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Systematic and biogeographical studies of the terrestrial Gastropoda of Madeira. With an annotated Check-list[1]

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The terrestrial Gastropod fauna of the Madeiran Archipelago is of crucial interest with regard to its high diversity and endemism, and its pronounced Tertiary relict character in connection with the Atlantic sea floor spreading. An adequate taxonomy is a basic requirement for all subsequent work. A general revision has been carried out, based on extensive material collected by the author, and on type material in museums. The revision has resulted in the description of one new genus, one new species and four new subspecies. Furthermore, specific state has been recognized for some taxa, and some species have been reduced to subspecific rank. In addition, four or five semispecies complexes have been recognized, and eight taxa (*i.e.* species and subspecies) have been renamed, owing to cases of synonymy or homonymy. One hundred and ninety of the estimated 259±3 taxa are endemic, all of which are of SW Palaearctic origin, mainly Mid-Tertiary, and in a few cases Late Tertiary. The absence of clear NW African affinities in the endemic element is striking. Relations to the other Mid-Atlantic archipelagoes (the Azores, Canary Islands and Cape Verde Islands) are discussed, and the enigmatic distribution pattern of the genera *Napaeus* and *Leptaxis* is pointed out. Of 25 genera with endemic species, 14 are peculiar to Madeira. The subfossil faunas of Piedade on Madeira and of Porto Santo are discussed, and the rather high percentage of now extinct taxa is pointed out. Attention is drawn to the fact that in late geological time the parts of the archipelago had more species in common than today, suggesting a considerable rate of faunal change, and that the present sharp inter-archipelago endemism may be to some extent secondary. There is no case where the subfossil evidence indicates that previous reproductive barriers were weaker than today. The results of the taxonomic-nomenclatural revision are concluded in an annotated check-list. In relation to its size, Madeira probably has the most diversified island Gastropod fauna in the world, with a striking display of adaptive radiation and niche specialization.

The following new taxa are described here for the first time, by diagnoses: *Hemilauria* nov. genus, *Actinella (Faustella) carinofausta* nov. spec., *Leiostyla (Leiostyla) vincta mauli* nov. subsp., *Caseolus (Caseolus) compactus vigiae* nov. subsp., *Actinella (Actinella) arcinella papilloscultpta* nov. subsp. and *Discula (Discula) polymorpha agostinhoensis* nov. subsp.

The following new names for previously described taxa are introduced in this paper: *Amphorella (Hypselia) cimensis, Caseolus (Caseolus) compactus areiensis, Caseolus (Caseolus) compactus betamajor, Caseolus (Caseolus) baixoensis, Caseolus (Caseolus) subcalliferus submajor, Actinella (Faustella) promontoriensis* and *Actinella (Plebecula) effugiens.*

The following previously infraspecific taxa are regarded as species: *Leiostyla (Leiostyla) arborea* (Lowe), *Leiostyla (Leiostyla) simulator* (Pilsbry), *Amphorella (Amphorella) grabhami* (Pilsbry), *Amphorella (Fusillus) tuberculata* (Lowe), *Steenbergia desertae* Mandahl-Barth, *Caseolus (Helicomela) solidus* (Lowe), *Actinella (Faustella) robusta* (Wollaston) and *Discula (Discula) pulvinata* (Lowe), in addition the renamed *Amphorella (Hypselia) cimensis, Caseolus (Caseolus) baixoensis* and *Actinella (Faustella) promontoriensis,* mentioned above.

For the first time recorded from Madeira are, furthermore: *Carychium tridentatum* (Risso), *Columella aspera* Waldén, *Truncatellina callicratis* (Scacchi) *Vertigo (Vertigo) pygmaea* (Draparnaud), *Vallonia excentrica* Sterki, *Acanthinula aculeata* (Müller), *Arion (Kobeltia) hortensis* auctt., *Arion (Kobeltia)*cf. *intermedius* Normand, *Hawaiia minuscula* (Binney), *Oxychilus (Oxychilus) draparnaudi* (Beck), *Oxychilus (Ortizius) helveticus* (Blum), *Zonitoides (Zonitoides) arboreus* (Say), *Limax (Lehmannia) valentianus* Férussac, *Deroceras (Deroceras) laeve* (Müller), *Deroceras (Deroceras)* cf. *lombricoides* (Simroth), *Helicella (Xeromicra) apicina* (Lamarck), and, in addition, unidentified juveniles of two further Helicid species. Some further species have previously been recorded under other names.

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[1] The present paper is a somewhat modified and extended version of a lecture held at the 3rd Scandinavian Symposium on Systematic Zoology, Finland, January 1982.

1. Introduction

Since the early 19th century the rich terrestrial Gastropod fauna of Madeira has attracted great interest, owing to its extreme diversity, high degree of endemism and pronounced Tertiary relict character. In recent times it has received further attention because of the archipelago's crucial position in relation to the spreading of the Atlantic sea floor. The topic has been discussed by several authors, such as Wollaston (1878), Watson (1892), Cockerell in several brief papers, by Pilsbry (scattered in the volumes of the Manual of Conchology), and, more recently, by Cook et al. (1972).

Much of speculation on the biogeography, ecology and evolution is, however, invalidated by inadequate taxonomy, or outdated by recent findings or concepts in the fields of palaeontology, palaeogeography, genetics and gastropod taxonomy in general. Particularly problematic is the fact that so little real information is available on the distribution and habitat selection of the different taxa. Species have been confused owing to inadequate taxonomy, or only a very rough circumscription of the distribution is given. Most museum material preserved is labelled "Madeira" or "Porto Santo" only. Evidently, samples from very different sites have been lumped together.

However, taxonomical differentiation, habitat selection, and competitive interaction, population dynamics and isolating mechanisms are intimately interwoven, and — to a considerable extent — manifested by the topographical distribution pattern. An adequate taxonomy is fundamental to all subsequent work.

In addition to the early works of Lowe, Wollaston, Albers, fundamental to all later research, important taxonomical revisions have been carried out by Pilsbry (Manual of Conchology, Vols. 19, 20 and 27), and Mandahl-Barth (1950).

The present author started field work on Madeira in 1970 in order to clarify — or partly even to reconstruct a knowledge of — the distribution, which had been lost, to work out the ecology and to obtain material for a taxonomical revision. Further collecting trips were made in 1972 and 1978. In 1981 the author had the opportunity to visit the ANSP Museum in Philadelphia to study type and other original material from Madeira. This contributed substantially to clarification of the taxonomy.

2. Nomenclatural revision

The results of the taxonomic revision are preliminarily concluded in the check-list. One new genus, one new species, and four new subspecies are described or indicated. The status of a considerable number of taxa, such as species, subspecies or infra-subspecies, has been re-evaluated. Cases which are still doubtful are indicated.

An important part of the survey is the general examination and revision of the nomenclature. In all, 10 established names have to be replaced, because of primary or secondary homonymy, discovery or rehabilitation of earlier names. In addition to the seven new names introduced in this paper and enumerated in the abstract, the following names are considered: *Craspedopoma (Craspedopoma) mucronatum* (Menke), *Caseolus (Leptostictea) hartungi* (Albers), *Disculella spirulina* Cockerell, and *Discula (Discula) calcigena* (Lowe). It is also demonstrated in some cases that names, based on Madeiran material, take a priority when the same taxon is described from elsewhere.

3. The physical and biotic background to the mollusc fauna

The Madeiran archipelago is situated about 700 kms from the coast of Morocco. In addition to the main island of Madeira there are two further groups of islands, Porto Santo and its adjacent islets and the three Desertas islands. The land area of the archipelago is < 800 km^2, of which more than 90 % is Madeira proper.

The climate is largely subtropical and oceanic, with slight differences between the warmest and the coolest month. The considerable variation in topography, local climate and habitats will not be considered here but have, in fact, great importance with regard to the diversity of the mollusc fauna. However, the major differences between the more temperate and partly very wet climate of the higher parts of Madeira and the relatively dry, warm and strongly insolated climate of Porto Santo, the Desertas and the southern and easternmost parts of Madeira should be mentioned. In the drier areas the soil is usually rather calcareous, on the higher and wetter parts decidedly leached and acid. The vegetation shows, correspondingly, great variation, but has been transformed to a great extent by man. The most important element is the laurel wood, which may be considered a Tertiary relict formation.

4. Geological evidence and history of biota

The Atlantic Islands have, with the exception of certain eastern marginal parts, a common volcanic origin, related to the Atlantic sea floor spreading. With some simplification it can be stated that they originated as ejecta from the Mid-Atlantic ridge, and their present distance from the ridge indicates the possible maximum time elapsed since their origin (Ostenso & Vogt 1967). Subsequent volcanic activity, including generation of islands off the axis, might have led to the concealment of early evidence. The oldest rocks in the Cape Verde Islands are estimated at 120 million years, in the Canary Islands at less than 20 million years (Ostenso & Vogt 1967, Wilson 1965), except for the easternmost islands, which include a considerably older basement of continental origin.

With regard to Madeira, there is considerable divergence in age estimates, ranging between 60 and 30 million years. It should, however, be born in mind that this is not the same as the time for emergence above sea level, when the island became available for biotic colonization. Palaeontological evidence (Krejci-Graf 1964, Watkins et al. 1966) indicates Miocene age, i.e. about 15 million years, but does not necessarily exclude higher ages. Much of the original bedrock of this time may have been eroded down and covered by younger deposits. Watkins & Abdel-Monem (1971), have demonstrated an age of 3.05±0.15 million years for lavas at an altitude of c. 840 m (site M22), i.e. more than 500 m above the Miocene reef deposits. Apparently a considerable terrestrial volcanic deposition must have preceded the period dated by Watkins & Abdel-Monem.

In conclusion, there is no conclusive geological evidence for when conditions allowed the terrestrial fauna to establish itself. This is decidedly of oceanic island character, with very few, easily dispersed indigenous vertebrate species: except for the lizard, *Lacerta dugesii,* and a seemingly indigenous, now extinct mouse species (Pieper 1981; acc. to Pieper, unpubl., similar records are known from other oceanic islands), only birds and three species of bat. Two of the latter are represented by separate subspecies. The frog, *Hyla meridionalis,* is undoubtedly introduced. Neither diversity nor endemism is very pronounced in the Insecta, which certainly depends on easy dispersal and considerable faunal exchange with the continent, with faunal replacement and prevention of speciation as consequences. High diversity and endemism is present in groups such as Diplopoda (Enghoff 1982) and Gastropoda, with a weak capacity for dispersal but an apparently strong capacity for radiation.

5. Diversity and endemism

As evident from the notes to the nomenclatural list, there are several cases when the border between species and subspecies is difficult to draw, owing to either intergrading variation, or lack of adequate material. I therefore use the term *taxon,* in the restricted meaning of species and well circumscribed subspecies, as the basic unit in comparisons. In fact, the border with taxa on an infra-subspecific level in the bewildering diversity of the Madeiran Gastropoda is also ill-defined in many cases.

The distinction of species and subspecies is therefore, to a certain extent, arbitrary. However, comments are made to all border cases, as far as present evidence permits.

Summarizing the nomenclatural list 259 ± 3[1] taxa are documented from the Madeiran archipelago. Three of these are still unidentified; furthermore, one (*Helicigona lapicida*) has been provisionally omitted from the list. It should be noted that the figure also includes the extinct, quaternary taxa. The distribution of the taxa groups with regard to the degree of indigenousness is shown in Table 1.

The limits between the groups 3-4:a, and 4: a-4:b in the table can be difficult to draw in particular cases and are, therefore, somewhat arbitrary. Absence from subfossil beds cannot be regarded as conclusive evidence of later introduction, as preservation takes place only under particular ecological conditions. Consequently, only a limited proportion of the extant species will come into question as subfossils. Further consideration has therefore been taken with regard to the distribution pattern in relation to human impact factors, particularly with regard to the consistency of the pattern.

The endemism is also pronounced on higher levels. Of 65 genera represented, 25 have endemic species on Madeira, and 14 of these are restricted to Madeira. A further six genera are shared with the other Atlantic Islands. One subfamily (Geomitrinae) is endemic to the Atlantic Islands, and this has the large majority of its species on Madeira. The land mollusc fauna of Madeira has, with exception of a few, widespread, mainly anthropochorous species, virtually nothing in common with the extant fauna of the adjacent North African mainland. The affinities are to be found in the early Tertiary of Europe.

A measure of the degree of diversity and endemism of the Madeiran Terrestrial Gastropoda is obtained by a comparison with the fauna of central and northern Europe. From this area, as it is delimited in the recent handbook of Kerney et al. (1979), 280 native or naturalized species have been recorded. Of these, 55 belong to the Mediterranean or the Carpato-Balcan fauna, and just touch the area at one or a few sites on the border. Including a few subspecies, the central and northern European gastropod fauna can be estimated at about 230 taxa. Very few of these are actually

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[1] Included as separate taxa, but of somewhat uncertain status are: *Leiostyla (Leiostyla) loweana transiens, Actinella (Faustella)* Form IV and *Discula (Discula) polymorpha pusilla.* Possible additions are: the edentate, recent form of *Truncatellina, Amphorella (Amphorella) tornatellina* f. *minor* and *Actinella (Actinella) laciniosa* Form II; even some further forms may come into question (cf. pertinent notes).

restricted to the region, and thus endemic in a strict sense. The area concerned is about 2.5 million km^2.

