ON THE ORIGIN, AFFINITIES, AND EVOLUTION OF THE LAND MOLLUSCA OF THE MID-ATLANTIC ISLANDS, WITH SPECIAL REFERENCE TO MADEIRA.[1]

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With 2 figures, 5 tables, and a tabular appendix.

CONTENTS

RESUMO. As faunas de moluscos terrestres dos Açores, Madeira, Ilhas Canárias e Cabo Verdes formam basicamente uma colecção relíquia, com afinidades pronunciadas com a fauna do Terciário antigo na zona Paleárctica ocidental. Neste trabalho são discutidas e revistas a composição, diversidade, endemismo e afinidades destas faunas de moluscos, sendo focada a atenção nos elementos indígenas. Uma revisão sinóptica ao nível do género dos

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[1] The present paper is a modified and extended version of a lecture held at the 8th International Malacological Congress, Budapest, Hungary, August 30, 1983, entitled: The Land Mollusc Fauna of Madeira and its significance in relation to the Development of the Mollusc Fauna of the Western Palearctic and the Atlantic Islands.

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moluscos indígenas é apresentada num apêndice tabular. No passado os elementos relíquia nas faunas foram sobrepostos por imigrantes do fim do Terciário e do Quaternário, estes últimos não tendo ainda dado origem a formas endémicas. Certos géneros, com uma significativa ou enigmática distribuição são discutidos, como por exemplo *Staurodon, Gibbulinella, Napaeus, Boettgeria, Phenacolimax, Janulus* e *Leptaxis*. Contudo, mesmo que as faunas tenham tido no início uma origem comum, é notável a excassez de grupos comuns aos vários arquipélagos. As diferenças entre as suas faunas são no todo bem explicadas pela história geológica (da qual é feita uma análise neste trabalho), pelos gradientes climáticos e pela posição das ilhas em relação aos continentes. A Madeira detém uma posição chave entre as ilhas do meio do Atlântico, com a sua acentuadamente diversidade e endemismo, como centro de evolução e dispersão para outros arquipélagos. Uma característica marcante da fauna indígena de moluscos da Madeira é que ela não tem virtualmente nada em comum com a fauna do noroeste africano adjacente; as afinidades são estritamente europeias. Isto é concebível se a posição paleogeográfica da Madeira no Terciário antigo, muito distante da África, fôr considerada. As montanhas submarinas a NE da Madeira podem então ter actuado como pontes para uma dispersão faunística a partir da Ibéria nessa altura.

ABSTRACT. The Land Mollusc faunas of the Azores, Madeira, the Canary Islands, and the Cape Verdes are basically a relict assemblage, with pronounced affinities to the Early Tertiary fauna in western Palaearctic. Composition, diversity, endemism and affinities of these mollusc faunas are reviewed and discussed. Attention is focussed on the indigenous elements. A synoptic review on the generic level of the indigenous Mollusca is given in a tabular appendix. On the old, relict elements in the faunas have been super-imposed Late Tertiary and Quaternary immigrants, of which the last-mentioned have not yet developed any endemic forms. Certain genera, with a particularly significant or enigmatic distribution are discussed, as *Staurodon, Gibbulinella, Napaeus, Boettgeria, Phenacolimax, Janulus* and *Leptaxis*. However, even if the faunas have primarily a common background there are remarkably few taxa in common between the archipelagos. Differences between their faunas are on the whole well explained by the geological history (of which a review is given), by climatic gradients and the positions of the islands in relation to the continental mainland. Madeira holds a key position among the Mid-Atlantic Islands, with its markedly high diversity and endemism, as a center of evolution and for dispersal to other archipelagos. A striking feature of the indigenous mollusc fauna of Madeira is that it has virtually nothing in common with the fauna of the adjacent NW African mainland; the affinities are strictly European. This is conceivable if the palaeogeographical position of Madeira in the Early Tertiary, remote from the African continent, is regarded. Present seamounts may have acted as «stepping-stones» for faunal dispersal from Iberia at that time.

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I. INTRODUCTORY REMARKS

The Mid-Atlantic Islands comprise four archipelagos, the Azores, Madeira, the Canary Islands and the Cape Verdes. In addition, there is a minute archipelago, the Selvage Islands, between Madeira and the Canary Islands, which is, however, not considered in this account[3]). For the sake of convenience the term Macaronesia is sometimes used for the Mid-Atlantic Islands together although this term is not free from objections. Owing to the incompleteness of taxonomical evidence (in particular for the Canary Islands and the adjacent area of mainland Africa) the figures given in the tables, with taxa grouped after various principles, are to some extent arbitrary. However, the knowledge is probably sufficient to admit a reasonably adequate picture of trends and relationships.

Madeira holds a central position among the Atlantic Islands, with regard to its geographical situation, diversity of its mollusc fauna and faunistic relations to the other archipelagos.

The terms *taxon/taxa* are used in the present account in the restricted meaning of species and well circumscribed subspecies, as the basic unit in comparisons. The distinction between species and subspecies is, indeed, illdefined in many cases. — The figures include extinct, subfossil taxa. As subfossil records are available for all islands concerned, the figures are thus compatible.

II. MADEIRA AND ITS LAND MOLLUSCA

The Madeiran archipelago is situated 700 km off the NW African coast. It is composed of 3 subgroups: Madeira proper, with a few adjacent islets, Porto Santo with several adjacent islets, and the three Deserta Islands. The total area is almost 800 km^2, of which 90% is Madeira proper.

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[3]) The terrestrial mollusc fauna of the Salvage Islands comprises one endemic subspecies, *Theba pisana macandrewiana* (Pfr) and 7 littoral species of wide distribution.

The archipelago is of vulcanic and in a strict sense oceanic origin[4]. The topographic relief is very marked, particularly on Madeira proper. The climate is subtropical and oceanic. However, there is a considerable climatic diversity (cf. Sjögren, 1974, with literature references), with a dry, partly semi-arid climate on Porto Santo, the Desertas and the lower southern and easternmost parts of Madeira proper. This contrasts with the more temperate and partly very wet climate on higher levels of the latter island. On the highest parts occasional snow and frost occur in winter. — The vegetation is correspondingly diversified (cf. Sjögren, 1979), the most significant community beeing the laurel wood, which is to be regarded as a Tertiary relict formation. Today the original vegetation is strongly affected by man, and over large areas destroyed or replaced by secondary vegetation. Remnants of the original woodland occur only in steep and inaccessible sites. The highest parts (up to 1850 m) are covered by montane heathland, largely heavily overgrazed and eroded, but with local remnants of stormbeaten scrub.

The topographical, climatic and vegetational diversity is, indeed, of fundamental importance for the highly diversified land mollusc fauna. In all 261 $\pm$ 3[5]) taxa have been recorded. Of these 219 are indigenous, of which 193 are endemic to the archipelago. There is a striking endemic differentiation within the archipelago which, however, will not be considered in the present wide context. The intra-archipelago diversity and relationships have been analysed by Cook & al. (1972).

III. DIVERSITY AND ENDEMISM OF THE LAND MOLLUSCA OF THE MID-ATLANTIC ISLANDS

A comprehensive synopsis of the land Mollusca is given in table 1. In this indigenous and introduced taxa, so far as can be estimated, are kept apart. Only the former element has a biogeographical significance, and the following discussion will be restricted to this.

A synopsis on generic level of the indigenous taxa of the Mid-Atlantic Islands is given in the appendix (p. 74). The sources, on which tables, the diagram and the appendix are based, are indicated in connection with the latter.

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[4]) The term oceanic is used in the biological meaning, indicating that islands have been isolated from the continent from the beginning, but not necessarily built up from the oceanic crust (i. e. oceanic in the geological sense), even if this, with few exceptions, is the case with the Mid-Atlantic Islands.

[5]) The taxa are listed in the paper by Waldén (1983). Since this was submitted for publication *Discocharopa aperta* (Möllendorff), introduced from the Pacific (Gittenberger & Ripken, 1983), as well as a so far undiscribed species of *Geomitra*, have been discovered. On the other hand, *Leptaxis granularis*, described by Groh (1983b), has proved to be a synonym of *L. psammophora* (Lowe).

TABLE 1. Distributional groups of Terrestrial Gastropoda of the Mid-Atlantic Islands.

