

WHEN THE GALÁPAGOS “FINCHES” ARE AZOREAN SNAILS

António M. de Frias Martins

*CIBIO-Açores, Centre for Research in Biodiversity and Genetic Resources, Department of Biology, University of the Azores, 9501-801 Ponta Delgada, São Miguel, Azores, Portugal
e-mail: frias@uac.pt*

ABSTRACT

On his way home, towards the end of the historic voyage of H.M.S. *Beagle*, Charles Darwin stopped by the Azores. He subsequently wrote a detailed report on the people and their life style, but had nothing to say about the archipelago's fauna and flora, except that everything reminded him of England. Yet, if Darwin was to return now, he would find evidence of evolution, mostly in the terrestrial molluscs. Of the 101 described species of land and fresh-water molluscs in the Azores (halophilic species excluded), 47 are endemic, and there is strong evidence for 28 additional species, not yet described. This wealth of endemism is distributed throughout the nine islands of the archipelago in patterns closely related to the age and the volcanic activity of each one. Examples are given of distributional patterns of endemic taxa, namely of the Oxychilidae and Enidae. Reference is made to the on-going research testing the speciation patterns seen in *Drouetia* in relation to the theory of punctuated equilibrium, as well as to the variability of *Napaeus pruninus* and reticulate evolution.

RESUMO

A caminho de casa, mesmo no fim da histórica viagem do *Beagle*, Darwin parou nos Açores. Escreveu um relatório pormenorizado sobre as gentes e sua maneira de viver, mas nada teve a dizer sobre a fauna e a flora local, excepto que lhe lembravam a sua velha Inglaterra. No entanto, se Darwin voltasse agora, poderia muito bem encontrar evidência de evolução, sobretudo nos moluscos terrestres. Das 101 espécies de moluscos terrestres e de água-doce descritas (exceptuando-se as espécies halófilas), 47 são endémicas, e há evidência forte para 28 espécies adicionais, ainda não descritas. Esta riqueza de endemismos distribui-se pelas nove ilhas em padrões

estritamente relacionados com a idade e a actividade vulcânica de cada ilha. São dados exemplos de padrões de distribuição de taxa endémicos, nomeadamente dos Oxychilidae e dos Enidae. Faz-se referência à investigação em curso associando os padrões de especiação em *Drouetia* e a teoria do equilíbrio pontuado, bem como a variabilidade de *Napaeus pruninus* e a evolução reticulada.

OCEANIC ISLANDS AND
ENDEMICISM: THE EXAMPLE
OF THE AZOREAN
MALACOFUNA

Evolution has been historically linked to islands, not because they are the only places where it happens but because they are more or less contained environments, suitable for in-depth studies. They are test tubes of evolution. Darwin (1859: 105) thought so when searching for answers to unravel the origin of species:

"If we turn to nature to test the truth of these remarks, and look at any small isolated area, such as an oceanic island, although the number of species inhabiting it is small, [...] yet of these species a very large proportion are endemic, - that is, have been produced there, and nowhere else in the world."

Yet, when Darwin landed on the Azores twenty three years previously, the fauna and flora he had an opportunity to examine

did not bring any revelation of striking endemism; instead, it reminded him of England:

"The rocks are covered in some parts by a thick brushwood about three feet high, and in others by heath, fern, and short pasture: a few broken down old stone walls completed the resemblance with the mountains of Wales. I saw, moreover, some old English friends amongst the insects; and of birds, the starling, water-wagtail, chaffinch, and blackbird." (Darwin, 1839: 369).

The evidence missed by Darwin – the land snails – was hiding beneath the fallen leaves of the remnants of the laurisilva.

The Azorean malacofauna, contrary to that of Madeira, was unknown at the time Darwin sailed aboard the *Beagle*. The first Azorean endemic mollusc, *Bulimus [=Napaeus] pruninus*, was described by Augustus A. Gould in 1848. It was only in 1860 that Arthur Morelet produced the first extensive work on the Azorean land snails. Of

the 69 species recorded, 32 were considered endemic. Backhuys (1975) compiled the second major list of the Azorean terrestrial malacofauna and, though raising the count to 99 species, of which 39 were endemic, he clearly stated:

"The present paper does not mark the end of the road, but rather it marks the starting point for further research. Many problems remain to be solved and many new and interesting facts will be discovered in the future" (p. 5).

The last count based on published records and preliminary lists fixed the total number at 114 species, of which 49 are endemic. If the halophilic Ellobiidae and supra-tidal Assimineidae and Truncatellidae are excluded, there are 101 species, 47 of which are endemic (Cunha *et al.*, 2010). Current research, however, points to an even greater number of endemics awaiting description and when they are would lead to a consequent rearrangement of taxonomic and biogeographical affinities (Table 1 and Figure 1; see also Martins, 2005). When the land and freshwater malacofauna of the Azores is updated with these descriptions (halophilic ellobiids and

supratidal prosobranchs excluded), the count will be about 129 species of which 75 are endemic, thus raising the percentage endemism to ~58%. If introduced species are excluded (those thought to have arrived after the 15th century, the beginning of the islands' human colonization), then the percentage of endemics would rise to ~79%, thus providing a more realistic scenario for the pattern of land snail evolution expressed in the islands.