The low diversity and endemism of the central and northern European mollusc fauna may be explained to a considerable extent by its pleistocene history, with extensive extinction and displacement of faunal elements. However, even a comparison with North America (N of Mexico), where the prequaternary fauna survived with much more limited displacements, shows a similar picture. This vast area, of 18 million km^2, with zones ranging from tropical to arctic tundra, houses about 760 species (Pilsbry 1939–1948), and a relatively modest number of subspecies.

Against this, the less than 800 km^2 of the Madeira archipelago houses 217 apparently indigenous taxa, of which 191 are endemic. A comparison with the mollusc faunas of the other Atlantic Island groups is made in Table 1. The outstanding character of the mollusc fauna of Madeira is apparent.

Panelius (1958) has pointed out the rather similar figures for anthropochorous species in each of the archipelagoes, and remarked that the level of endemism may have been 90 % or more, before human colonization. Only in the Azores was the degree of original endemism decidedly lower. European, and particularly Mediterranean, species dominate the introduced element.

The relationships of the endemic element in the Madeiran fauna will be considered in the following section. The relative position of the different archipelagoes is reflected in the composition of the indigenous element of the fauna. A western European element, probably of rather early cenozoic origin, is noticeable in the fauna of Madeira and the Azores, the NW African affinities of the Canarian fauna are obvious, as are the tropical African ones in the Cape Verde fauna.

The high diversity and endemism of the Madeiran mollusc fauna is outstanding in comparison not only with the other Atlantic Island groups, but with oceanic island faunas elsewhere in the world. Major islands, such as Madagascar or Cuba, with highly endemic faunas, are not considered in the present context, as they are not of oceanic origin in the strict sense. Islands with particularly high diversity and endemism are Mauritius (Germain 1921) and the Hawaiian Islands (Zimmerman 1948). The figure for the former island (area almost 1900 km^2), calculated on a consistent basis with regard to the various categories, is 151 specific-subspecific taxa, of which 83 are endemic. This is almost exactly the same as for Madeira proper: 157 and 83 taxa, respectively.

A provisional re-assessment of the figures of Zimmerman has been undertaken in order to make them reasonably compatible with those for Madeira. This has given the following results for Hawaii (18 major islands, numerous islets, total area almost 16 800 km^2): c. 1055 specific-subspecific indigenous taxa, of which all except about ten are endemic. The number of genera is 47, of which 25 are endemic to Hawaii. In addition there is about ten introduced species.

Hawaii has, by far, the richest oceanic island mollusc fauna in the world, with regard to diversity as well as endemic species. But if the individual islands are considered, it is in the same order of magnitude as for Madeira or Mauritius. It should be noted that extinct, subfossil species are included in all these comparisons.

Table 1. Distributional groups of terrestrial Gastropoda of the Atlantic Islands

	Azores[1] 2300 km^2		Madeira 800 km^2		Canary Islands[2] 7300 km^2		Cape Verdes[3] 3800 km^2	
	Taxa	%	Taxa	%	Taxa	%	Taxa	%
1. Endemic to the archipelago	41	41.8	191	73.7	141[4]	78.3	16	43.2[5]
2. Endemic to Atlantic Islands	3	3.1	3	1.2	4	2.2	–	–
3. Widespread species = with distribution outside Atlantic Islands	23	23.5	23	8.9	12	6.7	5	13.5[5]
4. Anthropochorous species								
a.) Naturalized	28	28.6	22	8.5	23	12.8	9	24.3[5]
b.) Strongly synanthropic, including adventives and accidental introductions	3	3.1	20	7.7			7	18.9[5]
Total	98	100.1	259	100.0	180	100.0	37	99.9

1) According to Backhuys (1975), critically reviewed and supplemented by the present author.

2) Preliminary estimate, according to Wollaston (1878), Odhner (1931, 1937) van Regteren Altena (1950), critically reviewed. No modern, monographic treatment of the Canary Islands terrestrial Gastropoda exists. Anthropochorous species probably under-recorded.

3) A preliminary estimate, based on a critical review of Wollaston (1878), Panelius (1958), and Groh (1983).

4) A liberal estimate. It is more probable that a revision would decrease the number of taxa, rather than the reverse. Of the approximately 30 Canarian taxa with NW African affinities, some may prove conspecific with continental species.

5) Five of the endemic taxa and five widespread members of the Cape Verde taxa have tropical African affinities or origin. Of the anthropochorous species three are widespread tropical, the remainder of European origin.

6. A review of the fauna-historical significance of endemic taxa above species level

To understand the causes of high diversity and endemism, and the historical significance of the mollusc fauna, it is necessary to consider the significant features of the different endemic groups.

In the Vertiginidae, *Staurodon saxicola,* endemic to Madeira, is the only palaearctic representative of the tropical subfamily Nesopupinae. However, in the Tertiary, from Oligocene to Miocene, related genera lived in Europe.

In the Pupillidae, extreme radiation has taken place in the genus *Leiostyla* on Madeira. Of a total of about 40 species in the Western Palaearctic, 25 are endemic to Madeira, together with several subspecies. The majority of the species have certainly evolved within the Madeiran archipelago, and show a striking adaptive radiation, being adapted to very different habitats. The genus is recorded from the European Oligocene, and the species there are similar to the more primitive species on Madeira (such as *cheilogona*) and also to species in western Europe, the Canary Islands and the not derived species of the Azores and Caucasus. All these belong to the subgenus *Leiostyla* s.s. The species of the other subgenera probably have a separate origin, but so far there is no palaeontological evidence of this. Other isolated, well circumscribed groups exist in the Causasus and on the Azores.

Discus in a very old, holarctic genus, recorded from Europe in Palaeocene and from N America in Eocene. Its origin may go far back in the Mesozoic, before the continents were fully separated. For the endemic Atlantic Island subgenera *Atlantica* and *Keraea,* however, no particular palaeontological evidence is available, and not much more can be stated than that they have an old palaearctic ancestry.

The vitrinid genus *Phenacolimax* is also an old one, with a wide, persisting distribution and known since the Oligocene in Europe. On Madeira, the Canary Islands and the Azores [1] it is represented by the endemic subgenus *Insulivitrina* (on the Canary Islands and the Azores also by the subgenera *Guerrina* and *Plutonia,* respectively). An interesting feature of the Atlantic Island species is that they are considerably larger than the continental species, which may be a result of evolution in an optimum environment, under relative freedom from stress from predators and competitors. The *Insulivitrinas,* primarily montane species, requiring relatively moist and cool conditions, have probably arrived on the Atlantic Islands in late Tertiary, when a climate of this kind began to develop.

The genus *Janulus,* possibly endemic to Madeira[2] was widespread in Europe from Oligocene and onwards. Even though the genus *Janulus* has a clear European origin, the subfamily Gastrodontinae, to which it belongs, is amphiatlantic and prevalently American. Its closest relatives seem to be American genera as *Gastrodonta.* This suggests that the group may have a very ancient ancestry, before the opening up of the Atlantic Ocean.

The African-Oriental-South European family Ferrusaciidae is represented on Madeira by three strictly endemic genera, comprising 14 species (in addition there are a few species of widespread genera). However, very little comparative anatomical and fossil evidence is available on the Ferrussaciidae, and the Madeiran genera in particular. Little more can be said about the Madeiran species than that they seem to have had a long evolutionary history in isolation. However, the three genera may have an at least diphyletic origin. The Ferrussaciidae is apparently an old group, represented since the Eocene in Europe by a number of genera, but none of these seems to be directly ancestral to any of the Madeiran genera.

Apart from the widespread genus *Balea,* the endemic Madeiran genus *Boettgeria* is the only representative of the family Clausiliidae on the Atlantic Islands. *Boettgeria* is a specialized, but not necessarily taxonomically isolated genus. Its affinities are still subject to dispute (Mandahl-Barth 1951, Zilch 1959-1960, Nordsieck 1979). However, it is clear that the affinities are to European Clausiliids, probably the SE European and neighbouring Asian subfamily Mentissoideinae, and not to the group in the Atlas region, belonging to subfamily Alopiinae.

One hundred and seven recorded taxa, thus substantially more than half the endemic fraction, belong to the helicid subfamily Geomitrinae, which is almost exclusively endemic to Madeira. Only a few species occur on the Canary Islands and the Azores and, insofar as they are endemic there, they may be derivates from the Madeiran stock. The Geomitrinae show extreme morphological and ecological differentiation, with seven of its ten genera endemic to Madeira, and some genera and subgenera even endemic to subgroups of the archipelago. The radiation within the Geomitrinae, however, is essentially an "inter-Madeira" problem, and should therefore

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[1] The old *Vitrina* record from the Cape Verdes, by Dohrn, was seemingly authentic (cf. Groh 1983: 179), but in lack of voucher material it cannot be stated which vitrinid genus is concerned.

[2] Records from Canary Islands have not been confirmed anatomically.

not be regarded in the present context on the relations of the fauna to the outside world. There is still no generally accepted opinion about its origin and systematic position, even if it is a primitive group — according to Mandahl-Barth (1950) the most primitive within the Helicidae. Largely the group must have evolved on the Atlantic Islands, and primarily on Madeira.

The genus *Leptaxis,* placed in a separate subfamily by several authors, is more widespread on the Atlantic Islands than the Geomitrinae, though, enigmatically, it is not found on the Canary Islands. It is an old genus, known already from the European Oligocene together with some extinct genera. Fossil records from Cape Verdes are regarded of Tertiary age by Kobelt (1896) by Groh (1983) as more probably of Quaternary age. One genus of doubtful systematic position, *Camaenopsis,* from the Lower Miocene of Morocco, is possibly also related to *Leptaxis.*

Finally, there is the prosobranchiate genus *Craspedopoma,* now endemic to the Atlantic Islands, which has the majority of its species on Madeira. In early Tertiary it was widespread in Europe, and has been recorded already from the Palaeocene.

Two genera endemic to Madeira, *Hemilauria* and *Lampadia* (Pupillidae and Helicidae, respectively), each with a single species, have not been discussed here. Not much more can be stated than that they are endemic and apparently rather isolated, without apparent affinities to any extinct or extant genus. Another peculiar, endemic form is *Helix (Idiomela) subplicata,* which seems to have a rather isolated position in the large genus *Helix.* This genus is rather young, first recorded from the Upper Miocene, and thus younger than the forms ancestral to the major part of the endemic Madeiran mollusca. *H. subplicata* may possibly represent an early, but specialized offshoot of the genus (cf. p. 274, note 78).

However, with our present state of knowledge, considerations on the systematic relations and significance of these forms with regard to the faunal history would be speculative, and are therefore omitted here. A few further endemic species, belonging to various widespread genera, and probably of relatively young origin, have also been disregarded here.

To summarize, all genera for which palaeontological evidence is available appear to have an origin, or affinities to genera in the early Tertiary European fauna, from Palaeocene to Oligocene. Other genera, such as *Boettgeria* and the Ferrussaciid genera, cannot be related to any extinct genus, and conditions speak in favour of a long, indepedendent evolution.

The high age, indicated by the mollusc fauna, may seem contradictory to available geological evidence (section 4), according to which an origin older than the Miocene does not seem probable, even if it cannot be entirely excluded. On the other hand, the ancestral fauna, from which the present fauna of the Atlantic Islands was derived, may have survived considerably longer under oceanic climate conditions at the border of the continent, than indicated by available fossil evidence.

However, the complete absence on Madeira of indigenous representatives of the geologically younger genera, which became dominant in NW Africa in the late Tertiary, probably partly replacing older genera must be considered in this context. This very definitely speaks in favour of the endemic gastropod fauna having been established on Madeira already in the Mid-Tertiary.

7. Discrepancies in the gastropod distribution pattern of the Atlantic Islands

In general there is a consistent pattern in the distribution of the terrestrial Gastropoda in the Atlantic Island region. Differences and peculiar features are, on the whole, well explained by climatic gradients and position in relation to the continental mainland. But, even if there are certain basic features in common, there are, nevertheless, striking signs of the isolation between the archipelagoes. Of the endemic species of the region, extremely few are distributed beyond a single island group, and none is known from all the groups.

In addition there are some cases which may seem inconsistent with the general pattern.

The Enid genus *Napaeus,* present in the European Eocene, but also with N African affinities, is represented by a considerable number of species on the Canary Islands and the Azores, but is completely absent on Madeira. This corroborates the general picture of absence of NW African affinities in the Madeiran mollusc fauna, but is enigmatic with regard to the Azoran fauna, which is even more remote from NW Africa in its affinities. Accidental dispersal from the Canary Islands directly to the Azores seems a more plausible explanation than local extinction on Madeira.

