

ORIGINS AND AFFINITIES OF THE FAUNA OF MADEIRA

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SUMMARY. The terrestrial fauna of Madeira contains more than 3300 species, of which about 900 are considered endemic to the island. The overall percentage of endemic species (ca. 27%) is high, although it varies considerably among the different groups.

The groups with the highest percentages of endemic forms are Reptiles (100%), Mollusca (62%), Diplopoda (59%), Acari (56%), Trichoptera (57%), Dermaptera (46%), Araneae (41%) and so forth.

Some remarkable examples of insular radiation are shown by Diplopoda (genus *Cylindroiulus*: 29 endemic spp.), Mollusca (genus *Leiostyla*: 25 endemic spp.) and Coleoptera (genus *Laparocerus*: 23 endemic spp.; genus *Tarphius*: 21 endemic spp.; genus *Trechus*: 20 endemic spp.).

Most of the faunistic groups present strong affinities with central european fauna with slightly weaker affinities with the mediterranean fauna. This tendency is the opposite to that found in the fauna of the neighbouring Canary Islands.

INTRODUCTION

Oceanic islands are of particular interest to the biologist because of their isolation, mode of origin, climatic characteristics and consequent biological peculiarities. It is known that island faunas and floras are generally disharmonic; important taxonomic groups found in continental zones are absent. Also, many species that inhabit oceanic islands have a wide ecological range, living in habitats from which they are excluded on continents.

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As a consequence of their isolation, island populations may diverge from their parental mainland populations and become distinct endemic species or complexes of species which are found nowhere else. For all these reasons, the study of island biotas has been of great importance in the development of current concepts of biological evolution and biogeographical theories.

GEOGRAPHICAL REMARKS

The Madeiran archipelago consists of three groups of islands: Madeira itself (728 km²) and two isolated rocks (Ilheu do Desembarcadouro e Ilheu de Fora), Porto Santo (43 Km²) and 3 offshore islands (Ilheu de Cima, Ilheu de Baixo and Ilheu de Ferro), and the Desertas (Deserta Grande, Ilheu Chao and Bugio).

Madeira is an oceanic island, about 15 Km long by 23 Km wide which rises to 1860 m (Pico Ruivo). It is about 3 million years old (Watkins & Abdel-Monem, 1971). Marked topographic relief produces considerable climatic diversity (cf. Sjogren, 1974 and references therein), the eastern part of the island being considerably drier than the rest (Punta de S. Lourenço). The original vegetation has been substantially altered by man, with large areas destroyed or replaced by secondary vegetation. The highest parts are covered by montane heathland and occasionally snow and frost occur in winter.

The current paper deals only with the fauna of Madeira proper, leaving aside the isolated rocks close to Punta de S. Lourenço (which harbour endemic species in some groups, e.g. Isopoda) and the other two island groups in the archipelago.

Considering that any zoogeographical considerations must be based on sound taxonomic work, the fauna of Madeira is one of the best studied in the World. More than one thousand scientific papers have been published on it.

VERTEBRATES

OSTEICHTHYES

The eel (*Anguilla anguilla*) is present in ravines in Madeira, where it is relatively common. As in other Atlantic archipelagos it is the only indigenous fish (Bertin, 1946). Recently (1961) Rainbow Trout (*Salmo gairdneri*) and Brown

Trout (*Salmo trutta*) have been successfully introduced from northern Portugal (MacCrimmon, 1971).

AMPHIBIA

Rana perezi is the only frog living on the island. This species was previously erroneously identified as both *Rana temporaria* (Bertin, 1946) and *Rana esculenta* (Sarmiento, 1948). According to Sarmiento (1948) frogs were introduced onto the island in 1834 by the first "Conde de Carvahal".

The presence of *Hyla meridionalis* was also recorded by Sarmiento (1948) after the first observation by Jate Johnson in 1885 (after Sarmiento, op. cit.). Nevertheless, Maul (1948) thinks that this species (*H. arborea* after Maul) became extinct on the island as nobody has since seen or collected the frog. The disappearance of *Hyla meridionalis* in Madeira, an island with a lot of suitable habitats, is enigmatical. In the Canary Islands both species (*R. perezi* and *H. meridionalis*) may live in sympatry in the same habitats without any obvious competition. Nevertheless, an introduced population of *H. meridionalis* has similarly disappeared in the island of Mallorca, Balearic Islands (Mayol Serra, 1985).

REPTILIA

Lacerta dugesii is the only species of reptiles living on the island and is endemic to Madeira, Desertas, Porto Santo, Salvagem Islands and Azores. Richter (1980) considered *L. dugesii* to be closely allied to the north-african species *L. perspicillata*.

AVES

Some 33 species of birds breed in Madeira at the present time, and these species can be grouped in three classes: a) endemic species, b) species with insular populations considered as differentiated endemic subspecies, and c) species in which the insular populations are undifferentiated from the mainland populations.

The first group comprises two endemic species: *Pterodroma madeira* and *Columba trocaz*. The populations of the Madeiran Gadfly petrels were considered until a short time ago as a subspecies of the Atlantic Gadfly Petrel (*Pterodroma mollis*), although several authors believe it to be two different species, the Freira (*Pterodroma madeira*) from Madeira and Fea's Petrel (*Pterodroma feae*) from Bugio (Bourne, 1983; Collar & Stuart, 1985; Zino & Zino, 1986).

Columba trocaz was considered as co-specific with *C. bollii* from the Canary Islands, although it is currently thought to be a well-differentiated species (Cramp, 1985; Collar & Stuart, 1985). *C. trocaz* lives in the laurel forest, as do the congeners - *C. bollii* and *C. junoniae* - in the Canary Islands. It might therefore be considered as a geographic relict related to these forests (see Baez, 1992).

There are also other endemic species whose distributions include some of the Atlantic archipelagos. So, *Apus unicolor* and *Anthus bertheloti* are endemic to the Canary Islands and Madeira, and *Serinus canaria* is endemic to Azores, Madeira and the Canary Islands. These three macaronesian endemics are closely related to the european species *Apus apus*, *Anthus campestris* and *Serinus serinus*, respectively (Volsøe, 1951).

The second group of Madeiran birds include those species whose insular populations are considered as endemic subspecies, such as: *Tyto alba schmitzi*, *Sylvia atricapilla heineken*, *Regulus ignicapillus maderensis*, *Motacilla cinerea schmitzi*, *Fringilla coelebs maderensis* and *Carduelis cannabina nana*.

