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MONOGRAPH

Barycypraea teulerei (Cazenavette, 1845) (Gastropoda Cypraeidae): a successful species or an evolutionary dead-end?

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ABSTRACT *Barycypraea teulerei* (Cazenavette, 1845) (Gastropoda Cypraeidae) is an unusual cowrie species, showing remarkable adaptations to an uncommon environment. It lives intertidally on flat sand/mud salt marshes, in a limited range, in Oman. On Masirah Island, humans probably drove it to extinction because of shell collecting. A new population, with a limited range, has recently been discovered, and this article describes observations I made on site in 2014. Evolution shaped this species into a rather specialized and successful life, but has also put it at risk. *Barycypraea teulerei* is well adapted to survive in its habitat, but at the same time is easily visible and accessible to humans, and this puts it at high risk of extinction. Evolution is indeed a blind watchmaker that '*has no vision, no foresight, no sight at all*'. And *B. teulerei* was just plain unlucky to encounter our species on its journey on our planet.

KEY WORDS Cypraeidae; *Barycypraea teulerei*; Biology; Evolution; Blind Watchmaker.

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INTRODUCTION

"*Natural selection, the blind, unconscious, automatic process which Darwin discovered, and which we now know is the explanation for the existence and apparently purposeful form of all life, has no purpose in mind. It has no mind and no mind's eye. It does not plan for the future. It has no vision, no foresight, no sight at all. If it can be said to play the role of watchmaker in nature, it is the blind watchmaker*".
R. Dawkins, The Blind Watchmaker, 1986.

Barycypraea teulerei (Cazenavette, 1845) (Gastropoda Cypraeidae) (Fig. 1) is one of only two relic species of the genus *Barycypraea* Schilder, 1927, along with the South African *Barycypraea fultoni* (Sowerby III, 1899) (Fig. 2). This genus is characterized by squat, heavy shells with a roughly triangular/pyriform shape. The mantle is always thin and almost transparent, whitish or pale brown, with little (*B. fultoni*) or no papillae (*B. teulerei*). Both species appear to be well adapted to sand and/or mud bottoms, although at very different depths. *Barycypraea fultoni* is a deep water species (Bergonzoni, 2012) while, as we will see in detail, *B. teulerei* is an intertidal one.

The genus comprises few fossil species, among them *B. ziestmani* Liltved et Le Roux, 1988 from the Alexandria Formation (Neogene), Port Elizabeth, S. Africa (Liltved, 2000), and the *B. caputviperae* species-complex from Indonesia (Miocene). The genus *Barycypraea* is morphologically and genetically linked to the genus *Zoila* Jousseaume,

1884, which is endemic to Western and Southern Australia. In this sense, the entire evolution of this cowrie lineage has always been strictly related to the Indian Ocean basin. The supposed similarity to the Venezuelan/Colombian *Muracypraea mus* (Linnaeus, 1758) and other allied fossil species of the Caribbean genus *Siphocypraea* Heilprin, 1897 [f.i. *S. problematica* (Heilprin, 1887)], seems not fully supported by molecular studies (Meyer, 2004).

A STORY OF A ONCE RARE SPECIES

Barycypraea teulerei was once an extremely rare species. In 1964, only 35 specimens were present in European collections (Schilder, 1964). Since 1969, only guesses were available about its distribution and habitat, since no one had ever reported a precise locality for the species. Specimens were labeled from different localities, including the Persian Gulf, Hormuz Strait, Aden, Arabian Sea, Red Sea, Port Sudan etc. (see Scali, 2013 for a detailed list), but in fact, no one knew where this species came from.