A closer look at Figure 1 reveals various biogeographic patterns and one peculiar situation. The terrestrial mollusc species of the Central Group of islands (Terceira, Graciosa, São Jorge, Pico and Faial) clump very obviously in that they share most of their endemics, thus reflecting their geographical closeness. A similar situation may be inferred for the Western Group (Flores and Corvo). The oddity appears in the Eastern Group, where Santa Maria has the least number of shared endemics but exhibits the greatest percentage of island endemics. Being by far the oldest island (8 Ma), Santa Maria was expected to have a high percentage of island endemics. Similarly, it was expected to constitute the colonization source for the re-

maining islands. However, the evidence presented in Figure 1, corroborated by the morphological and anatomical affinities of *Drouetia* (Figure 6), leads to a re-assessment of the role of Santa

Maria as the main focus for the colonization of the remaining islands of the archipelago, thus requiring additional explanation for the subsequent colonization of the other ones.

TABLE1. Distribution of the land and freshwater molluscs of the Azores, including species under description (halophilic ellobiids and supratidal prosobranchs not included). E, endemic (Azores); e, undescribed; I, introduced; M, endemic (Macaronesian); N, native. Cor, Corvo; Fai, Faial; Flo, Flores; Gra, Graciosa; Pic, Pico; Sjo, São Jorge; Sma, Santa Maria; Smg, São Miguel; Ter, Terceira.

Species	E/e	N	I	Cor	Flo	Fai	Pic	Sjo	Gra	Ter	Smg	Sma
<i>Pisidium casertanum</i>		x			x	x	x			x	x	x
<i>Hydrocena gutta</i>		M		x	x	x	x	x	x	x	x	x
<i>Craspedopoma hespericum</i>	E					E		E		E	E	
<i>Galba truncatula</i>			x								x	x
<i>Lymnaea peregra</i>			x								x	
<i>Physella acuta</i>			x							x	x	x
<i>Helisoma trivolvis</i>			x							x		
<i>Ferrissia fragilis</i>			x						x		x	x
<i>Deroceras caruanae</i>			x	x	x	x	x	x	x		x	x
<i>Deroceras laeve</i>			x		x	x	x				x	x
<i>Deroceras reticulatum</i>			x	x	x	x	x	x	x	x	x	x
<i>Arion distinctus</i>		x			x	x	x				x	
<i>Arion intermedius</i>		x		x	x	x	x	x		x	x	x
<i>Arion cf. flagellus</i>		x		x	x	x	x	x	x	x	x	
<i>Balea heydeni</i>		x		x	x	x	x	x	x	x	x	x
<i>Balea nitida</i>	E			E	E							
<i>Cochlicopa lubrica</i>		x		x	x	x	x	x	x	x	x	x
<i>Cachicopa lubricella</i>		x			x	x	x	x	x	x	x	x
<i>Discus rotundatus</i>		x		x	x	x	x	x	x	x	x	x
<i>Helicodiscus parallelus</i>			x							x		
<i>Helicodiscus syngleyanus</i>			x			x					x	
<i>Toltecia pusilla</i>		x			x	x	x	x	x		x	x
<i>Napaeus alabastrinus</i>	E						E			E		
<i>Napaeus atlanticus</i> [=forbesianus]	E						E	E	E	E		
<i>Napaeus delibutus</i>	E						E	E	E	E	E	
<i>Napaeus hartungi</i>	E											E
<i>Napaeus pruninus</i>	E										E	
<i>Napaeus tremulans</i>	E											E
<i>Napaeus vulgaris</i>	E										E	
<i>Napaeus sp. a</i>	e			e	e							
<i>Napaeus sp. b</i>	e							e	e		e	
<i>Napaeus sp. c</i>	e											e
<i>Euconulus fulvus</i>		x		x	x	x	x	x	x	x	x	x
<i>Ceciloides acicula</i>			x					x			x	
<i>Helix aspersa</i>			x	x	x	x	x	x	x	x	x	x
<i>Oestophora barbula</i>			x	x	x	x	x	x	x	x	x	x
<i>Oestophora lusitana</i>			x							x		
<i>Otala lactea</i>			x							x	x	x

