

The family Cypraeidae (Gastropoda Cypraeoidea) an unexpected case of neglected animals

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ABSTRACT

The family Cypraeidae Rafinesque, 1815 (Gastropoda Cypraeoidea), commonly called Cowries, are particularly well-known among shell collectors, because of their beauty and relative availability. While most species are common in shallow reef environments, some other are quite hard to find, because they may come from remote or hardly accessible habitats, or they are in fact just rarely found. Because of this rarity and beauty, several cowries get high market values among collectable shells. This relevant economic interest produced two kind of outcomes: a proliferation of taxonomic complexity, and a very detailed knowledge of every variation of a given species, making cowries collection one of the most specialized ones. Notwithstanding this, it is quite remarkable that cowries had attracted very little interest by biologists and professional malacologists. Few scientific studies are available to date. This review attempts to overview some of the major biological highlights of the Family, to promote future researches in this diverse group of gastropods.

KEY WORDS

Cypraeidae; Evolution; Biogeography; Speciation.

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INTRODUCTION

The family Cypraeidae Rafinesque, 1815, cowries (Gastropoda Cypraeoidea) comprises about 220 species of marine gastropods (but this figure may vary with different taxonomies, see f.i. Moretzsohn, 2014), widespread along the tropical and subtropical seas. Many species are commonly found in tropical shallow water reefs, although others are adapted to temperate waters and/or deep water environments. Most species are herbivorous grazers, but some are carnivorous, being more commonly sponge eaters.

The main characteristic of cowries (which is however shared by some other gastropods) is the

presence of a retractable mantle that covers the entire shell, when in full extension (Figs. 1–6). This makes the cowrie shell particularly shiny, because, at variance to most gastropods, shell layers are continuously deposited outside the shell itself, rather than in the aperture and inside. The mantle is seldom richly branched, with protrusions known as papillae (Figs. 1, 2, 4–6), that may have both respiratory and mimetic functions. When disturbed, the animal can quickly retract the mantle showing off the brilliant shell.

The amazing richness of shell and mollusk colors in cowries (as in many other mollusks as well) has been always an evolutionary puzzle.

Cowries are not toxic animals, as far as we know, so the brilliant colors of shells and mantles could not be considered as warning signals for predators (aposematism). Sometimes, the mantle, when fully expanded, may camouflage the shell itself (see f.i. the genus *Naria* Broderip, 1837, with fully branched mantle that may resemble algae tufts or coelenterate colonies) (Fig. 7).

In some other cases, the mantle is quite thin and almost transparent, so the shell is easily visible below (see f.i. the genus *Zoila* Jousseaume, 1884). Cowries are commonly cryptic (i.e. they hide) and nocturnal, and this is of course a clear adaptation to reduce predation. Nevertheless, some species, in their adulthood, graze freely in the open during the day (see f.i. the genera *Zoila*, *Barycypraea* Schilder, 1927; and *Cypraea tigris* Linnaeus, 1758). Such cowries tend to have heavy big shells, which is a clear adaptation to avoid predation by fishes and/or crustaceans. Some may also have deltoid shells, with a flat base, another clear adaptation to stick to rocky surfaces (thanks to a foot acting as a sucker) and prevent easy predation [see f.i. *Mauritia mauritiana* (Linnaeus, 1758), *Monetaria caput-serpentis* (Linnaeus, 1758), etc.].

Another environmental factor affecting shell structure is sea current and/or waves action. Generally cowries with thick and heavy shells are typical of turbulent waters. This feature is also variable among individuals of the same species, since lightweight shells tend to be more common in calm lagoons or in deeper waters, while heavy calloused shells are more easily found in the open ocean or in high surf waters.

THE UNUSUAL DEVELOPMENT OF A COWRIE SHELL

The cowrie shell follows a developmental pattern that is quite different from most mollusks. The first shell to be produced is the larval shell of the veliger (Fig. 8). While most species spend their larval time in the plankton, others have a direct intracapsular development (direct developers). Once metamorphosed, the shell keeps growing by adding whorls around its columella (Fig. 9). Eventually, during this growth, the shell may first resemble an *Oliva* shell (Fig. 10; i.e. ‘oliva stage’), or a *Bulla* (i.e. ‘bulla stage’).

In both such stages, the spire is well visible and the shell is very different from the adult one, both for its structure and color. The shell is very thin and all cowries are cryptic at this stage. This is easily interpreted as an adaptation to prevent predation. Although no secure data are available, many personal observations and info obtained from shell divers may point to the fact that cowries get to adulthood very fast, perhaps within few months from birth.

At the end of the juvenile stage, cowries undergo a deep change in their shells: the last whorl usually covers the entire shell, so the spire gets included in it, and it eventually bends over the columellar side to tighten the shell aperture (Fig. 1). This tightening is even more pronounced by the deposition of shell teeth, one of the most typical features of cowries (Fig. 12).

Cowries have no operculum, so teeth are an alternative strategy to make the aperture as narrow as possible, to prevent access to soft parts when the mollusk is retracted. Soon after teeth formation, the shell stops growing, and it starts thickening by deposition of shell and glaze layers, ending up into the typical thick and glossy shell (Fig. 12). The fact that cowries stop growing at adulthood is quite unusual among gastropods, which rather tend to have an undetermined growing pattern. Moreover, the growing rate and/or time to adulthood seem to be quite variable, even among the same species, ending up with a remarkable variability in adult shell sizes (see f.i. Okon, 2013a, b; 2014).

The shell of a cowrie mollusk is therefore quite different from most gastropod shells, as it evolved several unusual characteristics, including a relevant thickness, a very glossy surface, and a very narrow aperture. Moreover, many cowrie shells are brightly colored, making them quite visible to predators. Notwithstanding this, cowries are among the most successful gastropods in coral reefs, and they perform quite well in many other marine environments. As mentioned, some do not even hide at adulthood (see f.i. Fig. 13).