In March 1969, the very first specimens of *B. teulerei* were collected at Masirah Island (wrongly reported as Museera Island; Cross, 1969), a very remote island along the Oman coastline. *Barycypraea teulerei* appeared to live in very shallow water on sand/mud beds, and even outside the water during low tide. Since then, several malacologists made their way to Masirah to obtain specimens (see f.i. Williams, 1969; Luther, 1972; Charter, 1983) which soon became available for study and collection. One of the main sources was actually Dr. Donald 'Don' T. Bosch, who had a long service as a surgeon for the Sultanate of Oman. Dr. Bosch was the only surgeon in the entire country of 1.5 million people, and contributed to the modernization of health care in Oman. In recognition of his achievements, the Sultan of Oman awarded him with the "Order of Oman" in 1972. Don was also an extensive shell collector and a pioneer of Oman malacology. Many Oman species have been named by or after him (e.g. *Conus boschi* Clover, 1972, *Cymatium boschi* Abbott et Lewis, 1970, etc.), and he also dedicated some to his wife Eloise (e.g. *Acteon eloisae* Abbott, 1970). Because of Don Bosch and other shell collectors, thousand of specimens were easily available for a while, and the species became quite common in collections.

Eventually, in the early 90s, new fresh-collected *B. teulerei* began to disappear. By then, many collectors traveled to Masirah to collect specimens, without success. The species seemed to have simply vanished, probably due to over-collection and the relative ease of finding specimens by simply walking the flat beaches of the Island. Rumors were growing that this species had to be considered extinct.

In December 2012, after some unsuccessful trips to Oman, *B. teulerei* was found again by Massimo Scali and his family along the coastline of Oman (Scali, 2013; 2014), in a locality kept secret since then. The population was very healthy, with several thousand specimens freely grazing on a muddy flat bottom. Again, it was confirmed that this species lives in the intertidal zone. At low tide, *B. teulerei* does not hide itself under stones, as most cowries would do, and it is quite often completely exposed. In figure 3 you can see some in situ specimens during the sygyzian tide of 2014.

In December 2014, I was fortunate enough to join Massimo in his field trip to see this species on site. This article is basically a series of observations I've made that I hope will be of interest to the readers. I will discuss some of the aspects of the biology of this species, and I will express some considerations about its evolution.

THE HABITAT

Once I arrived at the place during the sygyzial tide of December 2014, I soon realized we were in an unusual habitat for a cowrie species. What I saw was basically a muddy salt marsh, covered with patches of algal mats and a few dark gray and orange sponges (Figs. 4, 5). No rock or evident coral to be found for kilometers. The only available hard substrate was a few *Pinna* sp. standing out of the bottom and a few dead bivalve shells. The mud was very anoxic, dark colored and stinking of sulfur. It was hard to walk on, at every step I remained glued in the mud. Despite this environment seeming quite inhospitable, a few minutes walking from the beach I found the first living *B. teulerei*. This mud flat is a relatively large area and we were walking, on average, 10–15 kilometers per day to observe *B.*