On the other hand, *Leptaxis,* which is well represented on all the other archipelagoes, is not found on the Canary Islands. The presence on the Cape Verdes suggests that the ancestral distribution of *Leptaxis* may have included the NW African coastal areas, and that its present absence form the Canary Islands may depend on local extinction rather than insufficient dispersal.

Whereas geological and, more indirectly, biogeographical evidence points to a roughly Mid-Tertiary beginning of terrestrial colonization for Madeira, and an even later one for the Azores, there are indications of an established older fauna on the Canary Islands (cf. Rothe 1964), which is partly of continental origin. This fauna seems to have been extensively destroyed by Mid and Late-Tertiary volcanic activity.

As a tentative hypothesis it can be assumed that genera such as *Hemicycla* and *Gibbulinella* are survivors of an ancient element in the Canarian fauna (*Hemicycla* is known from the European Miocene, and *Gibbulinella* already from the Cretaceous in Europe, the later together with *Staurodon* the only survivor of a palaeotropical fauna). The volcanic activity may have either prevented colonization by the specific Atlantic Island element, or largely destroyed a fauna of this kind. This may explain the notable paucity of the specific Atlantic Island element in the Canarian fauna: no specialized species of *Leiostyla,* one species of *Craspedopoma,* the (under all circumstances) faint presence of the Geomitrinae[1] and possibly *Janulus,* and the apparent absence of *Leptaxis* and the endemic Ferrussaciid genera. Besides *Napaeus* and *Hemicycla,* with a total of almost 70 taxa, the indigenous mollusc fauna of the Canary Islands is dominated by species with NW African affinities (some 30 taxa) of either small, easily dispersed and/or relatively late immigrants (16 taxa, among these the *Insulivitrinas*). *Canariella,* with some 10 taxa, with NW African as well as early Tertiary European affinities, is difficult to evaluate. The whole range, from endemic genera to to identical species, is represented in the indigenous element with NW African affinities.

Today these considerations are speculative, but the components of the pattern are distinct, and forthcoming research may allow a fairly firm assessment of the history of the mollusc fauna. In the first hand, better knowledge of the systematics, based on anatomical and other evidence, is desirable, particularly for the understanding of the relations between groups of the same genera, (such as *Napaeus, Actinella, Leptaxis*) present in different island groups. More adequate and precise geological knowledge is also indispensable for sound biogeographical considerations, particularly on chronology, sea level changes and the significance of events of catastrophic volcanism. The resolving of the complicated problem of later stages in the closing of the Tethys Sea and the position of the Atlantic Island groups relative to the African and European continent blocks of that time will probably be of the greatest importance for the interpretation of the history of the island biotas. Finally, "amalgamation" of evidence from different taxonomic groups would probably give answers to problems, which may seem enigmatic, when the perspective is restricted to a single group.

8. Aspects concerning a cladistic interpretation of the Gastropod fauna

The striking radiation of the endemic groups, with a clear correlation between the distribution pattern of many groups of taxa and the subgroups of the archipelago, seems fairly inviting for cladistic interpretation.

The hitherto performed survey has, besides topics of distribution and ecology, been concentrated on clarifying the taxonomical basis for subsequent research. A penetrative analysis of the relations between gastropod systematics and the distributional and ecological pattern is a task for the future. Until this has been carried out, attempts to make a cladistic interpretation would be unsubstantiated and speculative. For this reason only some selected items, of immediate interest with regard to forthcoming research, will be highlighted here.

The previous considerations on the geological history, phylogenetic relations and geographical background very definitely point to a Mid-Tertiary origin for a substantial part of the Madeiran terrestrial Gastropoda. It may go back to a few dispersal accidents only, and genera or even groups of genera may have a monophyletic origin. Present evidence and general considerations suggest that Madeira holds a central position in the development of the endemic element in the Gastropod fauna of the Atlantic Islands, but the possibility of mutuality must always be kept in mind. An analysis of the radiation must not be restricted to the relations between the Madeiran taxa, but must also consider related species-groups on the other Atlantic Islands.

It is a long jump from a presumed Mid-Miocene establishment of the terrestrial gastropod fauna to the Pleistocene, when subfossil evidence appears. In itself this evidence does not contribute to a cladistic interpretation of the radiation, but it introduces a time perspective which may throw some light upon how the evolutionary pattern might have been.

In designing cladograms for certain groups in the Madeiran terrestrial Gastropoda experimental systematic work would certainly be helpful, perhaps even indispensable. For testing and

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[1]) Except for the very local *Heterostoma* on Lanzarote, some of the small, anatomically not yet known Helicids may belong to *Actinella* and *Spirorbula.*

substantiating the tentative cladograms electrophoretic methods would be useful to quantify the genetic gaps as well as to sort out false assumptions. Indeed, these methods are effective mainly on the infrageneric level. For the higher phylogenetic relations we may have, at least at present, to rely on traditional morphological and palaeontological evidence.

9. The subfossil Piedade fauna on Madeira

The subfossil evidence on terrestrial Gastropoda of Madeira proper is restricted to the Piedade beds on Pta São Laurenço. As shown in Table 2 this fauna is very different from the local recent fauna. ^{14}C dating has indicated an age of 5 130 ± 70 years (Krejci-Graf 1964). Previous assumptions that the fauna was of Pleistocene age are thus definitively disproved.

The Piedade deposits originate from a former volcano on northern coast (Krejci-Graf 1964), now completely abraded. A substantial part of the gastropod fauna is of woodland type, and evidently emanates from higher levels of this volcano. Of 41 taxa recorded in the subfossil state only nine are identical with those now living in the vicinity. The faint representation of typical open terrain forms may depend partly on local ecological conditions, and partly on the fact that it was first after man had cleared the landscape that such species reached their present high abundances. With the possible exception of *Truncatellina linearis,* all the extinct taxa have systematic affinities which indicate that they may have lived in a wooded environment or, in extreme cases, in an open macchia type with sparse tree or bush vegetation.

Table 2. Composition of the fauna of Pta São Lourenço (shell-bearing species only).

Ecological group	Recent	Subfossil (Piedade)
Pronounced woodland taxa and species now confined to N Madeira	—	20
Extinct taxa, probably all woodland or "catholic"	—	10
Taxa living in light woodland as well as open terrain	6	7
Taxa largely restricted to open terrain	13	4[1]
Introduced species (or strongly favoured by synanthropic conditions)	6	—
Total	25	41

1) *Truncatellina linearis,* extinct, but probably conspecific with *Tr. molecula* (Dohrn 1869) of the Cape Verdes, probably indicates a warmer and drier climate than today.

But even if the differences between the recent and the subfossil fauna can be explained to a considerable extent by differences in the local ecological conditions, and supervening human influence, the record of nine species and two well defined extinct subspecies is an indication of a considerable shift in the overall ecological conditions. Two of the extinct taxa (*Caseolus bowdichianus* and *C. compactus betamajor*) are also present in the subfossil fauna of Porto Santo; furthermore *C. sphaerulus* is related to *C. subcalliferus,* still living on Porto Santo.

10. The subfossil fauna of Porto Santo

The subfossil deposits of Porto Santo are of a much more extensive and elaborate character than those on Madeira. There are local deposits in connection with nearly all the major hill complexes, and in many cases there is a well defined stratigraphy. Previously, the subfossil evidence has largely been treated *in toto,* not permitting more precise conclusions. Today, when an adequate taxonomical basis has been laid, working out the gastropod stratigraphy would centainly be a promising field. At present, however, only outline information can be given.

So far ^{14}C datings are available (Lietz & Schwarzbach 1971) the Porto Santo deposits are of Würm age, i.e. considerably older that the Piedade deposits. The mollusc stratigraphy has not been worked out, but shell-containing horizons in the extensive eolianite deposits have yieldid data of 13 480 ± 120 B. P. and 21 570 ± 350 B. P. A lower limit may be formed by a strand terrace of seemingly Tyrrhenian III age (^{14}C datings ≧39 500–43 000 B. P.), on which some of the terrestrial deposits rest, but Lietz & Schwarzbach do not exclude the possibility of still older strata. — The climate during the formation of the eolianites was, though fluctuating, largely cooler and drier than to-day, with prevailing NW winds. — It has not yet been stated if Holocene deposits, similar in age to those on Madeira, occur on Porto Santo, but field observations suggest that in places shells are of subrecent origin.

Considering that the Porto Santo deposits reflect the total fauna, it is not surprising that it is much richer than the merely local Piedade fauna. In all, 64 of the 85 indigenous taxa are recorded in the subfossil state from Porto Santo and its adjacent islets. Their distribution into different categories is shown in Table 3.

Of the 21 taxa, which have been found in a recent state only, 19 live under conditions in which subfossil preservation is not to be expected. They are extremely local, e.g. on islets, or live high up in the mountains. *Caseolus subcalliferus* is

Table 3. The indigenous terrestrial Gastropoda of Porto Santo and adjacent islets[1]. Number of taxa.

Distributional group	Recent	Recent and subfossil	Extinct
Endemic to Porto Santo	16	41[2]	15
Porto Santo and Madeira	1	3	4[3]
Widespread species	4	–	1
Total	21	44	20

1) Littoral species excluded.
2) Including 4 species, which have or may have died out
2) Including 4 species, which have or may have died out in recent time.
3) *Craspedopoma mucronatum* and *Cecilioides eulima* are still living on Madeira a proper.

represented by distinct subspecies in recent and subfossil state respectively, but it cannot be stated whether this reflects a chronological shift in the conditions, or if they have existed in parallel, the subfossil form belonging to a now extinct lowland race.

However, it is enigmatic that *Amphorella gracilis,* which is common on all the higher hill complexes, has never been found in the subfossil state. However, in general the Ferrussaciids are extremely rare in the deposits, and their present high abundance may be a consequence of the human transformation of the habitats.

Of the extinct taxa, eight are distinct species (one with two subspecies), and eight are subspecies of recent species or, in some cases, possibly separate but very closely related species. In addition to this, six recent species are conchologically more or less divergent in the subfossil state, though not sufficiently to discriminate them as subspecies.

Finally it should be noted that at the same time as the endemic element of Porto Santo was more diversified in the past, the fauna also had more in common with the fauna of Madeira proper. As mentioned, the now extinct *Caseolus bowdichianus* and *C. compactus betamajor* lived on both islands. Of the former there is, however, a series of forms approaching *C. punctulatus,* indicating that the taxon may be primarily of Porto Santo origin. The subgenus *Actinella* s.s. was represented on Porto Santo by *A. arcinella papillosculpta* and possibly also the subgenus *Faustella* by the somewhat obscure *A. crassiuscula.* Finally, there was a now extinct species on Madeira, *C. sphaerulus,* closely related to *C. subcalliferus,* as mentioned previously.

All the pertinent taxa belong to an indisputably subfossil fauna. There are no indications, in the form of apparently subrecent material, that they should have disappeared recently as a result of the human impact. On the other hand, recent collecting activity has unveiled further species common to the subgroups of the Madeiran archipelago, as well as the reverse: species may have disappeared since the days of Lowe and Wollaston. To what extent this disparity is real, or due to inadequate collecting, is difficult to say as yet. In every case it strengthens the picture of a constant change in the faunal composition, which does not necessarily have to be related to the present human influence.

Even if there have been considerable changes in the composition of the gastropod fauna during a geologically short period, the basic pattern in the distribution of most species has remained remarkably stable. They may have widened or reduced their distribution to some extent, but there are no profound changes. Subspecies or semispecies were localized to essentially the same parts of Porto Santo as today.

11. Semispecies problematics

The work of Wollaston is of particular interest as an early, but highly consistent attempt to comprehend the pattern of variation in an extensive faunal assemblage in the light of the Darwinian concept of evolution. With painstaking care he scrutinized every form, to define its systematic status and its relations to other pertinent recent or extinct taxa. To a degree, which is probably unique in malacology, subsequent research has essentially confirmed the taxonomy of the Madeiran Terrestrial Gastropoda assessed by Wollaston and his predecessor Lowe.

Watson (1892) concluded that the endemic species were generally distinct and unambigous. Cockerell (1922d) asserted a contrary opinion and stressed the presence of numerous critical forms.

As a conclusive result of the present revision it can be stated that in the overwhelming majority of cases it is quite clear which the taxa are, by which features they are defined, and how they are circumscribed geographically. It is quite another matter that it must be admitted that whether forms should be ranked as species or subspecies, particularly when isolated on different islands, can still be a matter of judgement. Experimental systematic work may contribute to conclusive answers in this respect.

There is a limited number of cases in which the specific delimitation is not quite unequivocal, and we may have to make do with semispecies. These presumed border cases are briefly reviewed here: further information is given in the annotated check-list.

In spite of extensive literature on phenotypic and genotypic variation, selection etc. (cf. comprehensive papers of Jones et al. 1977, Clarke et al. 1978) the relevance, and the particular implications of the semispecies concept with regard to the terrestrial Gastropoda has not yet been adequately analyzed. In the present paper the concept is used in a relatively unsophisticated way, the application perhaps best described with the following words: "systematic entities, which normally give the impression of distinct species, but in which the accidental occurrence of intermediate individuals or local populations indicate local and/or temporary hybridization, without affecting the prevailing integrity of the species". In practice the discrimination between overlapping variation and real hybridization can be very difficult. Careful observation of the detailed spatial occurrence and niche specialization, combined with morphometrical or experimental systematic studies, may lead to resolution of the problems. In the check-list the presumed semispecies are nomenclaturally treated as species.