<table>
<tr><th rowspan="2"></th><th colspan="2">Azores
2300 km²</th><th colspan="2">Madeira
800 km²</th><th colspan="2">Canary Islands
7300 km²</th><th colspan="2">Cape Verdes
3800 km²</th></tr>
<tr><th>Taxa</th><th>%</th><th>Taxa</th><th>%</th><th>Taxa</th><th>%</th><th>Taxa</th><th>%</th></tr>
<tr><td>1. Endemic to the archipelago</td><td>41 [1]</td><td>41.8</td><td>193 [2]</td><td>73.9</td><td>141 [2] [3]</td><td>77.9</td><td>16 [2]</td><td>43.2</td></tr>
<tr><td>2. Endemic to the Atlantic Islands</td><td>3</td><td>3.1</td><td>3</td><td>1.1</td><td>4</td><td>2.2</td><td>—</td><td>—</td></tr>
<tr><td>3. Widespread taxa = =distribution outside Atlantic Islands</td><td>23</td><td>23.5</td><td>23 [4]</td><td>8.8</td><td>12</td><td>6.6</td><td>5</td><td>13.5</td></tr>
<tr><td>4. Anthropochorous species</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>a) Naturalized</td><td>28</td><td>28.6</td><td>22</td><td>8.4</td><td rowspan="2">24 [5]</td><td rowspan="2">13.3</td><td>9</td><td>24.3</td></tr>
<tr><td>b) Strongly synanthropic, including adventives and accidental introductions</td><td>3</td><td>3.1</td><td>20</td><td>7.7</td><td>7</td><td>18.9</td></tr>
<tr><td>Total</td><td>98</td><td>100.1</td><td>261</td><td>99.9</td><td>181</td><td>100.0</td><td>37</td><td>99.9</td></tr>
</table>

NOTES :

1) **Napaeus** cf. **variatus** (Webb & Berth.) doubtful.

2) **Truncatellina linearis** (Lowe), **atomus** (Shuttl.), and **molecula** (Dohrn) are included here, tentatively regarded as subspecies of one species.

3) Figures for the Canary Islands are preliminary and approximative, in lack of a modern revision of the fauna. Some of the taxa described as endemic may prove conspecific with NW African taxa.

4) Note that **Cochlicopa lubrica** is regarded as represented by an endemic local form on Madeira.

5) Probably underrecorded.

TABLE 2. Levels of taxonomical differentiation within species groups (only indigenous taxa)

A. Taxa	Azores		Madeira		Canary Islands		Cape Verdes	
	Species	Subspecies (endemic to the archipelago)	Species	Subspecies (endemic to the archipelago)	Species	Subspecies (endemic to the archipelago)	Species	Subspecies (endemic to the archipelago)
Non-endemic species	18	—	16	—	8	1	4	—
Non-endemic species, represented by endemic subspecies	—	1 1)	—	1 2)	—	—	—	2
Littoral species	5	—	7	—	4	—	1	—
Endemics common to two or three archipelagos	3	—	3	1 3)	4	1 3)	—	1 3)
Endemic to a single archipelago	37 4)	3	144	47	122 appr.5)	17	12	1
Total indigenous taxa	67		219		157		21	
B. Endemics of total	Taxa/%		Taxa/%		Taxa/%		Taxa/%	
Endemic to Atlantic Islands	3/4.5		3/1.4		4/2.6		—	
Endemic to the archipelago	41/61.2		193/88.1		141/89.8		16/76.2	

NOTES :

1) **Balea perversa nitida** (Mousson).
2) Local form of **Cochlicopa lubrica** (Müller).
3) **Truncatellina linearis, atomus, and molecula, cf. table 1.**
4) Six of the species may possibly be subspecies (one **Leiostyla**, one **Napaeus**, four **Leptaxis**).
5) Some may be subspecies.

Cf. also further notes to table 1.

It can be seen from table 1 that a very high percentage of the total mollusc fauna is endemic, but also that remarkably few, in fact only 4 of the 395 taxa, endemic to the Mid-Atlantic Islands as a whole, are common to two or three archipelagos.

In table 2 the character of just the endemic as well as the indigenous taxa in general is elucidated in more detail. In this comparison terrestrial species of the marine supra-littoral zone are kept separate

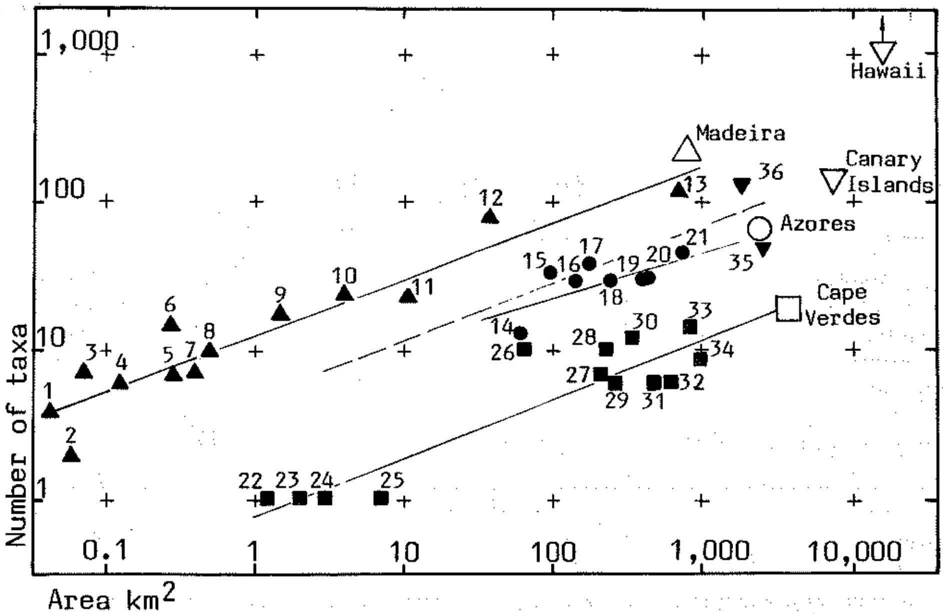

Fig. 1. Relation between area and number of taxa for indigenous terrestrial Mollusca of the islands listed in table 3. For the three Mid-Atlantic archipelagos, for which data for the individual islands are available, these have been plotted and regressions calculated. Omitted are: Sta. Luzia and some minute islets of the Cape Verdes, from which no data are available, and Corvo of the Azores, whose mollusc fauna is evidently very incompletely known (only one confirmed record). For Hawaii the arrow indicates an evidently higher figure, but exact data are not available (cf. table 5). For comparison the taxa-area curve of 8 high islands (including Mauritius and Réunion, plotted here) in the Indian Ocean has been indicated (broken line; modified after Peake, 1971). Subfossil, extinct taxa are included.

Extrapolation of the regressions to the total area of the archipelagos gives (actual number in parentheses): for Madeira 154 taxa (219), Azores 61 (57), Cape Verdes 21 (20).

Regressions (note: figures are plotted in double logarithmic scale):

Madeira :	$y = 12.841\,x^{0.370}$	$r = 0.9431$ ***
Azores :	$y = 5.940\,x^{0.299}$	$r = 0.6854$ ($p.$ $0.1 > 0.05$)
Cape Verdes :	$y = 0.786\,x^{0.396}$	$r = 0.9193$ ***

Indian Ocean Islands : exact equation not available.

TABLE 3. Comparison between endemism on generic, specific and subspecific level between the Mid-Atlantic Islands, Indian Ocean Islands and Hawaii

Archipelago/Island	*Area* km²	*Endemic taxa* *Species*	*Subspecies*	*Non-endemic indigenous species*	*Genera with indigenous species* *Endemic*	*Non-endemic*
Azores	2300	37	4	26	—	30
Madeira	800	144	49	26	14	32
Canary Islands	7300	122 appr.	19	16	9	29
Cape Verdes	3800	12	4	5	—	13
Mauritius	1900	78	5	49	1	29
Réunion	2500	20	2	28	—	18
Hawaii 1)	16800	747 appr.	305 appr.	10	25	22

NOTE :

1) A tentative reassessment of the last comprehensive review, by Zimmerman (1948), in order to make data reasonably consistent with those from the Mid-Atlantic Islands. Supplemented by data from E. Alison Kay (personal information). — No doubt the figures for the endemic taxa are too low.

S y m b o l s: Madeira ▲ : 1, Ilhéu da F^te^ da Areia; 2, Ilhéu das Cenouras; 3, Ilhéu de Fora do P^to^ S^to^; 4, Ilhéu de Fora da Madeira; 5, Ilhéu de Ferro; 6, Ilhéu de Cima; 7, Ilhéu de Agostinho; 8, Ilhéu Chão; 9, Ilhéu de Baixo; 10, Bugio; 11, Deserta Grande; 12, Porto Santo; 13, Ilha da Madeira. — Azores ● : 14, Graciosa; 15, Santa Maria; 16, Flores; 17, Faial; 18, São Jorge; 19, Terceira; 20, Pico; 21, São Miguel. — Cape Verdes ■ : 22, Ilhéu de Cima; 23, Ilhéu Grande; 24, Ilhéu Branco; 25, Ilhéu Razo; 26, Brava; 27, Sal; 28, São Vicente; 29, Maio; 30, São Nicolau, 31, Fogo; 32, Boa Vista; 33, Santo Antão; 34, São Tiago. — Indian Ocean ▼ : 35, Réunion; 36, Mauritsius. — Entire archipelagos: open symbols.

