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A biogeographical analysis of terrestrial isopods (Isopoda, Oniscidea) from the central Aegean islands (Greece)

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Abstract. Terrestrial isopods (Isopoda, Oniscidea) of forty-three central Aegean islands and islets are analysed from a biogeographical point of view. The oniscid fauna consists of sixty-nine species, thirty-two genera and fourteen families and is characterized by Aegean elements that have an eastern Mediterranean origin. Endemism is at the level of 20%, similar to that of oniscids from other Mediterranean archipelagoes. Analysis of species distribution through both idiographic and quantitative approaches (faunal similarity among islands using Jaccard's index, simple matching indices and the UPGMA clustering technique) resulted in

the recognition of a major disjunction between Kyklades-plus-Ikaria and eastern islands-plus-Astypalea and four noteworthy island groups: the eastern islands, Naxos-Ikaria, Amorgos, and all other Kyklades. Island similarities are generally consistent with the known palaeogeography of the area with the exception of Ikaria's placement with Naxos among the Kyklades. Also, the 'eastern' character of Astypalea is in conflict with evidence from other known taxa.

Key words. Oniscidea, Aegean, faunal similarity, biogeography clustering.

INTRODUCTION

The biogeography of the Aegean archipelago, and especially that of its central (Fig. 1) and southern parts, has been a centre of interest for many researchers during the last decades. Both palaeontologists (Creutzburg, 1963; Sondaar, 1971; Dermitzakis & Sondaar, 1979; Dermitzakis & Papanikolaou, 1981; Dermitzakis, 1990; Anastasakis & Dermitzakis, 1990 etc.) and neontologists (Rechinger, 1951; Greuter, 1970; 1971; Bertoldi, 1971; Runemark, 1971; Strid, 1972; Heller, 1976; Beutler, 1979; Aspöck, 1979; Mylonas, 1982; Sfenthourakis, 1994) have addressed the distributional and faunistic problems related to—and arising from the complex palaeogeography of the region. Throughout its rather short history, the Aegean archipelago has been subject to drastic changes due to the combination of large scale tectonic movements of land and the, mainly pleistocenic, eustatic movements of sea level. Contemporary islands of the central Aegean are the remnants of an extensive land (Ägäis) that connected Asia Minor to continental Greece until the lower Miocene (Papanikolaou & Dermitzakis, 1981). Breakdown started in the middle-upper Miocene (Fig. 2) with the disconnection of the Kyklades from the eastern islands. The latter remained part of Asia Minor until the upper Pleistocene (Dermitzakis & Papanikolaou, 1981). The Kyklades were afterwards subject to many episodes of departmentalization and temporary reconnections the history of which is not sufficiently known. The northwestern part of the Kyklades remained connected to continental Greece until the end of the Pliocene. During the glacial episodes of Pleistocene several groups of islands

were successively formed and disengaged and at least one island, Kea (6), reconnected with continental Greece (Greuter, 1971). The exact geography of the region during these periods is unknown but can be approximated by the 200 m and 120 m isobaths for the Riss and Würm glacial periods respectively (Fig. 1). The southern border (volcanic arc) of the central Aegean has been formed by volcanic activity that started in the Pliocene (Fig. 3B). The more recent volcanic island is Nisyros (38) with an age of *c.*1Ma. This island, together with its neighbouring islets Gyali (39), Pergoussa (40) and Pachia (41), has remained isolated from all surrounding lands throughout its history (Papanikolaou & Lekkas, 1991). All other parts of the volcanic arc, Milos (10), Thira (18) etc., have formed temporary connections to surrounding islands at some period of their existence.

An important issue that remains obscure is the possible formation of a secondary landbridge between the Kyklades and the eastern islands after their first disjunction in the Miocene. The dominant view among geologists does not support this possibility, but is not without exceptions (Creutzburg, 1963; Dermitzakis, 1987).

The presence of humans for more than 5000 years on all of the islands, even on the smallest islets, has altered completely, but in a more or less homogeneous way, their physical environment. Human activity is generally a factor causing increased 'noise' in biogeographical studies since both (anthropochorous) dispersal and extinction rates of several taxa may increase, breaking down the concordance between the distribution of species and palaeogeography. Even though expected, the extent (and existence) of this kind of human influence is something to be tested against