In the attempt to understand the peculiar adaptations of cowries, we first have to consider that the shell of Cypraeidae is generally thick and very compact, hard to brake, with a very narrow aperture, and the mollusk is usually very mucous, which makes the cowrie quite slimy. These joined characteristics are likely a good adaptation against predation,

because the thickness of the shell, the absence of possible holds, the slimy surface, and the relative unreachability of soft parts, may discourage most predators. In fact, such characteristics make predation by small fishes and crabs very difficult.

Actually, cowries are often wholly swallowed by big fishes, since they cannot easily crack them, although it sometimes happens with strongly beaked fishes. Another important source of predation are octopuses, that drill the cowrie shell and



Figures 1–6. Examples of mantles and papillae in Cypraeidae (all from Hawaii). Fig. 1. *Lyncina carneola propinqua* (Garrett, 1879); Fig. 2. *Talparia talpa* (Linnaeus, 1758); Fig. 3. *Luria tessellata* (Swainson, 1822); Fig. 4. *Lyncina lynx* (Linnaeus, 1758); Fig. 5. *Naria poraria* (Linnaeus, 1758); Fig. 6. *Ovatipsa chinensi amiges* (Melvill et Standen, 1915). Photos courtesy David Lum.

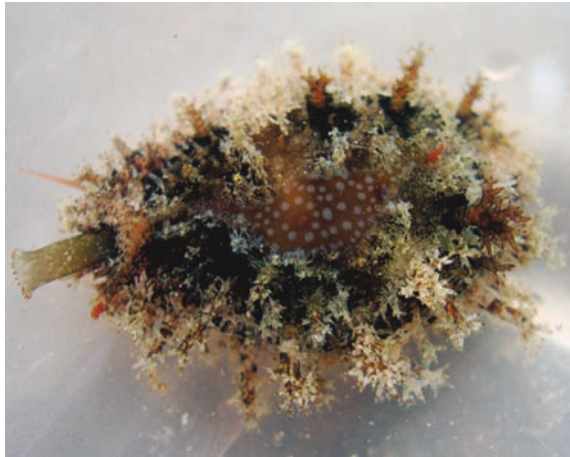
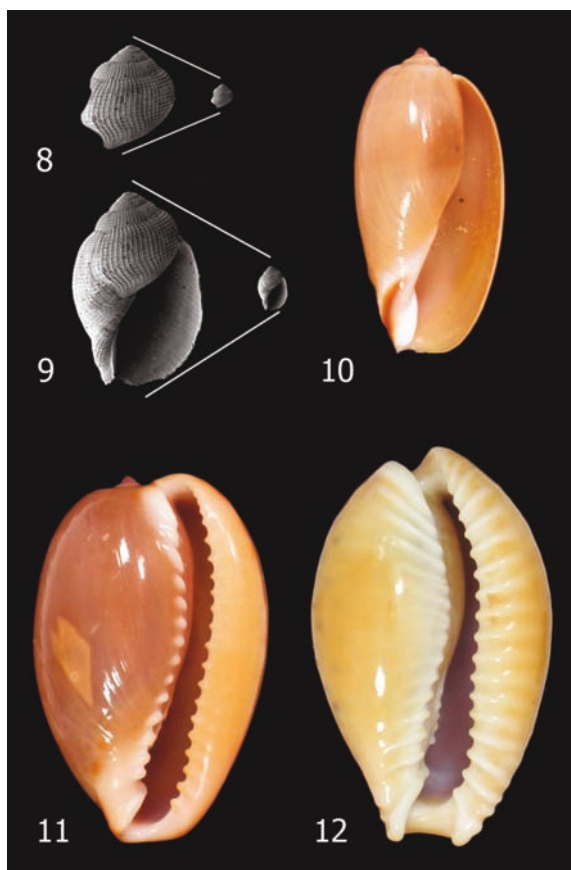


Figure 7. *Naria erosa* (Linnaeus, 1758) showing its extended mantle resembling an algae tuft (Zanzibar, Tanzania). The shell is barely visible in the middle of the dorsum, since the mantle is not fully extended.



Figures 8–12. Developmental stages of *Naria spurca* (Mediterranean Sea). Fig. 8. Veliger shell; Fig. 9. Young shell (just metamorphosed); Fig. 10. 'Oliva' stage; Fig. 11. Subadult; Fig. 12. Adult. Photos courtesy Andrea Nappo and Dario Marcello Soldan.

digest the mollusk, and eventually use cowrie shells (and others) to adorn their dens. Predations by shell drilling gastropods (e.g. Naticidae or Muricidae) seem to be much more rare.

COWRIES' REPRODUCTION

Cowries reproduction is quite remarkable too. Females lay eggs in clusters of capsules on hard surfaces and, at variance to many other gastropods, they hatch eggs by covering them with the foot (Fig. 14). Abandoned eggs may dye quite soon. This commitment in parental cares is unusual in marine gastropods, and it may be another reason for the success of this Family. When intracapsular development ends, planktotrophic larvae hatch and swim in the water column until they metamorphose. The length of larval stages may be different, and could be somehow related to the capacity of a given species to undergo local genetic diversification (i.e. subspecies and/or geographic races). Some species seem to have quite few divergent races, while others have a much higher geographically structured pattern.

On the other hand, direct developers seem to show different morphologies in different areas. In direct developers, young mollusks undergo intracapsular development and, since they feed at the expenses of accessory eggs in the capsule, they keep growing until they hatch as crawling snails. This development, evolved many times in cowries, especially in some temperate water genera (*Zoila*, *Cypraeovula* Gray, 1824, *Notocypraea* Schilder, 1927), has been often considered as an adaptation to improve the chances of larvae to find specific foods, like sponges they feed on. In fact, most direct developers are fully depending over limited food supplies, and they need to hatch as close as possible to their food, to increase chances of reaching adulthood.