S o u r c e s: critically revised figures from Backhuys (1975), Germain (1921), Groh (1983), Peake (1971 and unpublished), Waldén (1983 and unpublished), and Zimmerman (1948, also personal information from Dr. E. Alison Kay).

because their adaptation to a saline environment give them dispersal abilities, and a distribution pattern different from other terrestrial molluscs (with very few exceptions). — The refined data in table 2 show very clearly the endemic character of the fauna in all the archipelagos. It is also apparent that there is a significantly higher proportion of endemic taxa (ca. 90%) on Madeira and the Canary Islands, than on the other two groups.

The degree of diversity and endemism among the Mid-Atlantic Island groups, in comparison with certain other oceanic islands, with highly diverse and endemic mollusc faunas, is demonstrated in table 3. The range in numbers between the different Mid-Atlantic archipelagos reflects the considerable differences in ecological conditions and with regard to the faunal history.

The diagram, fig. 1, illustrates the number of taxa in relation to the area of islands and/or entire archipelagos. For the Azoran, Madeiran and Cape Verde archipelagos the numbers of taxa of the individual islands have also been plotted, and regressions calculated (for the Canary Islands updated, comparable figures are not available). The outstanding diversity and endemism of the Madeiran Mollusca is evident from table 3 and the diagram; in fact it is rivalled only by the Hawaiian Islands.

The number of taxa of the Madeiran archipelago is substantially higher (42%) than would be expected if extrapolated from the number of taxa/area relation. This reflects the pronounced intra-archipelago endemism (cf. Cook & al., *l. c.*) and vicariance pattern. For the Canary Islands the conditions are heterogenous, but if the comparison is restricted to the central-western islands, the old, not revised data from Wollaston (*l. c.*) indicate a similar situation, with a high degree of vicariance. For the Cape Verdes, on the other hand, the actual total number exactly corresponds to the calculated one, and for the Azores the latter number is only slightly lower than the real one. This reflects a basic faunal similarity of the individual islands, with only a slight tendency to intra-archipelago endemism and vicariating. The intra-archipelago distribution pattern and the relation of this to the ecological conditions is discussed in some length by Backhuys (1975, p. 268 ff.) for the Azores, and by Groh (1983a, p. 200 ff.) for the Cape Verdes.

IV. DISTRIBUTION AND CHARACTER OF THE ENDEMIC TAXA

In table 4 the endemic taxa have been grouped into categories, with regard to level of endemism (generic and specific/subspecific) and to the geographical range of endemism. The total figures, to which the fractions relate, refer to each individual archipelago.

On generic level, endemism is pronounced, especially on Madeira, but also in the Canary Islands. Endemism is considerably lower on the Azores, and on the Cape Verdes only one genus (*Leptaxis*), endemic to

TABLE 4. Distribution of endemic taxa in the Mid-Atlantic Islands

Archipelago	Endemic genera/Taxa total	Endemic genera/Species in common with other archipelagos	Endemic genera/Taxa endemic to the archipelago	Genera, endemic to the archipelago/taxa	% of total Genera/Taxa	Widespread genera/Endemic taxa	D:o/Endemic taxa in common with other archipelagos	D:o/Taxa endemic to the archipelago	% of total Genera/Taxa	Total Genera/Taxa
Azores	5/21				33.3/47.7	10/23			66.7/52.3	15/44
		1/1			6.7/ 2.3		2/2		13.3/ 4.5	
			?4/20[1]		26.7/45.5			8/21	53.3/47.7	
				—/—	—/—					
Madeira	20/154				69.0/78.6	9/42			31.0/21.4	29/196
		1/1			3.4/ 0.5		2/2		6.9/ 1.0	
			5/50		17.2/25.5			7/40	24.2/20.4	
				14/103	48.3/52.3					
Canary Islands	9/103				37.5/71.0	15/42			62.5/29.0	24/145
		1/1			4.2/ 0.7		3/3		12.5/ 2.1	
			?4/35 appr.[1]		16.7/24.1			12/39	50.0/26.9	
				4/64 appr.	16.7/44.1					
Addenda: Endemic species, insertae sedis				?/3	?/ 2.1					
Cape Verdes	1/5				9.1/31.3	10/11			90.9/68.8	11/16
		—/—			—/—		—/—		—/—	
			1/5		9.1/31.3			10/11	90.9/68.8	
				—/—	—/—					

NOTES :

1) Doubtful if **Napaeus** on the Azores and the Canary Islands are congeneric. For background data about the genera, see Appendix.

the Mid-Atlantic Islands, occurs. Both absolute and relative figures should be considered in this context. It is reasonable to regard the figures for endemic genera as an indication of the age of the mollusc fauna. The figures for widespread genera with endemic representation give a measure of subsequent colonization during later stages, and finally the widespread but indigenous species, which have not developed any endemic forms may have colonized the Atlantic Islands relatively late, not improbably as late as in the Quaternary (cf. tables 1 and 2). The degree of endemism on the specific/subspecific level is, indeed, higher than on generic level (disregarding the case of *Columella*, with a single endemic species common to three of the archipelagos), but the trend is roughly the same. — Indeed, factors as isolation from the continental mainland and secondary elimination of taxa also influence the figures.

The major part of the endemic radiation falls on families and genera, different for each island group. Only in the genus *Phenacolimax* is the degree of radiation roughly the same in all archipelagos, except for the Cape Verdes (where, in fact, the taxonomical position of the endemic Vitrinid recorded is uncertain). For the other genera, the differences in speciation suggest that colonization of the different archipelagos may be of rather different age.

In the Azores the Zonitidae shows the most obvious radiation, *Leptaxis* and *Napaeus* to a lesser degree, and still less in a few other genera. It is doubtful if this *Napaeus* is identical with the genus of the Canary Islands (cf. Backhuys, 1975, Hesse, 1933).

In Madeira there is a very striking, taxonomical as well as adaptive radiation in the genera *Leiostyla* and *Leptaxis,* in the Ferrussaciidae and the Geomitrinae. The last mentioned group comprises 108 of the 193 taxa endemic to the islands. A somewhat lower degree of radiation is present in the endemic genus *Boettgeria.*

In the Canary Islands 69 of the 141 endemic taxa belong to *Hemicycla* and *Napaeus,* in addition to which there is a more moderate radiation in *Monilearia* and *Canariella.* None of these genera is represented on Madeira. Reversely, *Leiostyla* and the Geometrinae, so highly differentiated on Madeira, show only a slight radiation on the Canary Islands. Other characteristic genera of Madeira are lacking in the Canary Islands, among which notably *Leptaxis,* and taken together all this evidence indicates rather profound differences in the faunal history of the archipelagos.

In the Cape Verdes the only genus with endemic radiation is *Leptaxis.*

V. AFFINITIES OF THE MOLLUSC FAUNA OF THE MID-ATLANTIC ISLANDS

The biogeographical affinities are estimated on palaeontological and taxonomical evidence and, when firm evidence of this kind is lacking, the more circumstantial evidence of distribution and palaeogeographical conditions has to be taken into account. All these approaches have their limitations, and it is apparent that the biogeographical model must be to some extent arbitrary.

The affinities of the indigenous Mollusca are summarized in table 5. It should be noted that the table is not directly compatible with the other tables. Endemic and widespread taxa can be grouped together by their presumed common origin. Littoral species are excluded in table 5 as being less relevant in the present discussion. However, it can be stated that the evidence from these is corroborative. The genera in question, or closely related extinct ones, belonged to the fauna on the northern border of the Tethys Sea, the beginning of the present Europe, already in the early Tertiary or even in the Jurassic.

The grouping is made largely on the basis of genera, but exceptions have proved necessary and these are considered in the notes to the table. For widely distributed genera the grouping has been made with regard to the most closely related species.

The trends in the affinities of the mollusc fauna are fairly consistent and are explicable in terms of climatic and geographical conditions, and by the faunal history. The northern Palaearctic element is rapidly decreasing southwards from the Azores, to nil on the Cape Verdes, where taxa with tropical African affinities form the larger group, but lack in the other archipelagos [6]). In the Canary Islands there is a considerable fraction of NW African (Maghreb Region) or closely related taxa, not present in any other of the island groups, with the exception for the problematic case of *Napaeus* in the Azores. Also the general Mediterranean element, which is not predominantly or exclusively NW African, is best represented on the Canary Islands and markedly decreasing towards the periferal Azoran and Cape Verde groups.

The most conspicuous difference between the mollusc faunas of Madeira and the Canary Islands is the complete absence of taxa with NW African affinities on Madeira, despite the fact that they hold a similar position relative to the African continent. It is also striking that only few of the taxonomical groups of the Canary Islands are lacking ancestral or closely related forms in the European Tertiary, whereas a derived element, without such closely related, extinct forms is dominating on Madeira.

As in the case of the endemic taxa in general, the representation of taxa with a background in the European Tertiary is strikingly lower in the periferal Azores and the Cape Verdes.

There are no indigenous (but some introduced) species on the Atlantic Islands, which have Nearctic or Neotropical background. Conse-

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[6]) *Zootecus*, now confined to the southern border of the Sahel region and the Cape Verdes, is recorded from Tertiary strata (Lower Pliocene or Upper Miocene) on Lanzarote, Canary Islands (Rothe, 1966).

