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FRONT PAGE

Palmadusta clandestina passerina
(Melvill, 1888).

Photo: **Valda Fraser**

THIS PAGE

Hole in the Wall, Transkei

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The Family Cypraeidae:

an unexpected case of neglected animals

By Marco Passamonti

Lyncina vitellus (Linnaeus, 1758)
Image: Valda Fraser

Abstract

Cowries are particularly well-known among shell collectors because of their remarkable beauty and relative availability. While most species are easily obtainable, being common in shallow reef environments, some others 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 are highly-priced collectible shells selling for thousands of US dollars. Monetary considerations have helped to generate two outcomes: a proliferation of taxonomic complexity, and a very detailed knowledge of every variation of a given species, making cowrie collections relatively specialized. Notwithstanding this, it is quite remarkable that cowries have attracted very little interest from biologists and professional malacologists. Few scientific studies are available to date. This review attempts to overview some of the major biological highlights of cowries in order to promote future research into this beautiful and amazingly diverse group of gastropods.

Introduction

The Family Cypraeidae Rafinesque, 1815 (cowries) comprises about 220 species of marine gastropods (but this figure may vary with different taxonomies, see Moretzsohn, 2014), widespread among 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, most 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 fully extended (Fig. 1). This makes the cowrie shell particularly shiny, because, in contrast to most gastropods, layers are continuously deposited outside the shell itself, rather than the interior. The mantle often has richly branched protrusions known as papillae (Fig. 1).

These may have both respiratory and mimetic functions. When disturbed, the animal can quickly retract the mantle, showing off its 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 their brilliant colors are probably not warning signals for predators (aposematism). Sometimes, the mantle, when fully expanded, may camouflage the shell (see the Genus *Naria* Broderip, 1837, the fully branched mantle of which may resemble algal tufts or coelenterate colonies) (Fig. 1 and 2). In some other cases, the mantle is quite thin and almost transparent, so the shell is easily visible below (see the Genus *Zoila* Jousseaume, 1884). Cowries are commonly cryptic (i.e. they hide) and nocturnal, and these are clear adaptations to reduce predation. Nevertheless, some species, as adults, graze freely in the open during the day (see 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 (with their feet acting as suction attachments) to prevent easy predation [see *Mauritia mauritiana* (Linnaeus, 1758), *Monetaria caputserpentis* (Linnaeus, 1758), etc.]. Other environmental factors affecting shell structure are sea currents and/or wave action. Generally speaking, the heavier the shell of a cowrie, the higher the turbulence of the water it lives in. This feature also causes variability 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 usually found in high surf waters.

The unusual development of a cowrie shell

Cowrie shells follow a developmental pattern that is quite different from most mollusks. The first shell to be produced is the larval shell of the

veliger (Fig. 3A). 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. 3B). In its juvenile stage of growth, the shell may first superficially resemble an *Oliva* shell (Fig. 3C; i.e. 'oliva stage'), or a *Bulla* (i.e. 'bulla stage'). In both stages, the spire is well visible and the shell is very different from the adult one, both in 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 rigorous data are available, observations by many shell divers suggest that cowries reach adulthood rapidly, perhaps within a few months after leaving their capsules. At the end of their juvenile stage, cowries undergo major changes in their shells: the last whorl usually covers the entire shell, so the spire gets included in it, and the labral edge becomes closer to the columella to narrow the shell aperture (Fig. 3D). This tightening is even more pronounced after the deposition of shell teeth, one of the most typical features of cowries. Cowries have no operculum, so denticles are an alternative strategy to make the aperture as narrow as possible, to protect living tissues when the mollusk is retracted. Soon after denticle formation, the shell stops growing and it starts thickening by deposition of shell and glaze layers, creating the typical thick and glossy shell (Fig. 3E). The fact that cowries stop growing at adulthood is quite unusual among gastropods, which tend to have an indeterminate growth pattern. Moreover, the growth rate and/or time to adulthood seem to be quite variable, even among the same species, resulting in a remarkable range of adult shell sizes (see Okon 2013a,b; 2014).

The shell of a cowrie mollusk differs from most gastropod shells by its evolution of multiple features, 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 as adults (see Fig. 4).

In our attempts to understand the peculiar adaptations of cowries, we first have to consider that the cowrie shell is generally thick and very compact, hard to break, with a very narrow aperture, and the mollusk is usually very mucous, which makes the cowrie shell 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.

Cowries are often swallowed whole by big fishes, since they cannot easily crack them, although it sometimes happens with strongly beaked fishes. Other important predators are octopuses that drill the cowrie shell and digest the mollusk, sometimes eventually using cowrie shells (and others) to adorn their dens. Cowrie predations by shell drilling gastropods (e.g. Naticidae or Muricidae) seem to be much less common.

Cowrie reproduction

Cowries reproduction is also quite remarkable. Females lay eggs in clusters of capsules on hard surfaces and, in contrast to many other gastropods, they protect their eggs by covering them with their foot (Fig. 5). Abandoned eggs may die quite soon. This intensive parental care 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 is variable, and may be related to the capacity of a given species to undergo