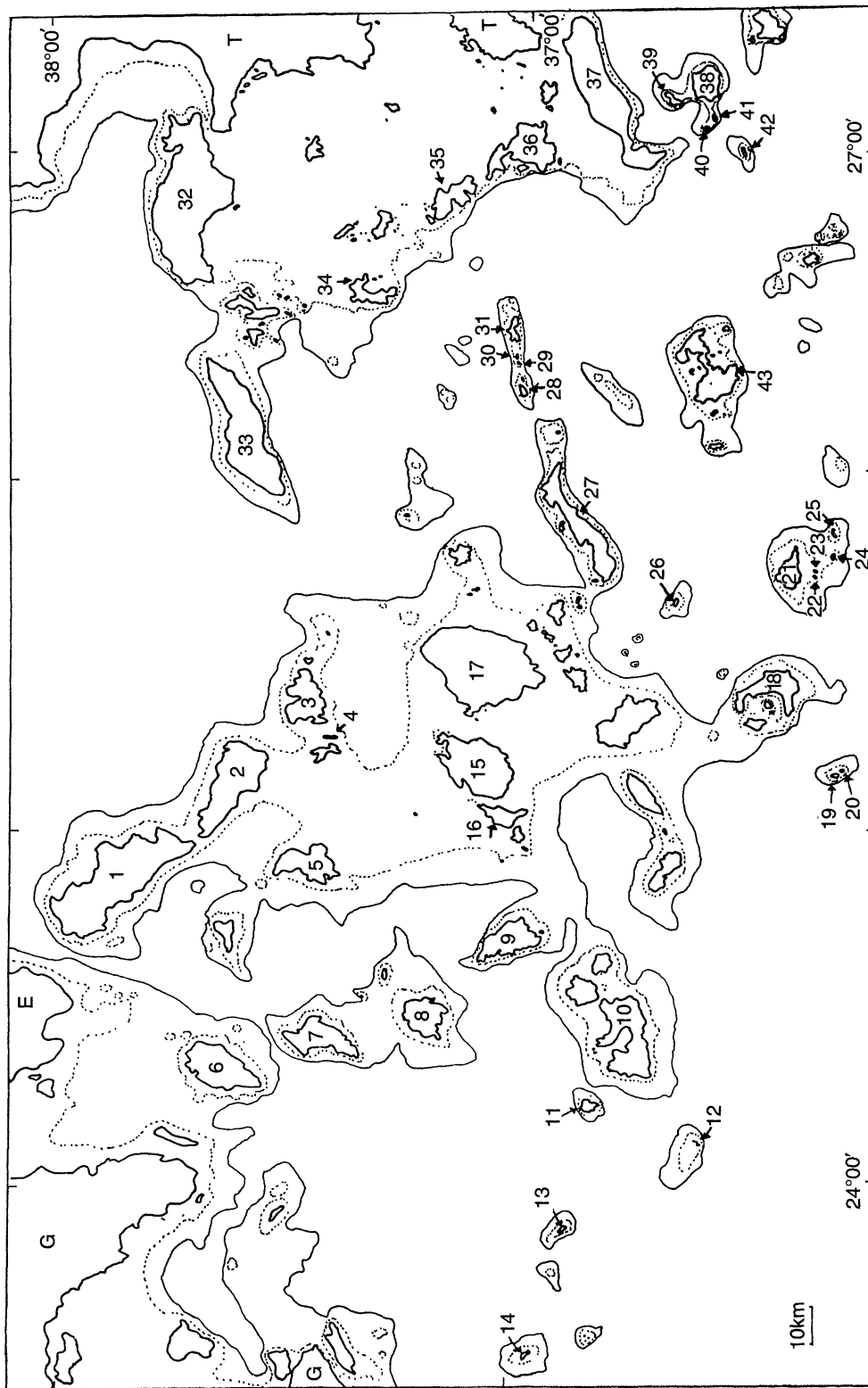


FIG. 1. The study area (central Aegean). 200 m and 100 m isobaths are shown with solid and dotted lines respectively. Kyklades: 1, Andros, 2, Tinos, 3, Mykonos, 4, Dilos, 5, Syros, 6, Kea, 7, Kythnos, 8, Serifos, 9, Sifnos, 10, Milos, 11, Antimilos, 12, Ananes, 13, Falkonera, 14, Velopoula, 15, Paros, 16, Antiparos, 17, Naxos, 18, Thira, 19, Christiani, 20, Askania, 21, Anafi, 22, Mikro Fteno, 23, Megalo Fteno, 24, Pachia (Kykladic), 25, Makra, 26, Anydros, 27, Amorgos, 28, Kinaros, 29, west Mavri, 30, east Mavri, 31, Levitha. Eastern islands: 32, Samos, 33, Icaria, 34, Patmos, 35, Leros, 36, Kalymnos, 37, Kos, 38, Nisyros, 39, Gyali, 40, Pergoussa, 41, Pachia, 42, Kandelioussa, 43, Astypalea. E: Evia (large island, very close to mainland, biogeographically regarded as part of continental Greece), T: Turkey (Asia Minor mainland). Island names in the text are followed by their serial number on this map.

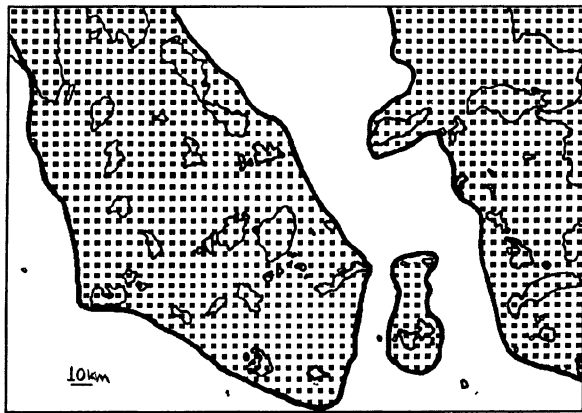


FIG. 2. Central Aegean in upper Miocene (land shown by dotted area) according to Dermitzakis & Papanikolaou (1981).

real data. Actually, it has played an important role for the land snails of the Kyklades (Mylonas, 1982), but no apparent effects on the reptile distribution of the same area can be seen.

The present paper aims to add more information on the biogeography of the central Aegean through an analysis of its terrestrial isopod fauna (Isopoda, Oniscidea). Oniscids of the central Aegean islands were hitherto known only from sparse records and their exact distribution remained unrecorded. An early attempt in biogeographic analysis by Strouhal (1937) was based on obsolete data and therefore his results cannot be regarded as valid. During subsequent years only a few more records of oniscidean species were added (Schmalfuss, 1979; Schmalfuss & Schawaller, 1984; Andreev, 1986). The present study is the first extensive and intensive study of central Aegean Oniscidea. Forty-three islands were studied in detail and the oniscidean fauna was found to be much richer than known from literature. Predictably, the actual distribution of most known species proved to be much wider, while several new species were also found.

It is not the purpose of this paper to deal with taxonomic issues. Suffice it to say that taxonomy of most species has been resolved at a sufficient level (Sfenthourakis, 1994) and that all new species have been already described elsewhere (Sfenthourakis, 1995; Schmalfuss & Sfenthourakis, 1995).