The uncertain status of some forms of the genus *Leiostyla* (see the check-list) is probably only a problem of lack of adequate and sufficient material. All these forms are known in a handful of specimens only, without locality data. When adequate material has become available — as for *L. sphinctostoma* and *arborea* — the taxonomical situation has become clear. For the likewise obscure *Actinella fausta* complex, resolution of the problems is now in sight. Preliminary evidence is presented here, in the notes 54–57 with Table 4 and the figures. Three species are seemingly involved, but with regard to a few yet doubtful specimens the evidence is ambiguous. These may represent a fourth, separate taxon, or hybrids between two of the other species, which in this case would have to be regarded as a semispecies pair.

The following pair of taxa usually appear as distinct species, but locally intermediate specimens have been found, suggesting a semispecies relation: *Boettgeria deltostoma* and *depauperata, Actinella bicarinata* and *echinulata,* very rarely also in *Amphorella oryza* and *tuberculata, Caseolus punctulatus* and *solidus.* For *Caseolus hartungi hartungi* (=*dealbatus* Lowe) and *hartungi fictilis* the evidence seems more in favour of the hypothesis that they are geographical subspecies not maintained by inherent reproductive barriers. *Heterostoma paupercula* is also possibly a complex of two semispecies.

The relations between the four forms of *Discula polymorpha,* existing together within a very limited area on Pta São Lourenço, as well between the forms of the same species on the Desertas Islands, are more complex. Cook & Pettitt (1979) studied the variation of a number of characters, but omitted to consider the underlying taxonomical problem. A tentative taxonomical interpretation is given in the note 67 to the check-list in the present paper. It may appear possible to explain the *Discula polymorpha* complex in terms of balanced polymorphism, but it seems that both subspecies and semispecies may be involved.

Finally it can be stated that there is no case in the wealth of forms in the Madeiran terrestrial Gastropoda which could be taken as evidence for sympatric speciation. Facts are best compatible with the assumption that geographic isolation or a strongly reduced gene flow must have preceded the establishment of balanced polymorphs as well as semispecies.

12. Some concluding remarks on the evolutionary process, dispersal and dispersal barriers

From the preceding, it can be concluded that the morphological differentiation on specific and lower levels has a very clear geographical background. The presence of distinct local races (such as *Discula polymorpha agostinhoensis,* and races of *Discula calcigena* and *Leptaxis nivosa*) on small islets, is most probably a consequence of the fragmentation of the larger islands and their mollusc populations. The distinctive character of these forms is probably due to local selective influence on small populations, in certain cases in combination with drift. Pettit (1977) has demonstrated that significant morphological changes have occurred in *Discula turricula* during little more than 100 years. He claimed that it is probable that the changes could be related to a shift in the local ecological conditions.

The founder effect may be working on a local level, enhancing the distinctive character of individual populations, but probably played no significant role in the development of the geographical pattern on a subspecific or higher level.

The evidence indicates that conditions favour rapid infraspecific differentiation and subsequent speciation, and that these processes are — for the majority of the taxa — not significantly counteracted by a gene flow due to dispersal. But at the same time it seems clear that changes in the faunal composition are constantly going on.

The fact that significant alterations in the faunal relation between Madeira and Porto Santo has taken place within the geologically short late Quaternary time can be extrapolated by some million years — corresponding to a plausible "life length" of a species — and fairly dramatic changes in the faunal composition can be postulated. Even if this is hypothetical, it gives reason for being reluctant to draw far-reaching conclusions from the recent distribution pattern.

After all, the geographical barriers between the parts of the Madeiran archipelago are modest, between 20 and 50 km. For most species a sufficient number of dispersal opportunities is certainly offered during their "life length", for a potential general colonization of the archipelago. Local adaption and niche specialization may have been more important for maintaining and enhancing the distributional pattern of the taxa than the primary geographical separation.

Theoretically (cf MacArthur & Wilson 1967, also Kew 1893, Rees 1965) it would be possible to calculate roughly the probability of dispersal accidents within the Madeiran archipelago from the evident fact that a significant exchange of Gastropod taxa has occurred between the Atlantic Island groups and over much wider distances. With the exception of some small, easily dispersed and widespread species, there is an almost total lack of endemic species common to two or more island groups. Over the distances concerned, there is virtually no gene flow able to counteract the speciation. Only *Heterostoma paupercula* s.l., with particular adaptions for overseas dispersal (cf. comments in Backhuys 1975 :215), has a distribution beyond a single archipelago.

The rather pronounced endemism above the species level between the parts of the Madeiran archipelago centainly depends less on insufficient dispersal than on difficulties in becoming established. Differences between genera in their innate capacity for adaption and ability to compete, as well as availability of pertinent ecological niches, may tend to strengthen the endemic separation. The secondary reduction of distinctive species groups, common to Madeira and Porto Santo, is consistent with this view.

The difficulty for newcomers to establish themselves was suggested as an explanation (section 6) of why the geologically younger NW African taxa had been unable to get a foothold on Madeira, with its well established earlier fauna. More directly the same is shown by the fact that those extensively spread species, which have been introduced by man in historical time, have been unable to colonize the more natural habitats to any significant degree.

As mentioned previously (section 9) six recent taxa are represented in the subfossil strata on Porto Santo, in forms morphologically more or less divergent from the recent. Properly analysed, these species will be able, together with more pronounced cases such as the sequence *Discula vermetiformis-subcarinulata-oxytropis,* to yield evidence on evolutionary rates. The presence of a considerable number of now extinct races of persisting species — or perhaps assemblages of semispecies — strengthens the picture of a rapid evolutionary turnover. The pattern may have been consistent with that demonstrated by Williamson (1981) for limnic Mollusca in the Turkana Basin. The considerable variaton on the subspecific level in several genera, particularly in *Discula* and *Actinella,* suggests that the material is available, from which new taxa can be recruited and, potentially, become dominant in suitable ecological niches and establish themselves as subspecies and species, when the overall ecological conditions change.

On the other hand, it should be noted that there are no signs of increased reproductive isolation during the period which is covered by conchological evidence. The species, or semispecies, seem to have been the same as today. The reproductive barriers, or the establishment of reproductively stable systems on a semispecies level, must be of a considerably higher age.

13. An annotated Check-list of the terrestrial Gastropoda of Madeira

The present list gives, in a very condensed way, a review of the knowledge upon which the present paper is based, but at the same time also points out the still unsolved taxonomical problems and cases of disagreement. In most cases it can be made here with brief references only. The full evidence has to be presented at a later stage of the survey.

The system largely follows Zilch (1959–1960). However, for the Helicidae the arrangement of Mandahl-Barth (1950) has been used, even though it must be admitted that his findings (particularly concerning the position of the Geomitrinae, *Leptaxis* and *Lampadia*) have not yet been "digested" and expressed in a generally revised system of the Helicidae.

Only synonyms of particular significance are given. For a more complete synonymy see the works of Mandahl-Barth (1950), Nobre (1931), Pilsbry (Manual of Conchology, pertinent volumes), and Wollaston (1878).

The following symbols are used:

- † Known in subfossil state only. Further species seem to have died out in recent time, but are not indicated here.
- * Anthropochorous species with a strongly synanthropous occurrence, in some cases accidentally only. About 22 further species are definitely or very probably of anthropochorous origin, but are now well established, and even naturalized (cf. comments to Table 1).

Note: Numbers of whorls are counted according to Ehrmann (1933, fig. 12).

It is the hope of the author that the list will offer a reasonably authoritative base for subsequent work on the Madeiran terrestrial Gastropoda. Considerable confusion, taxonomically as well as nomenclatorically, has also occurred in very recent time, and invalidated much ecological and biogeographical work.

Full descriptions and figures of new or revised taxa will be published later in a separate paper.

Subclass PROSOBRANCHIA
Order MESOGASTROPODA

Family Cyclophoridae

Craspedopoma (Craspedopoma) mucronatum (Menke 1830)[1]
Craspedopoma (Craspedopoma) monizianum (Lowe 1860)

Craspedopoma (Craspedopoma) lyonnetianum (Lowe 1852)
Craspedopoma (Craspedopoma) trochoideum (Lowe 1860)

Family Truncatellidae

Truncatella (Truncatella) subcylindrica (Linnaeus 1758)

Family Assimineidae

Assiminea (Assiminea) littorina (Delle Chiaje 1828)

Subclass EUTHYNEURA
Order BASOMMATOPHORA

Family Ellobiidae

Carychium minimum Müller 1774
Carychium tridentatum (Risso 1826)
Pseudomelampus exiguus (Lowe 1835)
Pedipes pedipes (Bruguière 1789)[2]
Ovatella (Ovatella) aequalis (Lowe 1835)
Ovatella (Myosotella) gracilis (Lowe 1835)
Marinula watsoni (Wollaston 1878)

Order STYLOMMATOPHORA

Family Cochlicopidae

Cochlicopa cf. *lubrica* (Müller 1774)[3]
Cochlicopa lubricella (Porro 1838)[3]

Family Vertiginidae

Columella aspera Waldén 1966
Columella microspora (Lowe 1852)
Truncatellina callicratis (Scacchi 1833)[4]
† *Truncatellina linearis* (Lowe 1852)[5]
Vertigo (Vertigo) pygmaea (Draparnaud 1801)
Staurodon saxicola (Lowe 1852)[6]

Family Pupillidae

Leiostyla (Leiostyla) cheilogona (Lowe 1831)
Leiostyla (Leiostyla) vincta vincta (Lowe 1852)
Leiostyla (Leiostyla) v. watsoniana (Pilsbry 1923)
Leiostyla (Leiostyla) v. mauli nov. subsp.[7]
Leiostyla (Leiostyla) irrigua (Lowe 1852)
Leiostyla (Leiostyla) loweana loweana (Wollaston 1878)[8]
Leiostyla (Leiostyla) l. transiens (Wollaston 1878)[9]
Leiostyla (Leiostyla) cassidula (Lowe 1852)
Leiostyla (Leiostyla) concinna (Lowe 1852)
Leiostyla (Leiostyla) laurinea (Lowe 1852)
Leiostyla (Leiostyla) sphinctostoma sphinctostoma (Lowe 1831)
Leiostyla (Leiostyla) s. heterodon (Pilsbry 1923)[10]
Leiostyla (Leiostyla) arborea (Lowe 1854)
Leiostyla (Leiostyla) simulator (Pilsbry 1923)[11]
Leiostyla (Leiostyla) fusca (Lowe 1852)[12]
† *Leiostyla (Leiostyla) wollastoni* (Paiva 1866)
Leiostyla (Leiostyla) laevigata (Lowe 1852)
Leiostyla (Leiostyla) recta recta (Lowe 1852)
Leiostyla (Leiostyla) r. macilenta (Lowe 1852)
Leiostyla (Leiostyla) millegrana (Lowe 1852)
Leiostyla (Leiostyla) corneocostata (Wollaston 1878)[13]
Leiostyla (Leiostyla) relevata (Wollaston 1878)
Leiostyla (Leiostyla) ferraria (Lowe 1852)
Leiostyla (Leiostyla) degenerata (Wollaston 1878)[14]
Leiostyla (Leiostyla) monticola (Lowe 1831)[15]
Leiostyla (Leiostyla) calathiscus (Lowe 1831)
Leiostyla (Leiostyla) abbreviata (Lowe 1852)
Leiostyla (Scarabella) cassida (Lowe 1831)
Leiostyla (Mastula) lamellosa (Lowe 1852)
Leiostyla (Wollastonula) gibba (Lowe 1852)
Lauria (Lauria) cylindracea (Da Costa 1778)
Lauria (Lauria) fanalensis (Lowe 1852)
Hemilauria limnaeana (Lowe 1852)[16]

Family Valloniidae

Vallonia costata (Müller 1774)
Vallonia pulchella (Müller 1774)
* *Vallonia excentrica* Sterki 1892
Acanthinula aculeata (Müller 1774)
Plagyrona placida (Shuttleworth 1852)[17]

Family Endodontidae

Punctum (Punctum) pygmaeum (Draparnaud 1805)
Punctum (Toltecia) pusillum (Lowe 1831)[18]
Helicodiscus (Hebetodiscus) singleyanus (Pilsbry 1890)[19]
* *Discus (Discus) rotundatus* (Müller 1774)
Discus (Atlantica) guerinianus guerinianus (Lowe 1852)[20]
Discus (Atlantica) g. calathoides (Lowe 1863)
Discus (Keraea) defloratus (Lowe 1854)

Family Arionidae

Arion (Arion) cf. *lusitanicus* Mabille 1868
Arion (Kobeltia) hortensis auctt[21]
Arion (Kobeltia) cf. *intermedius* Normand 1852[22]