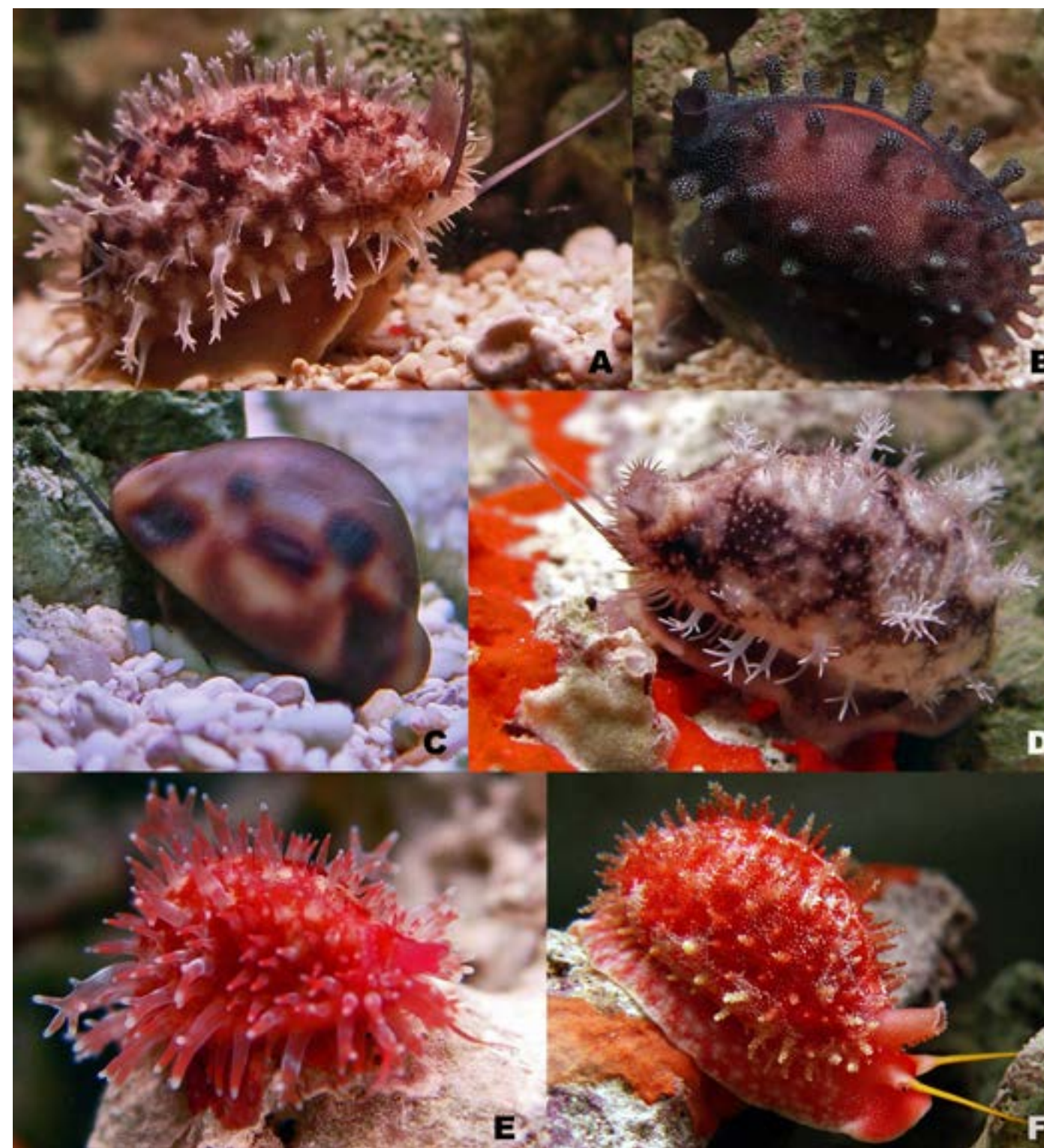


Fig. 1. Examples of mantles and papillae in Cypraeidae. **A.** *Lyncina carneola propinqua* (Garrett, 1879); **B.** *Talparia talpa* (Linnaeus, 1758); **C.** *Luria tessellata* (Swainson, 1822); **D.** *Lyncina lynx* (Linnaeus, 1758); **E.** *Naria poraria* (Linnaeus, 1758); **F.** *Ovatipsa chinensi amiges* (Melvill & Standen, 1915). Photo courtesy David Lum.



Fig. 2. *Naria erosa* (Linnaeus, 1758) showing its extended mantle resembling an algal tuft. The shell is barely visible in the middle of the dorsum, since the mantle is not fully extended.

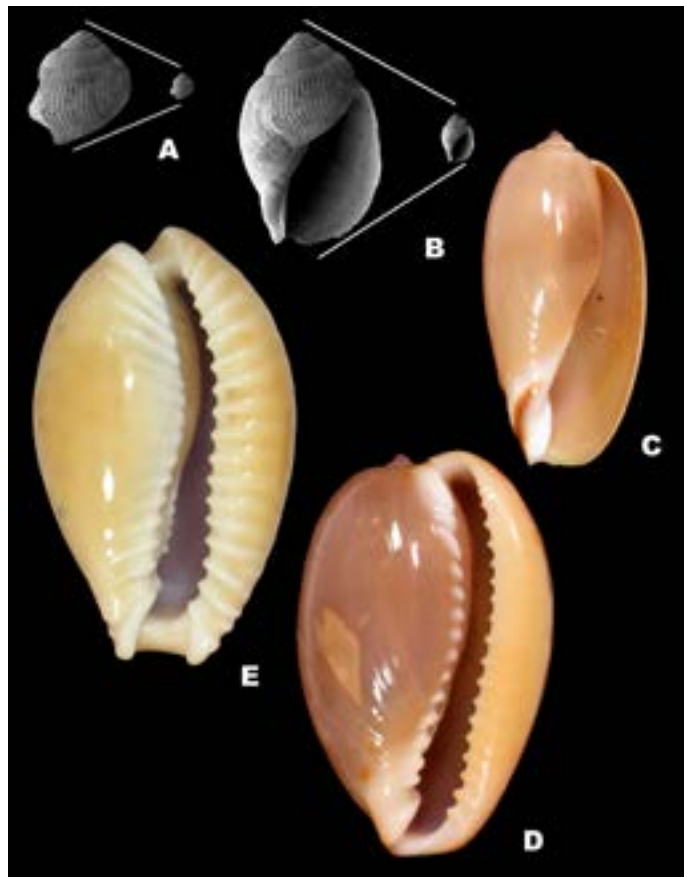


Fig. 3. Developmental stages of *Naria spurca*. **A** – Veliger shell, **B** – young shell (just metamorphosed); **C** – ‘Oliva’ stage; **D** – Subadult; **E** – adult.
Photo courtesy Andrea Nappo and Dario Marcello Soldan.

local genetic diversification (i.e. subspecies and/or geographic race formation). Some species have quite a few divergent races, while others have a much more restricted geographic pattern. Direct developers show different morphologies in different areas. In direct developers, young mollusks undergo intracapsular development and, since they feed at the expense of (i.e. cannibalize) other eggs in the capsule, they keep growing until they hatch as crawling snails. This pattern has evolved many times in cowries, especially in some temperate water genera (*Zoila* Jousseaume 1884, *Cypraeovula* Gray 1824, *Notocypraea* Schilder, 1927). Direct development has often been considered an adaptation to improve the chances of larvae to find specific foods, like sponges they feed on. In fact, most direct developers are fully dependent upon limited food supplies, and hatching as close as possible to their food supply increases their chances of reaching adulthood.

Distribution and biogeography

Cowries are subtropical marine animals (Fig. 6), so most of them live in the oceans between the two tropics. The highest number of species is found in the Indo-Pacific region; far fewer species live in the Atlantic (and the Mediterranean). Paulay and Meyer (2006) proposed an illuminating species richness map of Indo-Pacific cowries. The highest species richness is in the region going from the Philippines to Melanesia, especially along the boundary between the 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 and other reef-related organisms (see Malay *et al.* 2010). The region made up of ocean territories around 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



Fig. 4. Two *Zoila friendii jeaniana* (Cate, 1968) (f. *sherylae* Raybaudi Massilia, L., 1990) grazing their host sponge in the open.

Photo courtesy Daniel Edinger.



Fig. 5. *Erronea caurica* cfr. *quinquefasciata* (Röding, P.F., 1798) on eggs.

Photo courtesy Massimo Scali & Beautifulcowries Magazine.



Fig. 6. Distribution map of the living species of cowries.

