

Rediscovery of *Leptaxis vetusta* (Morelet & Drouët, 1857), a subfossil land snail from the Quaternary of Santa Maria (Azores)

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Abstract

Key-words: Late Pleistocene; Holocene; terrestrial gastropods; Santa Maria; Azores.

During a recent field work on the southern coast of the island of Santa Maria (Azores) a bulk sample of 37 shells and 25 fragments of *Leptaxis vetusta* was assembled from Late Pleistocene and Holocene slope deposits outcropping in the area. These specimens are the first of this rare subfossil species to be mentioned since the original descriptions of Arthur Morelet and Henri Drouët (1857). The purposes of our paper are a systematic and biometric description of *L. vetusta*. For the first time, the original type locality was localized with accuracy over the southern downslopes of Pico do Facho, between Figueiral and Prainha. The subfossil specimens were collected in slope deposits and detritic fans, overlying a fossiliferous marine deposit situated over the 2-3 m abrasion platform of Praia and Prainha bay. The age and factors associated to the extinction of this species are discussed, including the destruction of the original laurel cover and the colonization by *Otala lactea* (Müller, 1774), a continental helicid introduced and widespread in Santa Maria.

Resumo

Palavres-chave: Plistocénico superior; Holocénico; gastrópodes terrestres; Santa Maria; Açores.

Na sequência de trabalhos de campo realizados recentemente nas vertentes da costa sul da ilha de Santa Maria, foi possível efectuar uma colecção de 37 conchas e 25 fragmentos de *Leptaxis vetusta*, os primeiros desta rara espécie subfóssil a serem referenciados para além dos sintipos recolhidos por Arthur Morelet e Henri Drouët, em 1857. Nas páginas seguintes procede-se à redescção sistemática e ao estudo biométrico desta espécie subfóssil. A localidade tipo é, pela primeira vez, localizada com precisão, situando-se nas vertentes abruptas do Pico do Facho, entre Figueiral e Prainha. Os exemplares subfósseis foram recolhidos em depósitos de vertente, sobranceiros ao prolongamento ocidental da plataforma de abrasão de 2-3 m e do depósito marinho da baía de Praia e Prainha. As causas e idade relativas à extinção de *Leptaxis vetusta* são também discutidas, incluindo a sua relação com a destruição do coberto original de Laurissilva e com a proliferação de *Otala lactea* (Müller, 1774), um helicídeo introduzido a partir do continente e hoje extremamente abundante em áreas pouco florestadas da ilha.

Introduction

The Late Quaternary terrestrial gastropods from the Portuguese archipelagos of Macaronesia have been the focus of many naturalistic studies since the middle of the XIX century. One of the main reasons for such an interest was the particularity of those highly diverse insular land snails, usually considered as a relict of southwest Palaeartic faunas widespread in the Neogene of Europe and North Africa.

The modern land snail faunas of Azores and Madeira are a combination of autochthonous and introduced species, with a strong contribution of endemic Pupillidae, Enidae, Vitrinidae, Zonitidae, and helicids (s.l.) from subfamilies Leptaxinae and Geomitrinae (Waldén, 1983, 1984; Martins, 1999; Mordan & Martins, 2001). Many of these relict species are in course of extinction. Fossil evidences suggest that extinction episodes took place already in Pleistocene times, but their rate accelerated after the fifteen century, with the Portuguese colonization of

the archipelagos. Among other factors, the introduction of opportunistic land snails from the continent, and the destruction of the original laurel woods were apparently responsible for the decline and extinction of many insular species.

Autochthonous faunas are known as well from a multiplicity of subfossil assemblages, preserved in late Pleistocene and Holocene deposits outcropping near Caniçal (eastern Madeira), Porto Santo and Santa Maria islands. The subfossil terrestrial gastropods from Caniçal and Porto Santo form the rich and highly diverse ensemble of the whole continental deposits of Macaronesia (Waldén, 1983; Abreu, 2001). These faunas were known and exhaustively studied since the early researches of Lowe (1831). Large collections of subfossil specimens have been assembled from the Eolianitic Formation of Porto Santo (Soares, 1973; Silva, 1956, 1957, 1972; Callapez, 1989) a thick unit of calcareous eolic sands and interbedded paleosoils, covering nearly 2/3 of the island surface.

The occurrence of Quaternary deposits with remains of terrestrial gastropods is comparatively much more restricted across the Azores archipelago. The best examples can be found within the island of Santa Maria, on the eastern border of the group (fig. 1), where they are associated to coastal cliffs with pronounced slopes favourable to mass movements of volcanic and sedimentary debris, including blocks of Neogene marine limestone.