Species	E/e	N	I	Cor	Flo	Fai	Pic	Sjo	Gra	Ter	Smg	Sma
<i>Plutonia atlantica</i>	E					E	E	E		E	E	
<i>Aegopinella nitidula</i>			x				x					
<i>Hawaia minuscula</i>			x		x							
<i>Nesovitreia hammonis</i>		x		x	x	x	x	x	x	x	x	x
<i>Oxychilus alliarius</i>			x			x					x	
<i>Oxychilus</i> (D.) <i>agostinhoi</i>	E											E
<i>Oxychilus</i> (D.) <i>atlanticus</i>	E										E	
<i>Oxychilus</i> (D.) <i>batalhanus</i>	E										E	
<i>Oxychilus</i> (D.) <i>brincki</i>	E											E
<i>Oxychilus</i> (O.) <i>cellarius</i>			x	x	x	x	x	x	x	x	x	x
<i>Oxychilus</i> (O.) <i>draparnaudi</i>		x		x	x	x	x	x	x	x	x	x
<i>Oxychilus</i> (D.) <i>furtadoi</i>	E									E		
<i>Oxychilus</i> (?) <i>juvenostriatus</i>	E					E	E	E	E	E		
<i>Oxychilus</i> (?) <i>lineolatus</i>	E											E
<i>Oxychilus</i> ((D.) <i>miceui</i>	E									E		
<i>Oxychilus</i> (?) <i>miguelinus</i>	E										E	
<i>Oxychilus</i> (D.) <i>minor</i>	E					E	E					
<i>Oxychilus</i> (?) <i>ornatus</i>	E					E						
<i>Oxychilus</i> (?) <i>scoliura</i>	E									E		
<i>Oxychilus</i> (A.) <i>spectabilis</i>	E											E
<i>Oxychilus</i> (R.) <i>volutella</i>	E										E	
<i>Oxychilus</i> (?) <i>sp. a</i>	e											e
<i>Oxychilus</i> (?) <i>sp. b</i>	e											e
<i>Oxychilus</i> (?) <i>sp. c</i>	e											e
<i>Oxychilus</i> (?) <i>sp. d</i>	e								e			
<i>Oxychilus</i> (D.) <i>sp. a</i>	e			e								
<i>Oxychilus</i> (D.) <i>sp. b</i>	e			e	e							
<i>Oxychilus</i> (D.) <i>sp. c</i>	e				e							
<i>Oxychilus</i> (D.) <i>sp. d</i>	e				e							
<i>Oxychilus</i> (D.) <i>sp. e</i>	e				e							
<i>Oxychilus</i> (D.) <i>sp. f</i>	e								e			
<i>Oxychilus</i> (D.) <i>sp. g</i>	e								e			
<i>Oxychilus</i> (D.) <i>sp. h</i>	e										e	
<i>Oxychilus</i> (D.) <i>sp. i</i>	e										e	
<i>Oxychilus</i> (D.) <i>sp. j</i>	e										e	
<i>Oxychilus</i> (D) <i>sp. k</i>	e					e	e					
<i>Oxychilus</i> (D) <i>sp. l</i>	e											e
<i>Vitreia contracta</i>		x		x	x	x	x	x	x	x	x	x
<i>Zonitoides nitidus</i>			x		x		x				x	
Undescribed island endemic	-	-	-	1	4	-	-	-	4	-	3	9
Island endemic	-	-	-	-	7	1	-	-	-	3	9	13
Undescribed shared endemic	-	-	-	5	5	1	2	2	1	-	1	-
Shared endemic	-	-	-	4	7	13	15	15	10	16	12	6
Non endemic	-	-	-	27	30	39	40	33	31	39	49	40
TOTAL	75	20	35	37	53	55	57	50	46	58	74	68

VARIATION IN *DROUETIA*.

H_w: PUNCTUATED
EQUILIBRIUM ALIVE?

Table 1 shows that some taxa have undergone extensive radi-

ation in the Azores. The genus *Oxychilus* is remarkable in this respect, for it alone accounts for over one third of the endemic species present in the archipelago. Worth noting is that this

genus has no equivalent status among the endemic taxa of either Madeira or the Canary Islands. It is, therefore, a good candidate for the study of the processes, mechanisms and dynamics of evolution in the Azores.

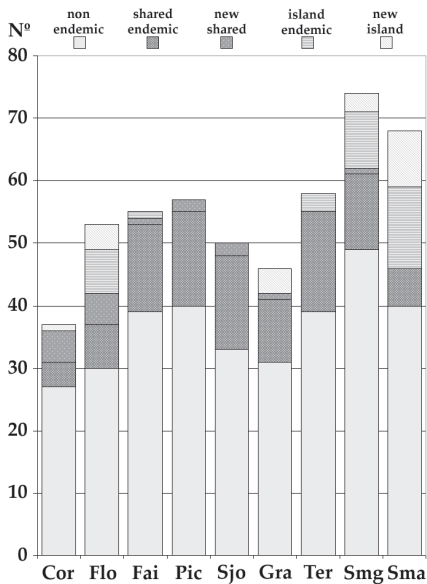


FIGURE 1. Cumulative representations of the distribution of terrestrial mollusc species throughout the various islands of the Azores. See Table 1 for abbreviations.

The endemic Azorean *Oxychilus* species flock is thought to have its origin in some pre-*Ortizius* type of snail arriving on the archipelago sometime during the Tertiary (Riedel, 1964), and to have lost their immediate

ancestral reference point with the Recent mainland European taxa. Azorean animals usually exhibit a more vivid coloration than European species, and can be grouped into two main categories, in relation to either the presence or absence of an umbilical perforation. The non-umbilicate forms are grouped under the subgenera *Drouetia* Gude, 1911 and *Atlantoxychilus* Riedel, 1964, whereas the umbilicate forms need more detailed studies to ascertain their phyletic relationships. *Drouetia* was proposed as a monotypic genus for *Helix atlantica* Morelet & Drouët, 1857, at the time thought to live throughout the archipelago. The anatomical studies of Riedel (1964) revealed a wealth of variability concealed within a usually less remarkable shell form. The subgenus *Atlantoxychilus* was created to accommodate the odd variety γ *spectabilis* of Morelet (1860), and the remainder of Morelet & Drouët's *H. atlantica* was split by Riedel (1964) into three subspecies under the subgenus *Drouetia*, which he later raised to specific level (Riedel, 1980). Subsequent studies (Martins, 1981, 1989a; de Winter, 1989) have contributed additional species.

An anatomical study of *Drouetia* conducted throughout the Azores by Martins (2005) revealed not only the presence of additional island endemics but also patterns of diversity, apparently consistent with the age of their host islands. These patterns were interpreted as representing various stages in the shaping of a species, that is, the process of speciation, as the role of colonization appeared to be of lesser influence. Thus: (1), young islands would display a greater amount of allotypic, demic, diversity but no overlap of distinct anatomical patterns, i.e., evidence of an early stage of speciation; (2), medium age islands would show speciation already clearly defined: there would be syntopic, inter-specific, variability but the species would be closely related and (3), old islands would also exhibit syntopic, interspecific, variability but the species would appear to be far less related than in the previous situation, having even progressed to the status of subgenus.