TABLE 5. Affinity groups (only indigenous taxa regarded; littoral species excluded)

	Azores		Madeira		Canary Islands		Cape Verdes	
	Taxa	*%*	*Taxa*	*%*	*Taxa*	*%*	*Taxa*	*%*
1. Widespread or northern species in W. Palaearctic, or closely related taxa	29	46.8	13	6.1	3	2.0	—	—
2. Prevalently Mediterranean species, or related taxa (genera extant in Europe)	4	6.5	8	3.8	12	7.8	4	20.0
3. Endemic taxa of W. Palaearctic Tertiary origin (now extinct in Europe)								
a) With the same or closely related genera in European Tertiary	17	27.4	62	29.2	102 appr.	66.7	7	35.0
b) Taxa belonging to genera, which have probably been derived on the Mid-Atlantic Islands	5	8.1	129	60.8	8	5.2	—	—
4. Taxa of NW African affinities	—	—	—	—	26	17.0	—	—
5. Taxa with tropical African affinities	—	—	—	—	— [1]	—	9	45.0
6. Taxa of uncertain affinities	7 [2]	11.3	—	—	2 [3]	1.3	—	—
Total	62	100.1	212	99.9	153	100.0	20	100.0

NOTES :

1) **Zootecus** lived on the Canary Islands in the Tertiary.

2) **Napaeus** spp.

3) «**Macularia**» spp. according to Wollaston (l. c.)

quently there is no evidence of pre-atlantic origin or transatlantic dispersal from west.

VI. SOME ENIGMATIC OR OTHERWISE INTERESTING MEMBERS OF THE ATLANTIC ISLANDS MOLLUSC FAUNA

The terrestrial mollusc fauna in the region which is today Europe, was dominated in the Mesozoic and the early Tertiary by a palaeotropical element. Two species, viz. *Staurodon saxicola* (Lowe) and *Gibbulinella dealbata* (Webb & Berth.), on Madeira and the Canary Islands respectively, are survivors of this palaeotropical fauna. The subfamilies to which they belong, Nesopupinae and Enneinae respectively, show a very wide and ancient tropical distribution pattern. Several other Macaronesian genera no doubt have an origin under similar tropical conditions in the early Tertiary, but have remained confined to the western Palaearctic.

As already considered *Leptaxis* and *Napaeus* have an enigmatically disjunct distribution, the former genus lacking on the Canary Islands, the latter present on the Canary Islands and the Azores, but absent on the interjacent Madeira. Alternative explanations concerning *Leptaxis* are that it became locally extinct on the Canary Islands or that it has never colonized these islands. In the latter case long distance dispersal from Madeira to the Cape Verdes seems decidedly less probable than that the two archipelagos have been colonized independently. The fact that *Leptaxis* is one of the very few of the Macaronesian genera to which there is a probable relative in the NW African Tertiary (*Camaenopsis* in the Lower Miocene of Morocco) suggests that the present distribution is a remnant of a wider distribution, which included part of NW Africa. However, as long as no information on the anatomy of the Cape Verde *Leptaxis* is available hypotheses on the systematic relation to the Madeiran-Azoran *Leptaxis* and possible origin can only be speculative.

In the case of *Napaeus* there is some evidence in favour of a diphyletic origin and subsequent convergence. Hesse (1933) has even suggested that the Azoran and Canarian (*Napaeus* s. s.) groups may belong to different subfamilies of the Enidae. Shells of *Napaeus* are known from the Eocene in Europe. — To resolve the problem a cladistic analysis, evaluating several characters and considering the continental Enidae, is required.

Janulus, with a few species on Madeira and the Canary Islands, is remarkable owing to its close relationship to the endemic Gastrodontinae in eastern N. America (especially *Gastrodonta; Poecilozonites*, endemic to the Islands of Bermuda, seems less closely related). However, *Janulus* cannot be considered as evidence of a direct faunal connection with the Nearctic. The genus was widely distributed in Europe, from the Oligocene to the end of the Pliocene (in England; Kerney, 1976), and has undoubtedly reached the Atlantic Islands from this region. But the Gastrodontinae are a very old group, and one of the very few for which there is evidence suggesting a distribution common to the Old and the New World before the northern part of the Atlantic began to open up. Indirectly, the persistence of *Janulus* offers evidence of very remote, preatlantic faunal connections.

Except for the widespread *Balea* the only Clausiliid genus of the Mid-Atlantic Islands is *Boettgeria* on Madeira. Its systematic position is still a matter of dispute, but it is evident that it is not related to the group in the Atlas region, which belongs to the subfamily Alopiinae, but with European Clausiliids. According to Nordsieck (1979) it belongs probably to the Mentissoidinae, whose extant distribution is SE European. Another group, whose systematic position is not well understood, in complete lack of anatomical evidence, are the endemic Madeiran Ferrussaciids. Tryon & Pilsbry (1908, p. 283) suggested a «genetical connection» with the Iberian *Cryptazeka,* which they also regarded as a probable Tertiary relict. They did not, however, substantiate this opinion, and in the recent paper of Gittenberger (1983) the taxonomical position of *Cryptazeka* is still regarded as obscure.

VII. ON THE GEOLOGICAL HISTORY OF THE MID-ATLANTIC ISLANDS

The geological evidence as to the age and history of the Atlantic Islands is highly complicated, of uneven accuracy and partly ambiguous. A detailed and comprehensive review is given by Mitchell-Thomé (1976, 1982). However, the now well established and elaborate theory of the Atlantic sea floor spreading gives a general framework for the understanding of the geological process and from which biogeographical speculation can proceed. Available facts are roughly consistent with the model proposed by Ostenso & Vogt (1967). According to this building up of the archipelagos was initiated at, or in close connection with the appearance of the pertinent part of the oceanic floor, lateral to the crest of the Mid-Atlantic ridge. The distance from the ridge can be used as a rough measure of the maximum time elapsed since this commenced. Conditions within the archipelagos, implying an, in general, younger age for islands in the westward direction, are compatible with this model. Indeed, some of the islands may have been generated by later vulcanism, off the spreading axis.

Common features to all the archipelagos (but not for all islands, depending on their individual age) are the presence of Miocene strata (Vindobonian), and marine terraces etc. from Pleistocene (Sicilian) and onwards. With the possible exception of Fuerteventura, in the Canaries, there is no evidence of folding in the region; when raised strata occur they are due to submarine vulcanic and vulcanic-tectonic processes.

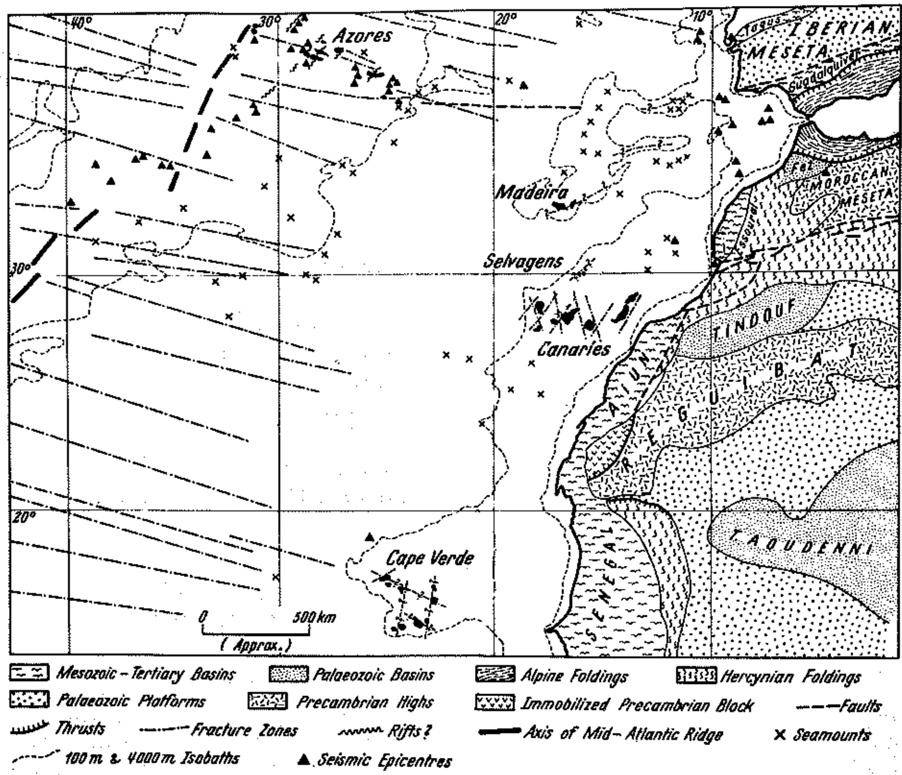

Fig. 2. The geographical location and geological environment of the Mid-Atlantic Islands. Features significant in relation to their development, particularly tectonic and stratigraphical, are indicated. — Somewhat modified after Mitchell-Thomé (1976).

(Reproduced by kind courtesy of Dr. R. Mitchell-Thomé, Luxembourg, and Gebrüder Borntraeger Ltd, Stuttgart).