Photo courtesy Mirco Bergonzoni.

for these similar distribution patterns could be both environmental and historical. Apparently the thousands of islands and reefs in Southeast Asia, as well as their highly diverse habitats, were central to a rich species radiation in cowries and other reef-related animals. Most of the widespread Indo-Pacific cowries probably originated in this area, and migrated (with varying success) outwards by larval dispersion.

The duration of veliger stages has been related to dispersion and speciation rates by Paulay and Meyer (2006). Although duration of veliger stages is only weakly correlated with species range, it is significantly related to the diversification of cowries in the Indo-Pacific basin: i.e. the lower the veliger time, the more the geographic/taxonomic diversification. Some Indo-Pacific cowrie species show very little geographic variation [see

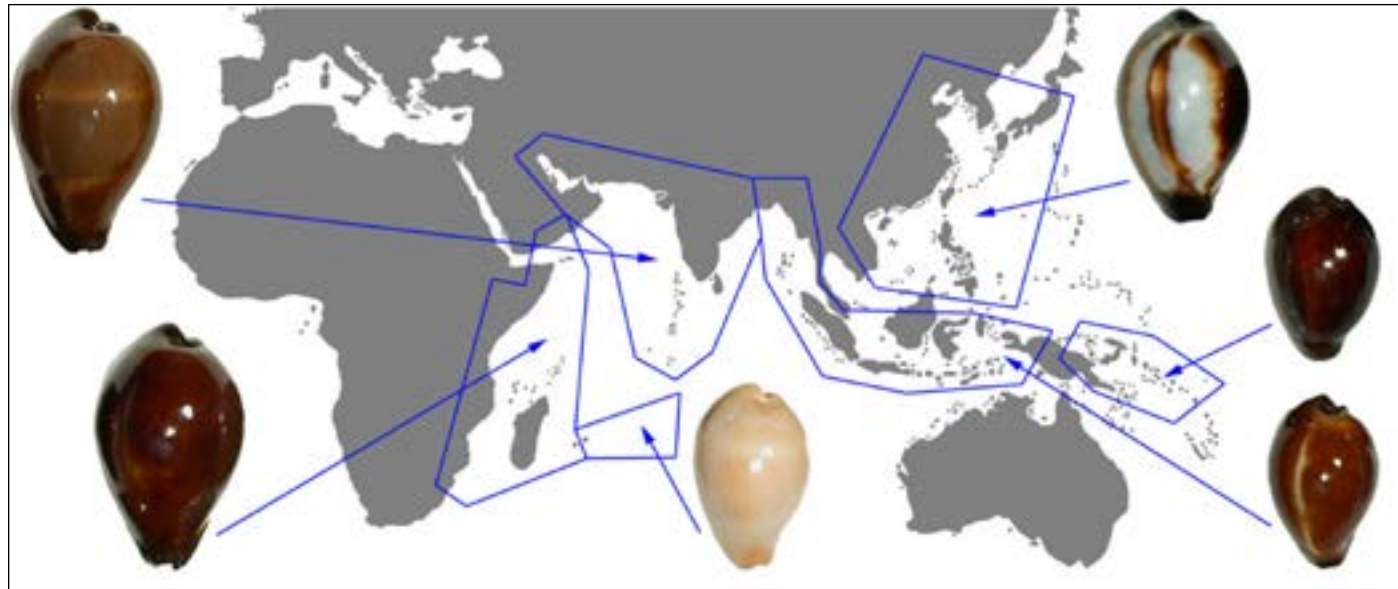


Fig. 7. Geographic diversification of the *Erronea onyx* species group. From left to right: *Erronea adusta adusta* (East Africa); *Erronea adusta nymphae* (Mauritius; Chagos); *Erronea adusta persica* (India, Oman, Persian Gulf); *Erronea adusta andamanensis* (East Indian Ocean); *Erronea adusta melanesiae* (South West Pacific); *Erronea onyx* (North West Pacific). Photo courtesy Mirco Bergonzoni.



Fig. 8. Examples of the variability of the *Leporicypraea mappa* species complex from different basins. Photo courtesy Mirco Bergonzoni & Cypraea.net.



Fig. 9. Examples of the variability of the *Zonaria pyrum* species complex. **1-4.** *Z. pyrum pyrum* (Gmelin, 1791) - Mediterranean Sea to Mauritania-Senegal (North of Dakar); **5.** *Z. pyrum insularum* Schilder, 1928 - Algarve (Portugal), Cadiz (Spain), Morocco, Canary Is.; **6-8** *Z. pyrum petitiiana* (Crosse, 1872) - South of Dakar (Senegal), Ivory Coast, Gabon, C. Verde; **9.** *Z. pyrum angelicae* (Clover, 1974) - North Gabon, Guinea Gulf (?); **10.** *Z. angolensis* (Odhner, 1923) - South Gabon, Luanda area (Angola). Photo courtesy Mirco Bergonzoni & Beautifulcowries Magazine.



Fig. 10. Examples of close relative pairs 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 eccentric locations. Above the line, the pairs considered as subspecies; below the line, the pairs considered as different species. From left to right: **1st row:** *Luria lurida* and *Luria lurida oceanica* (Ascension Is.); *Naria helvola* and *Naria helvola hawaiiensis* (Hawaii); **2nd row.** *Naria cernica* and *Naria cernica leforti* (Easter Island); *Naria acicularis* and *Naria acicularis sanctahelenae* (Ascension and Saint Helena); **3rd row:** *Monetaria caputserpentis* and *Monetaria caputdraconis* (Easter Island and Sala Y Gomez); *Cribrarula astaryi* (f. *lefaiti*) and *Cribrarula garciai* (Easter Island). Photo courtesy Beautifulcowries Magazine.

Monetaria caputserpentis, *Monetaria annulus* (Linnaeus, 1758)], while others are much more prone to produce local races/subspecies. Recent species have been studied in detail, including the *Erronea onyx* (Linnaeus, 1758) species complex (Bergonzoni, 2013), which differentiated into allopatric races (Fig. 7), and the *Leporicypraea mappa* (Linnaeus, 1758) species group (Fig. 8), which shows great biogeographic and evolutionary complexity (Bergonzoni & Passamonti, 2014). By analyzing such groups in detail, interesting examples of marine mollusk evolution have become apparent, including allopatric speciation events, incipient speciation, relevance of genetic flow for morphological diversification, etc. Other cowrie groups of interest still have to be analyzed

in detail, such as Genera *Cribrarula* Strand, 1929 and *Talostolida* Iredale, 1931, and the *Bistolida stolidia* (Linnaeus, 1758) and *Erronea caurica* (Linnaeus, 1758) species complexes, just to name a few.

