

## INTRASPECIFIC VARIATION AND THE HARDY-WEINBERG EQUILIBRIUM

Heiman E.L. \*)

**Abstract:** Intraspecific variation in many recent species of Cypraeidae is rather limited. Some of them seem to exist millions of years without substantial changes in their phenotypes. In others, about three dozen species, there are numerous forms. The latter inhabit mostly shallow water although they can be found sometimes in deeper water of 20-30 m and more. The conchological practice shows that intraspecific variation is especially high in the areas named here “geographical blind alleys” where populations of cowry species may consist of a limited number of individuals. This may violate the population equilibrium, which depends on certain conditions according to Hardy-Weinberg theorem. Two possibilities of the process of speciation in the Family Cypraeidae are shortly discussed: a gradual expansion of individuals of a species in new neighboring areas, and the results of high variability of populations in the “geographical blind alleys.”

**Key words:** Mollusca, Gastropoda, Cypraeidae, Hardy-Weinberg equilibrium, “geographical blind alley” areas, speciation.

Cypraeidae (cowries) are sexually reproducing marine molluscs living in populations, which may consist of colonies (smaller populations, groups of individuals of the same species). Such populations can be treated as Mendelian populations. It is accepted to consider that Mendelian populations have a gene pool that is the total of all the genes carried by the individual members of the population. When the individuals of the population are reproducing, their genes will pass into the gene pool of the following generations. Normally, the gene pool of a cowry population can be considered unlimited and no gene exchange between members of its individuals and individuals of other species (other Mendelian populations) takes place. The gene pool of widely distributed species may be divided into smaller gene pools of the colonies living in different areas.

### The Hardy-Weinberg equilibrium

Genes of the gene pool may have different forms (alleles). Different populations of the species may differ in the frequencies of some of these alleles. Theoretically Mendelian populations as a whole do not change with time; the frequencies of genes (and alleles) are the same. This follows from the Hardy-Weinberg theorem proven about a hundred years ago: “two or more gene alleles will have the same frequency in the gene pool generation after generation, until some agent acts to change that frequency.” In other words, in the ideally constant environmental conditions, Mendelian populations may not change with time.

Indeed, several species of living fishes and reptiles currently known to science look as if they did not change during dozens of millions of years. In Cypraeidae, the same can be said regarding *Bernaya teulerei* (Cazenavette, 1846), *Barycypraea fultoni* (Sowerby, 1903), and *Propustularia surinamensis* (Perry, 1811).

But many recent cowry species demonstrate such variability that even separating species may sometimes be difficult. There are many varieties in cowry populations.

One would think that this fact is in contradiction to the Hardy-Weinberg theorem but it only looks as such. The point is that the theorem is based on several assumptions. Violation of any of these may change the equilibrium.

The main assumptions are:

- 1) The population is large enough so chance fluctuations may be ignored.
- 2) A possible mutation is ignored.
- 3) Individuals with different alleles have neither advantages nor disadvantages in survival or in reproduction.
- 4) Mating is at random with respect to the alleles.

At least three stable mutants (the second condition above) in cowries are currently known. *Erronea erronea* (Linnaeus, 1758) form *azurea* from NW Australia has the bluish dorsum (normally grey-green). *Erosaria eburnea* (Barnes, 1824) living in the Pacific Ocean and *Notocypraea casta* Schilder & Summers, 1963 are characterized by the completely white shell. Shells of these taxa are rather uncommon. One can assume that the latter taxon is only a new mutant (a form) and not yet a separate population. Shells of the former superficially resembling those of *Erosaria miliaris* (Gmelin, 1791) are traditionally treated as different species. It seems to be a mutant of *E. miliaris*.

### Variable populations

Populations of the majority of living cowry species are not very variable and only a few forms can be observed in each of them in addition to morphometric differences between individuals.

Several others are very variable and include many forms.