A fact, which must be kept in mind, is that the age of the archipelago in the present context refers to the time when its basement began to be formed by submarine eruptions, and that the emergence of the islands above sea level, becoming available for biotic colonization, took place much later (e. g. for Madeira perhaps 30-60 million yr later).

The oldest strata, dating back to the lower Cretaceous, or possibly the Jurassic, are found in the easternmost Canary Islands and Cape Verdes. These sediments have the features of having been deposited in a relatively deep sea. For the easternmost Canary Islands there is strong evidence that their basement is, at least in part, a rifted fragment from the African plate, whereas the easternmost Cape Verdes are oceanic from the beginning. — In Lanzarote, one of the eastern Canary Islands, there are limestone beds of probably Pliocene age, possibly older (Hausen, 1959, Rothe, 1966), which contain land shells and eggs of flightless, struthionid birds. The latter very definitely indicate a land connection with the continent.

The geological evidence from the Central Canary Islands is highly complicated and heterogeneous, but these islands are evidently of oceanic origin and of roughly decreasing age in a westward direction (Mitchell-Thomé, 1982). The westernmost Hierro is decidedly younger, of Pliocene origin. For at least Gran Canaria, Tenerife and Gomera their existence as islands in the Miocene may be regarded as an established fact. In the Late Tertiary there was a very extensive vulcanism in the Canary Islands, probably largely of catastrophic character.

In the Cape Verdes, basaltic layers indicate that an archipelago may have existed already in Pre-Miocene time (> 30 million yr BP) but was eroded down, as the deposition of the Miocene sediments seems to have taken place at some depth. The history of the Cape Verdes (Mitchell-Thomé, 1983) shows a complicated pattern of intrusions, uplifts and faultings, not yet clarified in detail, but the present islands seem largely to be products of Late Tertiary vulcanism, continuing, at least on Fogo, in the Quaternary.

Indirect evidence indicates that the forming of Madeira commenced in the Late Cretaceous, and the presence of islands already in the Lower Tertiary is not excluded. The Miocene strata here have the character of coral reefs, offshore low islands, already considerably eroded down. The age of the archipelago may be ca. 15 million yr, though a considerably higher age is not excluded. The subsequent development is well documented by subaerial vulcanic layers from Late Miocene and later extensive deposition of tufas and basaltic lavas in the Pliocene-Pleistocene. In the course of time, uplift to 300-400 m took place. Structures under the late plateau basalts indicate a conspicuous erosion relief similar to the present. In addition, extensive lateritization indicates a humid, tropical climate. The vulcanism gradually ceased in the Quaternary, but eruptions have been dated as late as 1,000-2,000 yr BP in Madeira proper. In Porto Santo, which developed independently from Madeira, from a separate basement, vulcanism had already ceased in the Late Tertiary.

The Azores are situated on the slope of the Mid-Atlantic ridge with a WNW-ESE extension of 530 km. The westernmost islands are quite close to the crest of the ridge, and evidently of fairly young origin. The Miocene strata, visible only in the extreme east of the archipelago, were deposited in relatively shallow water, and it is possible that the eruptives here reached above sea level before the end of the Miocene. The central group seems to have been founded first in this period, and the islands here emerged in the Pliocene. Evidently the Azores is the youngest of the Macaronesian groups, and is today vulvanically and seismically the most active.

A crucial point in the development of the palaeogeographical pattern in the region of Madeira and the Azores, and therewith the conditions for faunal dispersal in the past, concerns the closure of the Tethys Ocean here. Connected with this is the kinematic interaction between the African, Iberian, and European plates, which meet here, and the opening of the northern part of the Atlantic, which started at about 80 million yr BP, i. e. about 70 million yr later than in the Central Atlantic (between Africa and the southern part of North America). The course of events is far from resolved, and will not be reviewed here. Only certain significant features, some of which do not seem quite compatible at present, should be considered.

Madeira is situated near the south-western end of a complex bank system, connected with the southern part of the Iberian plate and formed as a consequence of fracturing, igneous outpourings, tilting and finally uplift, during the compressive interaction between the plates. The process commenced in the Early Cretaceous, during opening of the Central Atlantic, and continued in several phases until the Mid-Miocene (Féraud & al., 1982). Available data are well correlated with sea floor spreading, and suggest that the bank system has been connected with Southern Iberia throughout the time. On the banks between Madeira and Iberia there are numerous seamounts, many of which have truncated summits (guyots), indicating abrasion during former island stages. The particularly well surveyed seamounts on the Gorringe Bank (Pastouret & al., 1980) show deeper abrasional terraces, formed in the Early Miocene and implying the existence of islands, considerably larger than the present Madeira. Evidently the seamounts must once have played a role as stepping-stones for faunal dispersal between Iberia and Madeira.

Other significant features are the very conspicious fault (Gloria Fault) in the eastern alignment close south of the Azores, a considerable dislocation of the magnetic anomalies along this fault, and an angle between the fracture zones. These features are believed to mark the oceanic extension of the present border between the African and the European plates. However, the bank system and Madeira are situated south of the east-north-east alignment of the fault. The two concepts, that of the fault as the border between the European and the African plates, and that of an uninterrupted connection between Iberia and the bank system, are not compatible, and this is a weak point in the theory. On the other hand, there is no evidence suggesting that sliding between Iberia and the bank system, and subsequent suturing, has occurred. Therefore it seems reasonable to assume that the connection has been uninterrupted at least since the opening of the Atlantic between America and Iberia, and the rotation of the latter commenced about 80 million yr BP.

Also to be considered are the relative movements between the African and Iberian plates. From about 150 milloin yr BP, or perhaps much earlier — estimates vary (cf. Coulomb, 1972, fig. 122, Hallam, 1981, Vegas

& Banda, 1982) — the African plate moved eastward, later followed by a more northern movement of the Iberian plate. This led to the opening of a considerable gap — the western extension of the Tethys — between Iberia/Europe and Africa, which reached a maximum in the interval between 135-50 million yr BP, when the bank system was essentially formed. After this period, and in connection with the Alpine orogenesis, the collisional phase commenced, leading to the suturing of Iberia to Africa in the Mid-Miocene. If we are going backwards from the Mid-Miocene, we will find that the palaeogeographical position of Iberia becomes increasingly remote from the African plate, the more as the nortwestern part of the latter (Maghreb region) was essentially formed at that time, by the Alpine orogenesis and the accretion of older, minor plates to the main African foreland (cf. Dewey & al., 1972).

VIII. AN ATTEMPT AT A GENERAL THEORY ON THE ORIGIN AND DEVELOPMENT OF THE TERRESTRIAL MOLLUSC FAUNA OF THE MID-ATLANTIC ISLANDS

As emphasized in this account the pronounced endemic element in the Macaronesian land mollusc fauna has its origin in the Early Tertiary Mollusca of Europe. Here a tropical mollusc fauna dominated in the Mesozoic and the early Tertiary (cf. Waldén, 1963, Peake, 1978). Extant, or closely related genera formed only a very minor fraction. Gradually the tropical genera were replaced by Palaearctic genera during the Tertiary (partly this element, in which primitive, orthurethran genera form a considerable part, may have immigrated from the north, where no palaeontological evidence is preserved). Relatives or descendants of this climatically fastidious fauna are today found in the South-East, in the Indo-Malayan region, and in the South-West, on the Atlantic Islands.

Already at an early stage in the opening of the North Atlantic the land mollusc faunas on both sides of the Atlantic were profoundly different; in addition there were great differences between faunas in western and eastern N. America, which were separated by a broad seaway. Only a few groups can, on the basis of direct or later fossil evidence, give any indication of a common, tropical mollusc fauna on the northern border of the Tethys Ocean. To these groups belong some genera in the families Ferrussacidae (*Cecilioides* and *Coilostele*) and Spiraxidae (recent *Poiretia* in the Mediterranean region, several extinct genera in the European Tertiary, several extant and fossil genera mainly in Central America), the genera *Pupisoma* and *Strobilops*, some genera of the marine supralittoral zone and finally the subfamily Gastrodontinae. None of these have an occurrence on the Atlantic Islands which can reflect a Pre-Atlantic origin. The endemic representatives of *Janulus* and of *Cecilioides* have a background in genera derived later in the Old World. In general, there were no profound changes in the New World fauna during the Tertiary, instead there was a rather straightforward evolution from the early genera, with later intrusions of Holarctic genera from the north, and additional tropical genera, mainly via the Central American land bridge, in the Late Tertiary. In this context it should be remembered that both the western and the eastern portion of N. America remained in contact with tropical, or at least warm-temperate conditions throughout the Tertiary, whereas drying and cooling in the Late Tertiary and the subsequent Pleistocene cold periods extensively eliminated the corresponding faunal element in Europe.