If we view time as expressed differently by the variously aged islands, a further step towards understanding the dynamics of evolution is possible: a test

of the theory of punctuated equilibrium (Eldredge & Gould, 1972). If the various steps toward speciation are circumscribed by the boundaries of the different islands, then the populations or communities contained within the *Drouetia* clade are bound to exhibit the characteristics of the various stages proposed by the theory, i.e.: (1), the diversity burst of the early stage, associated with severe ecological disturbance caused, in this case, by frequent volcanic eruptions; (2), an intermediate stage where species individuate during relatively long volcanic calmness (few thousands of years), the species still being closely related phylogenetically, and (3), the stasis stage where interspecific affinity and intra-specific variability are small, volcanic activity having ceased for more than a million years.

Evidence that species of *Drouetia* on various islands may meet these criteria comes from analyses of their reproductive anatomies. Pico, the youngest Azorean island (0.25 Ma), is an adequate candidate to exemplify the first stage. Martins *et al.* (2006) surveyed *Oxychilus* (*Drouetia*) *minor* Riedel, 1964 throughout Pico Island and

found that, although in general the samples of the various demes showed different patterns, within-deme variability was small and no overlapping patterns were detected. However, further research has shown the existence of two non-overlapping anatomical patterns corresponding to two different species, and a curious geographical distribution (Figures 2-3; Table 2). One pattern comprising demes a-e, typical of higher altitudes, extends longitudinally along the middle of the island. This shows strong anatomical affinity with *O. (D.) minor*, described from Faial Island, and with which it may be considered conspecific. The second pattern, with demes f-h, occupies the north-eastern side of the island along the coast. *Drouetia* is absent from the south-western side of the island.

Oxychilus (D.) minor has been the only *Drouetia* species recorded from Faial (Figure 4a). More extensive research, however, has revealed the existence of a sympatric, cryptic species, very similar to *O. (D.) minor* morphologically but readily distinguishable from it anatomically (Figure 4b). It is apparently identical to that found in f-h, on Pico Island, and it is plausible

that, as with *O. (D.) minor*, the populations on Pico have also migrated from Faial. A possible explanation for the anomalous distribution on Pico is related to its geological history, for the massive stratovolcano that dominates the whole north-western third of the island is only 40 thousand years old and there has been intense volcanic activity up to historical times on this half of the island (França *et al.*, 2003). This might, therefore, have had a great destructive impact on the island's earliest biota. It is hypothesized that *O. (D.) minor* (pattern one) arrived from nearby Faial, only 8 km to the northwest and was the first of these two species to inhabit Pico. The populations on the south-eastern tip of Pico survived the eruption of the mountain and, from there, progressively re-colonized the north *via* the centre of the island. The second pattern is still allotopic on Pico in relation to pattern one, whereas both are sympatric throughout Faial Island including in pristine, endemic areas such as Caldeira. It resulted probably from a much later colonization event, also from Faial, and is now spreading southward along the coastline.

The absence of *Drouetia* from the south-western side is less

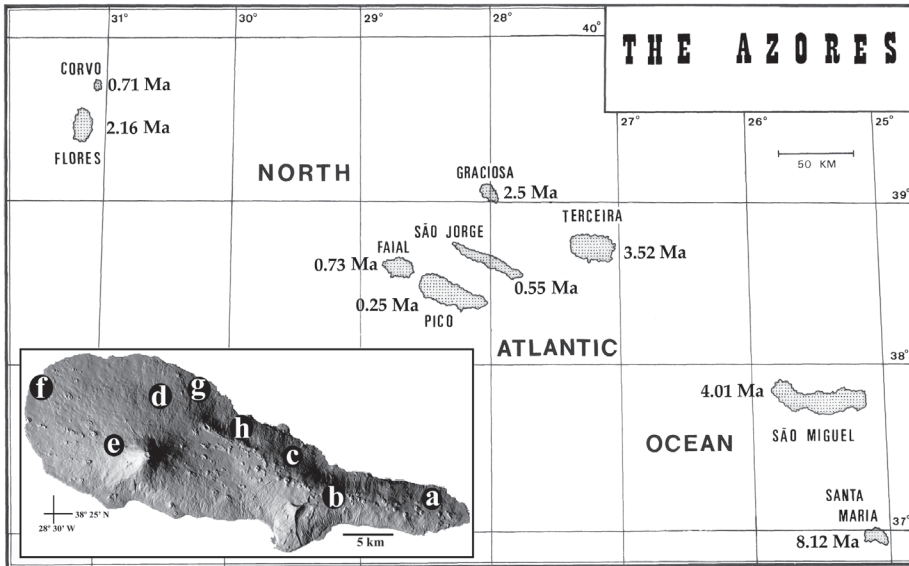


FIGURE 2. The Azores archipelago showing the ages of the various islands. Insert: Pico Island, showing the stations mentioned in the text. See Table 2 for abbreviations.

clearly justified, but could be tentatively explained by the overall youth of the island. Although intensive searches were conducted throughout Pico in 1995, 2005 and 2008, further research on this second largest island of the Azores, including molecular surveys, should yield more information on the relationships, rank-order and distribution of *Drouetia*, and help to clarify the geographical issues described earlier.

Relating the aforementioned evidence to the concept of punctuated equilibrium (Eldredge & Gould, 1972), namely the expect-

ed existence of a great amount of allotopic, demic, diversity but no overlap of distinct anatomical patterns, it can be said that those criteria for the first stage of the theory (allotopic, demic diversity) are somewhat obscured by the peculiar pattern of biogeographical distribution expressed on Pico. However, molecular analyses contrasting the populations on Pico and on Faial are expected to clarify the diversity patterns of the two cryptic species on both islands and will allow further inferences about the suitability of the application of the theory of punctuated equilibrium.