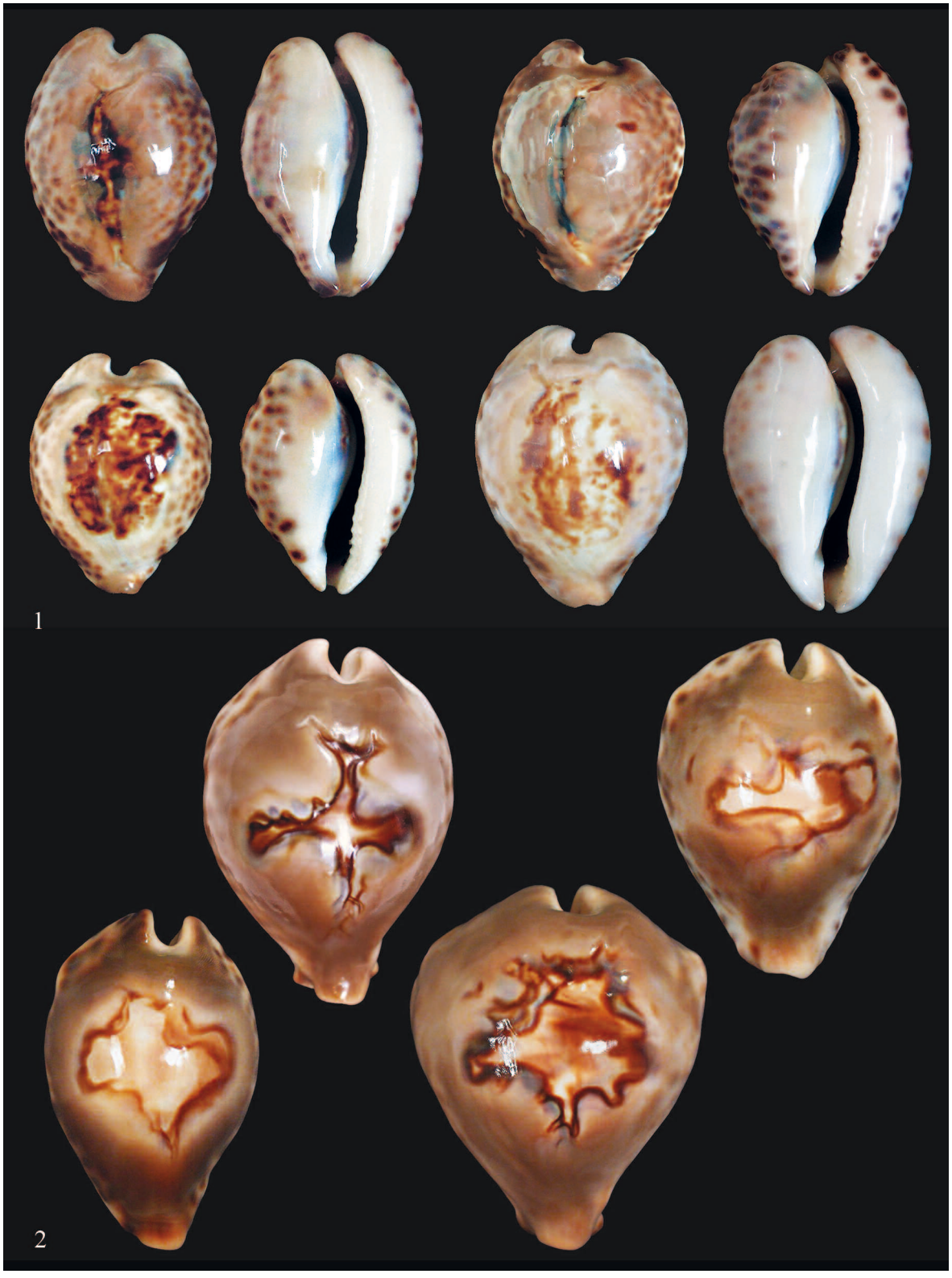

Figure 1. *Barycypraea teulerei*. Examples of variability of pattern of the species. Oman. Photo courtesy Massimo Scali and Beautifulcowries Magazine. Figure 2. *Barycypraea fultoni*. Examples of pattern and variability of the species. Mozambique and South Africa. Photo courtesy Mirco Bergonzoni and Beautifulcowries Magazine.

teulerei in situ. The other animals I was able to see were crabs, cuttlefishes, many bivalves, muricids, and some other cowrie species. Nevertheless, *B. teulerei* is by far the most common species in this environment. Its distribution is not even, however. *Barycypraea teulerei* tends to aggregate, and you can find dozens of specimens together in the same patch, then walk for minutes and not find one. What I observed is that the animals are active during the daytime, especially the small ones that I think may be males (see below). In many cases, they are heedless of being completely outside of the water. Walking on the flat for hours, I was also able to observe a few species of sea birds including small waders, flamingos and seagulls.

In comparing this to the previous known habitat of *B. teulerei* (which I indeed visited), the main difference is that at Masirah Island the sediment is sand, and the bottom is not anoxic. In Masirah, the above-mentioned algal mats and sponges are nowadays very rare, and the area looks more like a big sandy beach with scattered rocky patches. Nevertheless historical records, as well as a few very dead shells, witness that the area once hosted *B. teulerei*. My guess is that, besides collection pressure, there could have been some environmental change.

