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BIOGEOGRAPHIC PATTERNS OF THE AEGEAN REGION AND THEIR GEOLOGICAL ORIGIN

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ABSTRACT

Disjunctive patterns of distribution and island endemism are typical for the flora and fauna of the Aegean Archipelago. It is possible to explain their dispersal by tsunamis. One can observe a tendency of the phases of volcanic activity to be generally connected to the glacials. The phases of dispersal can be correlated with the phases of volcanic activity, whereas the endemic markings can possibly develop during phases of interglacial inactivity. Thereby island arc - marginal basin - systems as the Aegean Sea prove to be centres not only of recent geodynamic activity but also of biological origin of species.

THE PROBLEM OF LANDBRIDGES

The distribution of land mammals in the Mediterranean Neogene is a consequence of geokinematic and climatic events (STEININGER et al. 1985). Landbridges and drifting microplates make the faunistical exchange possible. But since the late Pliocene the land-sea-configuration as we presently know is finished. Because of this it is difficult to explain the conquest of the isolated Aegean islands by the Pleistocene mammals.

After the compilation by SCHRÖDER (1986) the intact Aegean land mass continued to the Miocene. In the Langhian-Serravallian stages the subsidence of intramountain basins started, followed by the synchronous collapses of the Northern Aegean Sea and the Cretan Sea in the Tortonian. The Asiatic mainland was totally separated from the Greek Archipelago. Crete and Karpathos were separated by a strait, but the Milos group still belonged to the Cyclade peninsula.

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In the Messinian the cut off from the Atlantic Ocean and the formation of evaporites followed. At Milos dolomitic marls are found over the crystalline basement. After the re-opening of the Mediterranean Sea in the Upper Miocene the configuration of the recent coast lines started. In the Pliocene Karpathos and Rhodes were also separated by a strait and Milos had no more land connections.

Since this time the landbridges from the Peloponnese via Crete and Rhodes or via the Cyclades to Turkey are not provable, with the exception of faunistical arguments. All authors discussed the presence of landbridges as a result of sinking sea levels with the ice ages, which should make a faunistical exchange possible. In some cases zoologists postulated landbridges or straits to explain the distribution of one or several species. An example is the so called "Karpathos-Trench", which was constructed by KUSS (1975) for the distribution of Quaternary dwarf deer.

It confuses, that the paleogeographic propositions change with animals and plants which are discussed. The investigations by DERMITZAKIS & SONDAAR (1979) have shown that the Pleistocene mammals of the Aegean Archipelago didn't live in an ecological balance. Because of this they concluded that there mostly has been a swimming colonization. In principle SONDAAR & DERMITZAKIS (1982) differentiated four original dispersal routes:

-- corridors via landbriges with balanced mainland fauna
-- filters via landbridges (especially peninsula connections) with unbalanced mainland fauna
-- the "sweepstake" over larger water barriers with unbalanced endemic fauna
-- "commuter"-routes over narrow water obstacles with unbalanced fauna of mainland species.

The swimming dispersal must also be postulated for the reptils, whose biogeographic distribution seems to be more confused than that of the mammals (see the maps by CYRÉN 1941). The swimming dispersal of the rodents and other small mammals is a problem. There are physiological limits set by the exposure and the food shortage. Therefore STORCH postulated even in 1977 a Quaternary landbridge between Crete and Rhodes, to explain the immigration of the mouse *Apodemus mystacinus*. Yet, the part of the birds, especially of predators, for the dispersal of mice and lizards is unclarified.

A special problem is the dispersal of landsnails. They cannot survive in salt water longer than several hours or days because of their osmotic limits. After MYLONAS (1982) in many cases the dispersal of landsnails seems only to be possible in context with "geological events". But of which kind such "geological events" should be ?

THE ENDEMIC HERPETO-FAUNA OF MILOS

The Milos island group at the western border of the Archipelago is very popular for its endemic herpeto-fauna. Here the Cyclades blunt-nosed viper (*Vipera lebetina schweizeri* WERNER) occurs, which points to its origin in Anatolia, so that herpetologists suspected a relic-endemism of the age before the Aegean collapse (WERNER 1938; WETTSTEIN 1953). This assumption is confirmed by the fact, that the Melian viper is ovipare as compared to the ovovivipare mainland race. So there is the question, whether there exist parallels to this potential relic-endemism in the Melian flora and fauna.

