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A BIOGEOGRAPHICAL ANALYSIS OF GREEK ONISCIDEAN ENDEMISM

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ABSTRACT

Despite our incomplete knowledge of Greek Oniscidea, a great number of species have already been described, of which 69% are endemic. This unusually high percentage of endemics is a result of intense speciation triggered by the complex topography, paleogeography, and ecological history of Greece. Using 100 × 100 km Universal Transverse Mercator (UTM) squares as Operational Geographic Units (OGUs), we mapped the presence of all endemic species known until 1995, and applied Parsimony Analysis of Endemicity (PAE) in order to find patterns of OGU relationships. In the procedure, we reduced the original data matrix in two successive steps, excluding uninformative and problematic species and OGUs. We analyzed separately the endemic species of the large genus *Armadillidium*, following the same procedure. The results lead to the recognition of two main biogeographic entities, the mountainous continental and the insular Aegean. These groups, and the relationships of OGUs on a finer scale, do not fully agree with the established paleogeography of Greece. Ecological factors, such as climatic change during the Pleistocene glaciations, must have played an important role in the shaping of modern patterns. This is also supported by the results of PAE for *Armadillidium* species, which are indicative of a recent ecologically induced pattern of differentiation.

INTRODUCTION

The present study is an attempt towards a biogeographic interpretation of the endemic Oniscidea (Crustacea, Isopoda) of Greece. Our knowledge of the distribution of Oniscidea in Greece has been significantly augmented during the last quarter of the century, thanks to the efforts of Dr. H. Schmalfuss (Stuttgart) and, to a lesser extent, a few other researchers. Even though the Greek oniscidean fauna is still incompletely known, it is possible to make it the subject of an informative biogeographic analysis since the presence of nearly two hundred valid species has already been documented, and 132 of them are endemic. The distributional limits of most of these species can be safely approximated at an operational geographic scale of some tenths of kilometers. Of course, large parts of Greece are still underexplored (Makedonia, Thraki, and most of

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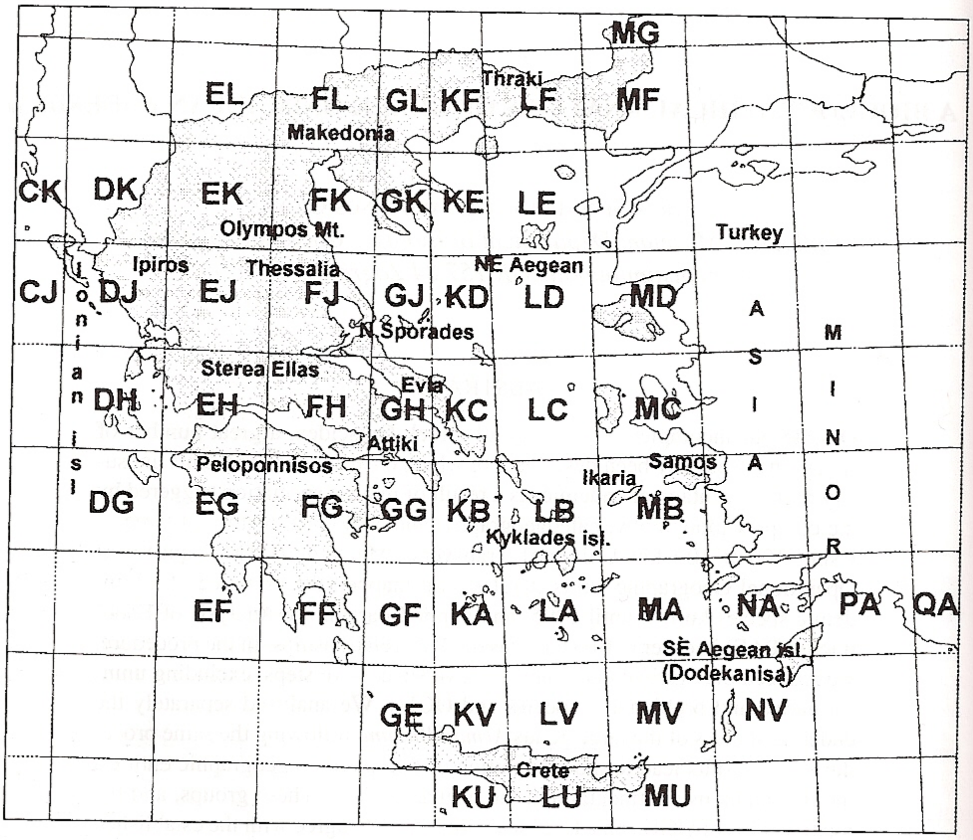

Fig. 1. Map of Greece showing the OGUs used (UTM squares) in the present analysis. The names of geographical regions mentioned in the text are also given.

the thousands of caves in Greece). Consequently, the future discovery of many more endemics is expected, especially when taking into account that almost all troglobitic species of Greek Oniscidea are endemic.