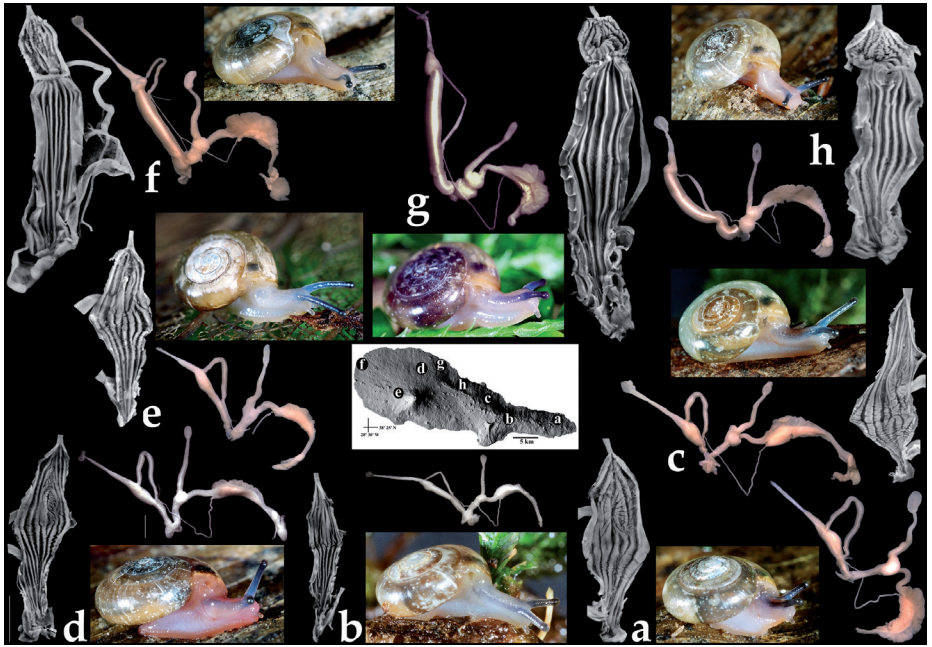


FIGURE 3. Variability in the coloration of the animal, morphology of the genitalia and internal morphology of the penis of *Oxychilus (Drouetia) minor* (a-e) and an undescribed species of *Drouetia* (f-h) from the various stations on Pico Island, as shown in Table 2. Scale bars = 1 mm.

França *et al.* (2003) considered that Flores is 2.16 million years old and has been free of volcanic activity for 3.000 years. Flores Island, then, is an appropriate candidate for verification of the second stage of punctuated equilibrium. That is, during relatively long periods of volcanic calmness, species individuate but remain closely related phylogenetically. Four widely sympatric species are found on Flores, and are readily separated by the ex-

ternal morphology of their shells and body coloration. Their anatomies, however, though different, reveal a similar pattern, indicating the possibility of a single ancestor (Figure 5). It appears, then, that here the criteria for the second phase of punctuated equilibrium are met.

The third stage – stasis – is seen on the island of Santa Maria, about 8 million years old and with no volcanic activity for over 3.5 million years. There are four

TABLE 2. Sampling sites (Stations) on Pico Island.

Sta	Locality	Altitude (m)	Co-ordinates	Characterization	date
a	Piedade	200	N 38° 25.874' W 28° 04.222'	Forest of <i>Accacia melanoxylon</i> , <i>Myrica faya</i> ; sparse undergrowth of <i>Hedychium gardneranum</i> ; stone walls	07-06-2005
b	Lagoa do Peixinho	850	N 38° 31.519' W 28° 23.365	Among <i>Selaginella kraussiana</i> and turf of semi-permanent pasture	14-02-1995
c	Caldeirões, Prainha do Norte	330	N 38° 27.620' W 28° 12.820'	Forest of <i>Cryptomeria japonica</i> , <i>Persea indica</i> , <i>Accacia melanoxylon</i> , <i>Pittosporum undulatum</i> ; undergrowth of <i>Hedychium gardneranum</i> , ferns.	24-11-2008
d	Ossada, Santa Luzia	350	N 38° 31.519' W 28° 23.365'	Forest of <i>Pittosporum undulatum</i> , <i>Accacia melanoxylon</i> ; <i>Hedychium gardneranum</i> ; stone walls, strewn rocks.	08-06-2005
e	Cabeço da Bola, Caminho da Montanha	1050	N 38° 28.703' W 28° 26.100'	Endemic vegetation: <i>Laurus azorica</i> , <i>Vaccinium cylindraceum</i> , <i>Viburnum tinus</i> , <i>Calluna vulgaris</i> , <i>Woodwardia radicans</i> , <i>Blechnum spicant</i> , <i>Festuca jubata</i>	09-06-2005
f	Mata do Hospital, Madalena	30	N 38° 32.098' W 28° 20.216'	Forest of <i>Pittosporum undulatum</i> , undergrowth of <i>Hedychium gardneranum</i> , <i>Pteridium aquilinum</i> , <i>Tradescantia fluminensis</i> ; stone walls	08-05-2005
g	Furnas de Santo António	20	N 38° 32.098' W 28° 20.216'	Forest of <i>Accacia melanoxylon</i> , <i>Pittosporum undulatum</i> , undergrowth of <i>Hedychium gardneranum</i> , <i>Pteridium aquilinum</i> , <i>Selaginella kraussiana</i> ; strewn rocks	10-06-2005
h	Chão Verde, São Roque do Pico	500	N 38° 29.456' W 28° 17.098'	Forest of <i>Pittosporum undulatum</i> , sparse <i>Accacia melanoxylon</i> , <i>Cryptomeria japonica</i> ; undergrowth of ferns; strewn stones	06-06-2005