THE STUDY AREA

The study area (Fig. 1) includes forty-three islands and islets that lie between $36^{\circ}10'$ and $38^{\circ}00'N$ and $24^{\circ}00'$ and $27^{\circ}25'E$ plus two more islets, Falkonera (13) and Velopoula (14), that lie between the former area and continental Greece. The total area is 4080 km^2 with 2572 km^2 in the Kyklades and 1508 km^2 in the eastern (Asia Minor) islands. The largest island is Samos (32) with an area of 476.2 km^2 and the smallest is Mikro Fteno (22) with an area of 0.025 km^2 . The highest mountain lies on Samos (32) (altitude 1434 m). All islands have a Mediterranean-type climate (Cs) and vegetation. Eastern islands receive more rainfalls but relative humidity of air is higher in central Kyklades. There is

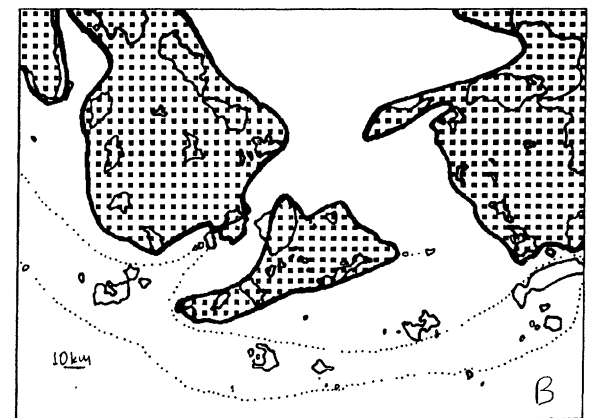
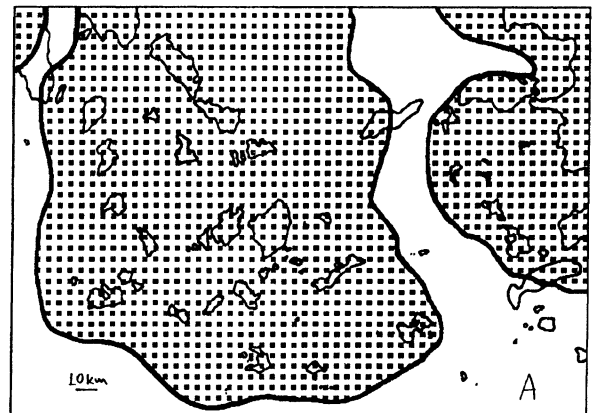


FIG. 3. Central Aegean in Pliocene, A: according to Creutzburg (1963) and B: according to Dermitzakis and Papanikolaou (1981). Area between dotted lines in 3B corresponds to the volcanic arc.

a climatic gradient among Kyklades, from north-northwest (more humid conditions) to south-southeast (drier with harsher summers). The range of mean annual rainfall for the whole study area is 360 mm (southern Kyklades) to 932 mm [Ikaria (33)], of mean annual temperature 18°C [Andros (1), Paros (15)] to 19.2°C [Milos (10), Ikaria (33)] and of mean annual relative humidity of air 65RH [Syros (5)] to 76RH [Paros (15)] (Theocharatos, 1978; Kotini-Zambaka, 1983).

The geomorphology of most islands is complex, with many hills, cliffs, mountains and small alluvial plains in between, especially where the numerous rivulets and streams (most of them dry) meet the sea. There are some small rivers on larger islands such as Samos (32), Naxos (17), Andros (1) and Ikaria (33) but, in general, running water is present only periodically during winter and spring on most other islands. The substrate of most islands comprises schists mixed with limestones whereas the southernmost islands are mainly, or completely, of volcanic origin and constitution [Milos (10), Antimilos (11), Ananes (12), Thira (18), Christiani (19), Askania (20), Anafi (21), Mikro Fteno (22), Megalo Fteno (23), Pachia (24), Makra (25), Kos (37), Nisyros (38), Gyali (39), Pergoussa (40) and Pachia (41)].

Both substrate and vegetation are markedly heterogeneous and this heterogeneity is the most important ecological characteristic of the study area. The influence of

humans on all aspects of the environment is profound and dates back to more than 5000 years BP. There is no island or islet that has not experienced constant perturbation by humans but the most extensive effects can be seen in the Kyklades which have been almost completely deforested during the last centuries.

Maquis is the commonest habitat type. In most places this has been degraded to mixed maquis-phrygana. Healthy dense maquis can be found on Andros (1), Ikaria (33), Samos (32), Naxos (17) and in small patches at hillsides on several other islands. Phrygana are extensively present on most islands. Coniferous forests (cypress and pine) are present only on the eastern islands, mainly on Samos (32), Kos (37) and Ikaria (33). Deciduous forests (oak) are present only as patchy remains of older formations at the boundaries of cultivated land, mainly on Kea (6), Samos (32), Ikaria (33) and Nisyros (38). The most important habitat type for terrestrial isopods is the banks and surroundings of streams with arboreal or scrubby hygrophilous vegetation. Nearly half the species of the study area can be found in these formations (Sfenthourakis, 1994). Other important habitats are the small swamps and salty grasslands that are often present just above the supralittoral zone around estuaries. Several other anthropogenic habitats, such as cultivated land and buildings, are also rich in isopods.

Small islets are also heterogeneous. Islets lying a few meters away from each other usually have completely different vegetational constitution and microclimatic conditions.

METHODS

Qualitative collecting for 132 days on forty-two islands and islets took place during the wet periods (October–May) of the years 1989–1993. In total, 298 sampling stations were tracked, distributed in such a way that all habitat-types and geographic subdivisions of each island would be sampled. The number of sampling stations per island is related to the size and heterogeneity of the islands. Effectiveness of collecting has been checked by repeated sampling on certain islands [Andros (1), Kea (6), Milos (10)] and proved to be at the level of 90% of total fauna, a percentage that is regarded as satisfactory for such studies. The distribution of species on islands is given in Appendix.

Data given by Schmalzfuss & Schawaller (1984) for the island of Thira (18) were also used in the analysis, corrected and completed with species found in Dr M. Mylonas' collection of isopods from the Kyklades.

Among-island and island-to-mainland shorter distances were measured on a 1:500,000 map.

Jaccard's index of faunal similarity (Jaccard, 1908) has been used as it is recommended for such analyses (Hengeveld, 1990) for its simplicity, easiness of interpretation and for not taking into account absences of taxa (not considering negative evidence as informative). Simple matching index (Brown & Gibson, 1983) has also been used for comparative reasons in the case of the reduced data matrix, where it seemed justified.

The unweighted pair-group method using arithmetic averages (UPGMA) clustering technique has been used

because it introduces the least distortion (Rohlf, 1970; Lee, 1980) and is most widely accepted. The cophenetic correlation coefficient (C.C.C.) served as a measure of clustering goodness of fit (Rohlf, 1992).