Family Vitrinidae

Phenacolimax (Insulivitrina) nitidus (Gould 1848)
Phenacolimax (Insulivitrina) marcidus (Gould 1848)
Phenacolimax (Insulivitrina) ruivensis (Lowe 1831)

Family Zonitidae

* *Hawaiia minuscula* (Binney 1840)
Vitrea (Vitrea) contracta (Westerlund 1871)
Nesovitrea (Perpolita) hammonis (Ström 1765)
Oxychilus (Oxychilus) draparnaudi (Beck 1837)
Oxychilus (Oxychilus) cellarius (Müller 1774)
* *Oxychilus (Ortizius) helveticus* (Blum 1881)
* *Zonitoides (Zonitoides) arboreus* (Say 1816)
* *Zonitoides (Zonitoides) nitidus* (Müller 1774)
Janulus stephanophora (Deshayes 1835)
Janulus bifrons (Lowe 1831)

Family Milacidae

Milax (Milax) gagates (Draparnaud 1805)
* *Milax (Milax) sowerbyi* (Férussac 1823)

Family Limacidae

Limax (Limax) maximus Linnaeus 1758
Limax (Limacus) flavus Linnaeus 1758
Limax (Lehmannia) valentianus Férussac 1823
Deroceras (Deroceras) reticulatum (Müller 1774)
Deroceras (Deroceras) laeve (Müller 1774)
Deroceras (Malino) cf. *lombricoides* (Simroth 1891)[23]

Family Euconulidae

Euconulus (Euconulus) fulvus (Müller 1774)

Family Ferrussaciidae

Cecilioides (Cecilioides) acicula (Müller 1774)
Cecilioides (Cecilioides) nyctelia (Bourguignat 1856)[24]
Cecilioides (Rhaphidiella) eulima (Lowe 1854)
Ferrussacia (Ferrussacia) folliculus (Gmelin 1790)
Amphorella (Amphorella) melampoides (Lowe 1831)
Amphorella (Amphorella) tornatellina tornatellina (Lowe 1831)
*Amphorella (Amphorella) t.*f. *minor* (Wollaston 1878)[25]
Amphorella (Amphorella) mitriformis (Lowe 1852)
† *Amphorella (Amphorella) grabhami* (Pilsbry 1908)
Amphorella (Fusillus) triticea (Lowe 1831)
Amphorella (Fusillus) oryza (Lowe 1852)[26]
Amphorella (Fusillus) tuberculata (Lowe 1852)[27]
Amphorella (Hypselia) producta (Lowe 1852)
Amphorella (Hypselia) iridescens (Wollaston 1878)[28]
Amphorella (Hypselia) cimensis nov. nomen[29]
Amphorella (Hypselia) gracilis (Lowe 1831)

Pyrgella leacockiana (Lowe 1852)
Cylichnidia ovuliformis (Lowe 1831)
† *Cylichnidia cylichna* (Lowe 1852)

Family Subulinidae

* *Subulina striatella* (Rang 1831)
Rumina decollata (Linnaeus 1758)

Family Clausiliidae

Boettgeria deltostoma (Lowe 1831)[30]
Boettgeria depauperata (Lowe 1854)[31]
Boettgeria obesiuscula (Lowe 1863)
Boettgeria lowei (Albers 1852)
Boettgeria exigua (Lowe 1831)
Boettgeria crispa (Lowe 1831)
Balea perversa (Linnaeus 1758)

Family Testacellidae

Testacella (Testacella) maugei Férussac 1819
* *Testacella (Testacella) haliotidea* Draparnaud 1801

Family Helicidae

Heterostoma paupercula (Lowe 1831)[32]
Heterostoma p. f. II
Steenbergia duplex Mandahl-Barth 1950[33]
Steenbergia desertae Mandahl-Barth 1950[34]
Geomitra (Geomitra) coronata (Deshayes 1850)
Geomitra (Geomitra) tiarella (Webb & Berthelot 1833)
Geomitra (Geomitra) moniziana (Paiva 1867).
Geomitra (Geomitra) grabhami (Wollaston 1978)
Geomitra (Geomitra) coronula (Lowe 1852)
Geomitra (Geomitra) delphinuloides (Lowe 1860)
† *Geomitra (Craspedaria) delphinula* (Lowe 1831)
Spirorbula obtecta (Lowe 1831)
Spirorbula latens (Lowe 1852)
Spirorbula squalida (Lowe 1852)
Spirorbula depauperata (Lowe 1831)
† *Spirorbula latina* (Paiva 1866)[35]
Caseolus (Caseolus) compactus compactus (Lowe 1831)
Caseolus (Caseolus) c. portosanctanus (Lowe 1854)
† *Caseolus (Caseolus) c. areiensis* nov. nomen[36]
† *Caseolus (Caseolus) c. betamajor* nov. nomen[37]
† *Caseolus (Caseolus) c. vigiae* nov. subsp.[38]
Caseolus (Caseolus) consors (Lowe 1831)
Caseolus (Caseolus) commixtus (Lowe 1854)
† *Caseolus (Caseolus) baixoensis* nov. nomen[39]
Caseolus (Caseolus) abjectus abjectus (Lowe 1831)
Caseolus (Caseolus) a. nesiotes (Wollaston 1878)
† *Caseolus (Caseolus) sphaerulus* (Lowe 1852)
Caseolus (Caseolus) subcalliferus subcalliferus (Reeve 1854)[40]
† *Caseolus (Caseolus) s. submajor* nov. nomen[41]
Caseolus (Caseolus) calculus (Lowe 1954)
Caseolus (Leptostictea) leptostictus (Lowe 1831)
Caseolus (Leptostictea) micromphalus (Lowe 1852)
Caseolus (Leptostictea) hartungi hartungi (Albers 1852)[42]
Caseolus (Leptostictea) h. fictilis (Lowe 1852)[43]
Caseolus (Helicomela) punctulatus punctulatus (Sowerby 1824)[44]
Caseolus (Helicomela) p. avellanus (Lowe 1854)
Caseolus (Helicomela) solidus (Lowe 1831)[45]
† *Caseolus (Helicomela) bowdichianus* (Férussac 1832)[46]
Disculella maderensis maderensis (Wood 1828)
Disculella m. taeniatus (Webb & Berthelot 1833)
Disculella compar (Lowe 1831)
Disculella spirulina Cockerell 1921[47]
Actinella (Actinella) lentiginosa lentiginosa (Lowe 1831)
Actinella (Actinella) l. stellaris (Lowe 1852)[48]
Actinella (Actinella) actinophora actinophora (Lowe 1831)
† *Actinella (Actinella) a. descendens* (Wollaston 1878)
Actinella (Actinella) arcta (Lowe 1831)[49]
† *Actinella (Actinella) arcinella arcinella* (Lowe 1854)[50]
† *Actinella (Actinella) a. papillosculpta* nov. subsp.[51]
Actinella (Actinella) laciniosa (Lowe 1852)
Actinella (Actinella) l.f. II[52]
Actinella (Faustella) arridens (Lowe 1831)[53]
Actinella (Faustella) fausta (Lowe 1831) = Form I[54]
Actinella (Faustella) carinofausta nov. spec. = Form II[55]
Actinella (Faustella) robusta (Wollaston 1878) = Form III[56]
Actinella (Faustella) Form IV[57]
Actinella (Faustella) obserata (Lowe 1852)
† *Actinella (Faustella) promontoriensis* nov. nomen = Form V[58]
† *Actinella (Faustella) crassiuscula* (Cockerell 1922)[59]
Actinella (Hispidella) armitageana (Lowe 1852)
Actinella (Plebecula) nitidiuscula nitidiuscula (Sowerby 1824)[60]
† *Actinella (Plebecula) n. saxipotens* (Wollaston 1878)
Actinella (Plebecula) giramica (Lowe 1852)[61]
Actinella (Plebecula) anaglyptica (Reeve 1852)
Actinella (Plebecula) effugiens nov. nomen[62]
Lemniscia michaudi (Deshayes 1830)
Lemniscia calva calva (Lowe 1831)[63]
† *Lemniscia c. veterna* Cockerell 1922
Lemniscia galeata (Lowe 1862)
Discula (Hystricella) bicarinata bicarinata (Sowerby 1824)
† *Discula (Hystricella) b. aucta* (Wollaston 1878)
Discula (Hystricella) echinulata (Lowe 1831)
Discula (Hystricella) leacockiana (Wollaston 1878)
† *Discula (Hystricella) echinoderma* (Wollaston 1878)[64]
Discula (Hystricella) oxytropis oxytropis (Lowe 1831)
† *Discula (Hystricella) o. subcarinatula* (Wollaston 1878)
† *Discula (Hystricella) o. vermetiformis* (Lowe 1854)
Discula (Hystricella) turricula (Lowe 1831)[65]
Discula (Discula) cheiranticola cheiranticola (Lowe 1831)
Discula (Discula) c. mustelina (Wollaston 1878)
Discula (Discula) polymorpha polymorpha (Lowe 1831)[66]
Discula (Discula) p. agostinhoensis nov. subsp.[67]
Discula (Discula) p. depressiuscula (Lowe 1852)
Discula (Discula) p. salebrosa (Lowe 1862)[68]
Discula (Discula) p. alleniana (Paiva 1866)
Discula (Discula) p. arenicola (Lowe 1831)
Discula (Discula) p. poromphala (Lowe 1852)
Discula (Discula) p. minor Mandahl-Barth 1950
† ? *Discula (Discula) p. pusilla* (Lowe 1854)[69]
Discula (Discula) calcigena calcigena (Lowe 1831)
Discula (Discula) c. discina (Lowe 1852)
Discula (Discula) c. maxima Mandahl-Barth 1950
Discula (Discula) c. gomesiana (Paiva 1866)
Discula (Discula) c. barbozae (Paiva 1866)
Discula (Discula) pulvinata (Lowe 1831)
Discula (Discula) attrita (Lowe 1831)
Discula (Discula) tabellata (Lowe 1852)
Discula (Discula) tetrica (Lowe 1862)
Discula (Discula) testudinalis (Lowe 1852)
† *Discula (Discula) cockerelli* (Noronha 1923)[70]
Discula (Discula) bulweri (Wood 1828)
Discula (Discula) albersi (Lowe 1852)
Discula (Discula) lyelliana (Lowe 1852)[71]
Discula (Callina) rotula (Lowe 1831)[72]
Discula (Mandahlia) tectiformis tectiformis (Sowerby 1824)
† *Discula (Mandahlia) t. ludovici* (Albers 1854)
Pseudocampylaea portosanctana (Sowerby 1824)[73]
Pseudocampylaea lowei (Férussac 1835)[74]
* *Candidula intersecta* (Poiret 1801)
* *Cernuella (Cernuella) virgata* (Da Costa 1778)
* *Helicella (Xerotricha) conspurcata* (Draparnaud 1801)
* *Helicella (Xeromicra) apicina* (Lamarck 1822)
* *Cochlicella acuta* (Müller 1774)
* *Cochlicella barbara* (Linnaeus 1758)
Caracollina lenticula (Férussac 1822)
Leptaxis (Leptaxis) erubescens erubescens (Lowe 1831)[75]
Leptaxis (Leptaxis) e. portosancti (Wollaston 1878)
Leptaxis (Leptaxis) e. advenoides (Paiva 1867)
Leptaxis (Leptaxis) e. hyaena (Lowe 1852)
Leptaxis (Leptaxis) furva (Lowe 1831)
† *Leptaxis (Leptaxis) chrysomela chrysomela* (Pfeiffer 1848)
† *Leptaxis (Leptaxis) c. fluctuosa* (Lowe 1852)

Leptaxis (Leptaxis) membranacea (Lowe 1852)
Leptaxis (Katostoma) wollastoni wollastoni (Lowe 1852)[76]
Leptaxis (Katostoma w. forensis (Wollaston 1878)
† *Leptaxis (Katostoma) psammophora* (Lowe 1852)
Leptaxis (Katostoma) nivosa nivosa (Sowerby 1824)
Leptaxis (Katostoma) n. planata (Lowe 1854)
Leptaxis (Katostoma) n. craticulata (Lowe 1852)
Leptaxis (Cryptaxis) undata undata (Lowe 1831)[77]
Leptaxis (Cryptaxis) u. vulcania (Lowe 1852)
Leptaxis (Cryptaxis) u. leonina (Lowe 1852)
Theba pisana (Müller 1774)
* *Otala (Otala) lactaea* (Müller 1774)
Lampadia webbiana (Lowe 1831)
* *Cepaea nemoralis* (Linnaeus 1758)
Helix (Cornu) aspersa Müller 1774
Helix (Idiomela) subplicata Sowerby 1824[78]

Species insertae sedis et dubiae

†? Geometrinae spec. nov.[79]
? *Trichia hispida* (Linnaeus 1758)[80]
? Hygromiinae ? spec.[81]
? *Helicigona lapicida* (Linnaeus 1758) ?[82]

Notes

1) Syn. *Craspedopoma lucidum* (Lowe 1831). — Cf. Zilch 1958, p. 53 and fig. 1.