Figure 3. *Barycypraea teulerei* wandering on a mud flat outside water at sygyzial low tide in December 2014. Oman.

Figure 4. The typical environment, at low tide, where *Barycypraea teulerei* are commonly found. Please note the algal patches. Oman. Figure 5. A close look of the sponge, common in the area, on which *Barycypraea teulerei* was seen eating. Oman.

In my opinion, *B. teulerei* needs the presence of sponges to establish a healthy population. During my observations, I was able to see a *B. teulerei* feeding on a dark gray/black sponge (Fig. 5), so I can confirm this species is spongivorous. However, I cannot exclude it feeding on algae too, but I have not seen any doing so. This is another characteristic that joins *B. teulerei* to the spongivorous *Zoila*.

REPRODUCTION AND LIFE CYCLE

Two other things are, in my opinion, necessary for *B. teulerei* to establish a healthy population. Firstly, dead bivalve shells. *Barycypraea teulerei* uses these shells to nest its eggs. When a female is brooding eggs (as all cowries do), she hides herself and the eggs on the underside of the valve. Females are hidden by the bivalve shell, but you can spot them because several males are commonly found close to them (Fig. 6). Females, on average, tend to be bigger than males, although this is not always true. Massimo Scali also spotted a male fecundating a female on eggs (Fig. 7). This may be an indication that eggs are fecundated while females lay them, and a reason why males compete for laying females.

Egg clusters are comprised of transparent capsules with brownish eggs inside. Immature capsules contain many eggs, but as development continues, only a few embryos per capsule are found. Embryos are easy to spot because they already have a formed shell (Fig. 8). Likely most of the eggs inside the capsule are only for embryo nutrition (nurse cells or intracapsular cannibalism?). It is therefore evident that this species has direct development and only one (or a few) newborns are hatching from each capsule. Direct development is, in cowries, considered an adaptation when a species depends on a limited food source (in this case sponges), so that newborns hatch close to their food source instead of being spread throughout wide areas as veligers. This direct development is again another similarity to *Zoila*.

When we arrived in December, many specimens were brooding eggs and we seemed to be right in the middle of the reproductive season. Air temperatures in Oman during December are not extremely hot, and during the day can reach 25–30°C. However, at night it can be as cold as 10°C or less.

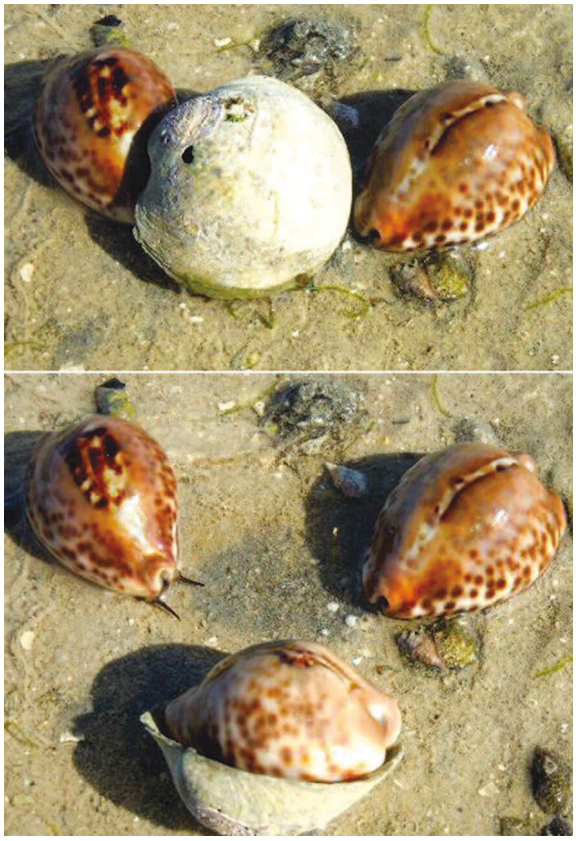

Figure 6. The typical behavior of a female breeding eggs. Above: the female is hidden under a dead bivalve shells, and two males are trying to fecundate. Below: same animals, after I turned the bivalve to make the female visible. Oman.