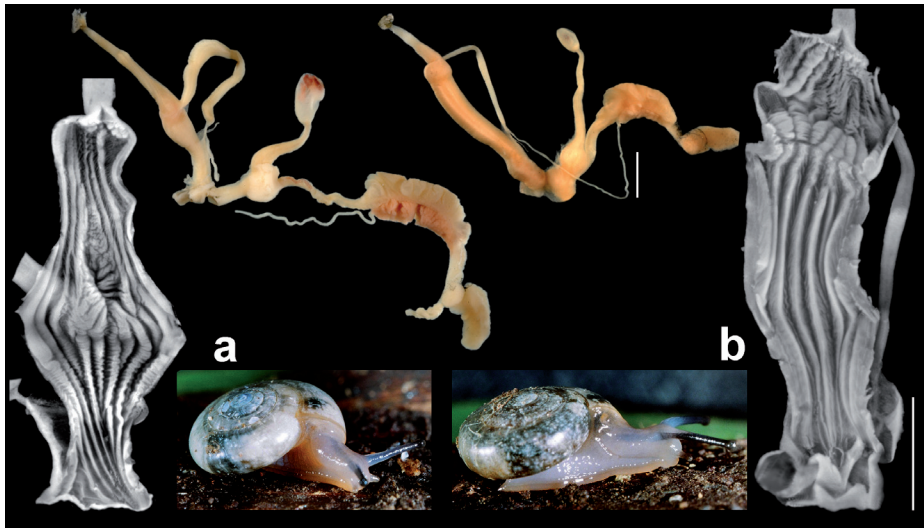


FIGURE 4. Variability in the coloration of the animal, morphology of the genitalia and internal morphology of the penis of *Oxychilus (Drouetia) minor* (a) and an undescribed species of *Drouetia* (b) from Ribeirinha, Faial Island. Scale bars = 1 mm.



FIGURE 5. Variability in the coloration of the animal, morphology of the genitalia and internal morphology of the penis of four undescribed species of *Drouetia* from Flores Island. Scale bars = 1 mm.

non-umbilicate species on Santa Maria, one placed under the subgenus *Atlantoxychilus* and the other three under *Drouetia* (Figure 6). Their intraspecific variability is comparatively small, that is, all variability is readily identifiable within each of the various species. This can, therefore, be interpreted as a stasis phase. Their anatomies are completely different but, on that basis alone, it is not possible to ascertain their phylogenetic relationships, namely if they have a common ancestry.

The evidence just presented, from selected islands, for the speciation of *Drouetia* as an example of punctuated equilibrium, is only one of a number of hypotheses being examined in the quest towards understanding the processes through which evolution happens and for the mechanisms that make it possible in the Azores Archipelago. Anatomy and morphology alone, though usually powerful indicators of patterns, are sometimes unable to give unequivocal answers to their ori-

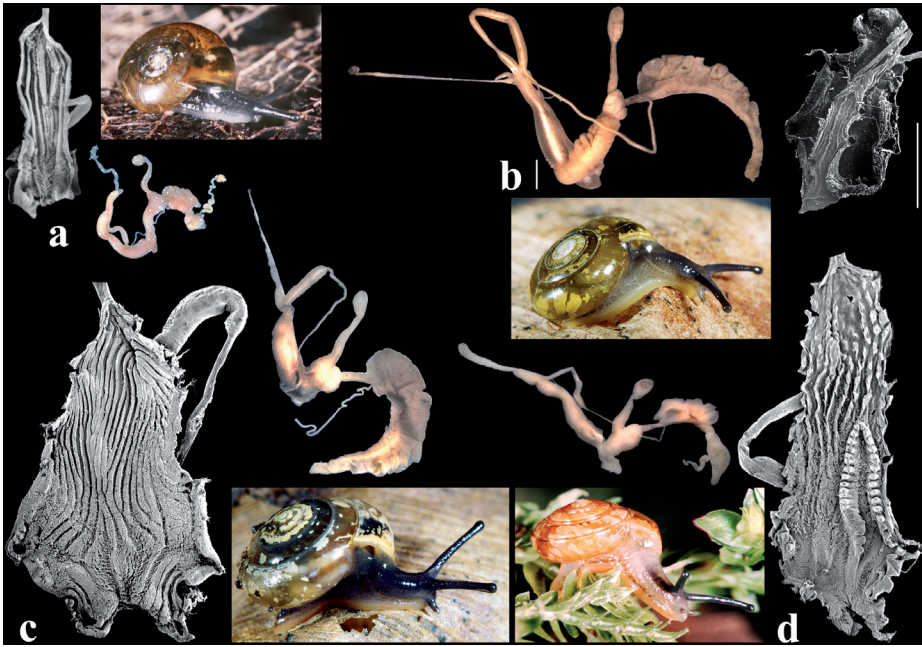


FIGURE 6. Variability in the coloration of the animal, morphology of the genitalia and internal morphology of the penis of species of *Oxychilus* from Santa Maria Island. **a**, *Oxychilus (Drouetia) agostinhoi*; **b**, undescribed species of *Drouetia*; **c**, *Oxychilus (Drouetia) brincki*; **d**, *Oxychilus (Atlantoxychilus) spectabilis*. Scale bars = 1 mm.

gins. A molecular study is underway to search for a phylogeny for *Drouetia*, to investigate aspects of population genetics and, thereby, to ascertain the phylogeographic relationships of demes, populations and species.

VARIATION IN *NAPAEUS PRUNINUS*. H_w: RETICULATE EVOLUTION?