Cowries have also colonized the Atlantic, although their species richness is much lower than in the Indo-Pacific. Most likely, this colonization was rather ancient, since the present cold currents off South West America (Humboldt Current) and South West Africa (Benguela Current) are strong barrier for larval dispersion and cowrie spreading. At present, no species seems to be able to spread from the Indo-Pacific to the Atlantic Ocean north of Namibia, or to South America. No cowries live



Fig. 11. Representatives of the South African Genus *Cypraeovula*. Photo courtesy Goncalo Rosa and Mirco Bergonzoni.

in the polar oceans. Nevertheless, Atlantic cowries have evident affinities with those in the Indo-Pacific. For instance, the Genus *Macrocypraea* Schilder, 1930 is present on both sides of the Isthmus of Panama, as it likely originated locally before the Isthmus closed. On the other side of the Atlantic, we have examples of pairs of allied species found in the Mediterranean and the Red Sea/Northwest Indian Ocean [*Luria lurida* (Linnaeus 1758)/*Luria pulchra* (Gray, 1824)], perhaps a Thetysian

residue. Some other genera are endemic to Northwest Africa and the Mediterranean (*Zonaria* Jousseume, 1884; *Schilderia* Tomlin, 1930). Finally, a peculiar distribution is found in the *Naria* species complex, including *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 pattern and timing of colonization of Atlantic and Mediterranean cowries is poorly understood, their phylogenetic relatedness to Indo-Pacific ones is evident. Detailed phylogeographic analyses are potentially of great interest to reconstruct the biogeological history of cowries in the Atlantic basin.

Larval stage duration of Atlantic cowries is correlated with morphologic diversification, similar

to the Indo-Pacific cowries. One paradigmatic example comes from the *Zonaria pyrum* (Gmelin, 1791) species complex (Fig. 9), one of the most beautiful Mediterranean and West African cowrie groups. Again, a short larval stage has been related to the extreme capacity to differentiate geographically, with different taxa spreading along the African coast (Bergonzoni, 2013).

Other interesting examples of evolution come from



Fig. 12. Extreme variability in *Zoila*. **A-C.** *Zoila friendii* subspecies/forms. **D.** *Zoila ketyana* subspecies/forms. **E.** *Zoila venusta* subspecies/forms. Photo courtesy Mirco Bergonzoni & Cypraea.net.



Fig. 13. The genus *Umbilia*. **A.** *Umbilia hesitata* species complex. **B.** *Umbilia armeniaca*. Photo courtesy Mirco Bergonzoni & Cypraea.net.



Fig. 14. *Barycypraea teulerei*. Two males approaching a female hatching eggs into a empty bivalve shell. Oman.



Fig. 15. *Barycypraea fultoni fultoni*. Natal, S. Africa. Photo courtesy Felix Lorenz & Beautifulcowries Magazine.

species/subspecies pairs in which one has a wide range, and the allied one has a peripheral endemic distribution. Fig. 10 shows some cases. Most of them are isolated endemics, likely of paraphyletic origin. Quite remarkably, they are treated much differently in established taxonomy: some are actually considered as full species, some other as subspecies, although no evident justification (other than subjective opinion) has been offered.

As mentioned, cowries were able to colonize temperate waters as well. This is particularly evident for South Africa and Western/South Australia, in which endemic genera evolved. In South Africa, the most striking evolutionary radiation is the Genus *Cypraeovula* (Fig. 11), which includes different closely related species that sometimes hybridize. 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) (Fig. 12). The *Zoila* cowries are spongivores and direct developers (see Fig. 4). *Zoila* micropopulation variation makes them one of the most complex and beautiful groups of marine organisms. *Zoila* are also the most coveted and expensive group of cowries sought by collectors. Genus *Notocypraea* is comprised of direct developers but it is less well-

studied than *Zoila*. Finally, the Genus *Umbilia* Jousseaume, 1884 (Wilson and Clarkson, 2004) is another striking endemic of temperate waters, distributed along the Southern and Eastern Australian coasts (Fig. 13).

Other direct developers are found as well, such as the Genera *Barycypraea* Schilder 1927 and *Muracypraea* Woodring, 1957. In all cases, direct developers have a very limited range. *Barycypraea teulerei* (Cazenavette, 1846) (Fig. 14), a shallow water direct developer (Scali, 2013; 2014), seems to be found in a limited area of Oman only. Its deep water relative, *Barycypraea fultoni* (Sowerby III, 1903) is found between Mozambique and South Africa (Bergonzoni, 2012) (Fig. 15). Another direct developer with little dispersal capacity is *Muracypraea mus* (Linnaeus, 1758), limited to the Gulf of Venezuela coasts and Guajira Peninsula in Colombia.

The molecular phylogenetics of cowries and their taxonomy

This field of cowrie biology has probably been the most thoroughly investigated. A huge phylogenetic reconstruction, based on DNA, has been proposed by Meyer (2003; 2004). The primary outcome of this pivotal work is an increased understanding of the

supraspecific (Subfamily, Genus) taxonomy of the Family. Quite remarkably, most of the Subfamilies and Genera proposed by older authors based upon shell morphology (see Schilder, 1939; 1966; Schilder & Schilder, 1938) have been confirmed by DNA studies. The Family Cypraeidae is now subdivided into 7 subfamilies (Archicypraeinae, Erosariinae, Umbiliinae, Cypraeinae, Bernayinae, Luriinae and Cypraeovulinae) and 48 genera (Moretzsohn, 2014). These arrangements have been accepted by many cowrie experts. Even if a relatively stable supraspecific cowrie taxonomy is now generally in favor, this is certainly untrue at species level and below. Most of the proposed taxonomies have been based on morphological analyses and subjective author opinions. Only a few DNA and/or detailed evolutionary studies are available to date. Moreover, a certain degree of taxonomic proliferation has been stimulated by monetary concerns: Many cowrie dealers want new names, because new, “rare” species and

subspecies are highly valued (at least temporarily) in the collector market. This is what I call ‘economic speciation’, with some humor, of course! This approach should be strongly stigmatized for two reasons: first, it produces an unnecessary proliferation of taxonomic names; and second, it usually has no biological basis.

Another problem comes from the rules of taxonomy, and this is particularly evident for species and subspecies names, which are governed by the International Code of Zoological Nomenclature. In my opinion, new species and subspecies names should not be introduced in taxonomy unless based on rigorous biological and evolutionary analyses. Nevertheless, specialized collectors need to have names to refer to specimens that are not important to evolutionary biologists, such local variants, unstable morphs, aberrations, etc. The use of ‘forma’ names should be a good compromise, because they meet collectors’ need for names



Fig. 16. *Zoila decipiens*. From left to right: black (normal), albino and rufinistic shells. Photo courtesy Drew Strickland.

and yet do not increase taxonomic complexity. Intraspecific names are not recognized by the ICZN. This approach is not without problems but it seems to me a reasonable compromise between two different, and sometimes conflicted, needs.