Figur 7. A male *Barycypraea teulerei* fertilizes with his penis (A) a female that sits on a bivalve shell (B). Oman. Photo courtesy Massimo Scali.

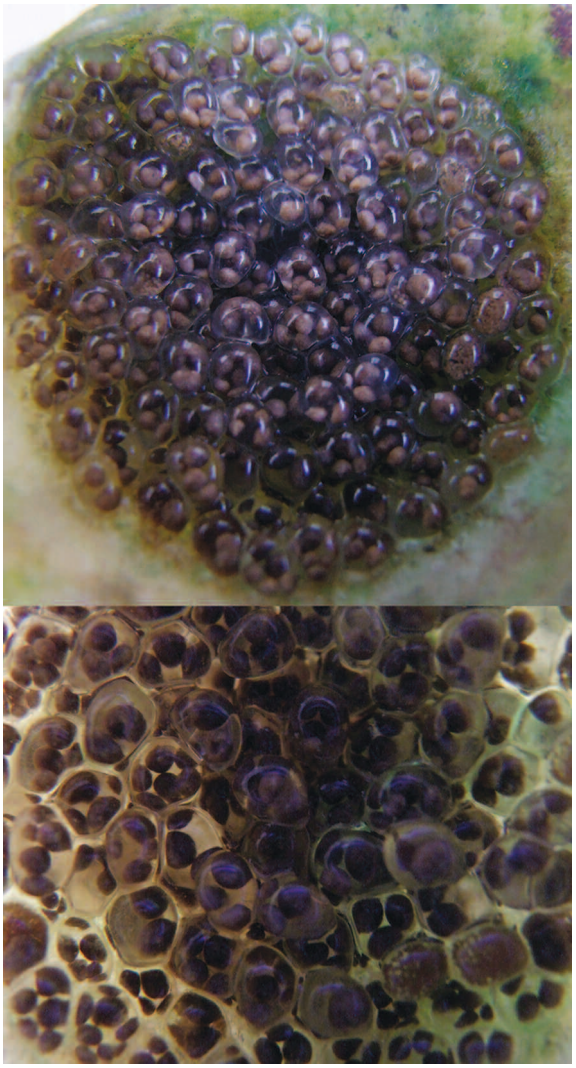

Figure 8. Two views of egg clusters inside bivalve shells. Please note that each capsule may contain different numbers of brownish eggs, and as soon as the embryos get bigger, the number of them decreases. Intracapsular cannibalism? Oman. Photo courtesy Massimo Scali and Beautifulcowries Magazine.

Our time at the site was basically the coldest part of the year, and I guess this is the main reason why *B. teulerei* reproduce during winter. This species is intertidal, so it is strongly influenced by solar heat and desiccation, and winter is the time of the year in which that is least likely to happen. The mud itself may also help in maintaining mollusk wetness and lowering temperature during air exposure. Moreover, water patches and little canals are still present in the mud flat, and some specimens (especially males) seem to take refuge in these when the tide is very low. Finally, almost no specimen showed an expanded mantle, and this is certainly a behavior for retaining moisture and reducing dehydration.

Another surprising observation, confirmed by previous reports at Masirah, is that we couldn't find any juvenile *B. teulerei*. All specimens were adults or, slightly sub-adult. Another important observation is that while adults are very visible and active, sub-adults are more mimetic and tend to hide below the algal mats. The fact that no young *B. teulerei* were found points sharply to the possibility that this species has a synchronized life cycle, and all reproducing mollusks found are the ones born from eggs of the previous year. Moreover, another observation is important: although *B. teulerei* shells are very heavy, no shell seems gerontic and most of them are undamaged. It seems likely they had no time to be damaged, and maybe this is because all those reproducing shells are just one year old and reached sexual maturity only a few weeks before we arrived.