For example, at least ten forms (not considering innumerable variants in the dorsal color and pattern) are known in *Cypraea tigris* Linnaeus, 1758 widely distributed in the Indo-Pacific region: in the West from Djibouti to South Africa, in the East to Polynesia. It is possible that such high a degree of intraspecific variation stipulated in the past adaptation of this species to new environmental condition and this process is still continued.

When the Red Sea was formed about 30 million years ago, a certain number of *C. tigris* apparently entered this new addition to the Indian Ocean. Malacologists believe that *C. pantherina* Lightfoot, 1786 evolved from *C. tigris* after a relatively small number of *tigris* individuals entered a new habitat (the Red Sea) and turned out to be isolated from the main genetic pool of the *C. tigris* populations (the first condition for stability of a population mentioned above was violated).

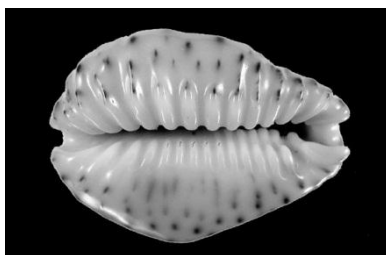
As a result the Red Sea is inhabited now by *Cypraea pantherina* while *C. tigris* is absent over there. Shells of *C. pantherina* are very similar to those of *C. tigris* and were often confused in old collections. There are reports in the literature regarding hybrids between *C. tigris* and *C. pantherina* in the area where the Red Sea turns into the northern part of the Indian Ocean. That confirms the above hypothesis regarding the origin of *C. pantherina*.

*C. pantherina* is also very variable having the same forms as *C. tigris* as mentioned in Heiman & Mienis (2000) and Heiman (2002a, b). The Gulf of Aqaba was formed later, probably about 5 million years ago (25 million years after the Red Sea was formed). One can separate conchologically populations of *C. pantherina* living in the southern Red Sea and those living in the Gulf of Aqaba; the latter are described in Heiman & Mienis (2001) as a subspecies.

Perhaps the same evolutionary process, which happened with *C. tigris* after formation of the Red Sea, was repeated after a partial separation of its northern part: the Gulf of Aqaba. As the first relatively small number of *C. tigris* settled in the Red Sea and after a long time evolved into *C. pantherina*, the first relatively small number of *C. pantherina* entered the Gulf of Aqaba and partly changed in this northern section of the Red Sea.



1. *E. nebrites* form labrospinosa.  
Near Hurghada, Egypt. Pleistocene.



2. *E. nebrites* f. labrospinosa.  
East Sinai



3. *E. erosa* f. labrospinosa  
Philippines

All this takes a lot of time as follows from another example. *Erosaria nebrites* (Melville, 1888) apparently underwent in the past the same process discussed above evolving in the Red Sea from *Erosaria erosa* (Linnaeus, 1758). Currently ten forms of it are known in the Gulf of Aqaba. As can be seen in Heiman (2002b, 2005) these forms of *E. nebrites* are very similar if not identical to forms of *E. erosa*, especially the form labrospinosa (Figs. 2-3) distinguished by very strong and produced labral teeth.

The latter form of *E. nebrites* is mostly found in the Gulf of Aqaba. In the northern part of the Gulf shells of this form may be common and their number may reach 20-30% of all shells of the species. This form is rarely found in quantity in the Red Sea proper. Shells of the same form were found in Pleistocene deposits near Urghada, Egypt, not far away from the Tiran Strait where the Gulf of Aqaba turns into the Red Sea. This means that conchologically *E. nebrites* seems to be the same during thousands of years from Pleistocene to our days. It is especially interesting that this form 'labrospinosa' was not known in *E. nebrites* until several years ago when it was found in an unusual place. The Hardy-Weinberg equilibrium does not mean the absence of evolution or the absence of variability in cowry populations. Probably, after establishing a cowry population in the new habitat (as with *C. tigris* and

*E. erosa* mentioned above) several forms in their populations survived natural selection. After that a number of individuals in the populations reached some critical quantity and the new population reached stability as a new species with a partly new phenotype.