Mutations and aberrations

Albinism and rufinism

Cowries display multiple interesting mutations and aberrations. Some of them, being rare and beautiful, are sought-after, highly-priced and well-known to most cowrie collectors. The biological causes of these changes are often unknown or neglected. I will highlight some of these here.

The first example comes from rare recessive mutations, such as cowries' albinism (producing white shells) or rufinism (producing orange shells) (Fig. 16). 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 necessarily associated with white and orange animals, respectively. This clearly indicates that genes for shell color are different from the genes for living tissue coloration. 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 cowrie shells have been proposed to be the result of different mutations in



Fig. 17. *Zoila rosselli satiata* and *Zoila rosselli satiata* f. *edingeri* (rufinistic). Both found at Point Quobba, W. Australia.

Photo courtesy Daniel Edinger and Beautifulcowries Magazine.

the metabolic pathways that produce brown/black pigments or "melanin". [For a detailed discussion see Passamonti and Hiscock (2013).]

In addition to their high collector value, the appearance of rare mutants within a population represents an interesting opportunity 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 Western Australia. This once quite large population was an important source of rosselli specimens, and many hundreds have been collected over the years. In addition to normal black shells, around 40 rufinistic specimens were found (f. *edingeri* Raybaudi Massilia, 1990) (Beals, 2013) (Fig. 17). These shells were collected over a limited time span, as the first ones were collected in 1988, and they disappeared soon after 1997. A perfect *edingeri* is now one of the most valuable *Zoila* shells, valued at about 20,000-30,000 US dollars. Why did the mutant disappear so quickly? One might think that it is because all orange shells were collected, so they 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 cowries may well produce 25% orange progeny shells, according to Mendelian proportions. The overall collecting pressure on BOTH black and orange specimens is the reason for the disappearance of orange shells: by reducing dramatically the total 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 gene pool, and no *edingeri* have been found since. This also means that the chances that this allele will appear again in Quobba are quite low, and that the *edingeri* rufinistic mutation simply no longer exists. Rufinistic shells are rarely found

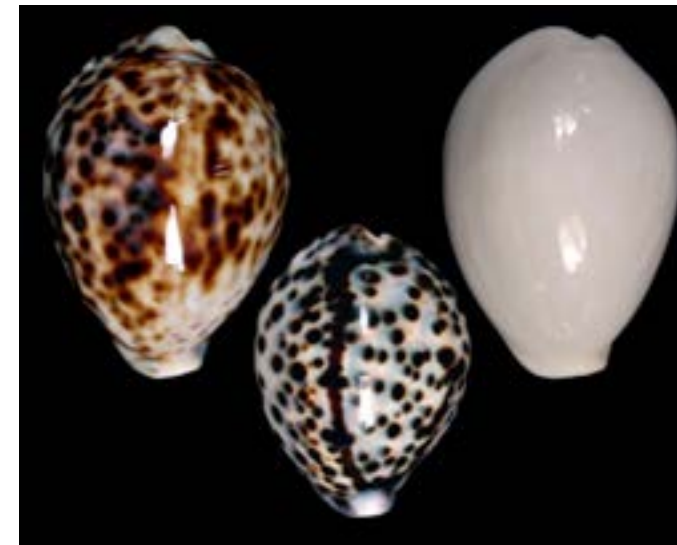


Fig. 18. Two normal *Cypraea tigris* along with an albino one.

Photo courtesy Mirco Bergonzoni & Cypraea.net.

within other *Zoila* species, as well as in some other cowries, so rufinism is likely caused by recurrent mutation(s). An independent rufinistic color form has been recently discovered in a distant south Western Australia *Zoila rosselli* population (see Lorenz, 2011; 2014).

Albinos are exceedingly rare among cowries. Although many cowries may be white or whitish, the rare albino mutants are only known for very few cowries [*Cypraea tigris* (Fig. 18), and *Zoila decipiens* Smith, 1880 (Fig. 16)]. What is quite interesting is that albino morphs have become fixed in some populations (i.e. ALL the shells are albino). Two paradigmatic examples are *Naria eburnea* Barnes, 1824 (Fig. 19) and *Erronea nymphae* Jay, 1850 (Fig. 7). 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 was established in a new area the albino allele became by chance the unique one (i.e. it was fixed).

Niger and rostrated cowries



Fig. 19. *Naria miliaris* (left) and *Naria eburnea* (right).

These aberrations appear to be restricted to some cowries and a single ovulid species [*Calpurnus verrucosus* (Linnaeus, 1758)]. It is evident that these two characteristics are the outcome of atypical cowrie shell development. As mentioned earlier, adult cowries stop growing, since the deposition of shell layers and pigments stops or strongly reduces. However, in some species, the signal to stop seems to work improperly, and the shell keeps growing by adding layers of shell and/or pigment. Such cowries develop a 'gondola shape' (rostration), and develop a deep black color (melanistic or 'niger' cowries). Both phenomena may appear together, or not, depending on species. Some species become melanistic and rostrated. Others may only be rostrated (these species do not have brown/black colors in normal adults). Also, the degree of rostration and melanism may vary among individuals (Fig. 20).

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 of Queensland. The biological causes of such



Fig. 20. Examples of different degrees of melanism and rostration in New Caledonian cowries. **A.** *Mauritia (Arabica) eglantina*; **B.** *Bistolida stolidia*.

aberrations are still unknown, and some have linked these phenomena to the presence of heavy metals (nickel?) in the water (Pierson and Pierson, 1975). What I think it is interesting is the likely genetic basis of melanism and rostration. 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 fail to stop at adulthood, as in normal cowries. Needless to say, we have no clue as to which genes could be involved in such processes, and this would certainly be a nice case study for developmental biologists.

Conclusions

In this paper I have tried to highlight some biological peculiarities of cowries which make them interesting objects for study 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' information is available. This manuscript is far from comprehensive; many other interesting cases could be highlighted. Nevertheless I hope that this short review has stimulated your interest in this amazing group of animals which certainly deserve more study. The collection of cowries, which is unfortunately so deeply money-driven, is certainly a restraint to biological studies. Some species are hardly accessible and collecting data are often vague (to hide sources of income for divers and dealers). On the other hand, an important collecting effort is a precious help for biologists. Perhaps for no other group of gastropods do we have such a huge amount of knowledge 'in the field'. We should therefore try to build a 'bridge' between two worlds (cowrie amateurs and biologists) so that both may benefit. Collectors will start to consider cowries not as just precious and beautiful objects, and evolutionary biologists/professional malacologists will become more

interested in cowries as rewarding animals for study. Only in this way, will the preconception that cowries are pretty but scientifically uninteresting animals will be justifiably overcome.

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Gastropodial MUSINGS

an informal column for questions, thoughts and answers

by Roy Aiken

The cabestana cutacea conundrum ...