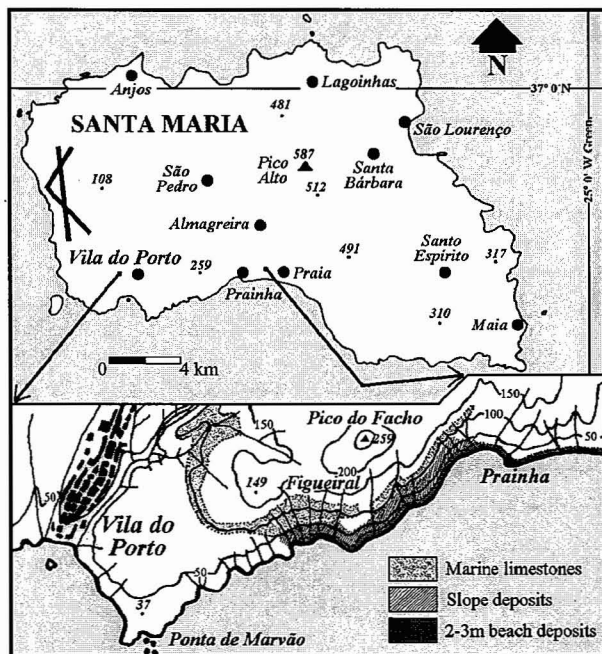


Figure 1 – Simplified map of Santa Maria, with a detailed view of the Southern coast of the island, from the harbour of Vila do Porto to the bay of Praia and Prainha. The area is dominated by the volcanic relieves of Pico do Facho (259m), and by a large band of Neogene marine limestone, which has been exploited for a long time in the local quarries of Figueiral. The cliffs from Figueiral to Prainha are partially masked by coalescent slope deposits, overlying a fossiliferous succession of Pleistocene beach sediments deposited over a 2-3 m abrasion platform (Callapez & Soares, 2000).

The French naturalists Henry Drouët and Arthur Morelet were among the first scientific explorers that had the privilege to observe these deposits. In 1857, during a long and well documented naturalistic voyage to the Azores (Drouët, 1866, 1870; Arruda, 1998), they visited Santa Maria for a week, and assembled a large collection of recent and subfossil terrestrial gastropods, including several species new to the science. These land snails were object of detailed systematic descriptions by Morelet & Drouët (1857), Morelet (1860) and Drouët (1861).

One of the most interesting land snails described by these workers was a subfossil helicid mentioned as "*Helix vetusta*" (Morelet & Drouët, 1857). This extinct gastropod from Santa Maria was expressively illustrated in hand coloured stamps from A. Morelet (1860). After the original diagnosis and comments of H. Drouët and A. Morelet, subsequent workers admitted the opinion that "*Helix vetusta*" was a valid species with shell morphology, form, colour pattern, and dimensions significantly different from the remaining Azorean Helicidae. Nevertheless, the occurrence of this *taxon* in the Quaternary deposits of Santa Maria needs an effective confirmation because A. Morelet and H. Drouët never specified the exact type locality, and no other specimens have been collected ever since (Backhuys, 1975).

The main purposes of our study are to retrieve "*Helix vetusta*" as a valid species of terrestrial gastropod, of exceptional importance to understand evolutionary and palaeobiogeographic patterns associated to the Quaternary land faunas of Azores. A bulk sample with 62 new specimens and fragments was recently collected, through geologic researches over the southern coastal slopes of Santa Maria. This field work also allowed an accurate determination of original type locality, as well a detailed sampling of the associated sedimentary deposits.

Systematic Palaeontology

| | |
|--|-------------------------------|
| Phylum | MOLLUSCA Linné, 1758 |
| Class | GASTROPODA Cuvier, 1797 |
| Subclass | PULMONATA Cuvier, 1817 |
| Order | STYLOMMATOPHORA Schmidt, 1856 |
| Family | Helicidae Rafinesque, 1815 |
| Subfamily | Leptaxinae Boettger, 1909 |
| Genus | <i>Leptaxis</i> Lowe, 1852 |
| (Type species: <i>Helix erubescens</i> Lowe, 1831) | |

Leptaxis vetusta (Morelet & Drouët, 1857)
(Plate 2, figs. 1-5)

- 1857 – *Helix vetusta* Morelet, & Drouët, p. 152.
- 1860 – *Helix vetusta*; Morelet, pp. 176-177, pl. 5, fig. 12.
- 1861 – *Helix vetusta* Mor. & Drouët; Drouët, p. 158.
- 1870 – *Helix vetusta* Morelet; Tristram in Godman, p. 109.
- 1878 – *Helix vetusta*; Wollaston, pp. 24-25.
- 1881 – *Helix vetusta*; Furtado, p. 7.
- 1888 – *Helix vetusta* Morelet & Drouët; Tryon, pp. 198-199, pl. 166, fig. 80a.
- 1895 – *Leptaxis vetusta* M. & D.; Pilsbry, p. 293.