If my hypothesis is correct, this would mean that *B. teulerei* is a cowrie with a very fast life cycle. Soon after December/January they hatch as small crawling snails. The snails, having thin shells, protect themselves from predators and desiccation by hiding inside the algal mats, which are actually quite intricate, and I guess these may also help in cooling the mollusks during the hot season low tides. Sponges are too small to be a suitable refuge even for the youngest snails. They develop this way until the beginning of the next reproductive season, when they complete development and start wandering for dead bivalve shells (if female) or other females (if males). Again, this peculiar life cycle, if confirmed, coincides quite remarkably with *Zoila*. Actually, *Zoila* newborns are very cryptic, as they hide inside sponges as protection from predation, and they only venture out into the open during reproductive season, when they reach adulthood and shells get thicker. *Zoila friendii*, for instance, broods eggs in the open (personal observation) just as *B. teulerei* does.

The complete development of *B. teulerei* is therefore spanning along the hot season. Oman is very hot during summer, easily reaching 40°C or more. I may imagine that, especially during low tide, the water could reach a very high temperature. Please

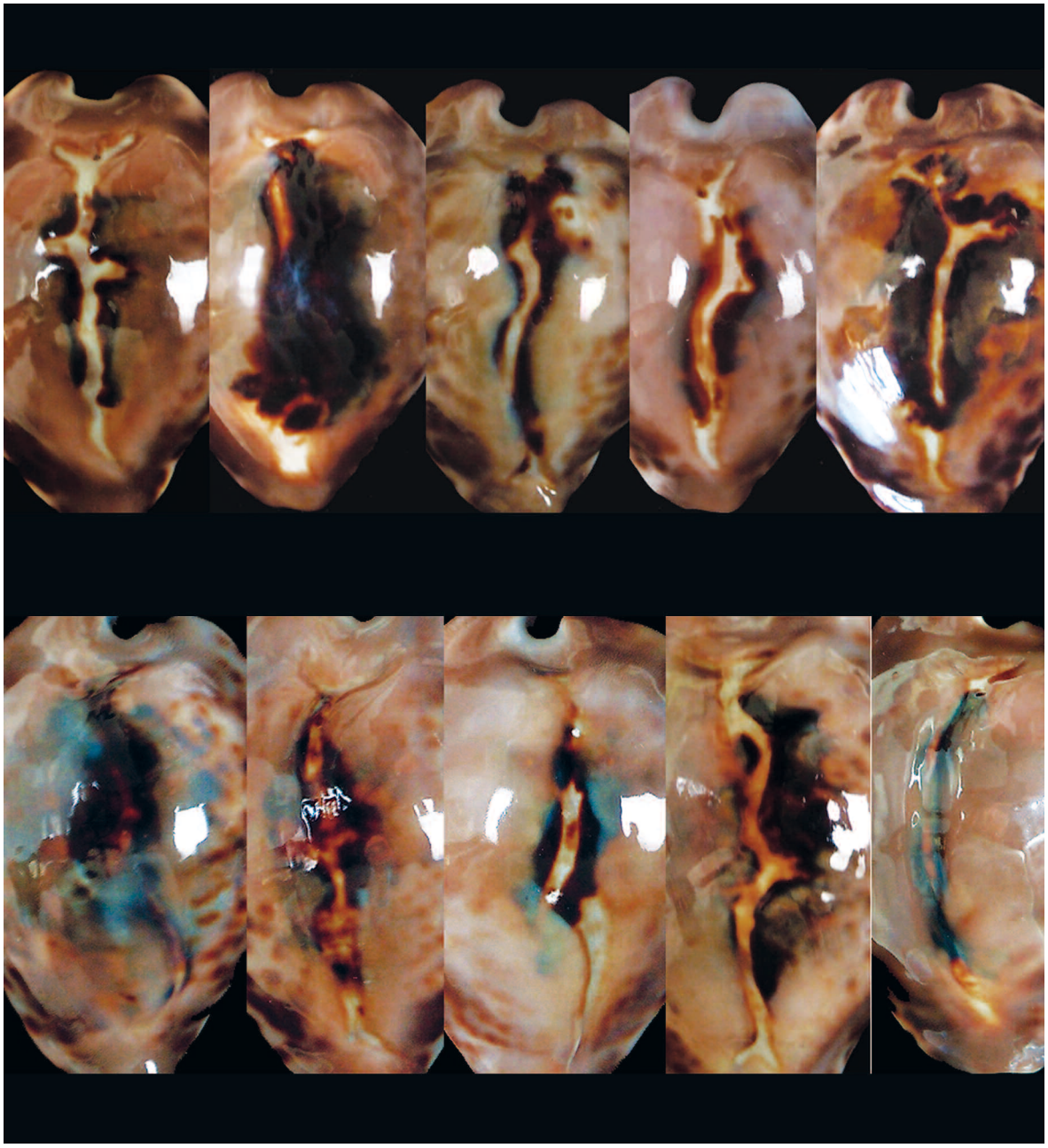

Figure 9. Examples of the variability of the dorsum in *Barycypraea teulerei*, some resembling a false aperture. Oman.

remember that this is a large lagoon flat and that the open ocean, which may be cooler, is quite distant. It is quite unbelievable, but apparently young *B. teulerei* are able to deal with these harsh conditions and reach adulthood with good success. A possibility is that *B. teulerei* migrates into shallow waters only to reproduce, and lives most of the year in deeper waters, where conditions are more stable. I do not think this is the case, because this species is not capable of fast movement, and the mud flat is several kilometers wide. Plus, I found most individuals very far from the deeper areas (actually the closer we searched to the open ocean, the less specimens were found). Moreover, it is unlikely that young *B. teulerei* are able to migrate back to the deeper water during their development, when they

are most vulnerable due to their thin shells. We also dredged for a few hours along the edge of the flat at a depth of 5–10 meters, and we found no *B. teulerei*, not even dead ones.