Nevertheless, the populations of some other "endemic" subspecies include also the Canarian populations, such as: *Falco tinnunculus canariensis*, *Accipiter nisus granti*, *Coturnix coturnix confisa*, *Turdus merula cabreræ* and *Petronia petronia madeirensis*.

Furthermore populations of some other "endemic" subspecies are found in three atlantic archipelagos: *Calonectris diomedea borealis* (Azores, Madeira, Canary Is.), *Larus argentatus atlantis* (Azores, Madeira, Canary Is.) and *Sylvia conspicillata orbitalis* (Madeira, Canaries, Cape Verde)

The final group includes those species in which the insular populations are undifferentiated from the mainland populations, such as: *Oceanodroma castro*, *Puffinus puffinus*, *Bulweria bulwerii bulwerii*, *Buteo buteo buteo*², *Alectoris rufa hispanica*, *Scolopax rusticola*, *Sterna hirundo*, *Columba livia*, *Apus pallidus brehmorum*, *Upupa epops*, *Erithacus rubecula microrhynchus*, *Carduelis carduelis parva*, *Carduelis chloris aurantiiventris* and *Passer hispaniolensis*.

² The madeiran populations were described as an endemic subspecies (*B. buteo harteri*). After JAMES (1984) these populations can not be differentiated from the mainland populations.

In conclusion, one can say that almost one-half (42%) of the birds that breed in Madeira have not obviously differentiated from the continental populations from which they originated. Therefore, their colonization is presumed to be recent. A time span of less than ten thousand years may be sufficient for isolated populations to undergo evolutionary changes (Bock, 1979).

One group of 14 non-endemic species are represented by 6 Madeiran endemic subspecies, 5 macaronesian endemic subspecies and 3 atlantic endemic subspecies, i.e., about 40 percent of the avifauna is subspecifically differentiated from continental populations. It can be assumed that their arrival may have taken place within the last 50.000 years, since this time span might be sufficient for such a differentiation (Fleming, 1962).

Finally, 2 species are strict Madeiran endemics and another three are Macaronesian endemics. These strict endemics represent only 6 percent of the avifauna (15 percent if macaronesian endemics are included) and this percentage is notably lower than that for endemism in other faunistic groups in Madeira: ca. 57% in Trichoptera, ca. 60% in Diplopoda, ca. 46% in Dermaptera, ca. 41% in Araneae, ca. 32% in Coleoptera, etc. If one takes into account that the age of the island is at least of about 3 m.y. (Watkins & Abdel-Monem, 1971) such a low level of differentiation within the avifauna is difficult to explain. Therefore, the avifauna must have undergone processes of faunal turnover, with a continuous cycle of colonization-extinction similar to that which is presumed to have occurred in others archipelagos such as New Caledonia, New Zealand (Mayr, 1965) or the Canary Islands (Baez, 1992). This opinion is also supported for the recent find of fossil birds that are not breeding on the island at the present time (Pieper, 1985).

The similar zoogeographic characteristics of the avifauna of Madeira and the Canary Islands (see Baez, 1992) can be explained by the proximity of the archipelagos and by having a common source area from which colonization occurred (Europe and Mediterranean subregion). Colonization may have been enhanced in the past by the presence of chains of islands between both archipelagos and the mainland which are now submersed (see Baez, 1982).

MAMMALIA

All the wild mammals from Madeira are synanthropic species which have been introduced to the island by humans (Mathias, 1988), e.g. rabbits (*Oryctolagus cuniculus*), rats (*Rattus rattus* and *Rattus norvegicus*), cats (*Felis catus*), ferrets (*Mustela furo*) and mice (*Mus musculus*). It is thought that

indigenous mouse populations existed before humans reached the island. These autochthonous mice reached a greater size than the current species (Pieper, 1981).

The only autochthonous extant mammals on Madeira are bats, of which 5 species are known: *Pipistrellus maderensis*, *Pipistrellus savii* (this record needs to be confirmed), *Nyctalus leisleri*, *Plecotus austriacus* and *Taderida teniotis*. All the species, except *P. maderensis*, which is endemic to Madeira and Canaries, have a wide distribution in the south of Palaearctic Region. *P. savii* and *T. teniotis* are also found in the Canary Islands. *P. austriacus* is closely related to *Plecotus teneriffae*, an endemic Canary Islands species, and might even be the same species (Ibañez & Fernandez, 1985).

INVERTEBRATES

NEMATODA

26 species of Nematoda are recorded from Madeira (Gadea, 1958; Sturhan, 1973a, 1973b, 1975). The Nematode fauna present cosmopolitan characteristics as do those of close archipelagos. All Madeiran species are widely distributed in Europe and North Africa, the most common species being *Plectus cirratus*, *Teratocephalus crassidens*, *Wilsonema auriculatum* and *Tylenchus filiformis*.

MOLLUSCA

About 230 living species of land molluscs have been recorded in Madeira. Of these some 219 are considered as indigenous and 144 of these are endemic (65 percent of the total). The high percentage of endemic genera shows the faunistic importance of this group: of 53 genera present, 15 (28%) are endemic (*Staurodon*, *Hemilauria*, *Boettgeria*, *Amphorella*, *Pyrgella*, *Cycichnidia*, *Steenbergia*, *Geomitra*, *Spirorbula*, *Caseolus*, *Disculella*, *Lemniscia*, *Discula*, *Pseudocampylaea* and *Lampadia*) and an other 5 are found only in other Atlantic archipelagos (*Janulus*, *Craspedopoma*, *Heterostoma*, *Actinella* and *Leptaxis*) (Waldén, 1984). Some genera have experienced a remarkable radiation into the island, such as *Leiostyla*, *Leptaxis* and *Boettgeria* (Waldén, 1983; Groh & Hemmen, 1984).

Besides these interesting endemics, about 20 species are synanthropic which have probably been introduced, e.g. *Milax sowerbyi*, *Discus rotundatus*, *Cochlicella barbara*, *Otala lactea*, *Cepaea nemoralis* and so on.

In summary, the land mollusc fauna of Madeira has, with exception of a few widespread 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 (Waldén, 1983).

NEMERTEA

Leptonemertes chalicophora is the only land Nemertea known in Madeira. This species is distributed in the Atlantic archipelagos of Azores, Madeira and Canaries and after Moore & Moore (1972) it might be considered as an endemic species of these islands.