The Mantel test of matrix comparison (Mantel, 1967; Rohlf, 1992) has also been used in order to check the influence of island-to-island geographic distances on faunal similarities. This test is approximated by the value of a *t*-parameter which is an estimation of the possibility that the observed Mantel *z*-statistic (the sum of products of the off-diagonal elements of the two matrices) is larger than the *z*-statistic resulting from infinite random permutations of the data matrices. If observed *z* is larger at a statistically significant level then the two matrices (here geographic distance and faunal similarity) are correlated.

RESULTS

Distribution

A total of sixty-nine valid species, thirty-two genera and fourteen families were found, while the presence of two more species remained ambiguous (Appendix). There are fifty-nine species, thirty genera and twelve families on Kyklades while on eastern islands there are fifty-three species, twenty-seven genera and fourteen families. Nine of the species were new for science (Schmalzfuss & Sfenthourakis, 1995; Sfenthourakis, 1995) and fourteen more were new records for the study area. The mean record increase per island was 533% while for seventeen islets all records were new.

The composition of the study area oniscidean fauna according to overall distributions of species and genera is given in Fig. 4. Aegean species constitute the main part of the fauna whereas European or Balkanic species are nearly absent. At the generic level Mediterranean elements outnumber all other categories. Mediterranean genera have differentiated in the Aegean giving rise to the special faunal constitution of the archipelago.

Asiatic elements (Asia Minor plus eastern Mediterranean) are well represented as can be also inferred by the percentage of Eurasiatic genera. From the non-Aegean Mediterranean elements holomediterranean are the most common while western Mediterranean species and genera are almost absent. Genera like *Helleria*, *Oritoniscus*, *Finaloniscus*, *Trichorhina*, *Acaeroplastes*, and *Tiroloscia* that constitute a large part of the oniscid fauna in western and central Mediterranean islands are absent from the Aegean, whereas the eastern genera *Schizidium* and *Nagurus* have their western distributional limits in the study area. There are also a few endemic Aegean genera such as *Rodoniscus* and *Cretoniscellus*.

Endemism is not extremely high (20%) but is significant when the endemics of central plus southern Aegean islands are considered (31%). The fauna of these two regions is very similar and they could be regarded as one biogeographical entity. In comparison, oniscidean endemism of the distant oceanic Canary islands reaches 60% (Rodriguez, 1991) while that of other Mediterranean continental islands, such as the Tuscan archipelago (Taiti

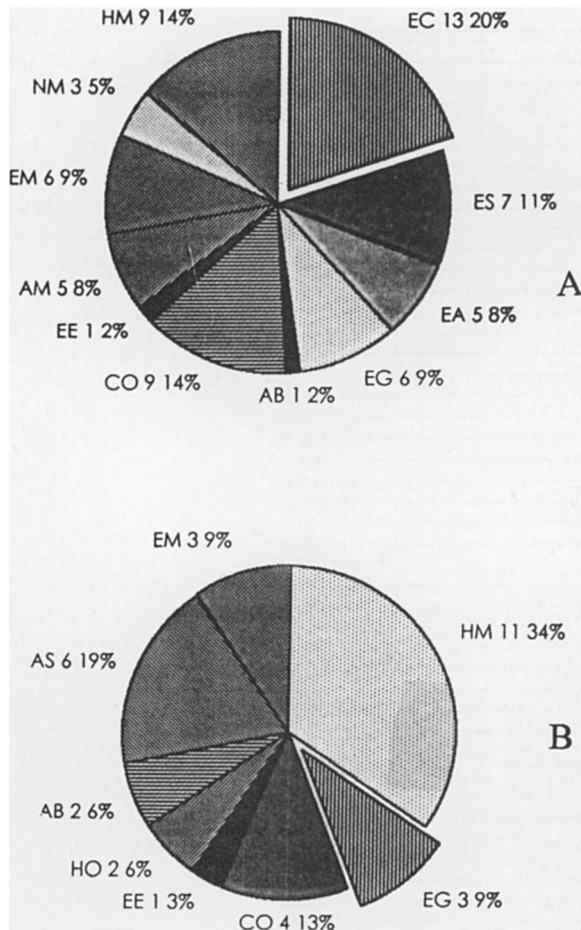


FIG. 4. Biogeographic analysis of central Aegean Oniscidea. A. Species (65 species excluding four of ambiguous taxonomic status) and B. Genera. HM, holomediterranean; NM, north Mediterranean; EM, east Mediterranean; AM, Asia-Minor; EE, European; AB, Adriatic-Balkan; CO, cosmopolitan or widely distributed; AS, Eurasiatic; HO, Holarctic; EG, endemics of Greece; EA, Aegean endemics; ES, endemics of southern Aegean; EC, endemics of central Aegean.

& Ferrara, 1989) and circumsardinian islands (Argano & Manicasterri, 1990), is at comparable levels (20% and 24% respectively).

The thirteen endemic species of the study area are distributed as follows: seven on Kyklades (12%), two on eastern islands (3.5%), one on the whole area, one on Kyklades plus Ikaria (33), one on eastern islands plus Naxos (17) and one on Kos (37) and Levitha (31). Nevertheless the real distribution of five of these (*Paraschizidium* spp.) could be wider because their cryptic behaviour makes their recovery somewhat circumstantial. There is also uncertainty about the distributional status of the eastern islands' endemics since Asia Minor oniscids are essentially unknown.

Only three species are local endemics of one island and two more are present on one big island plus one islet.

Endemism, as expected, is higher in the Kyklades that have been isolated for at least 2Ma. Nevertheless, it is lower than that of land snails (20%, Mylonas, 1982). This is possibly due to the more competent vagility of terrestrial

isopods. Reptiles, being more vagile than isopods, have an even lower endemism (Beutler, 1979; Mylonas & Valakos, 1990). Eastern islands were part of Asia Minor until the beginning of the Holocene and are not expected to host many endemic forms. The unique eastern island group that has never been connected with any other land [Nisyros (38) and surrounding islets] has risen above sea level only recently (about 1Ma) and all its fauna must have arrived later via dispersal. Nevertheless, one of the two eastern endemics is present on Nisyros (38) and its neighbouring islet Kandelioussa (42) (which is not volcanic) while the second is distributed on all eastern islands.