1930 – *Helix vetusta* Morelet; Nobre, p. 83.

1975 – *Leptaxis vetusta* (Morelet & Drouët); Backhuys, pp. 239-241.

Material: 37 adult specimens and 25 fragments from the slope deposits and detritic fans of Figueiral, Southern coast of Santa Maria Island, Eastern Azores.

Repository of specimens: all specimens were housed in the collections of palaeontology from the Earth Sciences Department of Coimbra University, Portugal.

Original diagnosis: «testa imperforata, groboso-conoidea, carinata, solidula, rugato-granosa, plerumque calcarea, interdum fasciis 2 rubiginis interruptis notata; anfr. 6 parum convexi, ultimo carinato, anticè deflexo, ad aperturam constricto; carina breviter compressa, demum crenulata; aperture perobliqua, ovato-angularis, fauce et peristomate in speciminibus quibusdam aurantio-fuscis; peristoma labiatum, marginibus callo crassiusculo junctis, supero vix expanso, columelari dilatato, planulato, apresso. Diam. maj. 19; min. 17, altit. 11 mill. - M. et D.»

Description: shell solid and thick, globular, conical above the periphery, with 6-7 flattened whorls and a deep suture. Body whorl strongly keeled at the periphery. Umbilicus entirely sealed. Aperture oblique and slightly elliptical, with a reflected outer lip, thickened, and flattened below. Columelar edge straight, with a compressed callus. Sculpture with slightly impressed growth-ridges, obliquely crossed by numerous rows of small and irregular folds and tubercles (Figure 2). Shell colourless, but sometimes with vestiges of original pigmentation: a dark-brown lip and reddish-brown spiral bands usually fused, and superimposed by a pattern of irregular whitish reticulation, resembling oblique radial bands.

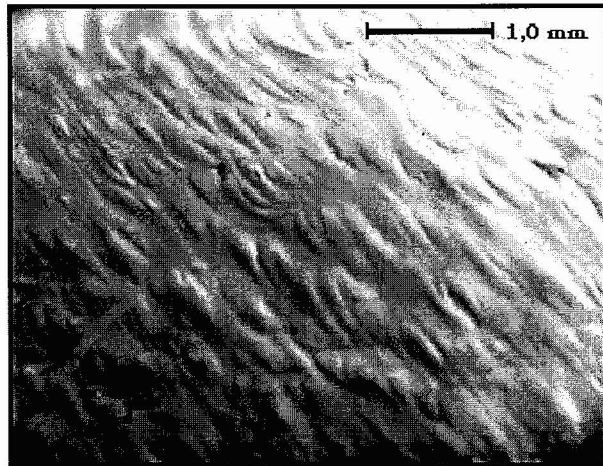


Figure 2 – *Leptaxis vetusta* (Morelet & Drouët, 1857) from Santa Maria, Azores. Detail of body whorl shell sculpture from specimen DCTSM26 (x11).

Dimensions: The dimensional variables (1) maximum diameter of shell, (2) minimum diameter of shell, and (3) shell height were measured from a sample of 30 well preserved adult specimens of *Leptaxis vetusta* (table 1). The maximum diameter observed reaches 19 mm (DCTSM5), and matches exactly with the value indicated by A. Morelet & H. Drouët. However, shell height shows a substantial variation when compared with the diameter. This variation results in the coexistence of specimens with acuminated spire, together with others with a more depressed shell, and a more pronounced keel on the last whorl (figures 3 and 4).