2) Syn. *Pedipes afer* (Gmelin 1790).

3) The species of *Cochlicopa* are conchologically well separated in the Madeiran material, but their size relations are not the same as in the European mainland material. The form referred to *C. lubrica* in Madeira is, on average, shorter than *C. lubricella.* This, on the other hand, agrees closely from the conchological aspect with the prevalent European form. In certain areas populations of a small form of *C.* cf. *lubrica,* similar to the Madeiran form, also occur in Europe.

4) Edentate specimens have also been found in Madeira. Their shell shape is similar to that of *T. callicratis,* and as this also occurs in in the edentate form (Geneva Basin, leg: J. Favre), they are tentatively referred to this species.

5) Probably conspecific with *T. molecula* (Dohrn 1869).

6) Including f. *seminulum* Lowe 1854, which falls within the normal variation of *S. saxicola.*

7) *Diagnosis:* Differs from the nominate form of *L. vincta vincta* by its less conical, more oblong shape with rounded apex and less outstanding peristome. The colour is light greyish-ochrous, with only a very faint indication of a band. Usually a small supracolumellar nodule. Differs from *L. v. watsoniana* in its smaller size, no subcolumellar fold. — Size: 3.33-3.74 × 1.95-2.15 mm, 5.4-5.7 whorls. — Madeira, leg: A. de Norohna. Also material in ANSP, Philadelphia (No. 354204). — *Etymology:* Named after G. Maul, former director of Museu Municipal, Funchal.

8) Including *"Pupa deformis"* Wollaston (1878).

9) The systematic status of this very poorly known form is still obscure. It may represent a distinct species, a local form of *loweana,* or a local hybrid between *loweana* and *cassidula.*

10) Tentatively maintained as a subspecies of *sphinctostoma.*

11) Tentatively considered a distinct species.

12) Lowe (1854) proposed the subgenus name *Craticula* for this species and *millegrana* and *ferraria.* Secondarily a type-species *(calathiscus)* was nominated by von Martens (1861), and later the group was extended to further species by Wollaston (1878). Later the name has been used by Pilsbry (1923) to include all strongly ribbed forms and, in most cases, also with strongly convex whorls. The group is, however, evidently an artificial one, due to convergence under dry ecological conditions, an there is no reason to maintain the name *Craticula.*

13) Including var. *resticula* Wollaston (1878).

14) Doubtful systematic status. No original specimens seen.

15) Including var. *pumilio* Wollaston (1878).

16) Till now known as *Columella limnaeana* (Lowe). For description see Pilsbry in Man. Conch., 27: 235-236. He states "that it is rather doubtful wheather it belongs to that genus". A close examination has unveiled the presence of a fine but distinct angular lamella in juvenile specimens. At about half-grown stage the lamella ceases and consequently larger specimens appear completely edentate. The lamella is an unmistakeable feature of the subfamily Laurinae. The simple and acute peristome, however, distinguishes this form from all other genera of the Laurinae. For this reason a new genus name, *Hemilauria,* is proposed here.

17) Syn. *Helix pusilla* var. *sericina* Lowe (1854), *H. debauxiana* Bourguignat (1863), *H. bussacona* Silva e Castro (1887). Systematic position somewhat uncertain. Cf. Gittenberger 1977.

18) *Helix pusilla* Lowe (1831) is the earliest name for a long number of independently described, but evidently conspecific forms, among which may be mentioned *Punctum tenuicostatum* (L. Pfeiffer 1846), *P. servilis* (Shuttleworth 1852), *P. micropleurus* (Paget 1854), *P. poupillieri* (Bourguignat 1864) and *P. hypocritum* (Dohrn 1869). Other species, such as *P. meridionale* Boettger 1905, may, in reality, be races belonging to the same superspecies complex.

19) Syn. *Helix scintilla* Lowe (1852). This name has priority, but as its identity has not been recognized until now, it is in accordance with ICZN 23b to make it obsolete in favour of the well established name *Helicodiscus singleyanus* (Pilsbry). The Madeiran form is identical with the nominate form of *H. singleyanus.* In the opinion of the present author *H. singleyanus inermis* (Baker 1929) is a distinct species.

20) Syn. *Discus semiplicatus* (L. Pfeiffer 1852).

21) Cf. Davies (1979). It is doubtful if the true *Arion hortensis* Férussac 1819 occurs on Madeira.

22) *A. intermedius* is a widespread and fairly variable species. That it may be an aggregate species cannot be excluded. — *A. intermedius* was placed in the section *Micrarion* by Hesse 1926. This is not sufficiently differentiated from *Kobeltia* to be regarded as a distinct subgenus.

23) Closely related to, and possibly conspecific with *D. panormitanum* (Lessona & Pollonera 1882) = *D. caruanae* (Pollonera 1891).

24) Seems to belong to a widespread Mediterranean complex. Synonyms are certainly *actoniana* (Benoit 1862), *rizzeana* (Benoit 1862), *petitiana* (Benoit 1862), possibly also *brondeli* (Bourguignat 1856) and *nanodea* (Bourguignat 1856). The latter is the earliest available of these names. The systematic grouping and synonymization of the vast number of nominal *Cecilioides* species is severely hampered by vagueness of many original descriptions, unretrievability of original material, and uncertainty of determinations of much museum material.

25) Probably not a true subspecies, merely an ecophenotype.

26) A variable species, though on the whole well separated from the *tuberculata* complex. Small and slender specimens, often with a relatively small aperture, seem to agree with *terebella* (Lowe 1852), but are connected with typical *oryza* by a continuous series of forms.

27) Two forms are found: a larger and a smaller (normal), which do not seem to intergrade.

28) Synonyms are probably: *gracilis* var. *ventricosa* (Paiva 1867, non Fischer 1807), *terebella* var. *laurentiana* (Pilsbry 1908).

29) Nov. nomen for *terebella* var. *subula* (Lowe 1854, non L. Pfeiffer 1839). It is doubtful whether the nominate species *terebella* (Lowe 1852) exists as a distinct taxon. Cf. above, note 23, *oryza*! Syntypic specimens in ANSP Museum, Philadelphia (No. 97199) seem to fall within the variation of *oryza.* No specimens freely separable from *oryza* have been found despite extensive field collecting during recent years. *A. cimensis* = var.*subula* (Lowe), on the other hand, appears as a distinct taxon.

30) *Clausilia maderensis,* Charpentier 1852, is an objective synonym (type specimen in Coll. Charpentier, Musée Zoologique, Lausanne). The description of *C. maderensis* by A. Schmidt (1868) fits *B. obesiuscula,* but is not based on Charpentier's material. A specimen in the Senckenberg Museum (SMF 68230/1), emanating from Parreys, is labelled *C. maderensis,* but actually belongs to *B. obesiuscula.*

31) The name *depauperata* covers an assemblage of forms, whose relationships are not yet fully understood. In some cases intermediate specimens have been found, suggesting hybridization with *deltostoma.* Perhaps the most adequate is to consider the two taxa as semispecies, even if this interpretation is tentative and not free from objections.

32) The validity of the genus name *Heterostoma* for *paupercula* is conditional (cf. comments by Mandahl-Barth, 1950, p. 15).

This species is fairly variable in size, colour, sculpture, apertural dentition etc. Edentate specimens are known. Two rather distinct forms are recognized.

Form I. Periphery somewhat keeled, the sides below sloping (c. 60°). Deep, sometimes very narrow umbilicus, with vertical whorl sides. Sometimes the spire is somewhat erected. Fig. 1. Cf. also Mandahl-Barth 1950, plate 5, fig. 6. Often white.

Form II. With rounded periphery, the sides below first vertical. Relatively shallow umbilicus, with rounded sides. Flat-spired. Usually brownish. Fig. 2.

Intermediate forms have also been found. It does not seem exluded that these forms represent a semispecies complex.

33) The status of *Steenbergia* as a separate genus must be considered conditional. Evidence is contradictory and apparently incomplete. The highly different anatomy of the distal genital parts, demostrated by Mandahl-Barth (1950) is puzzling. Backhuys (1975, p. 214-217) reports that specimens from the Azores, conchologically typical *H. paupercula,* have a genital anatomy characteristic of *Steenbergia* (epiphallus, penial flagellum). A reasonable explanation may be that we are dealing with a case of genital dimorphism, and that, in the Madeiran material, populations are prevalently, or exclusively, unimorphic in this respect, and that Mandahl-Barth happened to deal with such unimorphic material.

34) Known also from Madeira proper. No specimens of *desertae* intergrading with *duplex* are known, and considering its quite distinctive morphology it seems rather reasonable to accept it as a separate species. Nothing is known about its anatomy.

35) Occasionally subfossil specimens have been found, which are difficult to assign with certainty to *latina* or *depauperata,* suggesting that the reproductive isolation was not complete.

36) Syn. *Helix compacta* var. *δ pusilla* Lowe 1854. (p. 184; homonym of *Helix pusilla* Lowe 1831).

37) Syn. *Helix compacta* var. *β major* Lowe 1854 (p. 184). This is a synonym of *Helix major* Binney 1837 = *Triodopsis albolabris major* (Binney). The name *Helix spretta* is an unpublished manuscript name used by A. de Noronha for the concerned taxon. The assignment as a subspecies of *C. compactus* is tentative.

38) *Diagnosis:* Differs from *C. compactus areiensis* (= *C. compactus pusillus* (Lowe 1854)) by its basal striation. Often the ribs are interrupted into oblong papillae. On the apical side the marked ribs are papillate. — Size: 4.21-4.60 x 2.77-3.39 mm, 4.4-5.2 whorls. — Porto Santo, Vigia, leg: A. de Noronha. — *Etymology:* The name refers to the type locality.

The assignment as a subspecies of *C. compactus* is tentative.

39) Syn. *Helix commixta* var. *β pusilla* Lowe 1854 (p. 185. Homonym of *Helix pusilla* Lowe 1831). Judging from seemingly fresh shells, found in the southern slope of Pico de Baixo, the species may still survive.

40) Syn. *Helix sphaerula* var. *γ recens major trochoidea* Lowe 1854.

41) Syn. *Helix sphaerula* var. *β fossilis submajor trochoidea* Lowe 1854 (p. 185). This name is unlawful.

42) Syn. *Helix dealbata* Lowe 1831, non *Helix dealbata* Say 1821 = *Bulimulus dealbatus* (Say 1821). The description of *Helix*

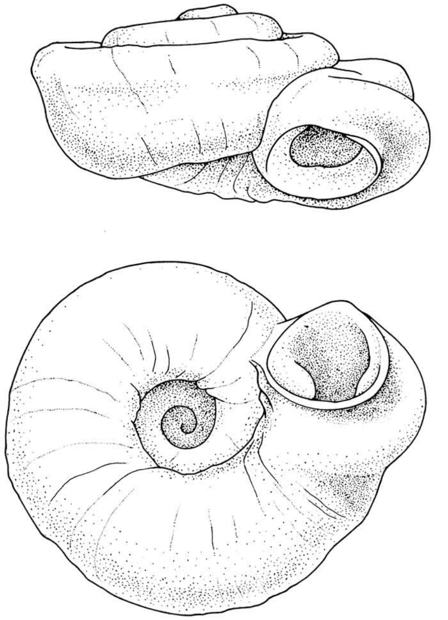


Fig. 1. *Heterostoma paupercula* (Lowe), Form I. — Porto Santo, Zimbral (Museu Municipal, Funchal). 5.49 x 2.57 mm, 4.2 whorls. 10 x.

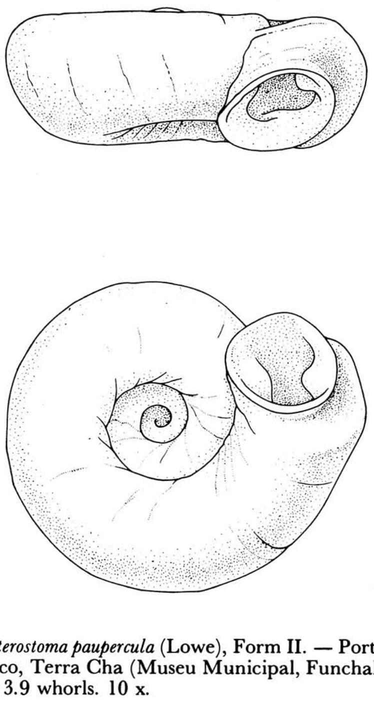


Fig. 2. *Heterostoma paupercula* (Lowe), Form II. — Porto Santo, Pico Branco, Terra Cha (Museu Municipal, Funchal). 4.81 x 1.88 mm, 3.9 whorls. 10 x.

hartungi Albers (published in February 1852) does not fit any taxon other than the one concerned here. The var. *minor* Paiva 1867 and *Geomitra (Disculella) cenourensis* Cockerell 1921 are included.

43) Original description published in March 1852.

44) Syn. *Helix punctulata* var. *α setulosa* Lowe 1831.