To the island group of Milos consists of the main island Milos the small islands Kimolos, Polyaigos, and Antimilos, which all belong to the South Aegean Island Arc. Especially in the deserted western part of Milos some macchia remains in the valleys around Profitis Ilias. Possibly this macchia is similar to the original vegetation.

The Melian macchia and its degraded phrygana are the common habitates of the Melian viper, whose colour and markings are perfectly adapted to the volcanic rocks of the island. The particulary poisonous and venomous snake occurs on Milos, Kimolos, Polyaigos and in a distinct race on Sifnos. Only from Milos also a pure red coloured form is known (KLEMMER 1982). The triangular head and the vertical pupils are distinct characteristics to distinguish the viper from the other Melian snakes. Among them an other endemic race is found: The Melian grass snake (*Natrix natrix schweizeri* L. MÜLLER). On Antimilos a race of *Elaphe quatuorlineata* (*E. qu. muenteri* BEDRIAGA) occurs, which is missing at Milos, but occurs also at Mykonos.

Of endemic lizards the Milos wall lizard (*Podarcis milensis milensis* BEDRIAGA) and *Lacerta trilineata hansschweizeri* L. MÜLLER are found at Milos. The Milos wall lizard is omnipresent at Milos, from the coastline up to the peak of Profitis Ilias. The lizard occurs also at Kimolos and Polyaigos, while at Antimilos and far away isles special races are found:

-- *Podarcis milensis schweizeri* MERTENS at Antimilos
-- *P. m. gerakuniae* L. MÜLLER at Falconera
-- *P. m. adolfjordansi* BUCHHOLZ at the Ananes isles.

At Antimilos the endemic Aegean wild goat occurs, called agrimi (*Capra aegagrus pictus* ERHARD), which is also found on Samothrake (SCHULTZE-WESTRUM 1963). This goat is closely related to the Cretan wild goat (*Capra aegagrus cretica* SCHINZ). In the past the "agrimi" of Antimilos occured also at Milos and its neighbour islands, as the name Polyaigos indicates, which means "many goats".

Other endemics are found among the orthopters, the isopods, and the landsnails. *Albinaria turrita* occurs in special races at Milos and Antimilos. But not all endemics are so very clearly developed as the potential relic-endemism of the Melian viper.

Especially strange is the fact, that also no parallels to the herpeto-endemism exist in the Melian flora. The only known phyto-endemite of Milos is *Genista melia* BOISS., a kind of broom, closely related to the Westmediterranean *G. scorpius* (L.) DC., missing today. At least the *Ophrys* group, a common orchid genus with a great variety, should have produced endemic forms. By specific investigations two types with endemic markings could be found, which were not known from Milos before. They are local races of *Ophrys omegaifera* H. FLEISCHM. and *Ophrys cretica* E. NELSON.

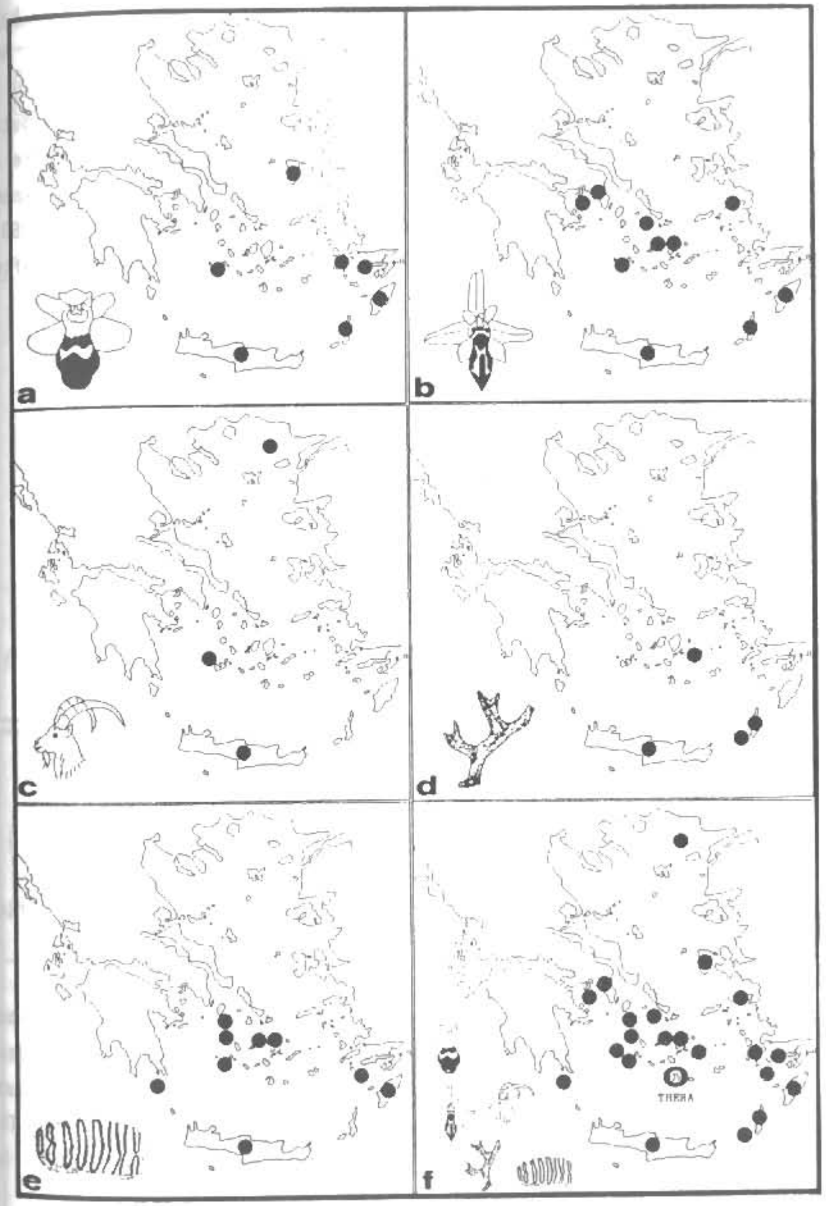
BIOGEOGRAPHIC DISPERSAL BY FLOOD WAVES (TSUNAMIS)