The origin and evolution of the Land Mollusca of the Mid-Atlantic Islands should be seen against this background, and the geological history reviewed in the previous chapter. On Madeira, biotic colonization had certainly taken place already in the Mid-Miocene, i. e. about 15 million yr BP though it seems quite possible that colonization may have begun already in the Oligocene. The dominance of the element with Tertiary European affinities, in contrast to the complete lack of the north-west African element in the mollusc fauna of Madeira, can be explained by the palaeogeographical position of Madeira, and decidedly speaks in favour of an early colonization, when Madeira was situated considerably more distant from Africa. Present day seamounts may have acted as stepping-stones at that time. An idea about the possibilities of passive dispersal (by winds, birds, in certain cases also drifting logs) of even rather large forms can be obtained from the study of Vagvolgyi (1976, cf. also Kew, 1893).

The taxonomic radiation may have taken place largely within the archipelago, from rather few propagules, and in direct interaction with the development of the topography and climatic and habitat differentiation. The persisting ancient character of the mollusc fauna suggests that there must have been fairly few arrivals in the Late Tertiary, but notably *Phenacolimax* may have arrived at that time, when elevation of the topography in combination with cooling of the climate may for the first time have offered conditions suitable for these essentially montane forms.

The question arises why there has not been any subsequent colonization of Madeira by the endemic north-west African elements, which had evolved since the Late Miocene, after suturing Iberia with Africa, when Madeira had reached its present position. It cannot be explained satisfactorily by the geographical barriers. Strong adaptation to the local environment and inability to compete with well established biota in respective areas, may be an essential explanation for this complete lack of faunal exchange.

The youngest, natural element in the Madeiran Mollusca are the representations of more northern, palaearctic taxa, which probably first arrived in the Pleistocene (or even later) and show little or no sign of taxonomic differentiation.

The markedly poorer and less radiated mollusc fauna of the Azores can, without constraint, be explained by the archipelago's considerably lesser age, more isolated position and that it was much more subject to climatic hazards during the Pleistocene, which may have impoverished the fauna. At the same time both position and climate favoured the influx of more northern Palaearctic taxa. Most conspicuous is the probably relatively early colonization, and subsequent radiation of European Zonitids (cf. discussion in Riedel, 1964). Part of the specific Macaronesian Mollusca may have arrived on the Azores from Madeira, especially less differentiated, young taxa, whose European ancestors already may have vanished.

In Chaper III the very high degree of intra-archipelago endemism and vicariance in the Madeiran group is noted, contrasting with the much lower degree of intra-archipelago endemism in the Azores (and still less in the Cape Verdes). From a strict vicariance biogeography aspect rather the contrary situation would be expected. Between the parts of the Madeiran archipelago the gaps are small, between 20 and 50 km, whereas the islands in the Azores are much more isolated from each other and spread over a large distance. Waldén (1983: 264-265) argues that local adaptation and niche specialization in the Madeiran Mollusca may have been more important for maintaining and enhancing the distributional pattern than the primary geographical separation.

In the Azores, on the other hand the low degree of intra-archipelago endemism and vicariance suggest that the present pattern of distribution may be young, perhaps partly due to Late Quaternary re-colonization after the climatic vicissitudes of the ice-ages.

In the other direction the paucity of the Cape Verde fauna may be seen not only in relation to actual, harsh ecological conditions, but also to the eliminating effect of climatic fluctuations at the margin of the Sahel region. However, an element with Tertiary European or endemic Macaronesian background has probably never had any strong representation on the Cape Verdes. In fact only two groups are represented here, *Leptaxis*, already discussed in Chapter VI, and the subgenus *Keraea* of *Discus*, the lastmentioned having closely related species on the Canary Islands. The relatively young (Pliocene) origin and the rather isolated position of the archipelago should also be taken into consideration. The tropical African element, outnumbering that with Macaronesian affinities, consists of small forms of widely spread genera, of little fauna-historical significance. Considering the evidence of extensive ice-age aridity and compression of the humid tropical zone in Africa (cf. Gellert, 1974, Fairbridge, 1964) some may even be Late Quaternary immigrants. It is also significant that there is a complete absence of larger African forms, which find their limit in adjacent Senegal. The low degree of intra-archipelago endemism and vicariance (cf. maps by Groh, 1983a) also indicates that the present distribution pattern is relatively young.

On the Canary Islands the three old, endemic genera *Hemicycla*, *Napaeus* (with reservations for the problematic relation to the Azoran group) and *Canariella* comprise about 80 taxa with well developed vicariating distribution. In addition there is the palaeotropical relic form *Gibbulinella*. It is difficult today to hypothesize to which extent the presence of the old genera should be explained by dispersal before or after the presence of the Tethys seaway between Europe and Africa, via NW Africa or more directly from Europe by long distance despersal, owing to the incompleteness of the taxonomical and palaeontological evidence. General palaeontological evidence indicates the existence of an older, continental fauna on the eastern Canary Islands, which seems to have been largely destroyed by the extensive vulcanism in the Late Tertiary, at the same time when most of the western islands were built up. The mentioned genera may be survivors of this old fauna, whereas most of the remaining endemic taxa are probably descendants of later Tertiary immigrants, partly from Madeira, partly from NW Africa. The decidedly lower degree of taxonomical radiation and specialization speaks in favour of this. More pronounced climatic vicissitudes in the Pleistocene than on Madeira may also have had some eliminating effects. Taxa of the more northern palaearctic type form quantitatively the most subordinate element in the Canarian mollusc fauna, just touching the archipelago and are certainly very late arrivals.

However, the still fairly inadequate taxonomical knowledge of the Canarian Mollusca, and the many debatable points in the geological history of the islands, prevents a penetrative discussion at present on how the fauna has evolved.

To conclude, it can be stated that the Canarian Mollusca have a more complex background than the Madeiran, resulting in that it is composed of more diverse faunal elements, at the same time as many genera are relatively little differentiated. In Madeira the original early Tertiary fauna is best preserved, but has also had a long, unbroken evolutionary differentiation owing to the relatively equable climatic conditions through time. The strong radiation of *Leiostyla*, the Geometrinae, the endemic Ferrussaciidae and, to a lesser extent, *Boettgeria* is striking. With this contrasts the sparse representation of the two former groups, and the lack of the two latter, in other Mid-Atlantic archipelagos. This emphasizes the role of Madeira as a center of evolution from which dispersal to other island groups may have occurred.

IX. SOME CONCLUDING REMARKS

The evolution and present distribution pattern of the Land Mollusca of the Mid-Atlantic Islands is very clearly related to the geological history of the islands, in connection with plate tectonics. The fauna has primarily its origin in the early Tertiary fauna of Europe. Evidence is largely in favour of a long, independent evolution within each archipelago, but later waves of colonization and climatic and geological events have complicated the pattern. In Madeira the mollusc fauna seems to have maintained most of its Tertiary character. It is possible to draw an outline history of the mollusc biota of the Mid-Atlantic Islands today, but several separate problems remain to be solved, before the historical concept is well-established and free from contradictions.

Significant taxonomical problems concern the relation between the two groups of *Napaeus,* as well as the relation of the isolated *Leptaxis* group on the Cape Verdes to the northern group of the Madeira-Azores. In general, the knowledge on the Canarian taxa is very incomplete, with regard to anatomy, taxonomy and evolutionary interpretation, as well as adequate sampling. Also the knowledge of the extant and fossil mollusca on the adjacent African mainland is quite insufficient. Even concerning the other archipelagos much detailed work remains before problems on radiation, possible faunal exchange between archipelagos (as well as within them) etc. could be treated adequately. In Madeira the endemic Ferrussaciidae are in particular need of anatomical and systematic study. It is desirable that systematic surveys are carried out on a basis of the entire group, not restricted faunistically to the taxa of a single archipelago; in addition characters ought to be studied methodically in a way which can produce evidence suitable for a cladistic analysis.

But an adequate interpretation also depends upon evidence from other fields, such as geology, palaeoclimatology and, in particular, concerning the complicated later phases in the closing of the Tethys Ocean, which coincided with the biotic colonization of Madeira and the Canary Islands, and subsequent early radiation of taxa.

A problem for the biogeographer is the fact that evidence pertaining to the palaeogeography, based on plate tectonics, orogenesis, eustatic changes, palaeoclimatology, and the general synchronization of geological events, is not readily available in integrated form. This is an indispensable requisite to forthcoming work in historical biogeography, and coordinated efforts by geo-scientists to produce this would be most welcome.

ADDENDA

Since the present paper was submitted for publication (April 1984) Dr. W. Rähle, University of Tübingen, West Germany, has kindly informed the author that he, during a recent visit to Madeira, found the following two species, not recorded there previously: *Helicodiscus paralellus* (Say) and *Deroceras panormitanum* (Lessona & Pollonera). These are *not* included in the figures, on which table 1 is based (in contrast to two additional species mentioned on page 54, foot-note 5). Both occur under unmistakeably synanthropic conditions on Madeira.

In a recent paper by Wiktor (1984) significant information about *Parmacella* on the Canary Islands is given.