PLATYHELMINTHES - TURBELLARIA

Four species, all widely distributed, are known from Madeira: *Bipalium kewense*, *Microplana terrestris*, *Microplana hovassei* and *Kontikia* sp. (Marcus & Marcus, 1959).

ROTIFERA

Schodduyn (1927) recorded 6 species belonging to the genera *Rotifer*, *Anuraea*, *Lepadella* and *Monostyla*, without any zoogeographic comments on their origin or distribution.

ANNELIDA

OLIGOCHAETA

Two species of aquatic worms (Naididae) have been recorded (Brinkhurst, 1969); the cosmopolitan *Nais communis*, and *Allonais paraguayensis*. Both species are widely distributed in America, Asia and Africa.

Concerning terrestrial worms, 11 species have been recorded on Madeira; most of them have a wide distribution in the Holarctic region (*Allolobophora caliginosa*, *Allolobophora chlorotica*, *Dendrobaena octaedra*, etc.). *Bimastus eiseni* has a Euro-american distribution and *Dendrobaena madeirensis* is distributed in Madeira and the north of the Iberian Peninsula (Zicsi, 1969; Michaelsen, 1903).

HIRUDINEA

Only one Palearctic species, *Dina lineata* has been recorded in the island (Sciacchitano, 1961).

ARACHNIDA

OPILIONES

A single species has been recorded in Madeira: *Phalangium opilio*. It is

widely distributed in the Palaearctic and also in North America (Schenkel, 1938).

PALPIGRADA

The mediterranean species, *Eukoenenia mirabilis*, is the only Palpigrad recorded in Madeira (Conde, 1984).

PSEUDOSCORPIONES

Fifteen species of Pseudoscorpiones are known in Madeira, two of them are endemics (*Paraliochthonius hoestlandti*) and *Pseudorhacochelifer coiffaiti*), one is endemic to Madeira and Azores (*Microcreagella caeca*), another one is endemic to Madeira and Canaries (*Calocheirus mirus*) and the remaining species have other European, Mediterranean or Iberian distributions (Pieper, 1981, 1990; MAHNERT *in litt*).

ACARI

About 55 species of Oribatida are known from Madeira; 12 of them (21.8%) are endemic (*Steganacarus similis*, *Archiphthiarius torosus*, *Damaeus interlamellaris*, *Cepheus undulatus*, *Neamerus lundbladi*, etc.). Two further species are endemics shared with other Atlantic archipelagos: *Liacarus madeirensis* (with Azores) and *Liacarus mucronatus* (with Canary Islands and Azores). The remaining species are european (17 spp. = 30%), holarctic (11 spp. 20%), mediterranean (5 spp. = 9%) afrotropical (1 sp. = 1.8%) or cosmopolitan (7 spp. = 12.7%) (Perez-Iñigo, 1988; Subias & Arillo, 1991).

Two endemic species of the family Ariophyidae belonging to the Acari Actinedida have been described, namely *Cymoptus vierai* and *Eriophyes barbujane*, both living on the laurel tree *Apollonias barbujana* (Carmona, 1987, 1988). Another endemic species is known from the intertidal zone: *Amhyadesia madeirensis* (Hyadesiidae) (Fain & Schuster, 1986).

25 species of aquatic Acari (Hydracnellae) have been recorded from Madeira, 21 of them are endemic, three are endemics to Madeira and Canaries and one species (*Sperchon brevisrostris*) is Palaearctic. All the endemics present close relationships to European species. One genus is also considered endemic to the island: *Maderomegapus* (Lundblad, 1942).

ARANEAE

There are about 150 species of spiders in Madeira, including in 98 genera and 32 families. About 55 species are endemic (37%) and this fauna generally shows close relationships with mediterranean fauna (Wunderlich, 1987, 1991).

Only a few genera have experienced a slight radiation, e.g. *Dysdera* (4 spp.), *Pholcus* (3 spp.), *Lepthyphantes* (3 spp.), *Philodromus* (2 spp.), *Centromerus* (2 spp.), etc. A genus is endemic: *Frontiphantes* (Linyphiidae) and it is monospecific (*L. fulgurenotata*). The remaining non-endemic species have mediterranean, palaeartic, holarctic, european or cosmopolitan distribution. Noteworthy among the mediterranean taxa is the presence of the "Black Widow" (*Latrodectus tredecimguttatus*) restricted to the xerix area of Punta de S. Lourenço.

CRUSTACEA AMPHIPODA

Three species of Gammaridae have been recorded (Dahl, 1958) in the island. *Pseudoniphargus* sp. is probably an endemic species. *Sarothrogammarus madeirensis* is an endemic species found only in Madeira, and *Chaetogammarus atlanticus* is a species distributed only on the Atlantic archipelagos (Azores, Madeira, Canaries).

Three species of Talitridae have also been recorded (Dahl, 1967): *Talitroides topitotum* has a Pacific and Indic distribution and has probably been introduced into the island with exotic plants, *Orchestia gammarellus* is a mediterranean species, and *Orchestia platensis* is widely distributed in both sides of the Atlantic. Both species of *Orchestia* live in the littoral zone.

COPEPODA

There are no data on this group, but Schodduyn (1927) recorded the genus *Cyclops* and Gadea (1958) recorded the genus *Bryocamptus*.

OSTRACODA

Three species have been identified unequivocally at present from Madeira: *Strandesia obliqua*, *Cypridopsis lusitanica* and *Potamocypris pallida*, all of them distributed in Europa or mediterranean subregion (Meisch & BRODDBAKER, 1993). A fourth species (*Heterocypris incongruens*) was seen in 1981 and 1986 in the fountains in Funchal (M.V. Hounscome, *pers com*).

CLADOCERA

Two cosmopolitan species have been recorded by Schodduyn (1927): *Chydorus sphaericus* and *Alona quadrangularis*.

ISOPODA

The diversity of the fauna of terrestrial Isopoda from Madeira is high and consists of 50 species (in the Canary Islands, La Palma which has a similar area harbours 13 species, and Tenerife, with almost threefold, has about 25 species). Of these 50 species, 8 are endemic to Madeira proper and 4 are endemic to Madeira archipelago. Two species are endemics shared with other Atlantic archipelagos (*Trichoniscus bassoti*, a cavernicolous species also living on the Canaries, and *Miktoniscus chavesi*, present also in Azores archipelago).