45) Syn. *Helix punctulata* var. *γ solida* Lowe 1831. This name is a junior secondary homonym of *Helix (Cyclodina) solida* Férussac 1821 = *Clausilia solida* Draparnaud 1805, but, in accordance with ICZN 59c, Lowe's name is valid.

46) The picture in plate 28 B in livr. 24 of Hist. Nat. gen & part. Moll., published in 1832, has to be considered as valid indication. A variable species, probably more than one taxon is covered by this name.

47) Syn. *Caseolus (Disculella) neospirorbis* Forcart 1965 = *Helix spirorbis* Lowe 1852, non *Helix spirorbis* Linnaeus 1758.

48) Somewhat vaguely differentiated from *A. lentiginosa lentiginosa.* Occasionally the two forms have been found distinct in mixed populations, sometimes with intermediates.

49) Including f. *minor* Wollaston (1878).

50) Madeira.

51) *Diagnosis:* Differs from the nominate subspecies by the papillae and, on average, the finer and somewhat irregular ribs. The umbilicus is narrow, but distinct. — Size: 3.99-4.38 x 2.54-3.02 mm, 4.5-5.0 whorls. — Porto Santo, subfossil, leg: H. W. Waldén. — *Etymology:* the name refers to the papillate surface sculpture.

Possibly a separate species. It was pointed out already by Wollaston (1878, p. 141) that *A. arcinella* from Madeira and Porto Santo, respectively, were slightly different.

52) A larger, raised form of doubtful systematic status. Distinct from the nominate form in samples. Possibly an ecologically conditioned growth form, but no habitat information available to prove this assumption.

53) Probably or *in partim* including *Helix capsella* Lowe 1854. The description is extensive, but does not give a clear idea of distinctive characters. Syntypic specimens in ANSP (No. 97081) unmistakably belong to *A. arridens.* The description may, however, have been based on material including what is called *A. carinofausta* below.

Note: *Helix capsella* Lowe 1854, non *Helix capsella* Gould 1851 = *Paravitrea capsella* (Gould 1851).

(54-57 general comments). The still very insufficiently studied subgenus *Faustella* appears to comprise a complex of forms, which have at least partly been covered by the name *fausta.* Some of these are, without doubt, distinct species but on the whole the evidence, at least partly, is suggestive rather than conclusive. A brief account will be given here, to substantiate the present, tentative interpretation of the *fausta* complex.

Table 4 gives certain outline data of the forms involved. Fig. 4 shows the limits of the clusters of the quotient $H_{apic.}/H_{bas.}$ (cf. Fig. 3) and the major diameter respectively, plotted against the number of whorls. The clusters are well defined and the state of *carinofausta* and *promontoriensis* as distinct species can scarcely be doubted, whereas the relation between *fausta* and *robusta* is more difficult to evaluate, owing to the presence of the doubtful specimens of Form IV. Comparisons between individual characters (Table 5) strengthens the picture that the forms are in general very well separated. The few exceptions refer to otherwise well separated pairs of taxa (cf. the cluster diagrams). With regard to other characters, such as shell shape, apertural armature and, to some extent, surface sculpture, there is in general a good correlation. The Form IV, which to some extent combiness features of *fausta* and *robusta,* though it seems to have its own characteristic appearance, has so far been omitted from the statistical analysis, owing to the very small material available — only four shells.

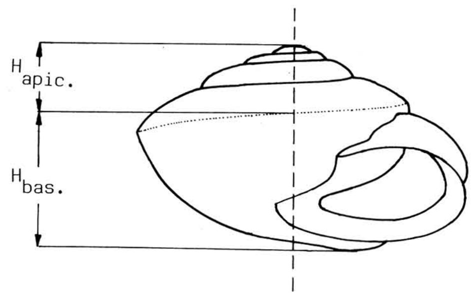


Fig. 3. Measures of height of apical and basal parts of the shell.

At the present state of research the analysis is hampered not only by the scantiness of material, but also by lack of geographical and ecological background data. The old material is generally labelled Madeira only (except for the subfossil *promontoriensis* from the Piedade beds), and fresh material, with adequate data, of these rare forms is accumulating very slowly.

54) *A. fausta* s.s. (verified by type material, ANSP 97099). Characterized by its relatively rounded shell, with blunt periphery. Usually the spire is relatively high and the 5.0-5.8 whorls more or less rounded. The basal callus is well developed, ending with a distinct knot. A parietal callus almost constantly present. — Fig. 5.

55) Differentiated from *A. fausta* by its carinate shell, lower spire and the 4.3-4.9 whorls usually fairly flat. The basal callus is even. Sometimes a weak parietal callus is present. The description of *Helix capsella* Lowe 1854, may have been based on material which included this form. However, the preserved type specimens (cf. note 53), and the fact that no indication of a parietal callus is given in descriptions by Lowe and Wollaston speak against this assumption. — *Etymology:* the name indicates the shell shape. — Fig. 6.

56) Similar to Form II *(carinofausta)*, but much larger, with a more pronounced striation and a parietal callus. The basal callus ending abruptly. — Fig. 7.

57) To some extent intermediate between Forms I and III. Judging from the very few (four) shells available it approaches *robusta* in shell shape, though is smaller on average. The basal callus may end with a knot, the parietal callus is weak. This

Table 4. Variation (mean and range) in taxa of the *Faustella* group.

Form/Taxon	Specimens examined	Diam.maj. mm	Height mm	Whorls[1]
I. *fausta* s.s.	33	6.31 (5.43-7.75)	4.27 (3.62-5.16)	5.5 (5.0-6.0)
II. *carinofausta*	22	5.43 (4.79-5.91)	3.27 (2.83-3.67)	4.4 (4.3-4.9)
III. *robusta*	20	7.60 (6.51-8.38)	4.94 (4.32-5.34)	5.8 (5.6-6.2)
IV. intermediates?	4	(6.55-7.30)	(3.97-4.95)	(5.3-5.8)
V. *promontoriensis*	26	6.05 (5.45-6.55)	3.64 (3.30-4.02)	5.1 (4.8-5.4)

1) Counted in accordance with Ehrmann (1933, Fig. 12)

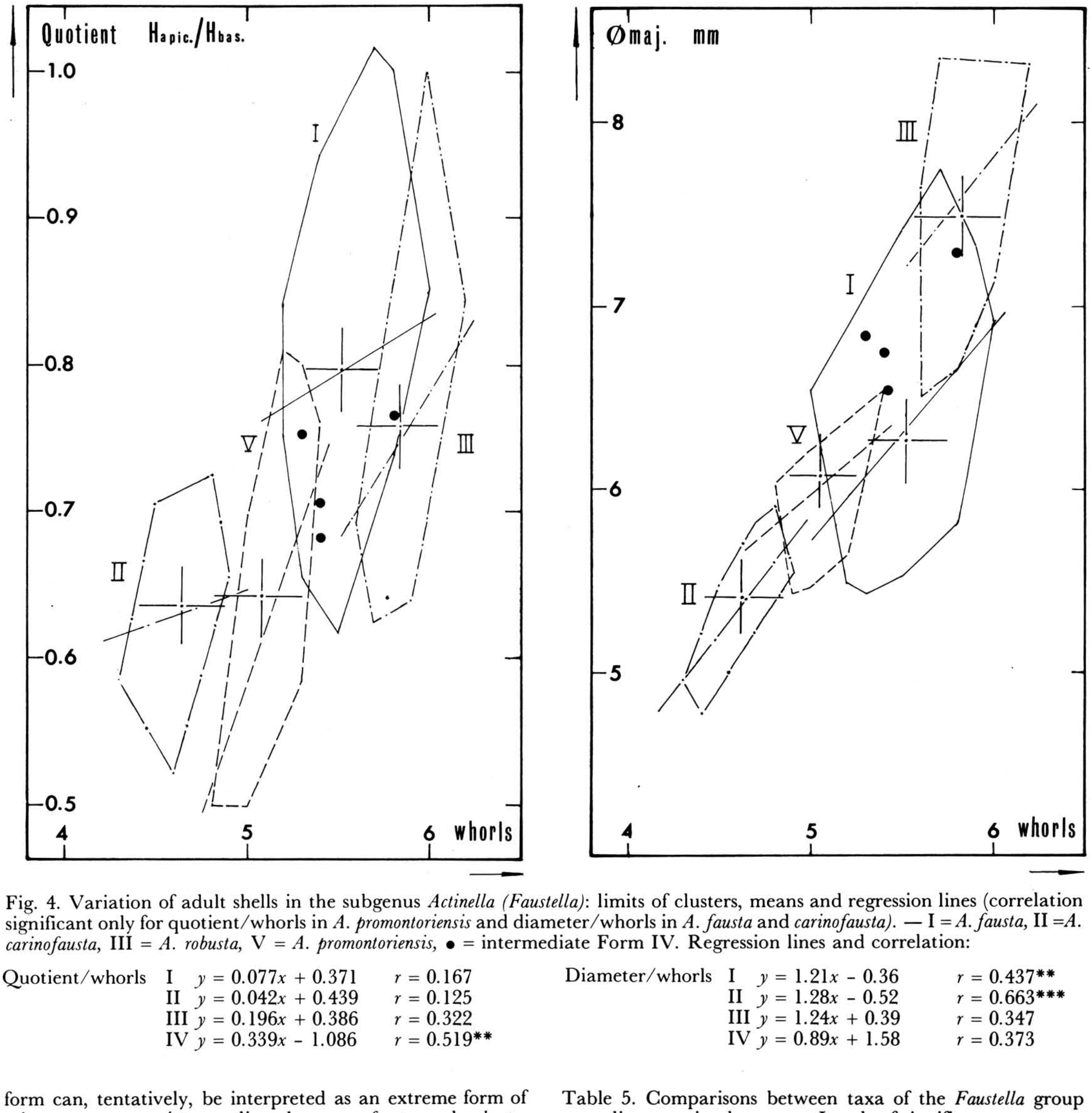


Fig. 4. Variation of adult shells in the subgenus *Actinella (Faustella)*: limits of clusters, means and regression lines (correlation significant only for quotient/whorls in *A. promontoriensis* and diameter/whorls in *A. fausta* and *carinofausta)*. — I = *A. fausta*, II = *A. carinofausta*, III = *A. robusta*, V = *A. promontoriensis*, ● = intermediate Form IV. Regression lines and correlation:

Quotient/whorls
I $y = 0.077x + 0.371$ $r = 0.167$
II $y = 0.042x + 0.439$ $r = 0.125$
III $y = 0.196x + 0.386$ $r = 0.322$
IV $y = 0.339x - 1.086$ $r = 0.519^{**}$

Diameter/whorls
I $y = 1.21x - 0.36$ $r = 0.437^{**}$
II $y = 1.28x - 0.52$ $r = 0.663^{***}$
III $y = 1.24x + 0.39$ $r = 0.347$
IV $y = 0.89x + 1.58$ $r = 0.373$

form can, tentatively, be interpreted as an extreme form of *robusta*, as a true intermediate between *fausta* and *robusta*, which in this case would form a semispecies complex, or — less probably — a separate species. — Fig. 8.

58) Syn. *Helix obserata* var. *β bipartita* Wollaston 1878. This name is preoccupied by *Helix bipartita* Férussac 1822 = *Thersites (Hadra) bipartitus* (Férussac 1822). Fig. 9.— *A. promotoriensis* shows clear affinities to the *fausta* complex, and not to to *A. obserata* (cf. Fig. 10). Characterized by the well developed subpalatal knot, parietal callus and blunt keel.

59) Tentatively assigned to *Faustella*. No material seen, lacking in the Coll. Cockerell (Professor Shi-Kuei Wu, University of Colorado, Boulder; unpubl.).

60) Including var. *pulchra* Paiva 1867 and var. *canicalensis* Lowe 1852. *A. nitidiuscula* shows considerable variation, but this does not seem to be of a character allowing division into subspecies. It may be of a partly phenotypic kind.

61) Uncertain whether or not a separate species.

62) Syn. *Helix lurida* Lowe 1831, non *Helix lurida* C. Pfeiffer 1828 = *Trichia (Edentiella) lurida* (C. Pfeiffer 1828).

Table 5. Comparisons between taxa of the *Faustella* group regarding certain characters. Levels of significance.