Amazing is the fact, that the Melian type of *Ophrys omegaifera* is closer to the Westmediterranean *Ophyrs dyris* MAIRE than to the Cretan race. The orchid was thought to be endemic at Crete, Karpathos, and Rhodes up to 1981 (BAUMANN & DAFNI), but was later also found at Chios, Kos, and the peninsula of Bodrum (BUTTLER 1986). The potential base form is the Asiatic *Ophrys fleischmannii* HAYEK, which also occurs at Crete and isolated at Attica and Hydra (see fig. 1 a).

The affinity of the Melian race to the Westmediterranean race shows, that in this case the centre of the differentiation must be suspected in the Aegean region. It it not possible to compare the origin of this separation with the separation in eastern and western races known from North Europe set by the Pleistocene icing over.

Also *Ophrys cretica* occurs at Milos in a distinct race. The species is related to *Ophrys kotschyi* H. FLEISCHM. & SOÓ, which is endemic to Cyprus. The distribution pattern is similar to *O. omegaifera* (see fig. 1 b). Noticeable is the fact, that these orchids are missing in the northern and southern Cyclades, whereas the Cretan Sea seems not to be a barrier. This disjunctive pattern of distribution with occurrence at Crete and Milos is similar to that of the wild goats (see fig. 1 c). This pattern returns in the distribution of Quaternary dwarf deer: Crete, Kasos, Karpathos, and on the other side of the Cretan Sea isolated at Amorgos (see fig. 1 d).

At last remember the Quaternary dwarf elephants, which have been found at Kithira, Crete, Rhodes, Tilos, and on the other side at the Cyclades Naxos,



a) *Ophrys omegaifera* H. FLEISCHMANN (after BUTTLER 1986 and own investigations)
b) *Ophrys cretica* E. NELSON (after BUTTLER 1986 and own investigations)
c) *Capra aegagrus ssp.* (after SCHULTZE-WESTRUM 1963)
d) Fossil Aegean dwarf deer (after DERMITZAKIS & SONDAAR 1979)
e) Fossil Aegean dwarf elephants (after DERMITZAKIS & SONDDAR 1979)

Fig. 1. Distribution patterns of selected plants and animals of the Aegean region and their projection (f).

Paros, Kithnos, Sifnos, and Milos (see fig. 1 e). MARINOS & SYMEONIDIS (1977) have shown, that the process of dwarfing must have happened at the islands. New investigations by DERMITZAKIS & VOS (1987) confirm this.

Surprising is the projection of all these patterns in one map: The outer points describe a circle around the island group of Thera, which was a centre of volcanic activity for the last 1.6 mio. years (see fig. 1 f). Thera became known for its catastrophic eruptions. After YUKOYAMA (1978) the Minoan tsunami was 89 m high at the centre and reached Crete after twenty and the Levantine coast after hundred minutes (see fig. 2).