DISTRIBUTION AND BIOGEOGRAPHY

Cowries are subtropical marine animals (Fig. 15), so most of them live in the oceans between the two tropics. The highest number of species is found in the Indo-Pacific Ocean, and far less species live in the Atlantic (and the Mediterranean). Paulay and



Figure 13. Two *Zoila friendii jeaniana* (Cate, 1968) (f. *sherylae* L. Raybaudi Massilia, 1990) grazing their host sponge in the open (Point Qobba, W-Australia). Photo courtesy Daniel Edinger.



Figure 14. *Erronea caurica* cfr. *quinquefasciata* (P.F. Röding, 1798) on eggs (Oman, Marisah Island). Photo courtesy Massimo Scali & Beautifulcowries Magazine.

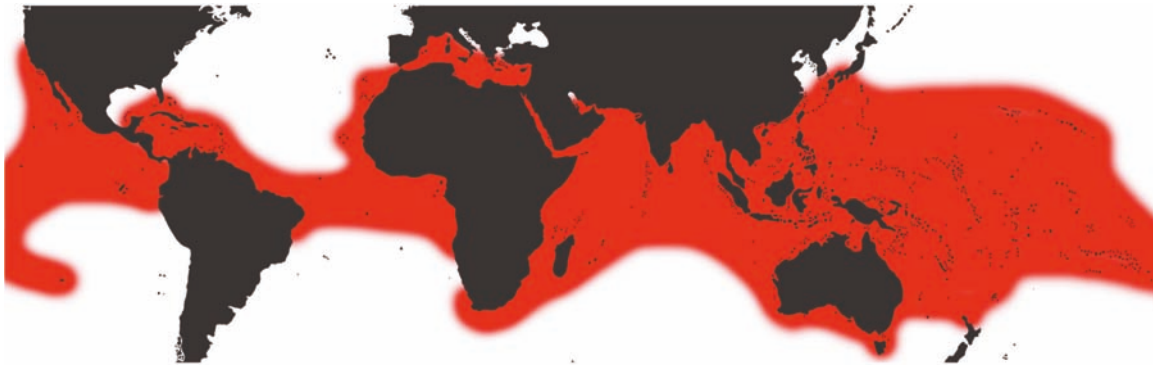


Figure 15. Distribution map of the living species of cowries. Photo courtesy Mirco Bergonzoni.

Meyer (2006) proposed a species richness map of the Indo-Pacific cowries. The highest species richness is in the region going from the Philippines to Melanesia, especially along the boundary between East Indian Ocean and West Pacific. Species richness significantly decreases going west towards Africa (although it locally increases again there), or east along the Pacific Ocean towards Polynesia and West America. Quite significantly, similar species-richness patterns have been found in reef-building corals, as in other reef-related organisms (see f.i. Malay & Paulay, 2010). In fact, the region comprising the ocean territories of Indonesia, the Philippines, Malaysia (Sabah), East Timor, Papua New

Guinea and the Solomon Islands, is known as ‘the coral triangle’, hosting more than 500 species of reef-building corals (Veron, 1995). The reasons for these similar species distribution patterns could be both environmental and historical. Apparently the thousand of islands and reefs in South East Asia, as well as their highly diverse habitats, were central to a rich species radiation in cowries and other reef-related animals. So that, probably, most of the widespread Indo-Pacific cowries have once originated in this area, and migrated (with different success) outwards by larval dispersion.

As mentioned, the duration of veliger stages has been again related to dispersion and speciation rates

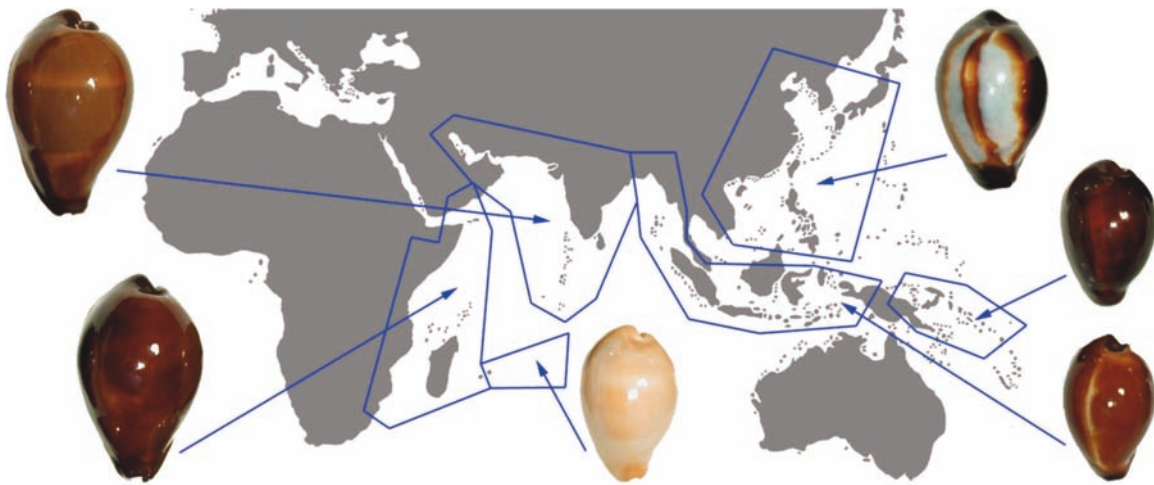


Figure 16. Geographic diversification of the *Erronea onyx* species group. From left to right: *Erronea adusta adusta* (East Africa); *Erronea adusta nymphae* (Mauritius; Chagos); *Erronea adusta persica* (India, Oman, Persian Gulf); *Erronea adusta andamanensis* (East Indian Ocean); *Erronea adusta melanesiae* (South West Pacific); *Erronea onyx* (North West Pacific). Photo courtesy Mirco Bergonzoni.