	I. *fausta*	II. *carino-fausta*	III. *robusta*
Whorls			
II. *carinofausta*	< 0.001	-	-
III. *robusta*	< 0.001	< 0.001	-
V. *promontoriensis*	< 0.001	< 0.001	< 0.001
Major diameter			
II. *carinofausta*	< 0.001	-	-
III. *robusta*	< 0.001	< 0.001	-
V. *promontoriensis*	0.05	< 0.001	< 0.001
$H_{apic.}/H_{bas.}$			
II. *carinofausta*	< 0.001	-	-
III. *robusta*	< 0.001	< 0.001	-
V. *promontoriensis*	< 0.001	0.7-0.8	< 0.001

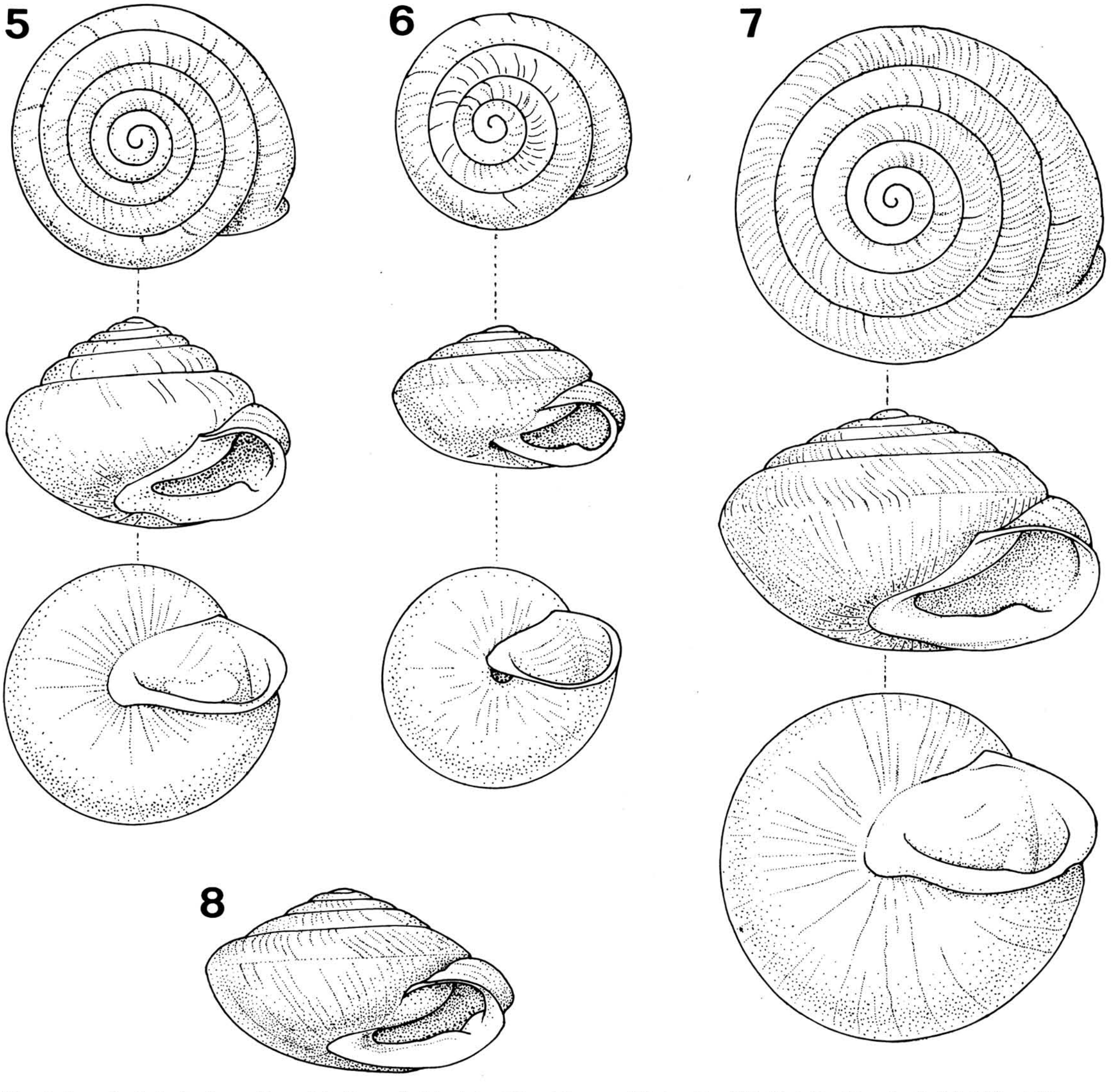


Fig. 5-8. — 5. *Actinella fausta* (Lowe) (= Form I). Madeira (Nat. Museum Wales, Cardiff; Melville-Tomlin Coll.) 6.32 x 4.35 mm, 5.8 whorls. — 6. *Actinella carinofausta* Waldén (= Form II). Madeira, Estreito de Camera de Lobos 27.I.1978 (Göteborgs. Nat. Hist. Museum). 5.23 x 3.15 mm, 4.5 whorls. — 7. *Actinella robusta* (Wollaston) (= Form III). Madeira (Nat. Museum Wales, Cardiff; Melville-Tomlin Coll.) 7.97 x 5.08 mm, 5.8 whorls. — 8. A doubtful, intermediate shell (*Actinella* Form IV). Madeira, Pousada dos Vinhaticos 9.II.1978 (Göteborgs Nat. Hist. Museum). 6.55 x 3.97 mm,, 5.4 whorls. — All figures 6x.

63) Doubtful whether or not congeneric with *L. michaudi.*

64) No original material seen. Relations to the other taxa of *Hystricella* obscure.

65) Including var. *α pererosa* Wollaston 1878.

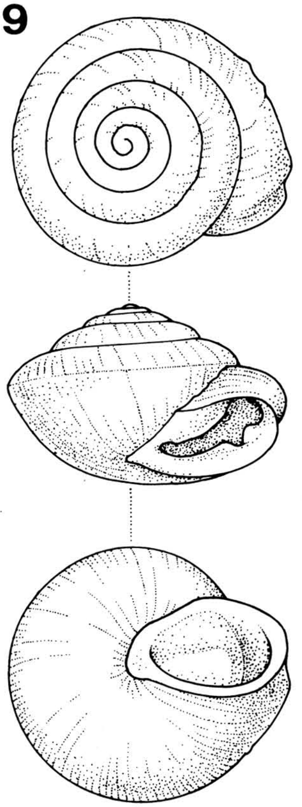
66) Taxonomy mainly according to Mandahl-Barth (1950), though it no doubt requires a general revision on the basis of an extensive material with adequate geographical and ecological background data. As in *A. nitidiuscula* the circumscription of subspecies is difficult owing to the fact that the correlation in the variation between different characters is, at least in some, cases, weak. This is clearly demonstrated in a study of variation by Cook & Pettitt (1979). However, these authors did not attempt to elucidate the taxonomy. No record of variance is given in their diagrams, and consequently these give no indication of possible cases of sympatric occurrence. The authors admittedly leave the basic taxonomical question open: are "one, two or more polytypic species" involved in the evolutionary radiation?

Even if some of the subspecies are less well defined, and their distinction may be a matter of dispute, they no doubt represent real systematic entities, and not more or less random products of independent variation of characters.

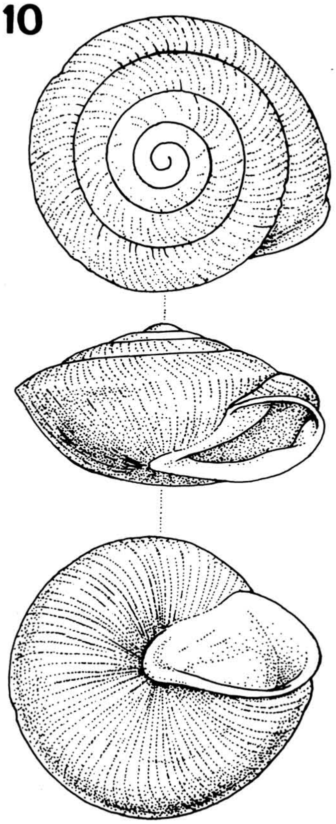
Judging from available evidence the subspecies *alleniana, arenicola* and *salebrosa* are conchologically well defined, even if the latter is not uniform throughout its large range. The subspecies *polymorpha* and *depressiuscula* show, on the other

Figs. 9–10. — 9. *Actinella promontoriensis* Waldén (= Form V). Madeira, Canical, subfossil (Nat. Museum Wales, Cardiff; Melville-Tomlin Coll.) 5.87 x 3.61 mm, 5.0 whorls. — 10 *Actinella obserata* (Lowe). Madeira (Senckenberg-Museum No. 139577, Coll. Moellendorff.) 6.22 x 3.19 mm, 5.1 whorls. — All figures 6 x.

9



10



hand, a considerable variation, which is intergrading, is greater than has so far been recorded in the literature, and demonstrates a considerable degree of independence between characters. No adequate distribution pattern information is available about the subspecies on the Desertas, which would permit testing of the real relations between the four subspecies recorded there.

A possible assumption is that the *polymorpha* complex may include two widespread, genetically largely isolated entities (species or semispecies) and even that some local form may have specific status.

67) The high-spired, strongly granulated form with blunt periphery, strictly limited to the easternmost islets of Madeira (Ilhéu de Agostinho and Ilhéu de Fora). Considered by Wollaston (1878, p. 172). Biometric information by Cook & Pettitt (1979, p. 48). — *Etymology:* after Ilhéu de Agostinho.

68) Syn. *Helix senilis* Lowe 1852, non *Helix senilis* Morelet 1851 = *Otala* sp.

69) In want of voucher material the status of this form in relation to other, related taxa in the Desertas group must be considered doubtful. The name *pusilla* is, in fact, not available, but as long as the actual status has not been proved, I see no reason for taking measures in this respect. If the taxon is ever synonymized with any other, the name of the latter will automatically take precedence.

70) Noronha (1923, p.85) indicates the existence of "two well separated varieties", but his description seems somewhat vague, and does not allow a definite assessment. Material, seen in the museum of Funchal, and found during my own field work corresponds to the primary description of the nominate form by Noronha.

71) Including var. *gigas* Wollaston (1878).

72) A single giant, subfossil specimen ($\varnothing_{\mathrm{maj.}}$ = 15.8 mm, H = 8.9 mm, whorls: 7.9) has been found in Vale de Touro, Porto Santo (voucher specimen in Funchal Museum).

73) Including var. *cimensis* Wollaston (1878), here regarded as a taxon on infrasubspecific level. According to Cockerell (1921a) this form is restricted to the summit of the islet Ilhéu de Cima. On lower levels of the same islet a smaller form, approaching the nominate form of *portosanctana,* occurs. Specimens converging with var. *cimensis* are reported from Pico de Ana Ferreira and Ilhéu de Baixo by Mandahl-Barth (1950).

74) Extinct in recent time. Highly variable, but no subspecies in the true sense discernible.

75) The taxonomy and nomenclature of *Leptaxis* unmodified according to Mandahl-Barth (1950).

Cockerell (1922c) draws attention to the fact that the name *Helix erubescens* Lowe 1831, is preoccupied by *Helix erubescens* (Solander) Lightfoot 1786, in Catal. Portland Museum p. 187, no 3973. Lightfoot refers to Lister's *Historia Conchyliorum,* plate 24, fig. 22. Dr. P. B. Mordan and Dr. J. F. Peake, BMNH, London, have, by kind compliance, informed me that this illustration is very poor, and as Lister's original specimen is lost, not more can be stated than that it may possibly have been a species of *Amphidromus.* The name *erubescens* Lightfoot (Lister) will therefore have to be rejected as a *nomen dubium.* The origin is only vaguely indicated by Lister: Ind. Or. (= East Indies), but this is sufficient to disprove Bequaert's assumption 1948 (Bull. Mus. comp. Zool. Harvard, 100, p. 30) that the S. American *Strophocheilus pudicus* (Müller) was concerned.

76) Including var. *subdubia* Wollaston (1878), intergrading

to *L. nivosa.* No locality is given but it seems that this form represents an extreme within populations, not a local form. Not seen by the present author.

77) Cockerell (1922c) asserts that *Helix groviana* Férussac is a senior synonym of *Helix undata* Lowe 1831. No such name is known, and it is most probably a misspelling of *Helix groyana* Férussac 1821 (in Tableau system. de la famille des Limacons Cochleae, p. 44). This name is, however, a *nomen nudum.*

78) Possibly extinct. — In addition to what is hitherto known about *H. subplicata* can be added that examination of subfossil material has shown that this species must have been viviparous, or at least ovoviviparous — so far known the only case in the genus *Helix.* Only few, remarkably large embryos were present in each adult shell. This indicates a low reproductive rate, in contrast to the prevailing condition in the genus *Helix,* where most of the species have very large egg-clutches. The combination of (ovo)viviparity, large embryos and low reproduction suggests a pronounced *K*-strategy, and probably represents adaptions to a very narrow ecological niche, in a biocoenotically "packed" environment. — Viviparity has also been demonstrated for *Boettgeria lowei* by Mandahl-Barth (1951), also from Porto Santo.

79) Juveniles of an extinct, probably Geometrinae species have been found at Ponta da Calheta, Porto Santo.

80) An apparently accidentally introduced species mentioned by Wollaston (1878: 81) and provisionally, but with explicit reservations, identified as *Trichia hispida.*

81)Two hispid, juvenile specimens of a so far unidentified species found on the southern slope of Pico do Facho, Porto Santo, by Th. Palm 4.2.1978.

82) Provisionally omitted from the list of Madeiran Gastropoda. The finding of autochtonous, subfossil *Helicigona lapicida* on Porto Santo is, for several reasons, highly improbable. Cf. comments by Wollaston (1878, p. 150) and Mandahl-Barth (1950, p. 40). It does not seem excluded that immature shells of the species, later described as *Discula cockerelli,* have been encountered.

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