The most interesting genus is *Porcellio* which includes 5 endemic species in the island (*P. maculipes*, *P. cataractae*, *P. scitus*, *P. atlantidum* and *P. gruneri*) and three other endemic species to Madeiran archipelago (*P. ferroi*, *P. xavieri* and *P. normani*). All of these endemic species belong to the "atlantic-group" that includes more species endemic to small islets close to Madeira island, Porto Santo, Canary Islands, Iberian Peninsula and north Africa. All of these endemics show relationships with mediterranean species.

Some of the remaining species have a mediterranean distribution as *Stenoniscus pleonalis* and *Haplophthalmus danicus*, or are cosmopolitan, as synanthropic species *Armadillium vulgare*, *Porcellio laevis* and *Agabiformius lentus*. However, most of the species have a european distribution and have probably been introduced by man, e.g. *Porcellio dilatatus*, *Porcellionides sexfasciatus*, *Trichoniscus pygmaeus* and so on (Vandel, 1960).

One introduced species, *Trichoniscus pusillus*, has parthenogenetic populations on the island, similarly to other groups in insular conditions, e.g. *Haploembia solieri* (Embioptera) and *Pycnoscelus surinamensis* (Dictyoptera) in the Canary Islands (Baez, 1982).

One interesting fact concerning the terrestrial isopod fauna of Madeira is its dissimilarity with the Canary Islands fauna. In many groups, the fauna of both archipelagos are closely related and share many endemics. Only one endemic species of terrestrial isopod is common to both archipelagos, although many Madeiran endemics show close affinities with canarian endemics, e.g. those species belonging to the family Porcellinidae (R. RODRIGUEZ, comm. pers.).

MYRIAPODA

SYMPHYLA

Three widely distributed species are known in the island. *Scutigerebella immaculatam* and *Symphylella vulgaris* may be subcosmopolitan and

Scolopendrellopsis subnuda is at least Holarctic. These three species have probably been introduced in Madeira as in other volcanic islands, e.g. Azores, Canary Islands, St. Helena and Hawaii (Scheller, 1961; Scheller & Baez, 1989).

PAUROPODA

Eleven species of Pauropoda have been recorded from Madeira. All belong to the genus *Allopaupopus*, three of which (27) are considered endemics (*A. brincki*, *A. dahli* and *A. laurinus*). Most of the remaining species have a wide distribution (*A. vulgaris*, *A. aristatus*, *A. gracilis*, *A. tenuis*, etc.) (Scheller, 1962).

CHILOPODA

Four species of Lithobiomorpha are known in Madeira; *Lithobius fulvicornis* is a subcosmopolitan species, *L. pilicornis* and *L. crassipes* are European-North African species, and *L. lusitanicus* is known from the Iberian Peninsula. All the four species have been probably introduced onto the island by man (Eason, 1984). The mediterranean species *Scutigera coleoptrata* is the only Scutigeraomorpha present in the island.

About 10 species of Geophilomorpha are known from Madeira (MINNELLI, 1980; in litt.); most of them are palaeartic or mediterranean species. Among the most common species are: *Nannophilus eximius*, *Haploschendyla europea* and *Geophilus flavus*. The latter has been introduced into many countries and probably also in Madeira.

DIPLOPODA

Fifty four species are known from Madeira proper, 32 of them are endemic to the island, and 3 spp. are endemic to Madeira and other Atlantic archipelagos (*Polydesmus brincki*, *Siphonocryptus canariensis* and *Cynedesmus formicola*; the record of *Cylindroiulus madeirae* from the Azores is probably due to anthropochore dispersal). The remaining species have a European, W-mediterranean, NW-African or cosmopolitan distribution and most of them probably have been introduced by man quite recently. *Ommatoiulus moreleti*, an iberian species, is a good example: it has been introduced to all the atlantic islands and its populations are very dense in many places.

Of the 32 endemic species, 29 (90%) belong to the genus *Cylindroiulus* and three to the genus *Acipes*. *Acipes* is a Macaronesian-Iberian genus, with 1 species from Spain, six species from Madeira and its satellite islets, and one from the Canaries. *Cylindroiulus* is a huge genus with approximately 100 species widely distributed in the W-Palaeartic. Considering *Cylindroiulus* species from Madeira as a monophyletic group, this species-swarm is of

considerable evolutionary and biogeographical interest. It appears to be a fine example of insular adaptive radiation in a small oceanic island, and thereby differs from the classical cases of adaptive radiation (Galápagos finches, Hawaiian drosophilids) where an "archipelago effect" has played a major role. It is also noteworthy that *Cylindroiulus* has radiated into several biotope types (forest, open land, mountain tops) and, within the forest, into several microhabitat types (Enghoff, 1982, 1983a, 1983b; Read, 1989).

INSECTA

COLLEMBOLA

Some 74 spp. of springtails are recorded from Madeira, of which 3 are endemic species: *Friesea laderoi*, *Arrhopalites maui* and *Sminthurus gamae*. Most of the remaining species are cosmopolitan or have a wide distribution: Palaearctic (30%), Holarctic (10%), subcosmopolitan (7%) and so on. There is only one Nearctic species (*Entomobrya mineola*) (Gama, 1986).

PROTURA

Nine species of Protura are known from Madeira, most of them appear to have been introduced. A genus (*Maderentulus*), two species (*Maderentulus maderensis* and *Eosentomon noseki*) and one subspecies (*Acerentulus confinis maderensis*) are endemic. All are closely related to european counterparts (Tuxen, 1982).

The six remaining species are distributed in Europe or in the Iberian Peninsula and, after Tuxen (op. cit.), have probably been introduced quite recently.

DIPLURA

Campodea quilisi is the only Diplura known in Madeira (Conde & Barbier, 1965). This species has a W-Mediterranean distribution and has also been recorded in the Canary Islands (Sendra & Baez, 1986).

THYSANURA

Five species of Thysanura are known in the island; tow of them are endemic to Madeira and the Canaries (*Ctenolepisma vierai*, *Dilta insulicola*), a third one is known from Madeira, Canary and Cape Verde islands (*Neoaasterolepisma myrmecobia*), and the two remaining species are synantropic and widespread (*Ctenolepisma lineata*, *Lepisma saccharina*), (Mendes, 1982, 1989).