Bulimus pruninus was the first Azorean endemic mollusc, de-

scribed by Augustus A. Gould in 1848 from material collected during the United States Exploring Expedition (1838-1842) in an unplanned stop at the Azores (São Miguel) (Colvocoresses, 1852). The specimens were originally thought to probably be from South America. Johnson (1964), apparently unaware of Morelet's (1860) extensive treatment of the land molluscs of the Azores, subsequently and tentatively attributed Gould's species to

Madeira Island. Morelet (1860: 180) commented upon this species as follows:

*"Le Bulimus pruninus est assurément l'espèce la plus remarquable de l'Archipel".*¹

He illustrated profusely the morphological diversity of shell coloration and texture, and considered under the same species name specimens from Terceira as well as those from Santa Maria, earlier described by Mousson (1858) as *Bulimus tremulans*. Backhuys (1975) revalidated Mousson's species from Santa Maria on account of the morphology of the reproductive system and, after the description of the specimens from Terceira as *Napaeus alabastrinus* by Martins (1989b), the locality of *Napaeus pruninus* became restricted to São Miguel, from where it was supposedly collected.

The coloration and texture of the shell are relatively constant in *Napaeus alabastrinus*, the former ranging from white to slightly coloured with purplish hues, and the latter from smooth to weakly rugose due to persistent growth lines. With *N. tremulans*, however, the coloration

ranges from dark-brown to yellowish, sometimes whitish, the background consistently darker in the first four or five whorls, marbled with lighter, longitudinal vermiculations or lines. The texture ranges from typically rugose in mountain specimens, vermiculations corresponding to raised ornamentation, to nearly smooth or with fine growth lines on those specimens from near-shore environments.

The reproductive systems of *Napaeus alabastrinus*, confined to Terceira and Pico, and of *N. tremulans*, only reported from Santa Maria, differ radically in the size and shape of the epiphallus, and in the length of the diverticulum. Their spermatophores are also extremely different, the one from *N. alabastrinus* being short with a curved head and the whole body with one loose helicoidal turn whereas that of *N. tremulans* is long and strongly coiled. The morphologies of the genitalia and of the spermatophores are highly constant throughout the populations of both species (Figure 7 a, i).

With *Napaeus pruninus*, however, the situation is quite different (Figure 7 b-h). The shells,

¹ *Bulimus pruninus* is surely the most remarkable species of the Archipelago.

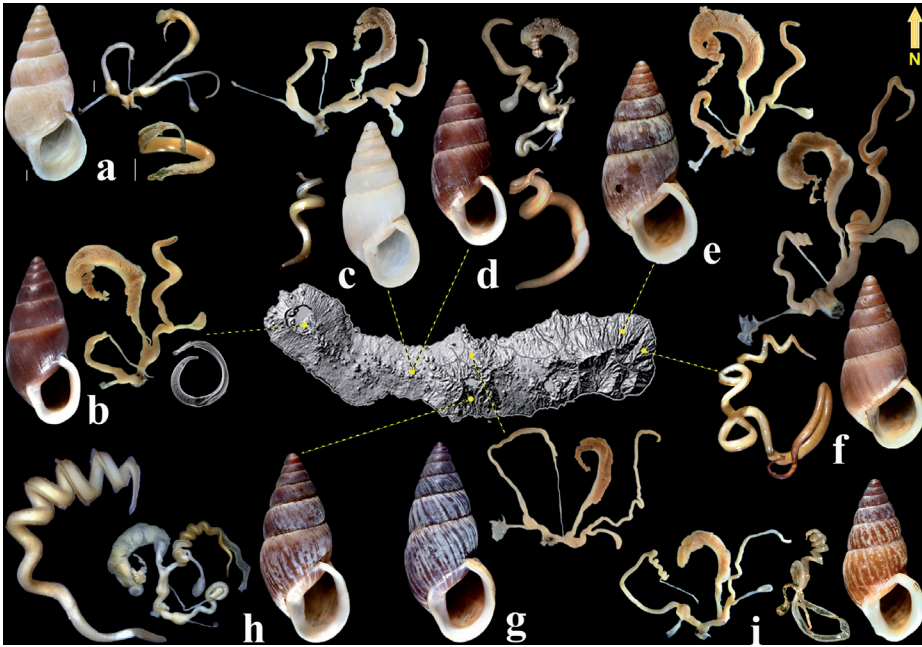


FIGURE 7. Variability in the morphology of shell, genitalia and spermatophore of species of *Napaeus*. **a**, *Napaeus alabastrinus*, Terceira (shell and genitalia, Fonte Dionísio; spermatophore, Silveira, Angra do Heroísmo); **b-h**, *Napaeus pruninus*, São Miguel (**b**, Sete Cidades; **c-d**, Pico do Fogo; **e**, Algarvia; **f**, Ribeira do Tosquiado; **g**, E of Gramas, Ribeira Grande; **h**, Rosário, Vila Franca do Campo); **i**, *Napaeus tremulans*, Pico Alto, Santa Maria. Scale bars = 1 m.

although typically deep purple, smooth in the western portion of São Miguel, range through the entire colour and texture patterns of the other two species, as do the genitalia and the spermatophores. Nevertheless, there is no clear correspondence between shell and genitalia/spermatophore morphologies indicative of an unambiguous relationship with either *N. alabastrinus* or *N. tremulans*.