Finally, what is the fate of the specimens that reached the first reproductive season? Do they survive to the next year? Is this species annual or not? Hard to say, but the fact that I could see very few damaged and no gerontic shells suggests that this species is rather annual, and after reproduction *B. teulerei* dies. If this is true, the population renews itself every year. It may seem strange that a mollusk forms such a hard, heavy shell in only one year, but there is no biological reason to disregard this hypothesis. On the other hand, it is true that we found very few dead shells, and there should be many more if they all die each year. It is also true that they can be easily burrowed into the soft mud bottom, so they would easily disappear. Nevertheless some dead shells are found beached as well.

PREDATION

How does *B. teulerei* deal with predators? As we mentioned, this species lives in open sand/mud flats, and they do not hide when adult. Moreover, several hundred specimens are found in relatively small areas. *Barycypraea teulerei* actually seems quite a successful species and, in fact, it is by far the most common cowrie in that particular habitat. Its behavior is quite the opposite of other cowries inhabiting the same area, f.i. *Naria turdus* (Lamarck, 1810) and *Palmadusta lentiginosa* (J.E. Gray, 1825), which are found hiding inside the algal coating of the numerous *Pinna* sp. found on the muddy bottom. And this is not because they are smaller, since some local *N. turdus* may be as big as *B. teulerei*, and with a similarly thick shell.

Among candidate predators, I may mention seagulls and crabs, which are common in the area, as well as other mollusks. However, very few shells (almost none) show signs of predation, and I have not seen any cracked shells on site or beached. Dead shells are also very rare, and when found, they do not show any sign of attack. It seems that predators are completely ignoring *B. teulerei*, an observation that was quite puzzling. Why should this species not be predated, and why does it actually seem to ignore predators? Is *B. teulerei* toxic, poisonous, or have a disgusting taste? Hard to say, but as far as I know, no toxic cowrie has ever been reported in literature. It is not unconceivable that perhaps they become toxic, repellent or disgusting by absorbing substances from their food sponges. Only targeted chemical analyses would possibly solve this issue.