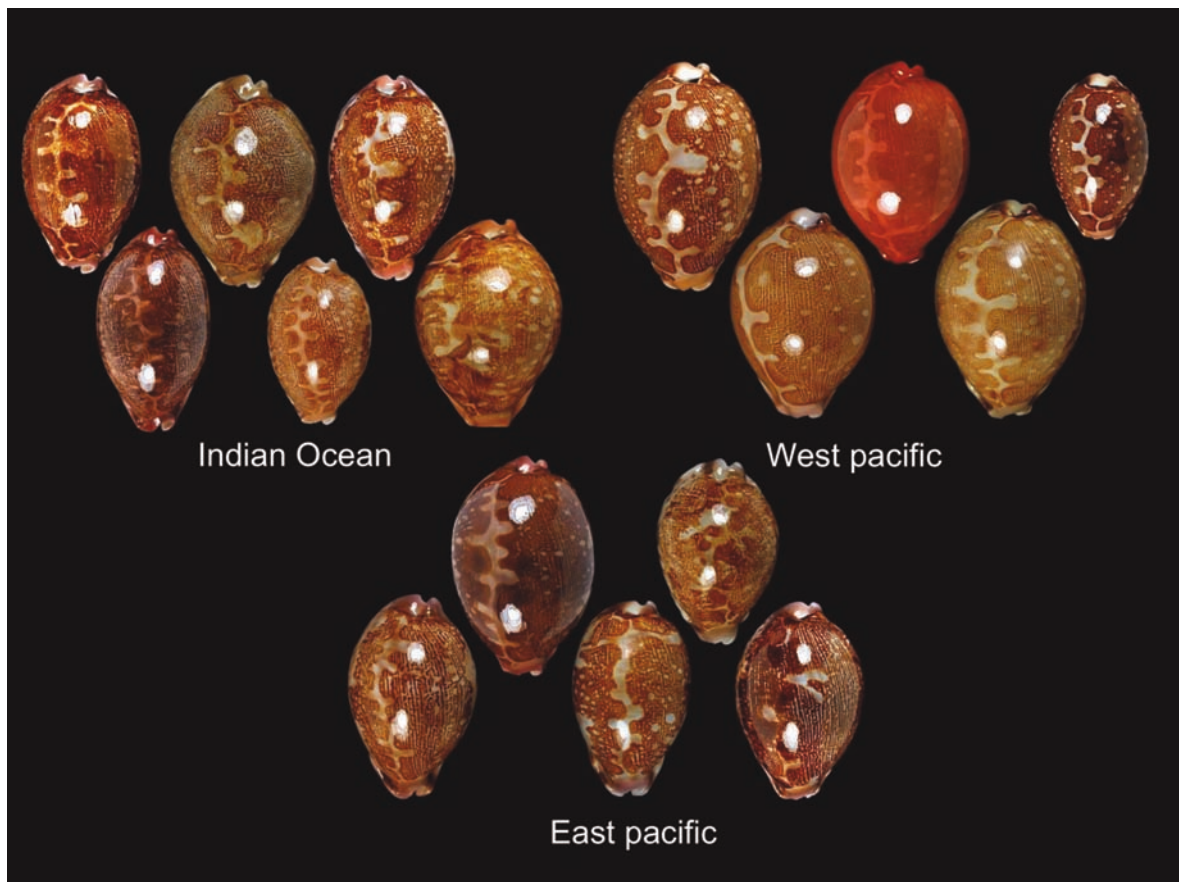
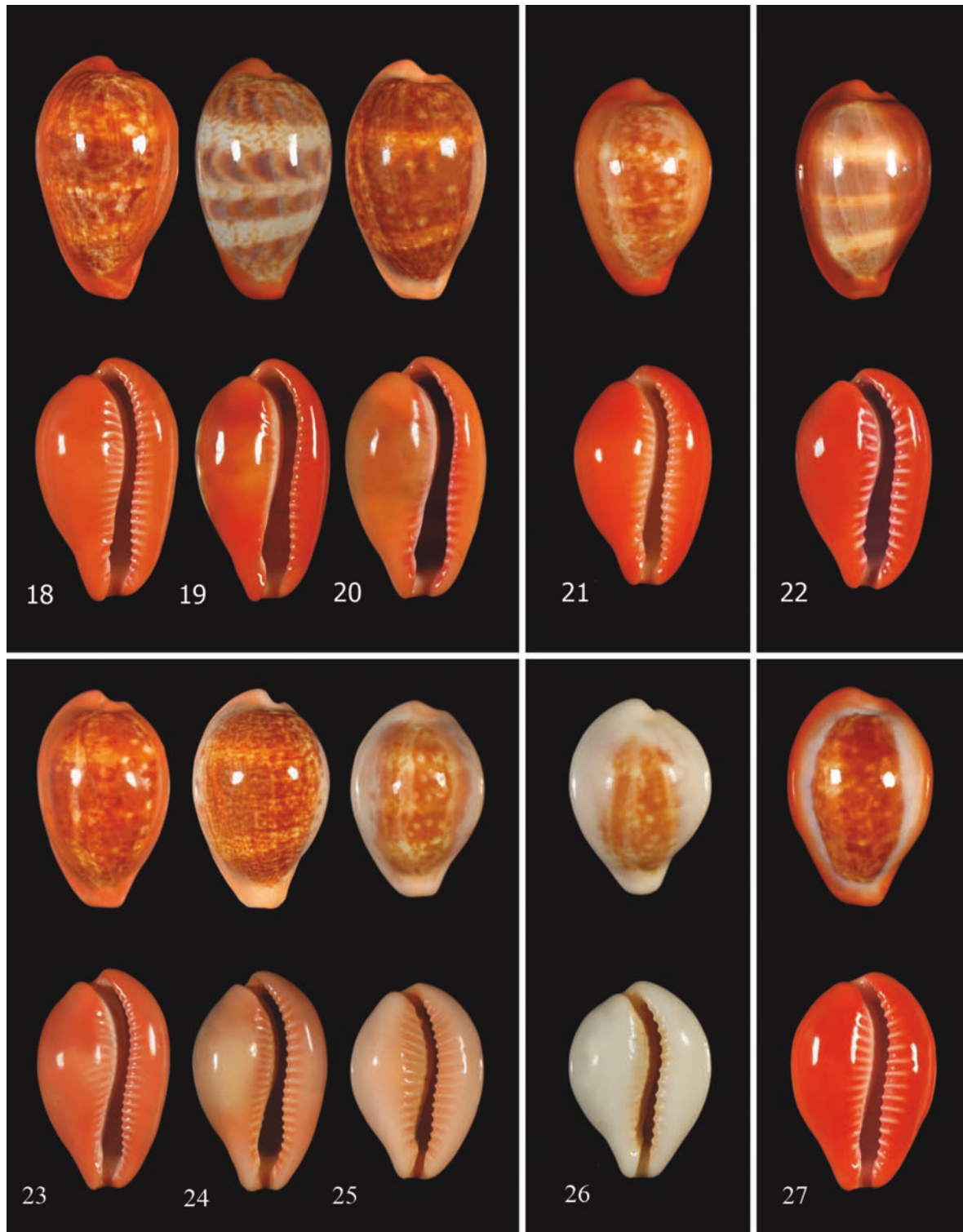
