The great snail debate

Figure 1. Mating of two hedge snails (Cepaea nemoralis). Hermaphrodites, individuals are simultaneously male and female. [Source: Photo © Michel Veuille]

The mutual attachment of these two hedge snails (Figure A) shows that they recognize themselves as the same species, although they are very different in appearance to our eyes endowed with colour vision, unlike theirs. The color variation of their shells is called polychromaticism. It depends on a set of two alleles of the same gene determining two characters: "pink" and "yellow". It was widely used in natural population genetics in the 1950s, when genes could only be studied if they determined a visible phenotype.

At a symposium held in *Cold Spring Harbor* (New York State, USA) in 1959 to mark the centenary of the Darwin's *Origin of Species*, this snail was the occasion for a great scientific controversy between "*breeders*" and "*neutralists*", which science historian William Provine humorously called *"the Great Snail Debate*". The Frenchman Maxime Lamotte, working with the mathematician Gustave Malécot, showed that phenotypic frequencies vary largely at random in natural populations, with selection explaining only 10% maximum of the variation between populations. This was the "neutralist" theory. This contradicted the data obtained on the same species by the British P.M. Sheppard, who also attended the symposium, who favoured the role of selection by predators, such as thrushes. This was the "selectionist" theory. According to him, allele frequency profiles varied essentially according to the microhabitat of snails. This reflected the fact that thrushes, capable of discerning colours, chased snails visually into the bushes (Figure B); the colour of the environment more or less altered their ability to perceive the different phenotypes. Sheppard was part of the school of Ronald Fisher, author of the founding book of evolutionary genetics: *The genetical theory of natural selection* in 1930. A spokesman for this school, E.B. Ford, believed that mutations could not reach a high frequency by chance, and therefore postulated that important polymorphisms such as snails should be due to selection by predators. For the American Sewall Wright, another founder of population genetics at the conference, chance is only interesting in evolution because it favours the action of natural selection. It can then free populations from local maximums, allowing allele frequencies to continuously evolve within populations. It was to suggest that Lamotte and Malécot were being misled by a subject of little importance.

Figure 2. Thrush anvil. Stones used by thrushes to break the shells of snails they have fetched from the surrounding bushes are called stones. Comparison of phenotypic frequencies among broken shells and in the remaining population was used to determine whether certain phenotypes protected snails by colour mimicry with the plant environment. [Source: Photo © Michel Veuille]

The epilogue of this debate came ten years later. In 1969, the Japanese Motoo Kimura and Tomoko Ohta interpreted the important diversity of molecular polymorphisms discovered in 1966 in the *Drosophila pseudoobscura* fly by Lewontin and Hubby and in humans by Harris. They demonstrated that this enormous amount of variation could only be explained if the majority of alleles fluctuated randomly. The result was a ten-year controversy following another ten-year controversy on the role of deleterious mutations. At the end of these debates, the neutralist theory triumphed. On the basis of Malécot's equations, Lamotte had given a message of humility for the celebration of the centenary of natural selection that the scientific community had not been able to hear.

It should be noted that the "neutralist theory of molecular evolution" [1] does not assert that natural selection does not exist, but only that the **majority of molecular polymorphisms are neutral**. However, it recognizes that the most important genetic changes to transform a species are selected. In 1982, the British mathematician Kingman gave the final form to the neutralist model with the *"theory of coalescence*", an extension of Malecot's equations on gene filiation. After seeing his work neglected for a while, Malécot (1911-1998) received definitive recognition. He is now .considered one of the founders of population genetics.

References and notes

[1] Motoo Kimura (1983) *The neutral theory of molecular evolution*, Cambridge University Press.