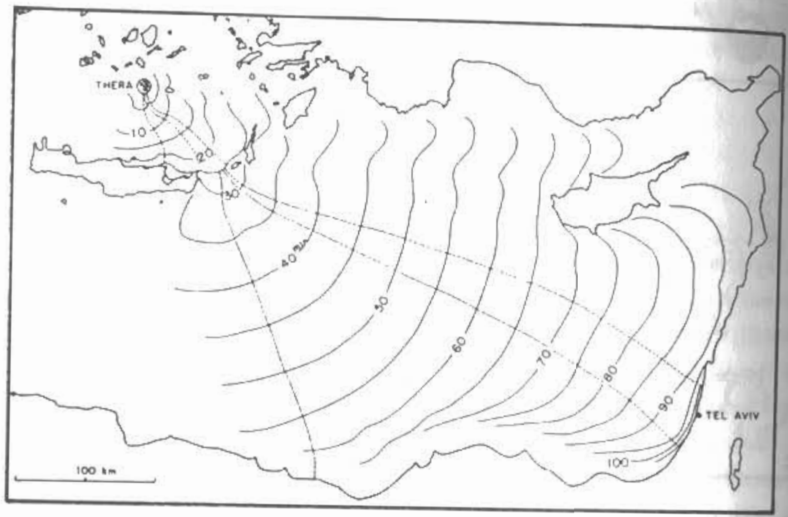


Fig. 2. Refraction diagram of the Minoan tsunami from Thera to Tel Aviv (after YUKOYAMA 1978).

It is plausible that such tsunamis devastated the Aegean coastal regions once again. Each time huge numbers of animals and plants were washed into the sea, in fact at the same time, which caused simultaneous landing of many individuums of one species. This is the requirement for the emergence of new races. The far-reaching dispersal of robust plants and animals seems to bepossible by currents.

One kind of robust animal is the Melian viper. The map shows the recent surface currents of the Mediterranean Sea (after LACOMBE & TCHERNIA 1972). The snake is found at the eastern mainland, also isolated at Cyprus and in Tunisia. Among them, in the centre of the Sea, lives the Milos endemite (see fig. 3 a).