Significant differences in size and morphology have resulted in the Cymatid *Cabestana africana/ cutacea/ dolarium* from Southern Africa, being split into two by some authors. D.H Kennelly illustrates *Cymatium dolarium*, Linne, for small shells exhibiting strong radial cords, and the much larger *africanum*, (A.Adams), with smooth body whorl.

Kilburn refers to "this most puzzling" *Cymatium* and mentions its generally accepted division into *africanum*, large, pointed, relatively smooth shells and *dolarium*, barrel shaped, with strong, bisected spiral cords. Steyn and Lussi lump them together, under *Cabestana cutacea*. Worms currently has *Cabestana cutacea* as being found in the Mediterranean, whereas *africana* is South African. Endemic to South Africa, they occur sympatrically.

Perhaps this group will only become clearer once DNA analysis is conducted in the future... The possibility remains that they represent two distinct species.



Figure 1 shows four shells all with the strong spiral cords, and three similar sized shells that are much smoother..



Figure 2 shows SA shells that actually bear a strong semblance to *cutacea* from Mediterranean

Figure 3 shows three lovely live dived colour varieties of the large *africana*.. this 'species' can reach 120mm



Figure 4 shows the relative size and morphology between the two



The Lorene Du Preez Shell Collection

On 16 November 2016 the Society lost one of its long-time members, Lorene Du Preez. Lorene had been an avid shell-collector since her youth and took over her mother's collection. This meant that apart from growing her collection into a significant and large one, she also had acquired a number of specimens that dated back to the early 20th century, and represented large and valuable shells which are seldom seen today.

Lorene was a graduate from the University of Stellenbosch and worked at the CSIR throughout her long career. She had a wide and diverse range of interests apart from conchology, particularly botany, zoology and geology.

On her passing, the Society learned that her next of kin had bequeathed her collection to it. This was a wonderful and thoughtful action and it will take the Society a long while to process all the specimens of the collection. In due course an article will be produced on the specimens in Lorene's collection, but the collection in the interim is in the safekeeping of the Society. We thank Lorene's next of kin for their generosity and look forward to being able to enrich the Society's conchological knowledge as we share in exploring her collection in the future.



It's all about the Water

BY KEN BROWN

In 2008, billions of commercially cultured oyster shells died on the Pacific Northwest Coast of the United States, threatening the collapse of a \$110 million industry. Scientists scurried to find the cause. Ocean water tests revealed a startling truth – the pH of the seawater had killed the oyster beds, as it had done to seeded beds every year since 2005.

Our oceans absorb massive amounts of greenhouse gases in the atmosphere – about a quarter of our emissions caused by burning coal, oil and gas result in major absorption of carbon dioxide (CO₂), which results in a fatal drop in the pH levels of the world's oceans, more commonly known as ocean

acidification ... and the process continues. We see images of a choking China, and India poisoning its air .. and ours.. daily, whilst another major global air polluter, the USA plays ostrich-head-in-the sand for short-term financial gain.

Since the beginning of the industrial era, our oceans have absorbed over 525 billion tons of CO₂, and at present this translates to a staggering 22 000 000 tons of CO₂ absorption a day. More than 2,400 new coal-fired power stations are under construction or being planned around the world. The new plants will emit 6.5 billion tonnes of carbon dioxide a year and undermine the efforts of the Paris climate conference to limit



Fig 1: Piles of discarded Pacific oyster shells destroyed after exposure to higher pH levels

global warming to 2°C.

Planetary evolution and adaptation is a slow process and many species have evolved slowly to suite their niches. Therefore an ocean which has become 30% more acidic in just the last 200 years compared to the past 50 million and which is growing exponentially more acid each year, has meant that this enormous and rapid change in seawater chemistry has not given marine life sufficient time to adapt. A drop in human pH of just 0.2 can cause seizures and death: in marine life similar drops have hugely harmful effects, and impact on growth reproduction and survival.

There is clear evidence that a number of seashells, and the shells of some marine creatures, are already beginning to dissolve with present levels of acidic seawater.

The chemistry of ocean acidification is simple. As CO₂ dissolves in seawater, it reacts with the water to form carbonic acid (H₂CO₃), and releases hydrogen ions (H⁺), which then bond with other molecules. pH is the scale used to measure the concentration of hydrogen ions, and acidity describes how many hydrogen ions exist in a solution. Oceanic pH has dropped from 8.2 to 8.1 since the Industrial Revolution, and is calculated to fall by another 0.3 to 0.4 units by the end of this

century at present levels. The scale may not seem significant, but it is logarithmic: for example, a pH of 6 is ten times more acidic than a pH of 7. The translation is frightening: at current levels of CO₂ absorption into our oceans, seawater pH will drop 120% by the end of the century, exponentially acidifying our oceans.

There is a double whammy in the chemistry though. Ocean acidification means that seawater will dissolve more and more carbonate-based species, from the shells of seashells and other marine animals to decimating coral reefs. However, seashells need carbonate (CO₃) as a key component to grow their shells. In order to make calcium carbonate (CaCO₃), shells and corals combine a calcium ion with carbonate from the surrounding seawater. Hydrogen ions however bond with carbonate ions, and in fact have a greater chemical attraction to carbonate than calcium. The result of the bonding between the hydrogen and carbonate is a bicarbonate ion, which is the second blow: seashells are unable to extract carbonate ions from the water, and cannot

use bicarbonate to grow their shells.

They are unable to grow new shells.

The loss of carbonate and the ability to produce calcium carbonate is not restricted to seashells, but includes many groups occupying many diverse niches, from coralline algae and zooplankton, to crustaceans and corals harbouring photosynthetic symbionts such as zooxanthellae.

In reef-building corals, present pH levels are responsible for between a 10 and 60% decrease in calcification rates. Coral reef ecosystems have served as cradles of evolution and development throughout Earth's biological history, and the destruction of reefs through acidification and global warming, will have an incalculable effect on the future of the entire planet, not just the simple seashell whose demise we will lament but not be inconsolable without.

Warming of the world's oceans is a reality as well, with catastrophic implications for coral reefs, and

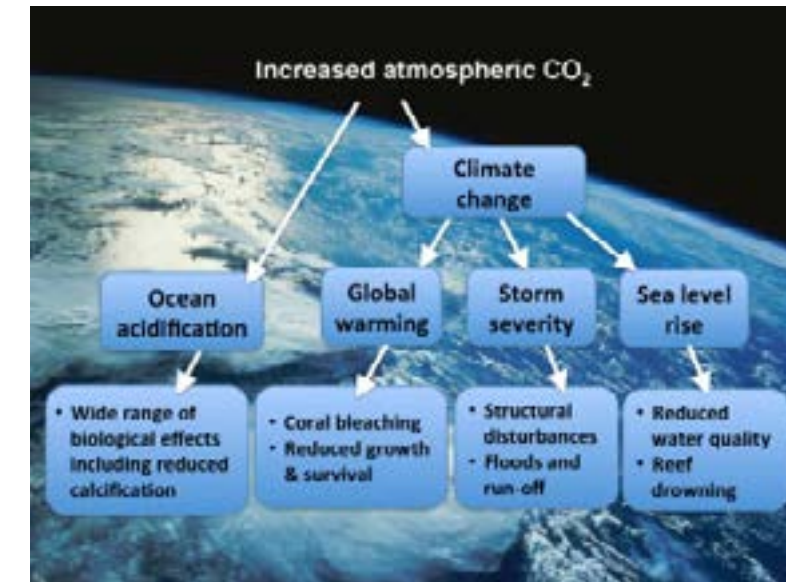


Fig 3. The multiple effects of increased carbon dioxide in the atmosphere

the huge diversity of marine life they spawn and shelter. Most coral reefs consist of stony corals known as scleractinian corals which obtain much of their diet from zooxanthellae, and which are the primary reef builders of the planet's tropical oceans.