APPENDIX. A synoptic table of genera, which are represented by indigenous species on the Mid-Atlantic Islands. — The table is somewhat summary, but present knowledge does not permit a consistent presentation on a more detailed level. The distributional status of the genera and cases of Tertiary occurrence in Europe are indicated. Cases of endemic subgenera are briefly considered. It should be admitted that estimates on indigenousness are somewhat restrictive compared with some other authors; it cannot be excluded that some few genera, omitted here, may have indigenous representatives, or that the presence in other archipelagos may actually be indigenous.

Based on critically revised data in the literature: for the Azores by Backhuys (1975), Riedel (1964), for Madeira by Waldén (1983), for the Canary Islands by Odhner (1931, 1937), Regteren Altena (1950), Riedel (1980), and the classical work of Wollaston (1978), for the Cape Verdes by Groh (1983a), Panelius (1958). In addition various sources, such as personal information and unpublished museum material, have been used.

Symbols:

×	presence
?×	taxonomical identity uncertain
×?	doubtful if indigenous
(×)	closely related genus in the Tertiary
*	the genus is represented by introduced species (refers only to genera, which have indigenous representatives in other archipelagos)

Notes to table of Appendix

1.) Endemic subgenera on the Azores and Madeira.
2.) Systematic position uncertain.
3.) Doubtful if Azoran and Canarian groups are congeneric.
4.) On the Canary Islands in the Pliocene.
5.) Small Subulinids of generalized type («*Opeas*») lived in Europe in the Early Miocene.
6.) Endemic subgenera on Madeira, Canary Islands and Cape Verdes.
7.) Two subgenera endemic to the Azores and the Canary Islands, respectively. The third subgenus, *Insulivitrina*, has, in addition to the several species on the Atlantic Islands, one species in the European Alps.
8.) The subgenus *Lyrodiscus*, endemic (fossil in England).
9.) Three endemic subgenera on the Azores.
10.) Systematic position uncertain.
11.) Also on the Canary Islands in the Pliocene.
12.) Subgenus *Idiomela* endemic to Madeira.
13.) Some of the «*Macularia*» spp. in Wollaston (*l. c.*).

Table

Major group Family Genus	Distribution type	Azores	Madeira	Canary Islands	Cape Verdes	The same or closely related genus in European Tertiary
PROSOBRANCHIA						
Hydrocenidae						
Hydrocena	wide, mainly tropical	×	—	×	—	—
Cyclophoridae						
Craspedopoma	endemic	×	×	×	—	×
Pomatiasidae						
Pomatias	wide, mainly Mediterranean	—	—	×	—	×
Truncatellidae						
Truncatella	littoral	×	×	×	—	×
Assimineidae						
Assiminea	littoral	×	×	×	—	×
BASOMMATOPHORA						
Ellobiidae						
Carychium	wide, prevalently holarctic	×	×	—	—	×
Melampus	littoral	—	—	—	×	×
Pseudomelampus	littoral	—	×	—	—	—
Pedipes	littoral	×	×	—	—	—
Ovatella	littoral	×	×	×	—	×
Marinula	littoral	—	×	—	—	×
STYLOMMATOPHORA						
Succineidae						
Quickia	Old World tropical	—	—	—	×	—
Succinea	wide	—	—	—	?×	×
Oxyloma	wide, holarctic	—	—	×	—	×
Cochlicopidae						
Cochlicopa	wide, holarctic	×	×	*	—	×
Vertiginidae						
Columella	wide, holarctic	×	×	×	—	×
Truncatellina	wide, old world	—	×	×	×	×
Vertigo	wide, holarctic	×	×	*	—	×
Staurodon	endemic	—	×	—	—	(×)
Chondrinidae						
Granopupa	Mediterranean	—	—	×	—	×

T a b l e (cont.)

Major group Family Genus	Distribution type	Azores	Madeira	Canary Islands	Cape Verdes	The same or closely related genus in European Tertiary
(STYLOMMATOPHORA cont.)						
Gastrocopta	wide, prevalently tropical	—	—	—	×	×
Pupillidae						
Pupilla	almost world-wide, not in S. America	—	—	—	×	×
Pupoides	wide, tropical	—	—	—	×	—
Leiostyla 1)	wide, western palaearctic	×	×	×	—	×
Lauria	wide, Old World	×	×	×	*	×
Hemilauria	endemic	—	×	—	—	—
Valloniidae						
Vallonia	wide, holarctic	×	×	*	*	×
Acanthinula	wide, western palaearctic	×	×	?×	—	×
Spermodea	wide, western palaearctic	×	—	—	—	×
Plagyrona 2)	Mediterranean	—	×	×	—	—
Enidae						
Napaeus 3)	endemic	×	—	×	—	×
Clausiliidae						
Boettgeria	endemic	—	×	—	—	—
Balea	wide, western palaearctic	×	×	—	—	—
Ferrussaciidae						
Cecilioides	wide, Old and New World	*	×	*	*	×
Ferrussacia	Mediterranean	—	*	×?	—	×
Amphorella	endemic	—	×	?	—	—
Pyrgella	endemic	—	×	—	—	—
Cylichnidia	endemic	—	×	—	—	—
Subulinidae						
Zootecus	wide, tropical	—	—	—4)	×	—
Pseudopeas	wide, tropical	—	—	—	×	—5)
Streptaxidae						
Gibbulinella	endemic	—	—	×	—	×

T a b l e (cont.)

Major group Family Genus	Distribution type	Azores	Madeira	Canary Islands	Cape Verdes	The same or closely related genus in European Tertiary
(STYLOMMATOPHORA cont.)						
Endodontidae *s. l.*						
Punctum	wide, holarctic-subtropical	×	×	×	×	×
Helicodiscus	wide, European-American	*	×	—	—	—
Discus 6)	wide, holarctic	×	×	×	×	×
Euconulidae						
Euconulus	wide, holarctic	×	×	—	—	×
Vitrinidae						
Phenacolimax 7)	wide, western palaearctic	×	×	×	?	×
Zonitidae						
Janulus	endemic	—	×	×	—	×
Zonitoides	wide, holarctic	×?	*	—	×?	×
Vitrea	wide, western palaearctic	×	×	×	—	×
Aegopinella	wide, western palaearctic	×	—	—	—	—
Retinella 8)	wide, western palaearctic	—	—	×	—	×
Nesovitrea	wide, holarctic	×	×	—	—	—
Oxychilus 9)	wide, western palaearctic	×	*	*	—	×
Vermetum 10)	endemic	—	—	×	—	—
Parmacellidae						
Parmacella	Mediterranean, Central Asian	—	—	×?	—	×
Helicidae						
Sphincterochila	Mediterranean	—	—	×	—	×
Heterostoma	endemic	×	×	×	—	—
Steenbergia	endemic	—	×	—	—	—
Geomitra	endemic	—	×	—	—	—
Spirorbula	endemic	—	×	?×	—	—
Caseolus	endemic	—	×	—	—	?×
Disculella	endemic	—	×	—	—	—
Actinella	endemic	×	×	?×	—	—

T a b l e (cont.)

Major group Genus	Distribution type	Azores	Madeira	Canary Islands	Cape Verdes	The same or closely related genus in European Tertiary
(STYLOMMATOPHORA cont.)						
Lemniscia	endemic	—	×	—	—	—
Discula	endemic	—	×	—	—	—
Pseudocampylaea	endemic	—	×	—	—	—
Cernuella	prevalently Mediterranean	×?	*	?×	—	×
Leucochroa	Mediterranean	—	—	×	—	×
Helicella	wide, western palaearctic	*	*	×	*	×
Trochoidea	wide, western palaearctic	—	—	×	—	×
Monilearia	endemic	—	—	×	—	×[11]
Caracollina	Mediterranena	*	*	×	*	×
Canariella	endemic	—	—	×	—	×
Leptaxis	endemic	×	×	—	×	×
Theba	prevalently Mediterranean	*	*	×	*	×
Lampadia	endemic	—	×	—	—	—
Hemicycla	endemic	—	—	×	—	×
Helix [12]	wide, western palaearctic	*	×	*	—	×
insertae sedis [13]	endemic?	—	—	×	—	—

REFERENCES

BACKHUYS, W.:
1975. Zoogeography and Taxonomy of the Land and Freshwater Molluscs of the Azores. — *Dissert.* 350 pp.

COOK, L. M., JACK, T., & PETTITT, C. W. A.:
1972. The distribution of land molluscs in the Madeiran archipelago. — *Bol. Mus. Mun. Funchal,* 26 : 5-30.

COULOMB, J.:
1972. Sea Floor Spreading and Continental Drift. — *Geophysics and Astrophysics Monographs,* 2, 184 pp.

DEWEY, J. F., PITMAN, W. C., RYAN, W. B. F., & BONNIN, J.:
1973. Plate Tectonics and the Evolution of the Alpine System. — *Geol. Soc. Amer. Bull.*, 84 : 3137-3180.

EVERS, A., KLEMMER, K., MÜLLER-LIEBENAU, I., OHM, P. REMANE, R., ROTHE, P., STRASSEN, R. ZUR, & STURHAN, D.:
1970. Erforschung der mittelatlantischen Inseln. — *Umschau*, 70 : 170-176.