It becomes clear that there are no definable areas of endemism inside the study area besides the preliminary distinction of the Kyklades from the eastern islands.

Characteristic distributions

Characteristic taxa are considered those with sufficiently known distributions, whose distributional limits are delineating a subregion inside the study area. Species with wider distributions, patchy records and problematic taxonomy are excluded from this consideration.

Protracheoniscus kalyrninus Sfenthourakis, 1985 is present on most large eastern islands [*Protracheoniscus babori* Frankenberger, 1938 replaces it on Kos (37)] but the genus is absent from the Kyklades. *Chaetophiloscia lagoi* (Arcangeli, 1934) is an eastern species that is also present on Astypalea (43), an island of questionable biogeographic position that lies at the 'borders' of the Kyklades and the eastern islands. On the other hand there is no 'Kykladid' species of Oniscidea on Astypalea (43).

Kykladic characteristic species are not distributed all over the Kyklades but remain restricted to some island sub-groups. *Echinarmadillidium cycladicum* Schmalzfuss & Sfenthourakis, 1995 is distributed on the central, western and southern Kyklades and reaches the Levitha (31) group to the east. *Porcellio werneri* Strouhal, 1928 is present only on the central Kyklades [Paros (15), Naxos (17), Amorgos (29)], *Ligidium cycladicum* Matsakis, 1979 on north-northwestern [Andros (1), Tinos (2), Syros (5), Kea (6), Kythnos (7)] and there is a number of species present only on one or two islands [*Schizidium tinum* Sfenthourakis, 1995, *Paraschizidium* spp. etc]. The Northwestern Kyklades host some species that are indicative of a recent connection with continental Greece [*Philoscia dalmatica* Verhoeff, 1901 on Kea (6), *Armadillidium atticum cythnium* Strouhal, 1937 on Kythnos (7), *Cretoniscellus strinatii* (Vandel, 1955) on Andros (1) and Tinos (2), *Monocyphoniscus caniensis* (Vandel, 1958) on Andros (1) and *Trichoniscus lindbergi* Vandel, 1958 on Tinos (2)]. No such species is present on any other island.

Of special interest are the species *Armadillidium ameglioi* Arcangeli, 1913, *Bathytropa granulata* Aubert & Dollfus, 1890 and *Ligidium ghigii* Arcangeli, 1928 that indicate a penetration of eastern elements into central and southern Kyklades [Naxos (17), Amorgos (27), Anafi (21)]. *Armadillidium insulanum* Verhoeff, 1907 and *Trachelipus aegaeus* (Verhoeff, 1907) are distributed on Kyklades, Samos (32) and Ikaria (33) but not on the other eastern islands

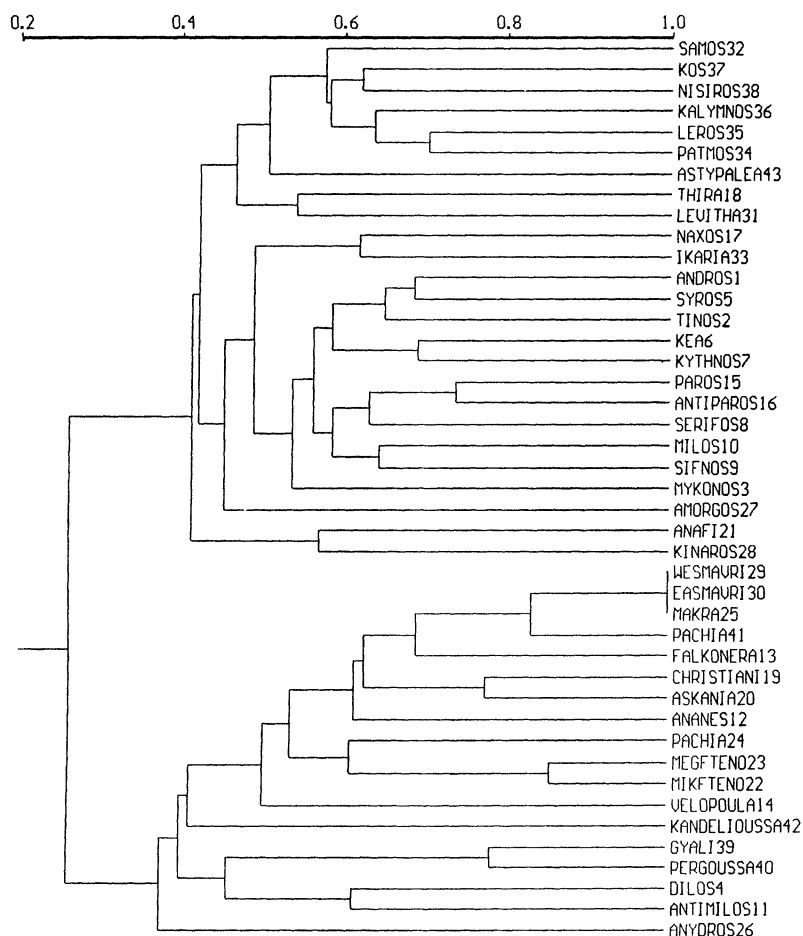


FIG. 5. One of the two UPGMA dendrograms of the whole set of islands and species (using Jaccard's index of similarity). C.C.C. = 0.88. The second has only minor differences. Numbers as in Fig. 1.

even though they have a wide distribution in the rest of Aegean.

The general picture is that island relationships, as depicted from the above mentioned distributions, follow an eastern–western geographic dimension with a major disjunction between the Kyklades and the eastern islands. Samos (32) and Icaria (33) share some elements with the Kyklades and the central Kyklades have a mixed faunal character influenced by eastern elements. The Northwestern Kyklades form a group not influenced by eastern elements but related to continental Greece.

Faunal similarity

The clues of the above mentioned idiographic approach are tested below by statistical methods which are more objective and robust.

When applying Jaccard's index on the complete species per island matrix, UPGMA results in two cluster topologies with equal C.C.C. (0.88). One of these is shown in Fig. 5. The second differs only at the relative position of four islands that form the group {[Levitha (31), Kinaros (28)], Anafi (21)], Thira (18)} connected next to Astypalea (43).