#### Areas where changes in cowry populations are most probable

The conchological observations show that several areas in the World Oceans exist where cowry populations may demonstrate more forms than in other places. This phenomenon was partly explained in the literature as the “founders effect” and the “atoll effect.” Both these cases are apparently connected with a limited number of individuals in populations that breaks the first condition of the Hardy-Weinberg equilibrium. There are different causes for these phenomena and correspondingly different consequences in the future.

The ‘founders effect’ deals with a new population. A population is small first but may grow and develop in the future in its own way and its individuals may finally be different from their predecessors.

The ‘atoll effect’ is a case when a population or a colony periodically decreases in numbers, grows up and develops again but it decreases in numbers again after a relatively short period of time.

Chances for a colony to develop in a new subspecies or in a species, in which new forms will prevail, are real mostly for the first case.

Another case is named here “geographical blind alley” similar to a situation in the northern part of the Gulf of Aqaba where contacts between individuals of a cowry population living here with individuals of the other parts of the relevant populations in the Gulf or in the Red Sea are naturally limited and a colony may be not large enough. This phenomenon shows itself in the existence of many forms as in the cases of the “founders effect.”

Cases of the “geographical blind alley” are observed not only in the northern part of the Gulf of Aqaba. There are many areas in the Indo-Pacific region with similar conditions: in the northern part of the Persian Gulf, in the North-East of the Andaman Sea, around the Hawaiian Islands, in French Polynesia, in the waters around Passover Island, around Australia, in the area of Mauritius-Reunion, in the South of Madagascar and in southern areas of South Africa. In these peripheral areas one can observe a high degree of variability of cowry populations and many forms, part of which already reached the subspecific level.

#### Speciation

Mayr (2000) explained one of the possible ways of the process of speciation by a gradual expansion of individuals of a species in new areas. After their settling there, changes in their biological characters may occur due to the adaptation to new environment. Healthy changes may gradually occur in the majority of individuals of new settlers and they may become partly different from their predecessors. Gradually they may reach a level of a geographical subspecies, and finally to build a separating mechanism of the specific level. All that takes a lot of time but examples of a similar process can be traced.

One of examples is *Notadusta punctata* (Linnaeus, 1771). This species is widely distributed in the Indo-Pacific region from Elat in the Gulf of Aqaba to French Polynesia. Here it is usually treated as a subspecies *N. punctata trizonata* (Sowerby, 1870). A marked difference of this subspecies consists of the visible smaller size of the shell and the dorsal pattern forming three zones and very small dark spots. It is easily separated from other populations of the species and can perhaps be treated as a species.

In the areas called here “geographical blind alley” many geographical subspecies are described. Perhaps these conditions are especially favorable for initiation of the process of speciation.

#### Literature

Heiman E.L. 2002a. Variability of cowry populations 18. Forms of *Cypraea tigris*. Triton 6:19-23.

...2002b. Cowries of East Sinai. Published privately. 208 pp.

2003. *Erosaria nebrites* form *labrospinosa*. Triton 8:17-18.

2005. Intraspecific variation in *Erosaria erosa* (Linnaeus, 1758). *Of Sea and Shore* 27(2):76-88.

Heiman E.L. & Mienis H.K. 2000. Variability of cowry populations 6. Two populations of *Cypraea pantherina*. Triton 2:17-23.

2001. *Cypraea pantherina ransraniensis* new ssp. from the East coast of Sinai. Triton 4:7-11.

Mayr E. 2000. Systematics and the origin of species from the viewpoint of a zoologist. 334 pp. Harvard University Press, Cambridge, Massachusetts, London.

Schilder F.A. 1962. Hybrids between *Cypraea tigris* Linnaeus, 1758 and *Cypraea pantherina* Solander, 1786

(Mollusca:Gastropoda). *The Veliger*, 5 (2):83-87.

\*) E-mail: heimel@netvision.net.il