Discussion: The anatomy of this endemic species is unknown, but the shell form, sculpture, and dimensions are congruent with the macaronesian *Leptaxinae*. According to A. Zilch (1959-60) and W. Backhuys (1975), this subfamily is represented by 3 recent and subfossil

Table 1

Dimensional shell measurements for 30 adult specimens of *Leptaxis vetusta* (Morelet & Drouët, 1857). The parameters considered are: (1) maximum diameter, (2) minimum diameter, and (3) shell height (mm).

| Reference number | Maximum diameter | Minimum diameter | Shell height | Reference number | Maximum diameter | Minimum diameter | Shell height |
|------------------|------------------|------------------|--------------|------------------|------------------|------------------|--------------|
| DCTSM1 | 18,1 | 16,4 | 15,1 | DCTSM16 | 17,1 | 15,7 | 14,7 |
| DCTSM2 | 17,8 | 16,6 | 14,9 | DCTSM17 | 16,5 | 15,6 | 14,6 |
| DCTSM3 | 17,0 | 15,1 | 13,4 | DCTSM18 | 18,2 | 16,3 | 14,3 |
| DCTSM4 | 17,3 | 15,8 | 14,2 | DCTSM19 | 15,4 | 14,7 | 13,4 |
| DCTSM5 | 19,0 | 16,8 | 13,8 | DCTSM20 | 16,9 | 15,8 | 15,7 |
| DCTSM6 | 16,7 | 15,4 | 12,8 | DCTSM21 | 16,8 | 15,5 | 13,3 |
| DCTSM7 | 16,3 | 15,5 | 13,0 | DCTSM22 | 17,4 | 15,7 | 14,3 |
| DCTSM8 | 18,1 | 17,0 | 15,1 | DCTSM23 | 18,0 | 16,6 | 13,5 |
| DCTSM9 | 16,9 | 15,4 | 13,2 | DCTSM24 | 17,4 | 15,9 | 15,9 |
| DCTSM10 | 17,4 | 15,9 | 13,8 | DCTSM25 | 18,1 | 17,9 | 14,9 |
| DCTSM11 | 17,1 | 15,4 | 13,6 | DCTSM26 | 17,3 | 16,2 | 14,6 |
| DCTSM12 | 16,7 | 15,7 | 14,2 | DCTSM27 | 15,0 | 13,8 | 12,6 |
| DCTSM13 | 16,4 | 15,2 | 14,1 | DCTSM28 | 16,2 | 15,3 | 12,4 |
| DCTSM14 | 16,6 | 15,7 | 12,8 | DCTSM29 | 16,7 | 15,7 | 14,3 |
| DCTSM15 | 14,5 | 13,6 | 11,8 | DCTSM30 | 15,6 | 14,5 | 13,2 |

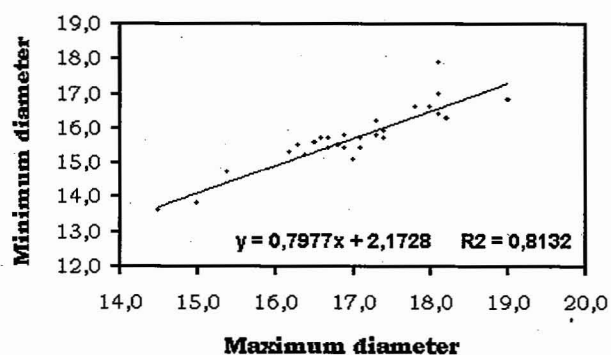


Figure 3 – Bivariate plotting, regression, and correlation coefficient of the relationship between the variables maximum diameter and minimum diameter (mm) of the 30 measured specimens.

genera: (1) *Leptaxis* Lowe, 1852, (2) *Lampadia* Albers, 1854 and (3) *Helixena* Backhuys, 1975. *Helixena* is a monospecific genus with egg-shaped shell, and restricted to Santa Maria (Backhuys, 1975); *Lampadia* is confined to Canarias and Porto Santo (*L. webbiana* Lowe, 1831). *Leptaxis* is the commonest and widespread genus of Leptaxinae, and is usually subdivided in three subgenera (*sensu* Mandahl-Barth, 1950): *L. (Leptaxis)* Lowe, 1852; *L. (Cryptaxis)* Lowe, 1854; and *L. (Katostoma)* Lowe, 1854. With a few exceptions, most modern species are grouped on the first of these subgenera.

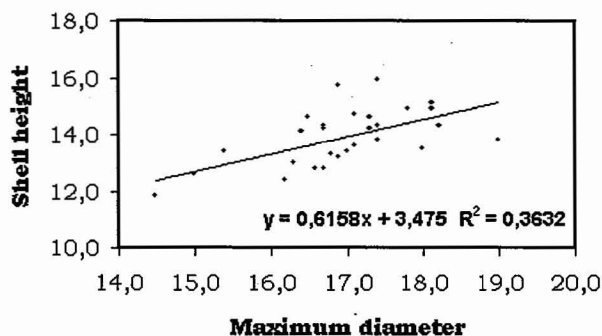


Figure 4 – Bivariate plotting, regression, and correlation coefficient of the relationship between the variables maximum diameter and shell height (mm) of the 30 measured specimens.