The zooxanthellae of scleractinian corals enable polyps to obtain the majority of their nutrients. The zooxanthellae are responsible for producing the calcium carbonate of the coral, which the polyps then excrete, slowly building up a skeleton, often on the foundation of generations of earlier



Fig 2: One of more than 2300 existing coal-based power stations in China – another 1171 are in the pipeline

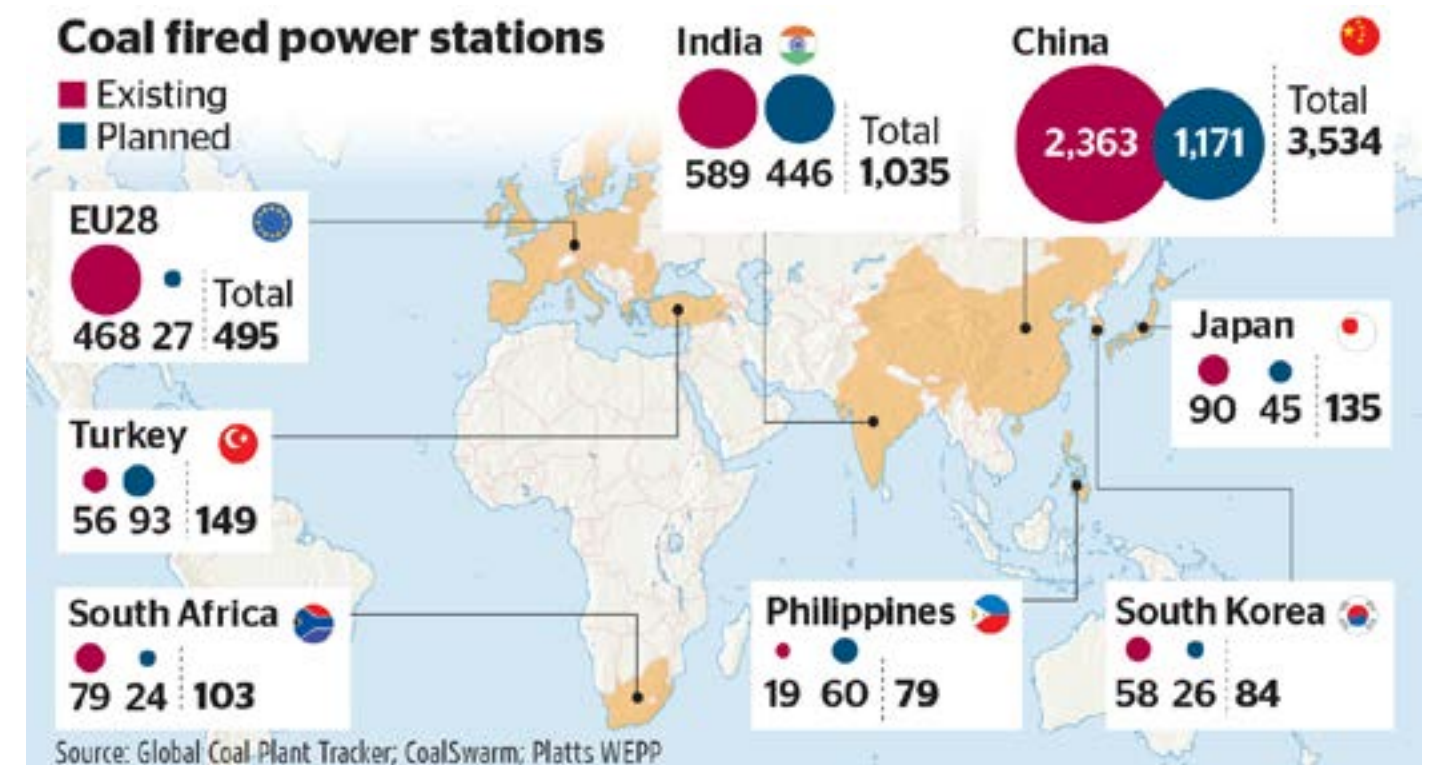


Fig 4. The number of major new coal-based power stations in the pipeline

skeletons, and in time colonies have built up the massive structures that are known as coral reefs. The presence of zooxanthellae is vital to the coral-building process particularly in open ocean waters which are nutrient poor: the coral animals provide a safe and stable environment and a source of nutrients; the dinoflagellates reciprocate by providing oxygen, carbohydrates and the alkaline pH necessary to enhance the rate of calcium carbonate deposition.

Coral reefs have significant economic value on a number of counts:

1. they provide income from tourism through visitors enjoying recreational activities such as sightseeing and diving
2. they are important breeding grounds and habitats for fisheries resources - about six million tons of fish are taken each year from coral reefs. Southeast Asia's coral reef fisheries alone yield about USD 2.4 billion annually from seafood
3. they protect coastlines from the effects of storm surges

4. they are vital reserves for global biodiversity
5. they are important carbon sequesters, taking carbon dioxide out of the atmosphere and mitigating atmospheric pollution and global warming
6. they release oxygen into the atmosphere through zooxanthellae photosynthesis

Zooxanthellae are incredibly sensitive to temperature changes and seawater temperature changes brought about by the greenhouse effect of global air pollution. A temperature change in seawater of several degrees will cause the zooxanthellae to eject from their coral hosts, dying and effectively ending the life of the coral.