The most profound pattern is the formation of two large

groups, one including all islands larger than 10 km² plus a few smaller, and the second including most islets. The size gap among larger islets and smaller islands (*c.* 10–35 km²) seems to be sufficient for the emergence of crucial faunal differences. Some marginal cases, such as Thira (18), Anafi (21), Levitha (31) and Kinaros (28) are exceptions whose uncertain position on the dendrograms can be attributed to: a) the poor oniscid fauna of the larger Thira (18) and Anafi (21), possibly resulting from their volcanic constitution and isolated position at the southern part of Kyklades, with harsher climatic conditions, and b) the relatively rich, for their size, fauna of the islets Levitha (31) and Kinaros (28).

The islet clusters do not follow any geographical or palaeogeographical pattern but are influenced by vegetational similarities and other ecological variables (Sfenthourakis, 1994). Additionally, islet faunal similarities are strongly biased by the small number of occurring species and, therefore, the resulting dendrogram is not interpretable in a biogeographically informative way.

On the other hand faunal similarities among larger islands are more informative and reveal several important patterns.

First of all, the eastern islands, minus Icaria (33), form a distinct group that includes Astypalea (43) while Icaria

(33) is clustered with Naxos (17) among the Kyklades. This first level disjunction is relative to the discussion of a recent landbridge formation between the Kyklades and the eastern islands (see Introduction). Even though faunal similarity cannot be directly translated to scenarios of land connections, it could be used as partial evidence in such discussions especially when analyses with other taxa give congruent results. Unfortunately this is not the case here. For land snails and reptiles *Astypalea* (43) belongs to Kyklades whereas Ikaria (33) has a unique character for most known taxa (Runemark, 1971; Strid, 1972; Aspöck, 1979; Beutler, 1979). One plausible scenario explaining the peculiarities of Ikaria (33) is the proposition of Creutzburg (1963) that the western half of the island was part of 'Kyklades' during Pliocene (but see Dermitzakis & Papanikolaou, 1981). This would have resulted in a composite Kykladid-eastern origin of the island.

Inside the group of eastern islands interrelationships are more or less as expected. The clusters of Leros (35)–Patmos (34)–Kalymnos (36) and Kos (37)–Nisyros (38) are more closely related to each other than each one with Samos (32) or *Astypalea* (43). Islands comprising the first cluster are geographically close and similar in size and habitat structure. Kos (37) and Nisyros (38) are probably related as source and colony since, as already stated, Nisyros (38) is a new volcanic island that never connected to other areas and Kos (37), being very close and much larger, is the most probable source of its fauna.

On the other hand Samos (32) is very different, both in environmental structure and climatic conditions, more distant from the 'chain' of other islands and with a much larger size. Consequently, its fauna is predictably different. *Astypalea* (43) is of uncertain palaeogeographic origin, isolated and with degraded vegetation. Therefore, its basal position is merely justified.

The interrelationships of the Kyklades are more complicated and unpredictable. Northern islands [Andros (1), Syros (5) and Tinos (2)] are grouped together at a high level of similarity, with the exception of Mykonos (3) which is poorly related to other groups. This must be due to its depauperate fauna caused by the degraded environment and the lack of running water. The position of Syros (5) in this group is in contrast with the results of Mylonas (1982) for land snails where Syros (5) was part of the central Kyklades. This cluster is related more with northwestern Kyklades Kea (6) and Kythnos (7). The western Kyklades together with Paros (15) form a separate group with Sifnos (9)–Milos (10) and Serifos (8)–Paros (15) as subgroups. The placement of Paros (15) among the western Kyklades is compatible with the palaeogeographic situation during the Pliocene (Fig. 3B). The close relationship of Milos (10) and Sifnos (9) is supported also by the presence of the endemic snake *Vipera lebetina schweizeri* Werner, 1935 on these two islands alone.

Naxos (17)–Ikaria (33) cluster is the sister group of all other Kyklades except for the basal Amorgos (27). This placement of Amorgos (27) cannot be explained in the same terms as that of Thira (18), Anafi (21) etc., because this island has a rich fauna also including many of the endemic species. Amorgos (27) has a unique faunal character and

its basal position for Kyklades is analogous to that of *Astypalea* (43) for eastern islands as both are lying at the 'borderline' of the two major subdivisions.

The above mentioned groupings have resulted from the analysis of the complete data matrix. It is reasonable, though, that the real distribution of some species is not fully recovered (e.g. for some halophilous and some cryptic species) and that taxonomic ambiguities concerning a few other species may have affected results. In order to overcome these obstacles a second cluster analysis was performed using a reduced data matrix not containing problematic and ubiquitous (uninformative) species. Reduced matrix contained fifty species (see Appendix) and twenty-one islands (all islets, Thira (18) and Anafi (21) were excluded for reasons discussed above).

UPGMA clustering with the Jaccard index gives two dendrograms with C.C.C. 0.77 and 0.75 respectively.

The best-fit dendrogram (Fig. 6) is much like those of the complete matrix analysis with one main difference. Samos (32) is now included in the Kyklades, closely related to the Naxos (17)–Ikaria (33) group. We should actually recognize four groups (since Mykonos (3) is not informative—see above): Samos (32)–Naxos (17)–Ikaria (33), Amorgos (27), Kyklades and eastern islands. In the second dendrogram Ikaria (33) is placed among Kyklades while Naxos (17) is related to Samos (32) among eastern islands.

The use of the reduced data matrix justifies with more reasonable grounds the application of a similarity index, such as simple matching, which considers 'common absence' of species as equally informative as common presence. This is so because the exclusion of problematic species from the data reduces the probability of using superficial 'absences' and, therefore, the remaining 'real absences' could reflect biologically interesting patterns. Application of simple matching index to the reduced data matrix results to four equally supported UPGMA dendrograms (C.C.C. 0.80). In all of them Samos (32) is again basal to all other eastern islands, Amorgos (27) is basal to all other Kyklades and Naxos (17)–Ikaria (33) is the sister group of the rest of Kyklades (Fig. 7). Differences among the four dendrograms arise from the interrelationships of western Kyklades and are of minor importance. The position of Nisyros (38) closer to the Leros (35)–Patmos (34)–Kalymnos (36) group is probably the result of the area-effect on 'common absences' [Kos (37), being much larger than Nisyros (38), hosts many species that are 'absent' from the latter island].