EPHEMEROPTERA

Mayflies are generally rather poorly represented in isolated islands. Only three species have been recorded from Madeira, two of them are very common species: *Baetis rhodani* (distributed all over Europe and northern Africa) and *Cloeon dipterum* a palaeartic species also distributed in the Atlantic archipelagos (Azores, Madeira and Canary Islands); the third one is endemic to Madeira and the Canary Islands (*Baetis pseudorhodani*) (Brinck & Scherer, 1961; Stauder, 1991). CLASEY (1966) recorded a female subimago belonging to an unidentified species of the genus *Centroptilum*.

ODONATA

Four species of dragonflies are known from Madeira: *Anax imperator* (Palaeartic), *Ischnura pumilio* (W-Palaeartic), *Sympetrum fonscolombei* (Palaeartic and Afrotropical) and *Sympetrum nigrifemur*. The latter species is endemic to Madeira and the Canary Islands and closely related to the european species *S. striolatum*. The Odonata fauna of Madeira is therefore clearly Palaeartic and all the species (except *S. nigrifemur*) are common in W-Europe.

DERMAPTERA

Eleven species of earwigs are known on Madeira, 4 of them (36%) are endemic (*Anechura schmitzii*, *Perirrhytus edentulus*, *Perirrhytus madeirensis* and *Perirrhytus pseudomadeirensis*), whilst the remaining seven species are cosmopolitan (*Anisolabis maritima*, *Labidura riparia*, *Forficula auricularia*, *Euboriella annulipes*, etc.) or palaeartic (*Forficula barroisi*) (Lange, 1991). After Brindle (1969) the geographic origin of these cosmopolitan or palaeartic species appears to be Europe or the Mediterranean subregion.

The genus *Perirrhytus* is endemic to Madeira proper.

DICTYOPTERA

About 13 species of cockroaches (Blattodea) have been recorded in Madeira, one of them is considered endemic (*Phyllodromica infumata*) and another one is restricted to the Azores and Madeira (*Phyllodromica chavesi*) (Princis, 1963). The remaining species have a world-wide distribution and most of them are synanthropic species, e.g. *Leucophaea maderae*, *Periplaneta americana*, *Periplaneta brunnea*, *Blattella germanica*, *Blatta orientalis*, *Pycnoscelus surinamensis* and so forth.

Only one species of the suborder Mantodea is present on the island, i.e. *Mantis religiosa*, distributed throughout W-Europe and north Africa.

ORTHOPTERA

Some 20 species of Orthoptera are known in Madeira, 6 of which are Tettigoniioidea, 6 are Grylloidea and 8 are Acridoidea. Four species (20%) are endemic (*Calliphona barretoii*, *Montana barretoii*, *Calliptamus madeirae* and *Euchorthippus madeirae*); the remaining species have a palaeartic distribution, a most of them being mediterranean (11 spp = 55%; e.g. *Ruspolia nitidula*, *Acheta hispanicus*, *Pseudomogoplistes squamiger*, *Chorthippus apicalis*, etc.), although four of them (20%) are distributed in the Old World (*Gryllus bimaculatus*, *Phaneroptera nana*, *Aiolopus thalassinus* and *Oedaleus decorus*) and one species has a cosmopolitan distribution (*Acheta domesticus*).

ISOPTERA

Three species of termites are known in Madeira. *Postelectrotermes praecox* is a endemic species that can be considered as a relict, the nearest neighbouring congener occurs on Aldabra (Lamb, 1980). Another termite on the island, *Cryptotermes brevis*, is a pantropical species widely distributed by man throughout the tropics. It is apparently restricted to Funchal, where it damages old buildings. Finally, *Reticulitermes lucifugus*, a W-mediterranean species, is considered by Lamb (1980) as a recent introduction onto Madeira.

EMBIOPTERA

The mediterranean species *Haploembia solieri* is the only Embioptera living in Madeira (Ross, 1966). The populations of this species in the island are parthenogenetic, as is common in other Mediterranean and Atlantic islands, e.g. Canary Islands. It is probable that this species has been introduced by man in the Atlantic islands.

MALLOPHAGA

There are two records of Mallophaga: *Goniodes dispar* on *Alectoris rufa* and *Halipeurus bulweriae* on *Bulweria bulweri* (Tendeiro, 1955; Edwards, 1961).

THYSANOPTERA

56 species of Thysanoptera have been recorded in Madeira (Zur Strassen, 1977, 1983). About 40-45% of these species must be considered as introduced; the remaining are considered autochthonous. Of these autochthonous species, five (8.9%) are endemic to the island (*Antillothrips repentinus*, *Hoplandrothrips maderensis*, *Hoplothrips lepidulus*, *Bacillothrips bagnalli* and *Gastrothrips mauli*), two species are endemic to Madeira and satellite islands (*Apterygothrips wollastoni* and *Haplothrips lundbladi*) and five species are endemic at least to two of the eastern Atlantic archipelagos.

Biogeographical affinities of this fauna are found in the northern Mediterranean area, whereas no close relationships exist with the southern Mediterranean fauna (Zur Strassen, 1977).

NEUROPTERA

14 species of Neuroptera are known from Madeira. Five of them (35%) are endemic to this island (*Hemerobius madeirae*, *Mallada sensitiva*, *Atlantochrysa sororcula*, *Atlantochrysa pseudoatlantica* and *Distoleon catta*). One species is endemic to the archipelagos of Madeira and the Canary Islands (*Semidalis candida*) and another one is endemic to Madeira, the Canaries and the Cape Verde islands (*Myrmeleon alternans*). The remaining species have an holarctic, circum-mediterranean, european or cosmopolitan distribution.

This fauna is dominated by Mediterranean taxa, although some endemic species show no close relationships with continental species (Ohm & Holzel, 1984).

PHASMIDA

There are no records of stick-insects in Madeira, although a specimen was found some years ago (BISCOITO, comm. pers.). It might be an fortuitous introduction and there are not more data on the presence of these insects in the island. A similar fact is known from the Canary Islands (Baez, 1982).

PSOCOPTERA

21 species of Psocoptera are known from Madeira, 5 of them are endemic of the island (*Caecilius marmoratus*, *Cerobasis maderensis*, *Trichopsocus coloratus*, *Trichopsocus brincki* and *Trichopsocus harteni*) and another two species are endemics that also occur on other Atlantic archipelagos (*Atlantopsocus adustus*: Madeira and Canaries; *Atlantopsocus chopardi*: Azores and Madeira). The remaining 15 species are W-Palaeartic (7 spp.), cosmopolitan (5 spp.), pantropical (2 spp.) and Holarctic (1 sp.).