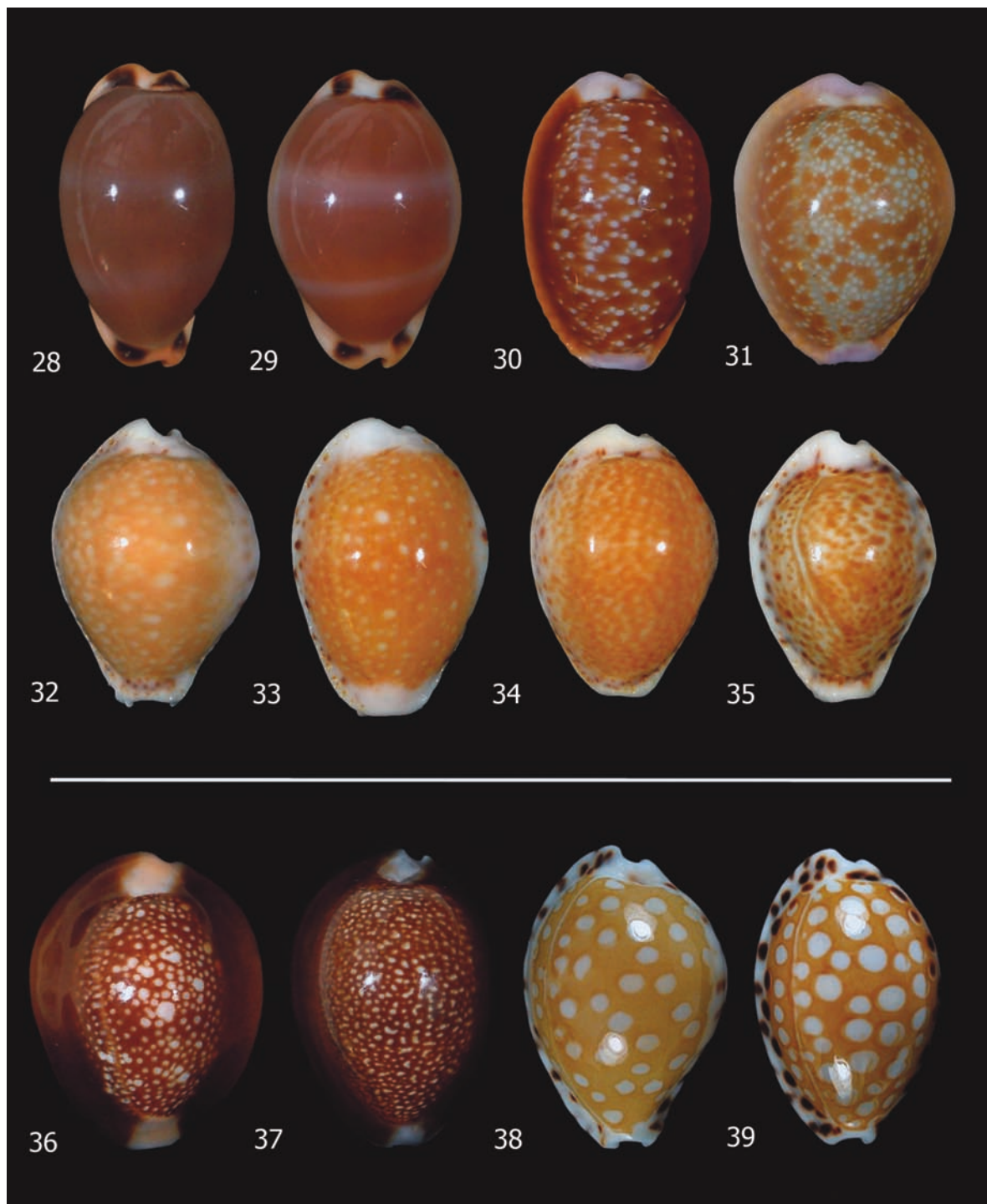