Combining evidence from all the above mentioned analyses leads us to the recognition of the following eminent island groups:

(1) Eastern islands [Samos (32), Leros (35)–Patmos (34)–Kalymnos (36), Kos (37)–Nisyros (38) and *Astypalea* (43)]. Samos (32) is also related to the Naxos (17)–Ikaria (33) group.

(2) Naxos (17)–Ikaria (33). This is a stable group of 'Kyklades' that is also related to Samos (32).

(3) Amorgos (27). It is always basal to the Kyklades-group. It has a unique faunal character and, according to the distribution of certain characteristic species, such as

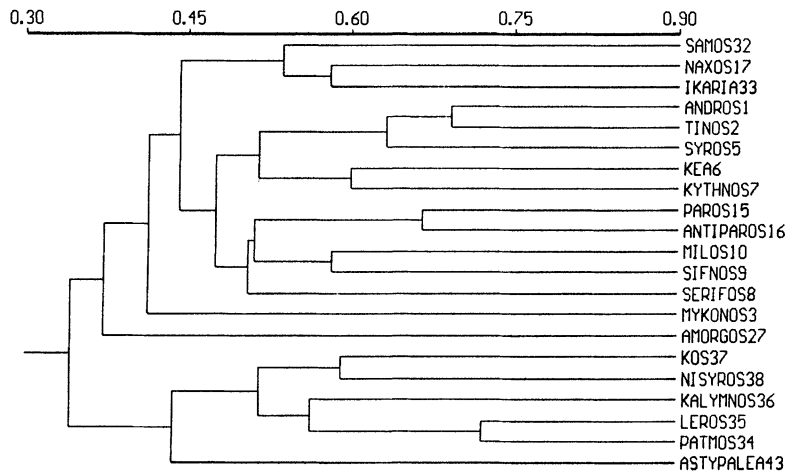


FIG. 6. Better supported UPGMA dendrogram (C.C.C. = 0.77) using Jaccard's index of similarity for the reduced data matrix, with twenty-one islands and fifty species.

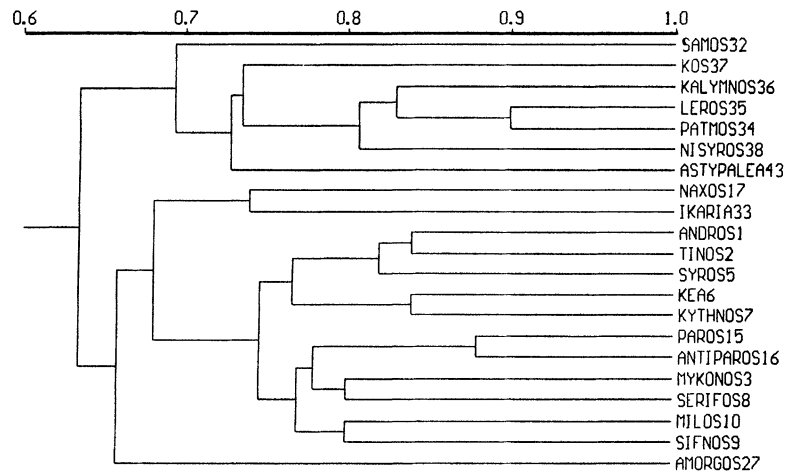


FIG. 7. One of the four equally supported UPGMA dendrograms (C.C.C. = 0.80) using simple-matching index of similarity for the reduced data matrix. The other three have only minor differences.

Porcellio wernerii and *Armadillidium ameglioii*, it is related more to the Naxos (17)–Ikaria (33) group.

(4) Other Kyklades. Inside this group relationships are more complicated but some infra-groups can be deciphered:

(4a) Northern Kyklades [Andros (1)–Tinos (2)–Syros (5)]. This is a stable infra-group related more to the northwestern group [Kea (6)–Kythnos (7)].

(4b) Northwestern Kyklades [Kea (6)–Kythnos (7)]. Although closer to the previous infra-group, they have affinities with western Kyklades too. Island groups 4a and 4b are influenced by continental Greek elements.

(4c) Western Kyklades [Milos (10)–Sifnos (9), Paros (15)–Antiparos (16), Serifos (8)]. The precise pattern of this infra-group inter-relationships is not sufficiently resolved.

It is expected, and in a sense trivial, that faunal affinity should be inversely related to geographical distance. In the present case this is quantitatively supported by the results of the Mantel-test of the correlation between among-island distance and similarity matrices for both similarity indices

TABLE 1. Results of Mantel-test for the correlation of among islands geographic distance and faunal similarity matrices (see text).

| | | |
|------------------|-----------|-------------------------------|
| Jaccard, | | |
| all species: | $t = 6.8$ | $P(z_{obs} < z_{exp}) = 0.01$ |
| Jaccard, | | |
| reduced matrix: | $t = 6.5$ | $P(z_{obs} < z_{exp}) = 0.01$ |
| Simple matching, | | |
| reduced matrix: | $t = 6.6$ | $P(z_{obs} < z_{exp}) = 0.01$ |

(Table 1). Correlation of matrices is highly significant in all cases. What could be interesting in this kind of analysis is the possible existence of profound deviations from the proximity-similarity rule that are either few, thus not traced by the test, or many, resulting in a negative result of the test. Such deviations can prove biogeographically informative as they reveal non-trivial disjunctions in need of historical or ecological explanation. In the present case there are two exceptions: the disjunction of the neighbouring Naxos (17)

and Paros (15), islands that never cluster together and the disjunction of Ikaria (33) and Samos (32). The Naxos (17)–Paros (15) disjunction is compatible with Pliocene geography (Fig. 3B) but for that of Ikaria (33) and Samos (32) some more complicated explanation, such as the hybrid-origin-of-Ikaria (33) hypothesis (see above), is needed.