The five endemic species are close to Palaeartic or european species (Lienhard, 1983; Meinander, 1966, 1975; Baz, 1989).

TRICHOPTERA

14 species of Trichoptera are known in Madeira proper, 8 of them (57%) are endemic of the island (*Synagapetus puntatus*, *Stactobia atra*, *Stactobia nybomi*, *Polycentropus flavostictus*, *Tinodes cinereus*, *Tinodes griseus*, *Tinodes merula*, and *Mesophylax oblitus*) and 3 are endemic to Madeira and Canaries (*Hydroptila fortunata*, *Oxyethira spinosella* and *Hydropsyche maderensis*). The

remaining three species have a wider distribution: *Hydroptila juba* which occurs in Portugal and Atlantic islands, *Hydroptyla vectis* which occurs in central and north Europe, and *Limnophilus affinis* which has a palaeartic range from Iceland to Japan (Nybom, 1965). As in the Canary Islands (see Baez, 1982) the trichopterous fauna presents a high percentage of endemic species and have general affinities with European fauna.

HEMIPTERA HETEROPTERA

Some 120 species of Heteroptera are known from Madeira (Lindberg, 1961). The most numerous families are Lygaeidae and Miridae, each of which include more than 30 species. Other important families are Pentatomidae, Anthocoridae and Coreidae, whilst several less-important families are represented by only a single species (Aradidae, Cimicidae, Microphysidae, etc.).

After Lindberg (op. cit.) about 17 species (14%) are endemic on Madeira proper (*Sehirus aeneus*, *Gonocerus madeirensis*, *Pionosomus madeirae*, *Chinacapsus atlanticus*, *Chinacapsus wollastoni*, *Velia maderensis*, etc.), 4 species are endemics on Madeira archipelago (*Nysius contiguus*, *Ischnocoris mundus*, *Esuridea lathridioides* and *Chinacapsus elongatus*) and 11 species are endemic to at least two atlantic archipelagos (*Tropistethus seminitens*, *Eremocoris wagneri*, *Tingis insularis*, *Wollastoniella obesula*, etc.).

About 50 species (40%) have a mediterranean distribution (*Tarisa flavescens*, *Piezodorus lituratus*, *Melanocoryphus superbus*, *Peritrechus gracilicornis*, *Nabis pseudoferus*, *Camtobrochis serenus*, etc.), 15 species (12%) are Palaeartic (*Peribalus vernalis*, *Plinthisus brevipennis*, *Orthops kalmi*, *Saldula pallipes*, etc.) and 8 species have a cosmopolitan distribution (*Nezara viridula*, *Ploiariola rubromaculata*, *Lyctocoris campestris*, etc.). Only one genus of Heteroptera is endemic to Madeira: *Chinacapsus*. This genus is the only one that is present as a species-swarm, having differentiated 7 species onto the island.

HEMIPTERA HOMOPTERA

APHIDOIDEA: About 122 species of Aphidoidea are known from Madeira (Ilharco, 1974, 1984). After Nieto et al. (1977) about 40 percent of them are cosmopolitan, 28% palaeartic, 12% holarctic and 6% have a mediterranean distribution. There are no species endemic to either Madeira or to the Atlantic archipelagos.

Coccoidea: About 79 species of Coccoidea are known from Madeira (Vieira et al., 1983), 5 of them are considered as endemic (*Aonidiella lauretorum*, *Aspidiotus madeirensis*, *Quadraspidotus laurinus*, *Luzulaspis cunhi*. and *Phenacoccus monieri*). The remaining species have either a subtropical (about 60%) or a palaeartic distribution (about 30%). VIERA et al. (1983) also consider that only 10 species may be indigenous to Madeira proper, almost all the others have been unintentionally introduced from Europe or subtropical/tropical regions, probably via imported plants.

Psylloidea: 8 spp. of Psylloidea are known from Madeira, 3 of them are endemic and closely related to mediterranean species: *Strophingia fallax*, *Arytainilla incuba* and *Arytainilla umbonata*; 2 species are madero-canarian endemics, 1 is known only from North Africa and Madeira and two species (*Trioza urticae* and *Trioza obliqua*) are widely distributed in the Palaeartic Region (Loginova, 1976).

Fulgoroidea: About 22 species of Fulgoroidea (belonging to the families Cixiidae, Issidae, Flatidae and Delphacidae) are known from Madeira. Ten of them (45%) are endemic to Madeira proper (*Hyalesthes madeirei*, *Cixius madeirensis*, *Issus maderensis*, *Calligypona bifurcata*, etc.) and one species (*Cyphopterus fauveli*) is endemic to the archipelago. Most of the remaining species have a palaeartic (*Megamelurus fieberi*, *Calligypona dubia*, *Calligypona leptosoma*, etc.) or mediterranean distribution (*Kelisia ribauti*, *Calligypona propinqua*, etc.) whilst one species is cosmopolitan: *Sogata furcifera*, (Lindberg, 1961).

The genus *Makarorysa*, with two sympatric species on Madeira (*M. madalta* and *M. madeco*) is a madero-canarian endemic genus (Remane & Asche, 1986).

Cercopoidea: Only one species of the family Aphrophoridae is known in Madeira: *Neophilaenus angustipennis*, considered so far as an endemic species in the Canary Islands and after Quartau & Andre (1988) it is probably a recent immigrant in Madeira.

Cicadelloidea: About 36 species of leafhoppers have been recorded from Madeira. Of these about 24 percent are endemic (*Aphrodes brachypterus*, *Typhlocyba maderae*, several species of *Asianidia*, etc.), about 43 percent are endemics species to Madeira and other Atlantic archipelagos, e.g. *Penthinia irrorata*, *Balclutha pellucens*, *Eupteryx capreola*, *Empoasca canariensis*, etc. Finally, the remaining species have an Holarctic, north-African or Afrotropical

distribution. It is probable that a significant proportion of these species (mainly those of Holoartic and worldwide distribution) have been introduced accidentally by man (LINDBER, 1961; Quartau, comm. pers.)