Figure 17. Examples of the variability of the *Leporicypraea mappa* species complex from different basins. Photo courtesy Mirco Bergonzoni & Cypraea.net.



Figures 18–27. Examples of the variability of the *Zonaria pyrum* species complex. Figs. 18–21. *Z. pyrum pyrum* (Gmelin, 1791): Mediterranean Sea to Mauritania-Senegal (North of Dakar); Fig. 22. *Z. pyrum insularum* Schilder, 1928: Algarve (Portugal), Cadiz (Spain), Morocco, Canary Is.; Figs. 23–25. *Z. pyrum petitiana* (Crosse, 1872): South of Dakar (Senegal), Ivory Coast, Gabon, C. Verde; Fig. 26. *Z. pyrum angelicae* (Clover, 1974): North Gabon, Guinea Gulf (?); Fig. 27. *Z. angolensis* (Odhner, 1923): South Gabon, Luanda area (Angola). Photos courtesy Mirco Bergonzoni & Beautifulcowries Magazine.



Figures 28–39. Examples of close relative couples of taxa of Cypraeidae. The one on the left is always the one with a wide distribution range, the right one is the endemic relative with its range limited to peripheral locations. Above the line, the couples considered as subspecies; below the line, the couples considered as different species, from left to right. Figs. 28, 29: *Luria lurida* (Mediterranean Sea) and *L. lurida oceanica* (Ascension Is.); Figs. 30, 31: *Naria helvola* and *N. helvola hawaiiensis* (Hawaii); Figs. 32, 33: *Naria cernica* and *N. cernica leforti* (Easter Island); Figs. 34, 35: *Naria acicularis* and *N. acicularis sanctahelenae* (Ascension and Saint Helena); Figs. 36, 37: *Monetaria caputserpentis* and *M. caputdraconis* (Easter Island and Sala Y Gomez); Figs. 38, 39: *Cribrarula astaryi* (f. *lefaiti*) and *C. garciai* (Easter Island). Photos courtesy Beautifulcowries Magazine.

by Paulay and Meyer (2006). Although duration of veliger stages is only weakly correlated to species range, it is significantly related to the diversification of cowries along the Indo-Pacific basin: i.e. the lower the veliger time is, the most is the geographic/taxonomic diversification. In fact, it is quite evident that some Indo-Pacific cowrie species show very little geographic variation, see f.i. *Monetaria caputserpentis*, *Monetaria annulus* (Linnaeus, 1758), while others are much more prone to produce local races/subspecies. Only because they have been recently analyzed in detail, I can mention here the *Erronea onyx* (Linnaeus, 1758) species complex (Bergonzoni, 2013a), which appeared to differentiate in allopatric races (Fig. 16), and the *Leporicypraea mappa* (Linnaeus, 1758) species group (Fig. 17), one of the most biogeographically and evolutionary complex cases among cowries (Bergonzoni & Passamonti, 2014). By analyzing such complexes in detail, very interesting cases on evolutionary history of marine organisms became

evident, including allopatric speciation events, incipient speciation, relevance of genetic flow for morphological diversification, etc. More case studies are really interesting, but they still have to be analyzed in detail, as f.i. the genera *Cribrarula* Strand, 1929 and *Talostolida* Iredale, 1931, and the *Bistolida stolidus* (Linnaeus, 1758) and *Erronea caurica* (Linnaeus, 1758) species complexes, just to name some.

As mentioned, cowries also colonized the Atlantic, although their species richness is much lower in this Ocean. Most likely, this colonization was rather old, since at present the cold currents of South West America (Humboldt Current) and South West Africa (Benguela Current) are evidently a strong barrier for larval dispersion and cowries settling. At present, no species seems to be able to spread from the Indo-Pacific to the Atlantic Ocean north of Namibia, or in South America. Of course no one lives in the Arctic Ocean as well. Nevertheless, Atlantic cowries have evident affinities with Indo-Pacific ones. For instance, the genus *Macrocyprea* Schilder, 1930 is present at both sides of



Figure 40. Representatives of the South African genus *Cypraeovula*. Photo courtesy Goncalo Rosa and Mirco Bergonzoni.

the Isthmus of Panama, as it likely originated locally before the Isthmus was closed. On the other side of the Atlantic, we have examples of couples of allied species found in the Mediterranean and the Red Sea/North West Indian Ocean [*Luria lurida* (Linnaeus 1758)/*Luria pulchra* (Gray, 1824)], maybe a Thetyan residue. Some other genera are endemic to this region (*Zonaria* Jousseaume, 1884; *Schilderia* Tomlin, 1930). Finally, a peculiar distri-

bution is given by the *Naria spurca* complex of species: this comprises three species, *Naria spurca* (Linnaeus 1758), *Naria acicularis* (Gmelin, 1791), and *Naria cernica* (Sowerby, 1870). The first is distributed in the Mediterranean/West Atlantic, the second along the East American coastlines, the latter is one of the most widely dispersed indopacific cowries. Although the exact colonization tempos and modes of Atlantic cowries are hard to speculate,



Figures 41–45. Extreme variability in *Zoila* from Western and South Australia. Figs. 41–43: *Zoila friendii* subspecies/forms. Fig. 44: *Z. ketyana* subspecies/forms. Fig. 45: *Z. venusta* subspecies/forms. Photos courtesy Mirco Bergonzoni & Cypraea.net.

their phylogenetic relatedness to Indo-Pacific ones is evident. Detailed phylogeographic analyses are potentially of great interest to reconstruct the geological history of the Atlantic basin, its past connections and/or geological changes.

Again, as for Indo-Pacific cowries, in the Atlantic as well the duration of cowries larval stages has been correlated by the rate of morphological diversification. One paradigmatic example comes from

the *Zonaria pyrum* (Gmelin, 1791) species complex (Figs. 18–27), spreads in the Mediterranean and West Africa region. Again, a short larval stage has been related to the extreme capacity to differentiate geographically, with different taxa spreading along the African coast (Bergonzoni, 2013b).

Another interesting case of evolution comes from cases of species/subspecies couples in which one has a wide range, and the allied one has a



Figures 46–47. The genus *Umbilia* (South and East Australia). Fig. 46: *Umbilia hesitata* species complex. Fig. 46: *U. armeniaca*. Photos courtesy Mirco Bergonzoni & Cypraea.net.



Figure 48. *Barycypraea teulerei* (Oman). Two males approaching a female hatching eggs into an empty bivalve shell.



Figure 49. *Barycypraea fultoni fultoni* (Natal, S. Africa). Photo courtesy Felix Lorenz & Beautifulcowries Magazine.

peripheral endemic distribution. Figures 28–39 show some cases. Most of them are isolated endemics, likely arisen paraphyletically. Quite remarkably, they are treated much differently in established taxonomy: some are actually considered as full species, some other as subspecies, although no evident reason (besides Authors' opinion) has been produced so far.