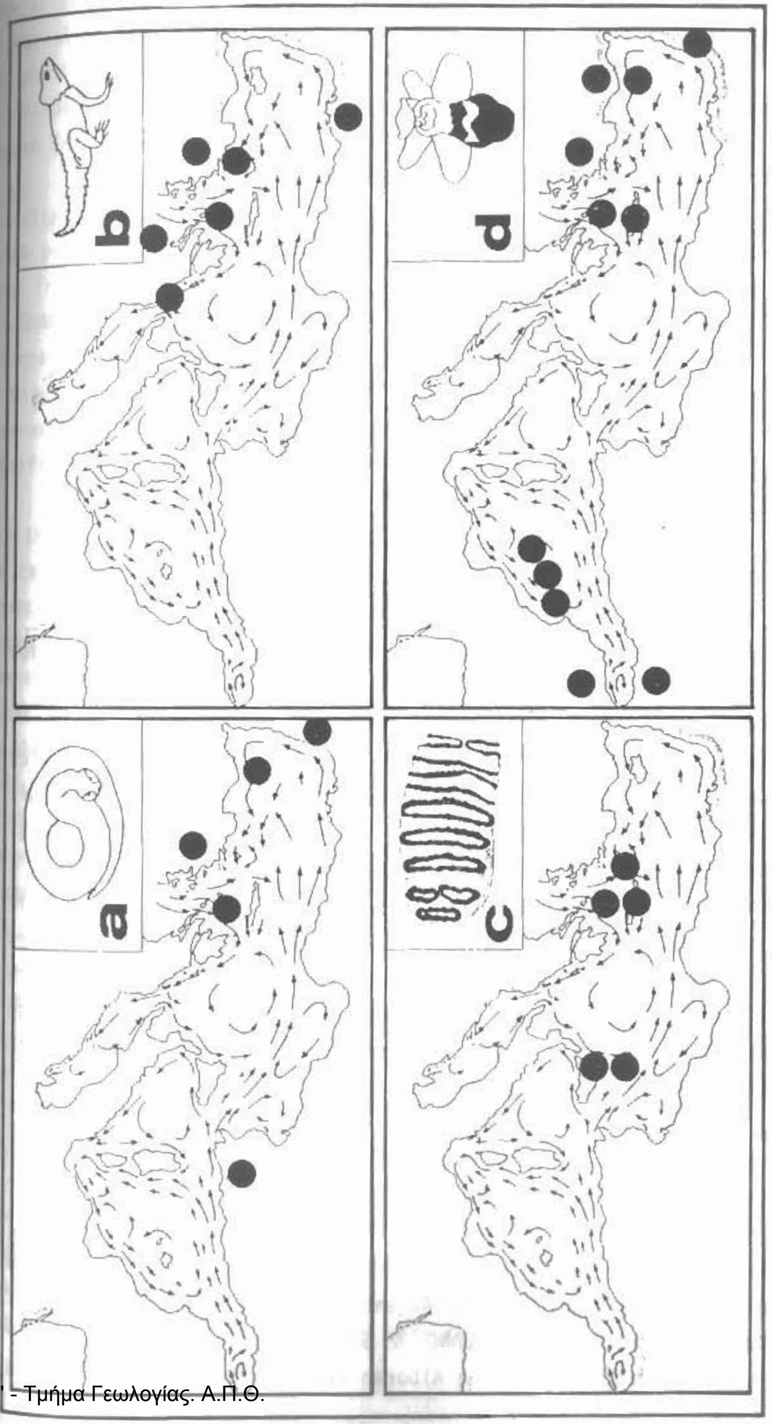


Fig. 3. Distribution patterns of selected plants and animals in context with the Mediterranean surface currents after LACOMBE & TCHERNIA 1972.

a) *Vipera lebetina schweizeri* WERNER (after JOGER 1984)
b) *Agame stellio stellio* L. (after MERTENS & WERMUTH 1960)
c) Dwarf elephants (mainly after DERMITZAKIS & SONDAAR 1979)
d) *Ophrys omegaifera complex* (after BAUMANN & DAFNI 1981; BUTTLER 1986 and own investigations)

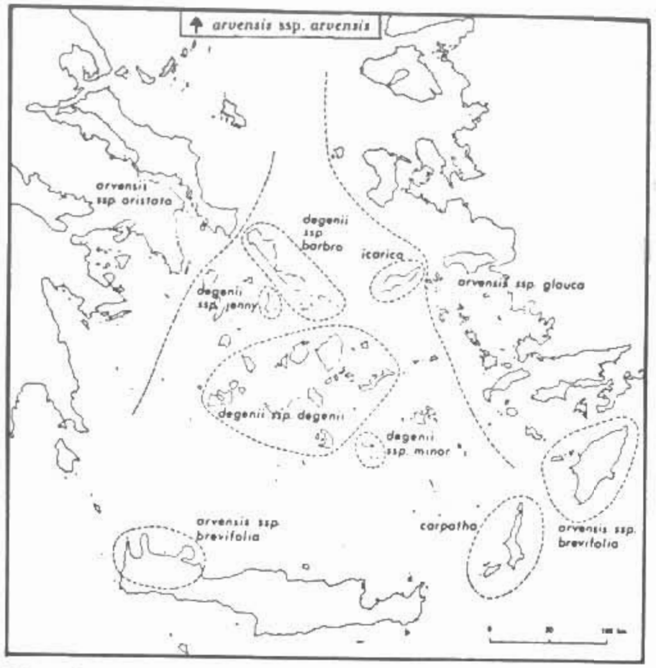


Fig. 4. Distribution pattern of the *Nigella arvensis* complex in the Aegean region (after STRID 1970).

Another kind of robust animal is the hardun (*Agama stellio stellio* L.), which inhabits Turkey and Lower Egypt. Isolated populations are known from the surrounding of Thessaloniki, from the central Cyclades (Mykonos, Delos, Paros, Antiparos, and Naxos), from Rhodes and Corfu (see fig. 3 b).

Following the recent currents via Corfu we reached Sicily and Malta. This is the route of the Greek west colonization in ancient times. Also, we find here the first remains of dwarf elephants out of the Aegean Sea (sea fig. 3 c). Much more westward *Ophrys dyris* MAIRE occurs, at the Balearic Islands and on both sides of Alboran Sea. Remember that *Ophrys dyris* is more similar to the Melian than to the Cretan race of *Ophrys omegaifera* (see fig. 3 d).