CONCLUSIONS

The oniscid fauna of the central Aegean islands is characterized by the poverty of continental elements and seems to have an eastern origin. Its level of endemism is indicative of relatively recent isolation and is comparable to that of other 'continental' island groups, such as the Tuscan archipelago. It can be labelled as an Aegean subdivision of the eastern Mediterranean fauna and is part of a wider central-plus-southern Aegean biogeographical entity.

The distributional analysis of this fauna has revealed several interesting patterns that help towards a resolution of the palaeogeographic history of the region. Idiographic analysis, such as that with characteristic species, even though recommended by certain authors (Hengeveld, 1990), can be criticized for speculative reasoning resulting mainly from ignorance of species distributional pattern causes (dispersal, extinctions, ecological constraints etc.) and from arbitrary (or no) interpretations of incongruent patterns. Nevertheless, in the absence of phylogenetic data, it has the advantage over the remaining overall-faunal-similarity approach in that it does not mangle the effects of patchy, underestimated and well-known distributions and does not treat all species as equally informative. On the other hand, similarity indices are not arbitrary and eclectic, and they compare the whole faunal constitution of islands without making any *a priori* explanatory assumptions. It is noteworthy that in the present work the conclusions of both approaches are similar and therefore it is very probable that they reflect some general underlying historical or ecological pattern. Human activity is not likely to have produced such congruent distributions. Since there are also no related patterns of known ecological factors (Sfenthourakis, 1994), history is the most possible agent of modern island relationships. Incompatible results from other taxa may reflect different times of faunal differentiation or a differential response to certain kinds of habitat disjunction.

The major subdivisions of the study area are mapped in Fig. 8. They are to some extent related to certain stages, mainly Pliocenic, of the region's palaeogeographic history. The separation of the Kyklades from the eastern islands is the major event reflected in oniscid distributional data, but with some peculiarities in the constitution of these island groups. These are the inclusion of Ikaria (33) in the Kyklades and Astypalea (43) in the eastern islands. What is more, the relationships of the Naxos (17)–Ikaria (33) group with Samos (32) stands as supporting evidence for the out-of-date hypothesis of secondary landbridge formation between the Kyklades and the eastern islands. According to the map of the Aegean at *c.* 800,000 yr BP given by Dermitzakis (1987), such a secondary landbridge could be present somewhere between Amorgos (27) and Leros (35). My

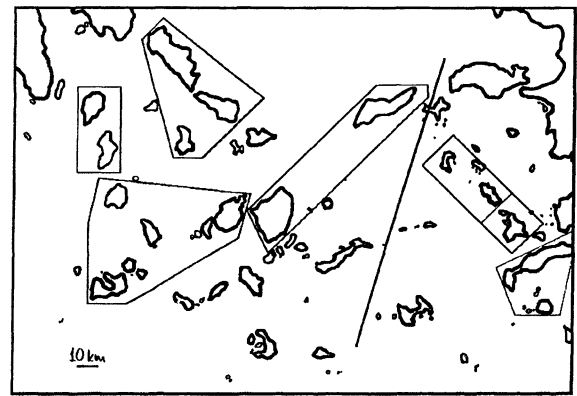


FIG. 8. The most eminent island groups that were recognized in the present analysis. Thick line shows the main disjunction between eastern islands and Kyklades.

results do not support this view, but instead, as already stated, the possibility of a Pleistocenic landbridge between Naxos (17) and Ikaria (33).

Small-scale questions on island-from-island separations cannot be answered at the level of resolution offered by oniscid-distribution analysis. On the contrary, a new problem for future research arises from conflicting evidence on the biogeographical position of *Astypalea* (43) coming from the distribution of terrestrial isopods and other taxa (molluscs, reptiles).

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APPENDIX 1—(cont'd)

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | | | | | |
|---|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|---|---|---|---|--|
| 41. <i>P. obsoletus</i> Budde-Lund, 1885 | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | | | |
| 42. <i>P. werneri</i> Strouhal, 1928 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 43. <i>Porcellionides prunosus</i> (Brandt, 1833) | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | |
| 44. <i>Proporcellio quadriseriatus</i> Verhoeff, 1917 | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | |
| 45. <i>Nagurus aegaeus</i> Schmalfuss, 1977 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 46. <i>Orthometopon phaleronense</i> (Verhoeff, 1901) | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 47. <i>Prottracheosicus babori</i> Frankenberger, 1938 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 48. <i>P. kalymnius</i> Sfenthourakis, 1995 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 49. <i>P. sp.</i> (not diagnosable females) | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 50. <i>Trachelipus aegaeus</i> (Verhoeff, 1907) | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 51. <i>Cylisticus convexus</i> (De Geer, 1778) | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 52. <i>Armadihidium ameghioi</i> Arcangeli, 1913 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 53. <i>A. atticum</i> cythnium Strouhal, 1937 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 54. <i>A. granulatum</i> Brandt, 1833 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 55. <i>A. insulanum</i> Verhoeff, 1907 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 56. <i>A. marmoratum</i> Strouhal, 1929 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 57. <i>A. vulgare</i> Latreille, 1804 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 58. <i>Echmarmadilidium cycladicum</i> Schmalfuss & Sfenthourakis, 1995 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 59. <i>Paraschizidium aegaeum</i> Sfenthourakis, 1995 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 60. <i>P. album</i> Sfenthourakis, 1995 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 61. <i>P. falkoneræ</i> Sfenthourakis, 1995 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 62. <i>P. levihæ</i> Sfenthourakis, 1995 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 63. <i>P. sp. aff. aticum</i> Sfenthourakis, 1990 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 64. <i>P. sp.</i> (ambiguous species) | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 65. <i>Schizidium hybridum</i> (Budde-Lund, 1896) | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 66. <i>S. oerizeni</i> (Budde-Lund, 1896) | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 67. <i>S. tunum</i> Sfenthourakis, 1995 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 68. <i>Trichoilidium malickyi</i> Schmalfuss, 1988 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 69. <i>Armadiillo tuberculatus</i> Vogl, 1876 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |

Species not included in reduced matrix: 1, 2, 14, 16, 17, 18, 19, 20, 21, 30, 40, 43, 58, 59, 60, 61, 62, 63, 68.

Numbers of islands as in Fig. 1.