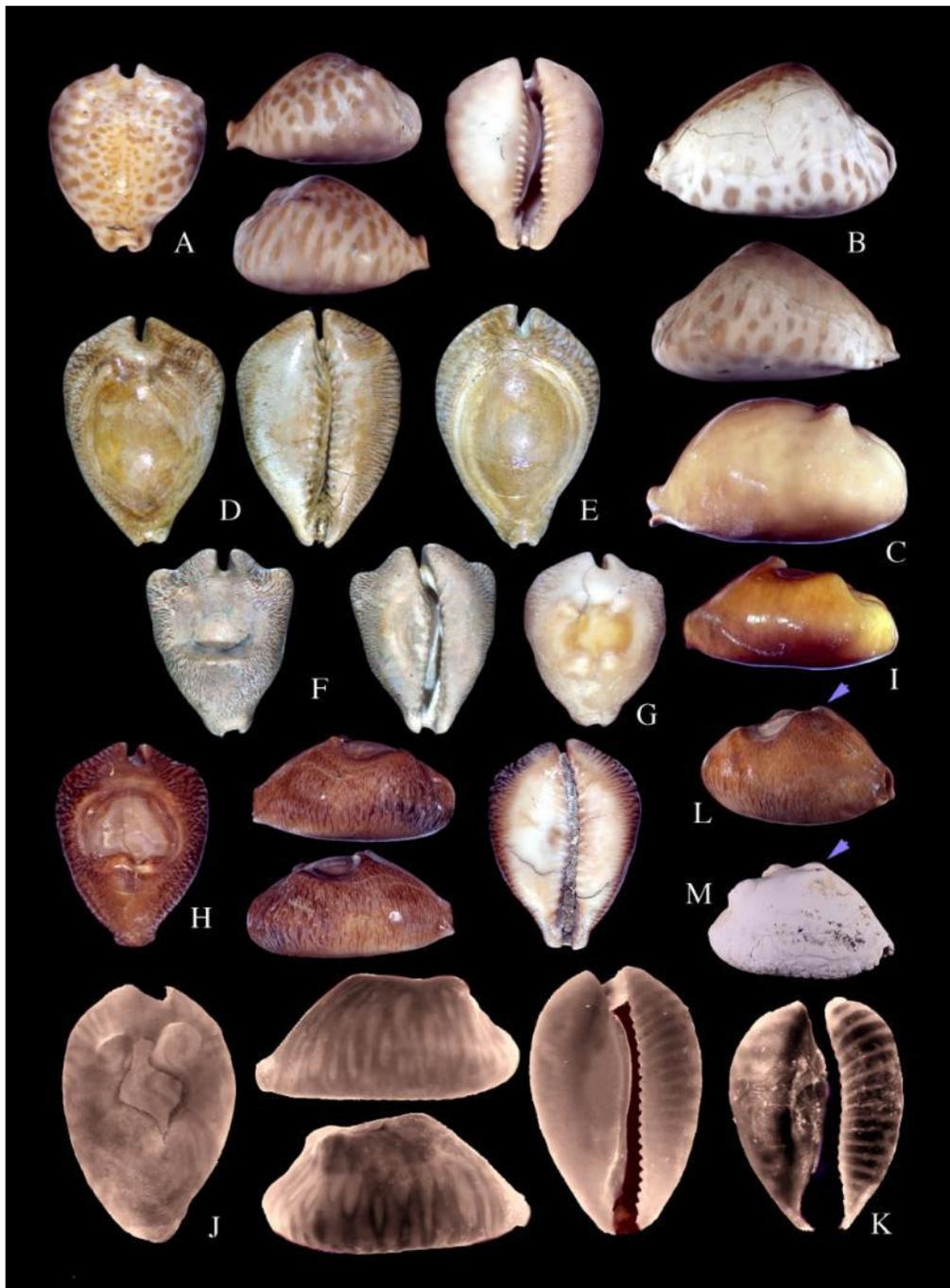
**Plate 2.** *Barycypraea fultoni fultoni* (Sowerby III 1903). Variations from Kwa-Zulu Natal, South Africa. **A**= 56 mm. Durban area, Kwa-Zulu Natal, ex pisce; **B**= 59 mm. Hibberdene, Kwa-Zulu Natal, at 125 meters; **C-E**= 59-64 mm. Pennington, Kwa-Zulu Natal, at 100-120 meters; **F, G**= 56-57 mm. Southern Kwa-Zulu Natal, at 100-150 meters; **H, I**= 61-64 mm. Umkomaas, Kwa-Zulu Natal, at 90-105 meters.



**Plate 3.** *Barycypraea fultoni massieri* Lorenz 1991. A-D= 55-75 mm. Southern Mozambique, at 75 to 125 meters; *Barycypraea fultoni amorimi* Raybaudi 1990 E-H= 68-77 mm. Southern Mozambique, at 150-250 meters.



**Plate 4.** *Barycypraea zietsmani* Liltved & Le Roux 1988 (47-65 mm) Pliocene (Alexandria Formation) near Coega, north of Gqeberha (formerly Port Elizabeth), South Africa.



**Plate 5.** A, B= *Muracypraea woodringi* Landau & Groves 2011 (38-52 mm), Late Miocene, Cativa, Colon, Panama; C= *Muracypraea henekeni* (Gabb 1873) (52 mm) Pliocene. Gurabo River, Dominican Republic; D= *Barycypraea murissimilis* (Martin 1879) (44 mm) Miocene, Nyalindung, Java, Indonesia; E= *Barycypraea beberkiriana* (Martin 1879) Miocene, Nyalindung, Java, Indonesia; F= *Barycypraea caputviperae* (Martin 1899) (34 mm) Miocene, Nyalindung, Java, Indonesia; G= *Barycypraea quadrinodosa* Fehse 2012 (32 mm) Miocene, Nyalindung, Java, Indonesia. Note the well-visible maltese-cross pattern; H, I= *Barycypraea caputviperae* (Martin 1899) (37-41 mm) Miocene, Nyalindung, Java, Indonesia; J, K= *Barycypraea zietsmani* Liltved & Le Roux 1988 (47-53 mm) Pliocene (Alexandria Formation) near Coega, north of Gqeberha (formerly Port Elizabeth), South Africa. Photos taken under UV light and inversed to display the color pattern; L, M= top: *caputviperae*, bottom: *zietsmani*, arrow pointing at the dorsal callus ridge these species had in common.



**Plate 6.** A-C= *Barycypraea teulerei* (Cazenavette 1846) (43-48 mm) Masirah Island, Oman, intertidally. The shell morphology of this strange cowry does not resemble any other living or fossil species, yet the molecules show it as closest related to *fultoni*; D= *Muracypraea mus mus* (Linnaeus 1758) (41 mm) Amuay Bay, Venezuela, shallow water; E= *Muracypraea mus bicornis* (Sowerby II 1870) (52 mm) Paraguana Peninsula, Venezuela, at 40 meters; F= *Muracypraea mus bicornis* f. *tristensis* Petuch 1987 (54 mm) Cabo de La Vela, Colombia, at 100-120 meters; G= *Muracypraea mus bicornis* f. *donmoorei* Petuch 1979 (48 mm) Goajira Peninsula, Colombia, at 60-80 meters; H= *Muracypraea mus bicornis* f. *insolatia* Lorenz 2017 (48 mm) Paraguana Peninsula, Venezuela, at 60 meters; The variability of the dorsal tubercles, the dentition, the formation of the anterior extremity, and the color pattern is remarkable. Molecular data reveals that all the living members of *Muracypraea* are very closely related.