The genus *Leptaxis* is essentially represented on the modern faunas of the Azores by a few species and subspecies of the *L. azorica* group. The geographic pattern exhibited by these terrestrial gastropods was probably originated through several steps of radiation and colonization, compatible with the age and geologic history of the islands (Riel *et al.*, 2001). *L. azorica* has a thin and translucent globose-depressed shell, quite different from the thick conical shell of *L. vetusta*. As T. Wollaston (1878) pointed out, there are no other *Leptaxis* on the Portuguese archipelagos of Macaronesia that can be compared with *L. vetusta*, except for the larger forms of *L. chrysomela fluctuosa* (Lowe, 1852) from the Eolianitic Formation of Porto Santo. The reasons for such a comparison were the pronounced spiral keels of both species, as well the straight and thick basal outer lips and the strong original coloring

of its shells. Nevertheless, the shell of *L. chrysomela fluctuosa* is much more compressed and discoid, and the keel is sharper than in *L. vetusta*; the shell microsculpture of both species is also distinct.

A type locality for “*Helix vetusta*”

The original diagnosis of “*Helix vetusta*” was published in the Journal of Conchylologie of July of 1857, as part of a preliminary notice of Arthur Morelet and Henri Drouët, concerning the systematic descriptions of 12 new helicid species from the Azores archipelago. This notice was complemented, a few years later, by detailed systematic descriptions, concerning the whole Azorean land snail faunas, and complemented with many geographic data (Drouët, 1859, 1861; Morelet, 1860).

About “*Helix vetusta*” the latter works of A. Morelet and H. Drouët are concordant with the idea that this species is a subfossil gastropod endemic from Santa Maria. Unfortunately, these French naturalists never indicated a precise location for the original, and probably very restricted sampling area. A remark of H. Drouët (1861) that “*Helix vetusta*” was abundant and «paraissait vivre dans les agaves ou contre les rochers», suggests not only a recent extinction, but also that this helicid was a common and widespread species. In spite of these data, subsequent naturalists that visited Santa Maria were unable to find any new specimens. The descriptions and figures by G. Tryon (1870), T. Wollaston (1878), F. Furtado (1881), H. Pilsbry (1895), and A. Nobre (1930) are product of bibliographic researches after the original works of Morelet and Drouët. W. Backhuys (1975) also yields a description of *Leptaxis vetusta* based on the figured syntypes.

The location of the original sampling area for *Leptaxis vetusta* can be indirectly determined after A. Morelet (1860), when this worker writes about the Neogene and Quaternary deposits of the island. A. Morelet and H. Drouët visited Santa Maria at June of 1857, together with the German geologist George Hartung (Drouët, 1870; Arruda, 1998). They made careful observations along the southern downslopes of Pico do Facho, near the localities of Prainha and Figueiral. For many years, this area was the ground of a flourishing quarry activity based on the exploration of Neogene limestones. It is also sure that A. Morelet and H. Drouët visited the beach deposits of Prainha bay, as well the large slope deposits of Figueiral. After A. Morelet (1860): «A partir du niveau des eaux, on remarque un massif de conglomérats et de roches ignées, surmonté de plusieurs lits de sable et de fragments roulés [...]. La couche supérieure, riche en coquilles marines, s'étend presque horizontalement [...]. Au-dessus de cette formation, règne un dépôt considérable de tuf jaune, entremêlé de basalte, qui revêt les pentes du Facho et se prolonge à une grande distance. En avançant vers l'est, on voit, près du hameau de Praya, sur les escarpements de la côte, a une élévation de 120 a 130 mètres, plusieurs lits de cailloux roulés, enveloppés dans la masse volcanique. C'

est aussi là, mais a l'étage inférieur, que l'on peut observer, dans une marne trappéenne, formant de hautes falaises, des débris de coquilles terrestres dont quelques-unes vivent encore dans l'île, tandis que d'autres ont disparu». This clear and comprehensible description confirms the existence of slope deposits with subfossil land snails in the southern coast of Santa Maria, overlying a succession of beach deposits exposed near Prainha. The syntypes of "*Helix vetusta*" were certainly collected there, because A. Morelet (1860) remarked that this species « fit partie de la création que l'on y rencontre aujourd'hui, et disparut [...] ». On retrouve effectivement, dans les mêmes tufs volcaniques, la plupart des mollusques terrestres qui vivent actuellement dans l'île [...]. La couche inférieure, de nature sablonneuse, renferme, en outre, des coquilles marines qui paraissent identiques à celles de notre époque».