COLEOPTERA

The beetle fauna of Madeira proper includes 58 families and about 817 species (approximately 875 spp. are known from Madeira archipelago, Erber in litt.). Around 260 species are considered endemic. When considered by family, some have no endemic species (Clambidae, Corynetidae, Cleridae, Dryopidae, Dermestidae, Ostomidae, Nitidulidae, Endomychidae, Bruchidae, etc.), whilst others are comprised of 20% endemic forms (Hydrophilidae, Orthoperidae, Staphylinidae, Liodidae, Throscidae, Byrridae, Buprestidae, Lyctidae, Curculionidae, etc.). The representatives of some families are all endemics (percentage 100%) such as Melyridae and Phytidae (Lundblad, 1958; Erber, in litt.).

Comparatively few families contain endemic genera (considering only Madeira proper): Carabidae (*Elliptosoma*), Liodidae (*Stereus*), Orthoperidae (*Clypeastodes*), Staphylinidae (*Xenomma*), Colydiidae (*Prostheca*, *Ploeosoma*) and Curculionidae (*Stenotis*, *Echinosomidea*). Most of these endemic genera are monotypic. There are also other endemic genera distributed in all the archipelago, as for instance *Ptinodes* (Ptinidae), *Hadrus* (Tenebrionidae), *Ellipsodes* (Tenebrionidae), *Anillobius* (Curculionidae), etc.

Species-swarms are notable in some genera: *Laparocerus* (Curculionidae, 23 spp.), *Tarphius* (Colydiidae, 21 spp.), *Trechus* (Carabidae, 20 spp) and *Acalles* (Curculionidae, 7 spp). The beetle fauna of Madeira is so abundant that it is almost impossible to carry out an overall faunistic analysis, but most of the species have an european origin and the endemic species have european affinities. A well studied family, Chrysomelidae, will be useful as an example (Erber, 1986): around 36 species are known from Madeira archipelago, 8 of them (22%) are endemic to Madeira proper, 1 is endemic to the Madeiran archipelago and another two are endemic on Madeira archipelago and the Canaries. Seventeen (47%) are members of European and Mediterranean faunas.

STRESIPTERA

Pseudoxenos heydeni is the only one species of Stresiptera known from Madeira. This species have a W-palaeartic distribution and attacks to wasps of the family Eumenidae (Kinzelbach, 1978).

LEPIDOPTERA

RHOPALOCERA: 16 species of butterflies (Papilionoidea) are known from Madeira. Only one species (6%) is endemic: *Pararge xiphia*. The insular populations of four European species are considered as endemic subspecies: *Pieris brassicae wollastoni*, *Gonepteryx cleopatra maderensis*, *Hipparchia aristaeus maderensis* and *Lycaena phalaes phlaeoides*. The remaining species have a wide distribution in the Palaearctic and Mediterranean (*Colias crocea*, *Vanessa atalanta*, *Pararge aegaira*, *Neohipparchia statilinus*), one is Oriental (*Vanessa indica*), one is Nearctic (*Danaus plexippus*) and three have a subcosmopolitan distribution: *Artogeia rapae*, *Cynthia cardui* and *Lampides boeticus*. Finally, two more species are vagrant and visit Madeira occasionally: *Issoria lathonia* and *Hypolimnas misippus*.

HETEROCERA:

a) Macroheterocera: The Macroheterocera fauna includes some 76 species, the most numerous families being Noctuidae and Geometridae; 19 of them are endemic (25%) as *Herbulotina maderae*, *Idaea maderae*, *Eupithecia atlantica*, *Noctua teixerai*, *Mesapamea maderensis* and so on. Most of the remaining species have a wide distribution throughout Europe, Asia and Africa, including those typically migratory species as *Acherontia atropos*, *Hyles euphorbiae*, *Perigea capensis*, etc. Finally, some species have a cosmopolitan distribution as *Hyles lineata*, *Agrotis ipsilon*, *Peridroma saucia*, *Heliotis armigera*, etc.

b) Microheterocera: The fauna of Microheterocera includes 21 families and about 190 species. The most numerous families are Pyralidae (52 spp.), Tortricidae (25 spp.), Gelechiidae (16 spp.), Blastobasidae (18 spp.) and Tineidae (16 spp.). Most of the species have a European distribution and most of the endemic species also have European affinities. Other species show different distributions: Mediterranean, Palaearctic, Tropicopolitan, etc.; some of them are cosmopolitan, including some pest species such as *Opogona sacchari* or *Pyralis farinalis*.

There are no endemic genera and only the genus *Blastobasis* (Blastobasidae) shows any remarkable radiation. Most of the 18 species present are endemic to Madeira.

DIPTERA

The Diptera fauna of Madeira includes 63 families and about 380 species; the most numerous families are Chironomidae (36 spp; Baez & Armitage, 1990), Muscidae (30 spp.), Syrphidae (24 spp.), Sphaeroceridae (22 spp.), Ephydriidae

(20 spp.) and so on. A total of 53 species are considered endemics (ca. 14%), although the percentage of endemics varies considerably between different families. Several have a high percentage of endemic forms, e.g. Lauxaniidae (100%), Therevidae (100%), Tipulidae (70%), Dolichopodidae (50%), Limoniidae (40%), etc. There is only one endemic genus: *Azaisia* (Rhinophoridae) whilst another one is endemic to Madeira and the Canaries: *Teneriffa* (Dolichopodidae). Some genera show substantial radiation: *Sapromyza* (Lauxaniidae, 8 spp.), *Machimus* (Asilidae, 3 spp.), *Nephrotoma* (Tipulidae, 3 spp), *Psilocephala* (Therevidae, 2 spp.), etc. About 20 species are endemic to Madeira and Canaries, 7 spp. are endemic to Madeira and Azores and 10 spp. are endemic to the north Atlantic archipelagos (Madeira, Canaries and Azores).

The remaining species are mostly european (25%), holarctic (17%) or palaeartic (10%), and most of the endemic species cited have european affinities. Species with mediterranean distributions are poorly represented (6,5%), as are afrotropical species (0,5%). About 45 species (ca. 12%) are cosmopolitan, most of them synanthropic, and in some families the percentage of these species is very high, e.g. Drosophilidae, Fannidae, etc.

SIPHONAPTERA

Dasypsyllus gallinulae gallinulae is the only flea recorded in Madeira proper (SMIT, 1957). However it is thought that most of the "domestic" species are also found there, e.g. *Pulex irritans*, *Ctenocephalides canis*, *Stenoponia tripectinata*, *Ctenocephalides felis*. All of them have been recorded from the smaller islands of the Madeira archipelago: Porto Santo and Deserta Grande (Hopkins & Rothschild, 1953, 1956, 1962).