The sad prognosis is that coral reefs are under heavy pressure. Already 27% of world's coral reefs are permanently lost and with current trends, a further 30% is at risk of being lost in the coming thirty years. With such devastating levels of destruction, the social and economic implications for the millions of people who depend on coral reefs are of great concern. Over 39% of the world population now live within 100 kilometres of the

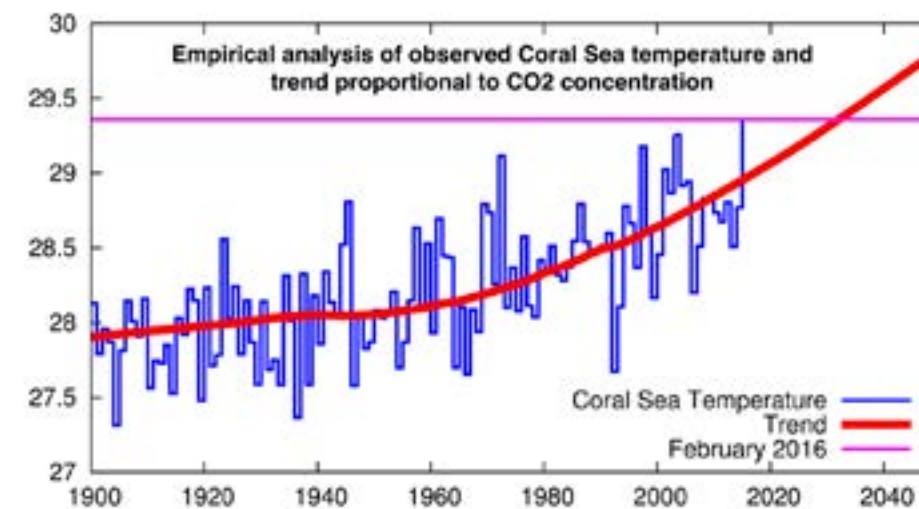


Fig 5: Even the most robust of seashells shows evidence of corrosion due to higher seawater pH



coast and many people in these areas depend on reefs. Reefs protect coastlines and reef fish provide a source of nutrition and income. Poverty increases and food security decreases as fish stocks are depleted. This drives fishermen further toward the use of destructive methods to catch what little there is left. Destructive reef practices by impoverished communities include dynamite blasting and cyanide poisoning in seafood capture, usually for Asian markets. Land-based pollution is another major threat to coral reefs as untreated sewage from urban areas and runoff from chemicals used in agriculture cause sedimentation and mass algal growth. Currently 22% of the world's coral reefs are under medium to high risk from these land-based sources of pollution, and 60% of all coral reefs are at risk from human destruction.

The odds appear to be inevitably piling up against the long term survival of our humble seashell. Water pH will significantly inhibit growth of shell structure, stress the animal and its ability to reproduce, and will in fact dissolve shells as pH



levels increase. The looming destruction of our coral reefs predominantly as a result of water temperature increases will mean that the home to one of our planet's most productive and diverse ecosystems, from the actual corals to the fish, crustaceans, molluscs, seabirds, sea turtles, sea snakes, echinoderms and cetaceans will all be at severe risk.

So let us collect and sagaciously concern ourselves with nomenclature, gem quality and current placement of our beloved shells, ... are we fiddling whilst Rome burns?

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Naudoliva caitlinae

The Hunt for an Elusive Species

BY PHILIP JOOSTE

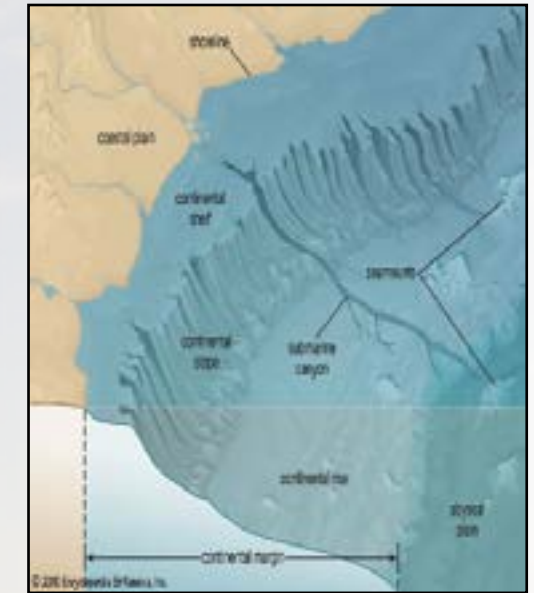


Naudoliva caitlinae Kilburn, 1989 was known originally from a few beached specimens found occurring between Kidd's Beach Xora Beach, about 30 km south and 70 km north of East London, respectively. Specimens of *Naudoliva caitlinae* were very seldom seen and, when found, were usually in poor condition.

Their elusive habitat was long-discussed and it was thought to be relatively shallow, presumed to be between 30 to 40m, and also possibly in sand.

Following the original discovery and description, specific effort was made to locate their habitat. Between 1996 and 2002 they were actively searched for by diving and dredging off East London, from Nahoon to Bosbok Strand, in water depths ranging from 20 to 40m. Many other species were found during this time by dredging on sand in these areas, including *Marginella susanae* J.H. Veldsman & Jooste, 2009, *Marginella mosaica* Sowerby II, 1846, *Marginella bairstowi* Sowerby III, 1886 and small numbers of *Marginella nebulosa* (Röding, 1798). Also found were specimens of *Melapium lineatum* (Lamarck, 1822), *Amalda contusa* (Reeve, 1864), *Amalda trachyzonus* Kilburn, 1975, some *Pseudoliva* species (similar to *Pseudoliva ancilla* Hanley, 1860), and many others.

Many species were found by diving, including some of the local Cypraeidae, Conidae and other species, but *Naudoliva caitlinae* remained hidden. In 2000 the search effort expanded to include deeper water territories. The search parties involved resorted to dredging, using bigger boats and learning how to deal with the strong currents prevailing off the Eastern Cape coast. Searches started off East London, mainly around the Kwelera area, and ventured near the Continental Shelf.



Dredging here on a shale bottom, the search parties found some very interesting and rare species, including *Cypraeovula kesslerorum* Lorenz, 2006, *Cypraeovula capensis profundorum* Seccombe, 2003, *Triviella immelmani* Rosenberg & Finlay, 2001, *Conus velliesi* (S.G. Veldsman, 2016), and others. Also found, after getting to know the area, was the first *Naudoliva caitlinae*. It was dead taken, but very fresh. This was in 2002, and, following this discovery, all involved thought that the habitat of this elusive species had finally been discovered – but another specimen was not found again for quite a few years. This, indeed, is the marque of a true rarity!

In 2012, after having explored the East London area quite well, and having come slightly shallower (between 93 and 95m), search parties finally found the first live-collected specimen on a shale bottom, amongst lots of dead and broken shells. In this period, three live and three good quality dead specimens were found. Although the habitat – following a 16-year search – had finally been found, the species remained exceptionally rare, and the original search group had to wait another



two years before two more live and three more dead specimens were found.

So to sum up from my personal experience, I think that *Naudoliva caitlinae* is probably a deeper water species that rarely will be found shallower than 90m. They seem to prefer a coarse, shale habitat,

covered with broken shell pieces.

This species will also undoubtedly remain rare, in consideration of their habitat which is around 20km offshore near the Eastern Cape Continental Shelf – an area wrought with challenges and very difficult to dredge.