AEGEAN ENDEMISM AS A RESULT OF VOLCANIC PHASING

In contradiction to the distribution pattern of the *Ophrys omegaifera* complex the recent surface currents from the Atlantic Ocean run through the strait of Gibraltar into the Alboran Sea. HUANG & STANLEY (1972) have shown by sedimentological examinations, that in the Alboran Sea with the glacials changed

the directions of currents. This is an important indication of the glacial dispersal of the *Ophrys omegaifera* complex (see fig. 3 d). Another clear indication of glacial dispersal is the pattern of the *Nigella arvensis* complex: The distribution limits of the races are congruent with the glacial coast lines of the Aegean Sea (see fig. 4, after STRID 1970).

It must also be asked, whether Thera was the unique source of volcanic activity at glacial times. Potentially all volcanos at the South Aegean Island Arc which produce lavas of low viscosity are possible. A compilation of radiometric data from the literature (ANGELIER et al. 1977; FYTIKAS et al. 1976, 1984; HUIJSMANS 1985) shows, that primarily the Nisyros-Yali group before the Turkish westcoast plays an active part in the Upper Pleistocene (see tab. 1). The rocks of Nisyros, mapped by DAVIS (1968), are nearly the same as those of Thera. So Nisyros could be the second important source of tsunamis with biogeographic significance.

But the table of radiometric data of Aegean volcanic rocks in context with the data of the marine oscillations of the ice ages exposes another surprise: One can observe a tendency of the phases of volcanic activity to be generally connected to the glacials. The possible cause for this synchronism could be the fluctuations in the body of Aegean Sea water in the rhythm of ice ages: Crustal erosion and magmatic differentation during the interglacials, extension and volcanism during the glacials. Then the phases of dispersal can be correlated with the phases of volcanic activity, whereas the endemic markings could possibly have developed during phases of interglacial inactivity. This is exactly the case shown by the distribution of the *Nigella arvensis* complex. And this is also an explanation for the common occurence of mainraces and endemics as the *Ophrys omegaifera* complex shows. The dwarfing of the Pleistocene mammals was associated with interglacials, too (see DERMITZAKIS & VOS 1987).

It seems, that the dispersal by tsunamis is the normal way of dispersal for orchids from the Aegean Sea to the West Mediterranian, because the disjunctive patterns of distribution are very normal. For example the orchid *Anacamptis pyramidalis* L. C. M. RICHARD occurs as the dwarf race *urvilleana* SOMMIER & CARUANA GATTO at Crete and after BUTTLER (1986) also at Malta and Gozo, in fact here together with the base race, but flowering earlier.

In the Aegean the dispersal by tsunamis may be the normal way of dispersal for all robust animals and plants which can actively swim or passively drift: Many mammals, reptils, arthropods. Because of the short times of the tsunami spreading the dispersal of small rodents and landsnails may be possible. In some cases it could be, that only the eggs were dispersed (spides, orthopters, isopods).

Volcanic area	K/Ar-age (mio. y.)	Mediterranean Sea Phase of fluctuation
Edessa	1,9 / 1,8	Postpliocene regression
Volos	1,6 / 1,5 / 1,4	Calabrian (indiff.)
	1,2	Postcalabrian regression
Psathoura	0,7	Milazzian ingression
Lichades	0,5	Roman regression
Kamena Vourla	1,7	Calabrian (indiff.)
Methana	0,9 / 0,8	Syrian regression
	0,6	Roman regression
	0,3	Tyrrhenian regr./ingr.
Milos	0,5	Roman regression
	0,9	Syrian regression
	1,0	Sicilian ingression
	1,1	Postcalabrian regression
	1,7 / 1,5	Calabrian (indiff.)
	1,8	Postpliocene regression
Thera	1,6 / 1,5	Calabrian (indiff.)
	0,6	Roman regr./Milazzian
Kos	1,6	Calabrian (indiff.)
	1,0	Postcalabrian regression
Yali	0,024	Post-Monastir regression
Nisyros	0,2	Post-Tyrrhenian regression

Tab. 1. Radiometric data of Aegean volcanic rocks in context with the Quaternary fluctuations of the Mediterranean Sea. Data after ANGELIER et al. 1977; FYTIKAS et al. 1976, 1984; HUIJSMANS 1985.

The plants of *Nigella arvensis* complex have buoyant balloon-formed seed capsules; the orchids have very resistant small seeds.

Thereby island arc - marginal basin - systems as the Aegean Sea prove to be not only centres of recent geodynamic activity but also of biological origin of species. Similar systems are located at the West Pacific border (Bearing Sea, Sea of Okhotsk, Sea of Japan, East China Sea, South China Sea, Sunda Shelf and Indonesia, Coral Sea, Tasman Sea) and in Central America (Carribean Sea).

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