As mentioned, cowries were able to colonize temperate waters as well. This is particularly evident for South Africa and West/South Australia, in which endemic genera evolved. In South Africa, the most striking evolutionary radiation is the genus *Cypraeovula* (Fig. 40), including different closely related species that sometimes hybridize too. On the other side of the Indian Ocean, in Western Australia, another striking example of colonization of temperate waters is the genus *Zoila* (Lorenz, 2001; Wilson and Clarkson, 2004) (Figs. 41–45). The *Zoila* cowries are sponge eaters and direct developers, and this caused a flourishing of local races, making them one of the most taxonomically complex groups of marine organisms. Along with *Zoila*, another similar case is the genus *Notocypraea*, which is however much less known in detail. Finally the genus *Umbilia* Jousseaume, 1884 (Wilson and Clarkson, 2004) is another sticking Australian endemism of temperate waters, as it is distributed along the East and South coast (Figs. 46, 47).

Other cases of direct developers are found as well, such as the genera *Barycypraea* and *Muracyprea* Woodring, 1957, and few others. In all

cases, these species have a very limited range. F.i. *Barycypraea teulerei* (Cazenavette, 1846) (Fig. 48), a shallow water direct developer (Scali, 2013; 2014), seems to be found in a limited area of Oman only, while the deep water relative *Barycypraea fultoni* (Sowerby III, 1903) is found between Mozambique and South Africa (Bergonzoni, 2012) (Fig. 49). Another case of direct developer with little dispersal capacity is *Muracyprea mus* (Linnaeus, 1758), limited to the Gulf of Venezuela coasts and Guajira Peninsula in Colombia.

THE MOLECULAR PHYLOGENETICS OF COWRIES AND THEIR TAXONOMY

This is probably the field of cowries biology that has been more thoughtfully investigated. In fact, a huge phylogenetic reconstruction, based on DNA, have been proposed by Meyer (2003; 2004). The primary outcome of this pivotal work is an ultimate tuning of the sovraspecific taxonomy of the family. Quite remarkably, most of the subfamilies and genera proposed by older Authors on morphology (see f.i. Schilder & Schilder, 1938; Schilder, 1939; 1966;) have been confirmed by DNA.

The family Cypraeidae is now subdivided into 7 subfamilies (Archicypraeinae, Erosariinae, Umbiliinae, Cypraeinae, Bernayinae, Luriinae and Cypraeovulinae) and 48 genera (Moretzsohn, 2014), and this arrangement has gained a very good agreement among cowrie experts.

Even if a relatively stable sovraspecific taxonomy has been reached in the Family, this is certainly untrue for species level and, even more, below it. Most of the proposed taxonomies are based on morphological analyses, as well as on Authors' opinions. Only few DNA data and/or detailed evolutionary studies are available to date. Moreover, a certain degree of taxonomic proliferation has been certainly triggered by economic factors: in fact, many cowrie collectors want new names, so that a new named cowrie gets a much higher value in the market. This cause what I'd call 'economic speciation', with some humor, of course! This approach should be strongly stigmatized for two reasons: 1st, it produces an unnecessary proliferation of taxonomic names; 2nd, it has no biological bases in most cases.

Another problem comes from the rules of taxonomy, and this is particularly evident for species and subspecies names, which are under the provisions of the International Code of Zoological Nomenclature. In my opinion, new species and subspecies names should not be introduced in taxonomy if not based on rigorous biological and evolutionary analyses. Nevertheless, specialized

collectors need to have names to refer to morphologies that are just not so important for evolutionary biologists, like local variants, unstable morphs, aberrations, etc. The use of 'forma' names should be a good compromise, because they, one side, meet collectors' needs for names, and, the other do not increase taxonomic complexity (i.e., infrasub-specific names are not under the provisions of the Code). This approach is not without problems, of course, but it seems to me the only possible compromise between two different, and sometimes contrasting, needs.

MUTATIONS AND ABERRATIONS

Albinism and rufinism

As it happens in all living beings, cowries may show some interesting mutations and aberrations. Some of them, being rare, may produce some of the most sought-after and priced cowries, so all collectors know them very well. On the other hand, their biological causes are quite unknown or neglected. I try to highlight some of them here.



Figure 50. *Zoila decipiens* from Broome area, W-Australia. From left to right: black (normal), albino and rufinistic shells. Photo courtesy Drew Strickland.

The first example comes from rare recessive mutations, such as cowries' albinism (producing white shells) or rufinism (producing orange shells) (Fig. 50). These phenotypes are evidently due to rare mutations affecting the genes for shell color. It is quite remarkable that white or orange shells are not necessary associated to white and orange animals, respectively. This clearly points out to the observation that genes for shell color are different from the ones of the soft parts. For this reason, it would be inaccurate to call such specimens 'albino' or 'rufinistic', but I use these terms here for simplicity. Both rufinistic and albino cowries have been proposed to be the result of mutations over the same metabolic pathways producing brown/black pigments (melanin?). For a detailed discussion see Passamonti and Hiscock (2013).

Besides their high collecting value, the appearance of rare mutants within a population represents an interesting case to study the dynamics of allele frequencies, and the effects that collecting pressure may have on the variability of natural populations. A paradigmatic example is that of *Zoila rosselli satiata* Lorenz, 2002, from Fitzroy Reef, Quobba Point, North West Australia. This once quite large population was an important source of rosselli specimens, and many hundreds have been collected over the years. Among normal shells, around 40 rufinistic specimens were found (f. *edingeri* Raybaudi Massilia, 1990) (Beals, 2013) (Fig. 51). These shells were collected over a limited time-lapse, as the first ones were collected in 1988, and they disappeared soon after 1997. Why the mutant disappeared so fast? One may think that this is because all orange shells were collected, so they



Figure 51. *Zoila rosselli satiata* and *Z. rosselli satiata* f. *edingeri* (rufinistic). Both found at Point Quobba, W-Australia. Photo courtesy Daniel Edinger and Beautiful-cowries Magazine.

could not produce orange progeny anymore. However, this is not fully the case: since rufinistic mutations are likely recessive (i.e. they may 'hide' in heterozygous individuals), two heterozygous black mates may well produce $\frac{1}{4}$ of orange shells, according to Mendelian proportions. So, the overall collecting pressure (on both black and orange specimens) is rather the reason of this disappearance: by reducing dramatically the number of individuals, the population underwent a strong 'bottleneck', which is well known in evolutionary biology to reduce genetic variability. Because chances for rare alleles to pass throughout a population bottleneck are very scarce, the rufinistic allele was soon lost from the population, and no *edingeri* was found since then. This also means that the chances that this allele will appear again in Quobba are quite low, and the *edingeri* rufinistic mutation is simply no longer existing. However, rufinistic shells are found within many other *Zoila* species, as well as in some other cowries. So rufinism is likely a case of recurrent mutation. F.i. an independent rufinistic morph has been recently evidenced in another *Zoila rosselli* population (see Lorenz, 2011; 2014).