Some clues may also come from the shell. As mentioned, *B. teulerei* has a very heavy shell. Its thickness is certainly an adaptation to prevent cracking by fishes, crabs or sea birds, as well as drilling by muricids or naticids. Moreover, its squat shape might also be an adaptation to perfectly adhere it to the bottom (as in many other cowries). However, I may also argue that the peculiar pattern of the dorsum could have an adaptive function, although this is just a guess. In fact, even if the dorsum is characterized by a variable pattern (basically no two specimens are alike), most shells show a neat double dorsal line, framing a central groove, especially when the shell is thicker. More uncommonly, they show a dark blotch in the middle of the dorsum. Other kinds of patterns are rarer. In figure 9 you can see an overview of the variability of the dorsal patterns. Contrarily to the dorsum, the mouth is quite wide and uncolored. Considering all this, my guess is that the flashy dorsal color in this species might be either an aposematic coloration (in case the mollusk is toxic or has a bad taste), or, maybe, could represent a sort of 'false aperture' that may distract sea birds from the vulnerable parts of the animal. I may imagine seabirds being fooled and peck at the dorsum of the cowrie, which is actually a very hard part of the shell, completely disregarding the real aperture, where the mollusk would be more vulnerable. Of course this is just a guess, but it is of course not the first such case known in nature: for instance, you may find something similar in false eyes of fishes, which are adaptations to drive predators' attacks to parts of the body that are less sensitive or critical for survival.

Finally, please also note that this species has no teeth along its aperture, a characteristic that is very rare in cowries, even if some specimens may have some little denticles. Teeth in cowries have a particular function, i.e. to narrow the aperture to prevent attacks from predators, since cowries have no operculum. Evidently this species has no need

for teeth, and teeth, which are found in all other *Barycypraea*, are on their way to being lost. This is a very well known evolutionary process: no selective constraints (i.e. no need for teeth) allow accumulation of mutations, which result in the gene products having less or no function (i.e., the genes or the proteins involved in teeth production being partially or wholly inactivated).

AN EVOLUTIONARY DEAD END?

All this considered, *B. teulerei* shows a plethora of remarkable adaptations to a very specific environment, which makes this species an outlier among cowries: i) it lives in the intertidal zone on sand/mud flats, where other cowries are rarer; ii) it is active during the day, at variance to other cowries; and iii) it is strictly dependent on a specific habitat and food source. Nevertheless it performs quite well when all these conditions are present, so we can say that this species appears very well adapted to its environment. Evolution has done "a good job" with this species. And, in fact, *B. teulerei* has no significant predators, at least when they are adult and freely grazing and mating in the open.

On the other hand, its distribution range seems quite limited, maybe because of its specialist way of life. The absence of free-swimming larvae is certainly another concurring factor. We tried to find *B. teulerei* elsewhere along the Oman coast, with no success, although more research needs to be done. Unfortunately, the very limited distribution makes this species a highly vulnerable one.

Actually the main concern for the survival of *B. teulerei* does not come from predators, but from humans. It was quite bad luck for *B. teulerei* to find a species collecting it in large numbers for its beauty, rather than for its taste. And it was bad luck indeed that this species is commercially valuable to collectors. The limited range does the rest. The story of the Masirah population teaches us that *B. teulerei* is indeed in high danger of extinction. That is why the new locality should absolutely remain secret, and I am not giving any precise indication as to where it is. It is also my opinion that this species should be protected by law.

The life history of *B. teulerei* is, no doubt, a remarkable one. Evolution shaped this species to a rather specialized and successful life. At the same time, it has put *B. teulerei* at risk. Evolution is a blind process and of course it could not foresee that, at a certain point, this species would have encountered another one: humans, predating it for its shine, beauty and striking colors. Evolution shaped *B. teulerei* to survive in its habitat, but at the same time made it so easily accessible to humans, and its highly specialized life puts it at risk of extinction. Evolution is indeed a blind watchmaker that '*has no vision, no foresight, no sight at all*' (Dawkins, 1986). And *B. teulerei* was just plain unlucky to encounter our species during its journey on our planet.

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