HYMENOPTERA

The Madeiran Hymenoptera fauna includes 31 families and more than 500 species. About 18-20% of the species are considered endemics with european affinities. whilst most of the remaining species have a european distribution. Some species are holoartic, and others have a cosmopolitan distribution, mainly those synanthropic species.

As in other groups, many species are known only from Madeira and the Canaries. Some examples are: *Pteromalus ametrus* (Pteromalidae), *Xenomerus canariensis* (Scelionidae), *Zaglyptus rufus*, *Dichrogaster tenerifae*, *Campoplex praeacuppator* (Ichneumonidae) and so on.

Only two families contain endemic genera, i.e. Pteromalidae (*Makaronesa*, *Mauleus*) and Diapriidae (*Mantara*) (Graham, 1975, 1981, 1984). A few genera

have split into a species-swarm: *Makaronesa* (6 spp.), *Bethylus* (3 spp.) and *Hormius* (3 spp.).

GENERAL CONCLUSIONS

The terrestrial fauna of Madeira contains more than 3300 species, the most numerous groups being Coleoptera, Hymenoptera, Diptera, Lepidoptera, Hemiptera, Mollusca, and Araneae (see Table 1). About 900 species are considered endemic to the island.

Most of the faunistic groups present strong affinities with the central european fauna and slight weaker affinities with the mediterranean fauna. This tendency is opposite to that found in the fauna of the neighbouring Canary Islands (cf. Baez, 1982).

If one accepts the geological evidence that Madeira is an oceanic island, i.e. an island which has never been connected with a continent, the fauna must have been acquired by air or transoceanic colonization, and the seamount along the Madeira-Iberian crest may have provided stepping stone islands in early times (see Baez op. cit.).

The overall percentage of endemic species (ca. 27%) is high if one takes into account the area of Madeira. It is known that the number of endemic species on islands is generally higher in bigger islands (Wilson, 1988; cf. Baez, 1982). The percentage of endemic species varies considerably among the different groups (see Table 1). With the exception of the Reptiles (with only one endemic species on the island, i.e. 100% endemism), the groups with the highest percentages of endemic forms (more than 50%) are: Mollusca (62%), Diplopoda (59%), Acari (56%) and Trichoptera (57%). Notable groups with less than this proportion are Dermaptera (46%), Araneae (41%), Neuroptera (35%), Coleoptera (31) and so forth.

The number of endemic genera is high in Mollusca (15 genera) and Coleoptera (8 genera) and there are 3 endemic genera in Hymenoptera and one endemic genus in the following groups: Acari, Araneae, Protura, Dermaptera and Diptera. Finally, some remarkable examples of insular radiation ("species-swarms") are found in the Madeiran fauna, e.g. the genus *Cylindroiulus* (Diplopoda, Julidae; 29 spp.), *Leiostyla* (Mollusca, Pupillidae; 25 spp.), *Laparocerus* (Coleoptera, Curculionidae; 23 spp.), *Tarphius* (Coleoptera, Colydiidae; 21 spp.), *Trechus* (Coleoptera, Carabidae; 20 spp.), *Acalles*

(Coleoptera, Curculionidae; 7 spp), *Sapromyza* (Diptera, Lauxaniidae; 8 spp.), *Leptaxis* (Mollusca, Helicidae, 6 spp.) and *Boettgeria* (Mollusca, Clausiliidae; 7 spp.).

TABLE 1: Total number of species, number of endemic species, percentage of endemic species and number of endemic genera of the terrestrial groups of the fauna of Madeira proper.

(* = introduced; ** = endemic to Atlantic archipelagos; *** = endemic to Madeira and Azores).

GROUP	Nº spp.	Nº spp. endemic	% spp. endemic	Nº genera endemic
VERTEBRATA				
Osteichthyes	3*	-	-	-
Amphibia	1*	-	-	-
Reptilia	1	1	100	-
Aves	33	2	6	-
Mammalia	5	(1**)	-	-
INVERTEBRATA - OTHER THAN ARTHROPODA				
Nematoda	26	-	-	-
Turbellaria	4	-	-	-
Nemertea	1	(1**)	-	-
Rotifera	6	-	-	-
Annelida				
Oligochaeta	13	-	-	-
Hirudinea	1	-	-	-
Mollusca	230	144	62	15(+5**)
INVERTEBRATA - ARTHROPODA				
Palpigradi	1	-	-	-
Pseudoescorpiones	14	2(+1***)	14	-
Opiliones	1	-	-	-
Acari	83	40(+2**)	48	1
Araneae	150	55(+20**)	37	1
Crustacea				
Isopoda	50	12(+2**)	24	-
Others	9	1(+1**)	11	-

(continued)

GROUP	Nº spp.	Nº spp. endemic	% spp. endemic	Nº genera endemic
Symphyla	3	-	-	-
Pauropoda	11	3	27	-
Chilopoda	15	-	-	-
Diplopoda	54	32(+3**)	59	-
Collembola	74	3	4	-
Protura	9	2	22	1
Diplura	1	-	-	-
Thysanura	5	(2**)	-	-
Ephemeroptera	3	(1**)	-	-
Odonata	4	(1**)	-	-
Dermaptera	11	4	36	1
Dictyoptera	14	1(+1***)	7	-
Orthoptera	20	4	20	-
Isoptera	3	1	33	-
Embioptera	1	-	-	-
Mallophaga	2	-	-	-
Thysanoptera	56	7(+5**)	12	-
Neuroptera	14	5(+2**)	35	-
Phasmida	1*(?)	-	-	-
Psocoptera	22	5(+2**)	22	-
Trichoptera	14	8(+3*)	57	-
Heteroptera	120	21(+11**)	17	-
Homoptera	268	27(+16**)	10	-
Lepidoptera				
Rhopalocera	16	1	6	-
MacroHeterocera	76	19	25	-
MicroHeterocera	190	35(?)	18(?)	-
Coleoptera	817	260	31	8
Stresiptera	1	-	-	-
Diptera	383	58(+37**)	15	1
Siphonaptera	1	-	-	-
Hymenoptera	500	100	20	3
TOTAL:	3341	860(+111**)		

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