FAIRBRIDGE, R. W.:
1964. African Ice-Age Aridity. — In: *Problems in Palaeoclimatology*, pp. 356-363, J. Wiley & Sons Ltd.

FALKNER, G.:
1974. Über Acanthinulinae aus dem Obermiozän Süddeutschlands (Gastropoda: Pupillacea). — *Arch. Moll.*, 104 : 229-245.

FÉRAUD, G., GASTAUD, J., AUZENDE, J.-M., OLIVET, J.-L., & CORNEN, G.:
1982. $^{40}Ar/^{39}Ar$ ages for the alkaline volcanism and the basement of Gorringe Bank, North Atlantic Ocean. — *Earth and Planetary Science Letters*, 57 : 211-226.

FRIAS MARTINS, A. M.:
1981. *Oxychilus (Drouetia) agostinhoi* new species (Stylommatophora: Zonitidae) from the Azores Islands, its anatomy and phylogenetic relationships. — *Occ. Papers Moll. MCZ*, 4 : 245-265.

GELLERT, J. F.:
1974. Pluviale und Interpluviale in Afrika. Geologisch-paläoklimatologische und paläogeographische Fakten und Probleme. — *Petermanns Georgr. Mitt.*, 118 : 104-115.

GERMAIN, L.:
1921. Faune malacologique terrestre et fluviatile des Iles Mascareignes. — *Mém. Soc. Zool. France, Suppl.*, 495 pp.

GITTENBERGER, E.:
1983. On Iberian Cochlicopidae and the genus *Cryptazeka* (Gastropoda, Pulmonata). — *Zool. Meded. Rijksmus. Natuurl. Hist. Leiden*, 57 : 301-320.

GITTENBERGER, E., & RIPKEN, T. E. J.:
1983. *Discocharopa aperta* (Möllendorff, 1888) (Pulmonata, Charopidae) on Madeira. — *Basteria*, 47 : 58.

GROH, K.:
1983a. Revision der Land- und Süsswassergastropoden der Kapverdischen Inseln. — *Arch. Moll.*, 113 : 159-223.
1983b. Eine neue *Leptaxis*-Art aus den quartären Schneckensanden von Porto Santo (Madeiren) (Pulmonata: Helicidae). — *Arch. Moll.*, 114 : 59-64.

HALLAM, A.:
1981. Relative Importance of Plate Movements, Eustasy, and Climate in Controlling Major Biogeographical Changes Since the Early Mesozoic. — In: NELSON, G., & ROSEN, D. E.: *Vicariance Biogeography: a critique*, pp. 303-330. Columbia Univ. Press.

HAUSEN, H.:
1959. On the Geology of Lanzarote. — *Soc. Sci. Fenn., Comment. Phys.-Math.*, 22 : 4, 211 pp.

HESSE, P.:
1933. Zur Anatomie und Systematik der Familie Enidae. — *Arch. Naturgesch.*, N. F., 2 (2) : 145-224.

KERNEY, M. P.:
1976. Mollusca from an interglacial tufa in East Anglia, with the description of a new species of *Lyrodiscus* Pilsbry (Gastropoda: Zonitidae). — *J. Conchol.*, 29 : 47-50.

KEW, H. W.:
1893. The dispersal of shells. — *Internat. Scient. Ser.*, 75, 291 pp.

KREJCI-GRAF, K.:
1964. Die mittelatlantischen Vulkaninseln. — *Mitt. Geol. Ges. Wien*, 57 : 401-431.

LIETZ, J., & SCHWARZBACH, M.:
1971. Quartäre Sedimente auf der Atlantik-Insel Porto Santo Madeira-Archipel) und ihre paläoklimatische Deutung. — *Eiszeitalter u. Gegenwart*, 22 : 89-109.

MANDAHL-BARTH, G.:
1950. Systematische Untersuchungen über die Heliciden-Fauna von Madeira. — *Abh. senckenb. naturf. Ges.*, 469, 93 pp.

MITCHELL-THOMÉ, R. C.:
1976. Geology of the Middle Atlantic Islands. — Geb. Borntraeger Verlag, 382 pp.
1982. The geological settings and characteristics of the Atlantic Islands: — *Acta Geol. Acad. Scient. Hung.*, 25 : 395-420.
1983. The Cape Verde Archipelago and African affinities. — *Bol. Mus. Mun. Funchal*, 35 (155) : 175-206.

NILSSON, T.:
1983. The Pleistocene. Geology and Life in the Quaternary Ice Age. — F. Enke Verlag, 651 pp.

ODHNER, N.:
1931. Beiträge zur Malakozoologie der Kanarischen Inseln. Lamellibranchien, Cephalopoden, Gastropoden. — *Ark. Zool.*, 23 : 14, 116 pp.
1937. Little-known Land Mollusca from Madeira and La Palma (Canary Islands). — *Proc. Malac. Soc. London*, 22 : 353-364.

OSTENSO, N. A., & VOGT, P. R.:
1967. Steady State Crustal Spreading. — *Nature*, 215 : 810-817.

PANELIUS, S.:
1958. The Land and Freshwater Molluscs of the Cap Verde Islands. — *Soc. Scient. Fenn., Comment. Biol.*, 18 (3) : 3-30.

PASTOURET, L., AUZENDE, J.-M., LE LANN, A., & OLIVET, J.-L.:
1980. Temoins des variations glacio-eustatiques du niveau marin et des mouvements tectoniques sur le Banc de Gorringe (Atlantique du Nord-Est). — *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 32 : 99-118.

PEAKE, J. F.:
1971. The evolution of terrestrial faunas in the western Indian Ocean. — *Phil. Trans. Roy. Soc. Lond.*, 260 : 581-610.
1978. Distribution and Ecology of the Stylommatophora. — In: *Pulmonates*, 2A : 429-526. Academic Press.

REGTEREN ALTENA, C. O. VAN:
1950. The Limacidae of the Canary Islands. — *Zool. Verh. Rijksmus. Natuurl. Historie Leiden*, 11, 34 pp.

RIEDEL, A.:
1964. Zonitidae (Gastropoda) der Azoren. — *Bol. Mus. Mun. Funchal*, 18 (66) : 5-58.
1980. Genera Zonitidarum. — Backhuys Publisher, 197 pp.

ROTHE, P.:
1964. Fossile Strausseneier auf Lanzarote. — *Natur und Museum*, 94 : 175-187.
1966. Zum Alter des Vulkanismus auf den östlichen Kanarien. — *Soc. Scient. Fenn., Comment. Phys.-Math.*, 31 (13) : 1-80.

SCHWARZBACH, M.:
1974. Das Klima der Vorzeit. — F. Enke Verlag. 3rd Ed. 380 pp.

SJÖGREN, E.:
1972. Vascular Plant Communities of Madeira. — *Bol. Mus. Mun. Funchal*, 26 : 45-125.
1974. Local Climatic Conditions and Zonation of Vegetation on Madeira. — *Agronomia lusit.*, 36 : 95-139.

SOLEM, A.:
1979. A theory of land snail biogeographic patterns through time. — In: *Pathways in Malacology*, pp. 225-249. Bohn, Scheltema & al. Publishers.

TRYON, G. W., & PILSBRY, H. A.:
1906-1926. Manual of Conchology. — Pertinent Volumes 18-27.

VAGVOLGYI, J.:
1976. Body size, aerial dispersal and origin of the Pacific land snail fauna. — *System. Zool.*, 25 : 465-488.

VEGAS, R., & BANDA, E.:
1982. Tectonic Framework and Alpine Evolution on the Iberian Peninsula. — *Earth Evolution Sciences*, 4 : 320-343.

WALDÉN, H. W.:
1963. Historical and taxonomical aspects of the Land Gastropoda in the North Atlantic Region. — In: *North Atlantic Biota and their History*, pp. 153-171. Pergamon Press.

1983. Systematic and biogeographical studies of the terrestrial Gastropoda of Madeira. With an annotated Check-list. — *Ann. Zool. Fennici*, 20 : 255-275.

WENZ, W.:
1961-1962. Gastropoda, 1, Allgemeiner Teil/Prosobranchia. — In: *Handb. Paläozool.*, 6 : 1, 2nd. Ed., 1639 pp.

WIKTOR, A.:
1983. Parmacellidae of the Mediterranean Area and Canary Islands (Gastropoda, Pulmonata). — *Malak. Abh. Mus. Tierk. Dresden*, 9 : 82-96.

WOLLASTON, T. V.:
1878. Testacea Atlantica or the Land and Freshwater shells of the Azores, Madeiras, Salvages, Canaries, Cape Verdes and Saint Helena. 588 pp.

ZILCH, A.:
1959-1960. Gastropoda, 2, Euthyneura. — In: *Handb. Paläozool.*, 6 : 2, 834 pp.

ZIMMERMAN, E. C.:
1948. Insects Hawaii. I. Introduction. — *Univ. Hawaii Press*, 206 pp.