As a conclusion, the *locus typicus* for "*Helix vetusta*" can be defined as the south and southeast slopes of Pico do Facho, from the limestone quarries of Figueiral to the west end of Prainha bay. This coastal area of pronounced slopes can be accessed from Prainha beach westwards, following a long fringe of cliffs exposed at low tide. The sedimentary succession observed starts with a 2-3 m beach deposit (Berthois, 1951; Berthois, 1953; Zbyszewski & Ferreira, 1961; Zbyszewski *et al.*, 1961), with (1) a basal conglomerate made of large rounded clasts of volcanic rocks; (2) algal encroachments with articulated pholads (*Lithophaga aristata*), (3) front-beach sands with abundant debris of *Ervillia castanea* (Callapez & Soares, 2000), and (4) white sands with debris of land snails, including shells of *Leptaxis vetusta*. Over these deposits, the slopes of Figueiral are covered by a thick succession of detritic fans, containing Neogene limestone, clay and

volcanic debris, as well a rich assemblage of subfossil land snails. Our bulk sample was assembled from these slope deposits.

Palaeoecology and causes of extinction

Leptaxis vetusta is characterised by a thick and solid shell, quite different from the fragile and translucent shells of the remaining autochthonous helicids widespread in Santa Maria. It is interesting to observe that the short distribution area of this species is close to the band of Neogene limestones of Figueiral-Prainha, and matches with the slope deposits with calcarenite debris accumulated below these outcrops. In fact, it is well known that the lime content of soils is an important factor for the segregation of shells. Many terrestrial gastropods from calcareous biotopes have thick and solid shells. According to this factor, it is reasonable to assume that *Leptaxis vetusta* was adapted to a geographically restricted environment of Santa Maria, characterized by soils and rocks with a larger content of carbonates.

Why became extinct this helicid? The explanation for the decline and extinction of this species is surely associated to environmental changes occurred inside its area of habitat, during last centuries. Evidences include (1) the destruction of the original laurel cover of Santa Maria, and the anthropic introduction of new botanic species; (2) a colonization by the introduced and opportunistic *Otala lactea* (Müller, 1774), one of the commonest and widespread land snails of the island. Subactual specimens of *Otala lactea* are common in the slope deposits of Prainha, where they occur together with coloured *Leptaxis vetusta*. This fact shows that the extinction of this endemism was very recent, and probably favoured by adverse ecologic competition.

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PLATE 1



Figure 1 – The type area for *Leptaxis vetusta* (Morelet & Drouët, 1857): Southern coast of Santa Maria observed from Prainha westwards, with the 2-3 m abrasion platform exposed at low tide. The pronounced slopes of Figueiral are visible near the left border of photo. Many of our specimens were collected in the red slope deposits illustrated in this figure.



Figure 2 – The beach deposit of Prainha and the overlying slope deposits: (1) basal conglomerate with large clasts of volcanic rocks; (2) algal encroachments with *Lithophaga aristata*, (3) beach sands with abundant *Ervillia castanea*; (4) white sands with land snails, including rare *Leptaxis vetusta*; (5) slope deposit with reddish-brown clays and subfossil gastropods, including fairly common shells of *Leptaxis vetusta*.

Plate 2

Fig. 1a-1c – Reproduction of the original figurations of A. Morelet (1860). Syntype of "*Helix*" *vetusta* Morelet & Drouët, 1857, fossils from Santa Maria, Azores (x1).

Fig. 2a-2c – *Leptaxis vetusta* (Morelet & Drouët, 1857). Slope deposits 1 km westwards from Prainha, Santa Maria, Azores. Specimen DCTSM26 (x2).

Fig. 3a-3b – *Leptaxis vetusta* (Morelet & Drouët, 1857) Pigmented shell from the slope deposits; same locality. Specimen DCTSM46 (x3,5).

Fig. 4a-4c – *Leptaxis vetusta* (Morelet & Drouët, 1857). Slope deposits. Specimen DCTSM12 (x2).

Fig. 5a-5c – *Leptaxis vetusta* (Morelet & Drouët, 1857). Slope deposits. Specimen DCTSM14 (x2).

PLATE 2



1a



1b



1c



2a



2b



2c



3a



3b



4a



4b



4c



5a



5b



5c