Albinos are much more rare among cowries. Although many cowries may be white or whitish, the rare albino mutants are only known for very few cowries [f.i. in *Cypraea tigris* (Fig. 52), and *Zoila decipiens* Smith, 1880 (Fig. 50)]. What is quite interesting is that albino morphs may became fixed in some populations (i.e. all the shells are albinos), hence they are not rare mutants anymore: two paradigmatic examples are *Naria eburnea* Barnes, 1824 (Fig. 53) and *Erronea nymphae* Jay, 1850 (see Fig. 16). Both are clearly related to non-albino relatives, *Naria miliaris* (Gmelin, 1791) and *Erronea adusta* (Lamarck, 1810), respectively. These are likely cases in which the 'albino' allele was fixed into a new population because of a 'founder effect', i.e. when a new population had established in a new area the albino allele become by chance the unique one (i.e. it was fixed).

Niger and rostrated cowries

This is another interesting feature, which appears to be unique to some cowries and only one ovulid species, *Calpurnus verrucosus* (Linnaeus, 1758). It is evident that these two characteristics are the outcome of the unusual developmental scheme

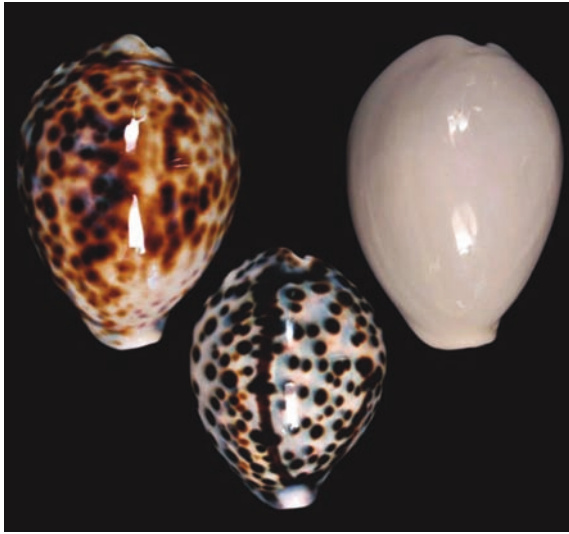


Figure 52. Two normal *Cypraea tigris* along with an albino one (Madagascar and Philippines). Photo courtesy Mirco Bergonzoni & Cypraea.net.



Figure 53. Two species of the genus *Naria*. *Naria miliaris* from China (left) and *N. eburnea* from New Caledonia (right).

of cowries' shells. As mentioned, adult cowries stop growing, since the deposition of shell layers and pigments stops or strongly reduces. However, in some specimens, the signal to stop seems not to work properly, and the shell keeps growing by adding layers of shell and/or pigment. Hence such cowries quickly get a 'gondola shape' (rostrated), as well as a deep black color (melanic or 'niger' cowries). Both phenomena may appear together, or not, depending on species. Some species become melanistic and rostrated altogether, others may only be rostrated (these are the ones that do not have brown/black colors in normal adults). Also, the degree of rostration and melanism may vary among individuals (Figs. 54, 55).

Even if such phenotypes are occasionally found over the entire range of some cowrie species, it is quite remarkable that they get much more common in two specific areas: the southern reefs of New Caledonia, and the Keppel Bay area in Queensland. The biological causes of such aberrations are still unknown, and some have linked these phenomena to the presence on heavy metals (nickel?) in the water (see, f.i., Pierson and Pierson, 1975). What I think it is interesting is the presumable genetic base of melanism and rostration: as mentioned, both could easily be interpreted as a malfunctioning of genetic regulation of shell development. The pattern of expression of

developmental genes is somehow affected (by metals? by other environmental factors? by mutations?), and the genes for deposition of shell color and layers just fail to stop at adulthood, as it happens in normal cowries. Needless to say that we have no clue on which genes are involved in such processes, and this would certainly be a nice case study for developmental biologists.

CONCLUSIONS

In this paper I tried to highlight some biological peculiarities of cowries, making them interesting case studies to many aspects of evolutionary biology, not only for taxonomy. Cowries are very interesting marine organisms, and, even if they have been studied by very few professional biologists, they are well known by amateurs, and a huge amount of 'first-hand' data are available. This manuscript is far to be complete, and many other interesting cases could be highlighted; nevertheless I hope that this short review has attracted your interest to this amazing group of animals, that certainly deserves more studies. The collection of cowries, which is unfortunately so deeply money-driven, is certainly a restraint to biological studies, since some species are hardly accessible and collecting data are often vague (to preserve a relevant



Figures 54, 55. Examples of different degrees of melanism and rostration in New Caledonian cowries.
Fig. 54: *Mauritia (Arabica) eglantina*; Fig. 55: *Bistolida stolidia*.

source of income for divers/dealers). On the other hand, an important collecting effort is a precious help for biologists, since maybe for no other group of gastropods we have such a huge amount of knowledge ‘in the field’. We should therefore try to build a ‘bridge’ between the two words (cowries amateurs and biologists) that both may benefit: collectors will start to consider cowries not as just precious and beautiful objects, and evolutionary biologists/professional malacologists as interesting animals to study. Only this way, the preconception that cowries are just pretty but uninteresting animals will be definitively overcome.

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