Preliminary molecular analysis seems to have complicated the situation even further, by integrating a third species into the equation (Figure 8). The analysis clearly separates *N. alabastrinus* from the other two species, but leaves unresolved the presence in *N. pruninus* of similar genitalia and spermatophore morphologies (Figure 7 a, b). On the other hand, there is no definite separation between *N.*

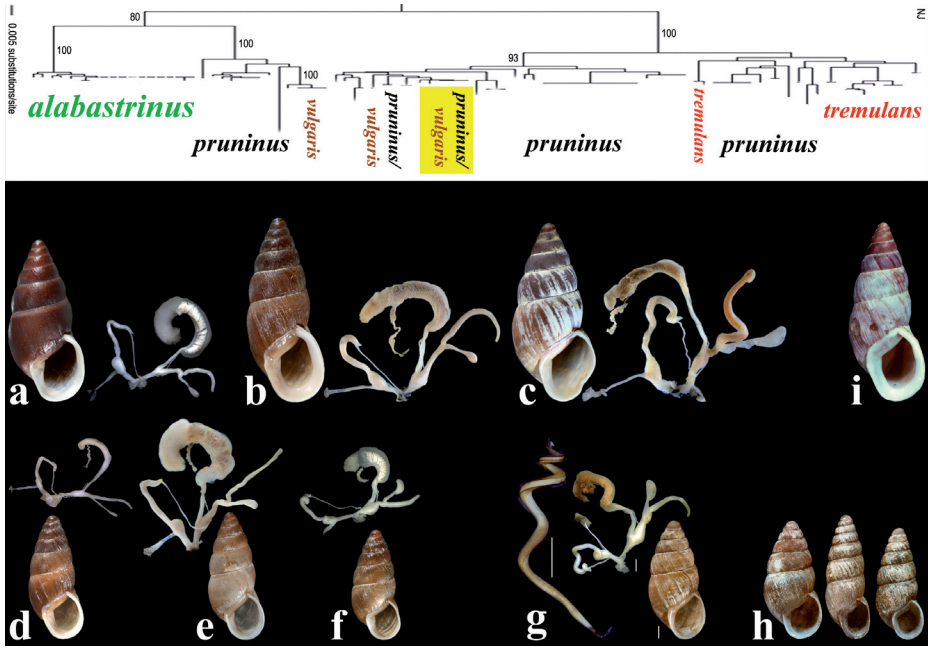


FIGURE 8. Molecular, morphological and anatomical variability in *Napaeus*. a-f, Cluster of specimens from Pico do Fogo, São Miguel (yellow rectangle) in a cladogram obtained from COI, ranging from typical *Napaeus pruninus* to *Napaeus vulgaris* (f); g, shell, genitalia and spermatophore of *Napaeus vulgaris*, Pico do Fogo, São Miguel; h, *Napaeus vulgaris*, syntypes BMNH 93.2.4.1134-6, São Miguel; i, *Napaeus pruninus*, figured holotype USNM 5485 (Johnson, 1964). Scale bars = 1 mm.

tremulans and *N. pruninus*, thus rendering somewhat irrelevant the differences in genitalia and spermatophore morphology. Furthermore, the topology of what was supposed to be an out-group, *Napaeus vulgaris*, clustering with the typical *N. pruninus*, brings even more confusion to an already unclear situation.

A basic question comes to mind as a possible way to unravel the above described con-

fusion: did *Napaeus alabastrinus* and *N. tremulans* originate from *N. pruninus*? Or could we, instead, be confronted in São Miguel, where all patterns merge, with a case of reticulate evolution?

Morelet (1860) put forward a working hypothesis in relation to this problem, that is, introgression. On the basis of shell morphology alone, he had already recorded the wide vari-

ability of *N. pruninus* and its overlap with that of *N. vulgaris*. He wrote, when commenting about *N. vulgaris*:

“Chez certains individus, les traits du B. pruninus prédominant [...]; elle [the shell] conserve d’ailleurs la taille habituelle du vulgaris; mais les mêmes caractères, en s’affaiblissant graduellement, finissent par se confondre chez d’autres spécimens, d’une manière tellement intime avec ceux de l’espèce voisine, qu’il n’est plus possible d’assigner à chacune d’elles ses limites” (p. 186)².

The French naturalist then proceeds to give the explanation:

“Lorsque l’on considère cette dégénérescence du Bulimus pruninus, dont les traits caractéristiques se confondent avec ceux d’une espèce totalement différente, qui emprunte à celle-ci sa petite taille et sa transparence pour lui donner sa forme et ses couleurs, on ne trouve d’autre

explication à cette singularité qu’une alliance adultérine entre les deux mollusques” (p. 187)³.

IF DARWIN WERE TO VISIT THE AZORES AGAIN...

The two situations just considered provide ample justification to view the Azorean islands as a cradle of evolution, real test tubes where theories dealing with the processes and the mechanisms governing evolution can be tested. The privileged geographical location of the archipelago and the spatial grouping and diverse ages of its islands provide us with an ideal laboratory to catch evolution red-handed.

If Darwin were to visit the Azores again, he probably would not have to hand all the ingredients necessary to come up with the concept of evolution, but he certainly would have readily available the solu-

2 In some specimens, the features of the *B. pruninus* predominate [...]; [the shell] retains otherwise the usual size of the *vulgaris*; but the same characters, gradually becoming fainter, end up mixing in other specimens, in so intimate a manner with those of the neighbor species, that it is no longer possible to assign to each their own limits.

3 Once this degenerescence of the *Bulimus pruninus* is considered, where the characteristic features are confused with those of a totally different species, which borrows from this one its small size and transparency to give it its shape and colours, one does not find any other explanation for this singularity but an adulterine alliance between both molluscs.

tion for some of the clarifications his theory would benefit from. And, then, the emblematic Galápagos finches could well be Azorean land snails.

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