Previous biogeographic work on Greek Oniscidea (Sfenthourakis, 1996) has dealt with particular geographic subunits of Greece (central Aegean). There are very few papers dealing with the biogeography of Greece on a large geographical scale, and these are mostly paleogeographical (Greuter, 1970; Dermitzakis and Papanikolaou, 1981; Dermitzakis, 1990).

MATERIALS AND METHODS

The present study is based on the distributional data of terrestrial isopods (Oniscidea) of Greece that have been published up to 1995, inclusive (Andreev, 1984, 1985, 1986; Schmalfuss, 1979, 1981a,b, 1982, 1983, 1984a,b, 1985a,b, 1986, 1988a,b, 1989, 1990a,b, 1991, 1993, 1994, 1995; Schmalfuss and Schawaller, 1984; Schmalfuss and

Sfenthourakis, 1995; Sfenthourakis, 1991, 1992a,b, 1993, 1994, 1995a,b). Valid species of the most differentiated and problematic genus, *Armadillidium*, have been defined according to the revisions by Schmalfuss (1981b, 1982, 1984a, unpublished data).

We divided Greece into 100 × 100 km squares, hereafter denoted as Operational Geographic Units (OGUs), according to the Universal Transverse Mercator (UTM) coding (Fig. 1). OGUs with zero species occurences (purely marine, unexplored areas, or areas with no endemics—EE, FE, EF, GK, LD, and MG) have been excluded, together with OGUs CK, CJ, LC, and PA that contain only small parts of land. For the sake of simplicity, the small triangular corrective UTM "squares" (not shown on map) between the G and K columns have not been considered, as they do not affect the distribution mapping. The number of informative OGUs has been reduced to 45.

In order to examine OGU interrelationships we used Parsimony Analysis of Endemicity (PAE) (Rosen, 1988). PAE is a method of biogeographic analysis that introduces the methodology of cladistics into the analysis of presence/absence data sets. Even though its properties are still under study, it has proved useful in the few cases where it has been applied (Morrone, 1994; Maldonado and Uriz, 1995). PAE is supposed to give information on historical relationships of analyzed units (OGUs), as it considers the presence and absence of endemic taxa as apomorphic and plesiomorphic binary states, respectively, and uses parsimony algorithms to find "synapomorphies"—hence "phylogenetic" relationships—among OGUs. Nevertheless, PAE cannot be considered as a method of vicariance (or cladistic) biogeography since it does not take into account the phylogenetic relationships among endemic taxa.

In the first step of analysis, we used the complete data matrix (species × OGUs). Next, we excluded the least dependable and the uninformative data points (troglobitic and halophilic species, species present in one OGU, and OGUs containing one species). Finally, in the last step, we merged OGUs that formed eminent clades during the previous steps, if they also constituted geographically reasonable entities, and we analyzed merged areas as new OGUs. Additionally, we applied PAE on the distribution of endemic species of the large genus *Armadillidium* (excluding autapomorphic "states" —species with unique occurences). All analyses were performed by the PAUP Version 3.1 software (Swofford, 1993).

RESULTS

ONISCIDEAN ENDEMISM IN GREECE

As shown in Table 1, the total number of valid oniscidean species of Greece described until 1995 is 192, 132 of which are endemic. These endemic species belong to 14 (of a total of 17) families and 35 (of a total of 48) genera, 9 of which are also endemic (*Acteoniscus, Cretoniscellus, Graeconiscus, Minoscellus, Rodoniscus, Xeroporcellio, Kithironiscus, Trichodillidium, Paxodillidium*). Five of them are confined to caves (*Acteoniscus, Cretoniscellus, Graeconiscus, Minoscellus, Kithironiscus*), one (*Rodoniscus*) is endogean, and only three have epigean species (*Xeroporcellio, Trichodillidium, Paxodillidium*). Endemic genera belong to four families:

Table 1
Numbers of total known endemic, troglobitic, and endogean species of Greek Oniscidea in each genus and family. E—Endemic, G—Endogean, T—Troglobitic

Family	Genus	Total	Endemic	Troglobitic	Endogean
Tylidae	*Tylos*	1			
Ligiidae	*Ligia*	1			
	Ligidium	7	5		
Trichoniscidae	*Acteoniscus* E, T	1	1	1	
	Alpioniscus T	6	6	6	
	Buddelundiella T	1	1	1	
	Cretoniscellus E, T	3	3	3	
	Graeconiscus E, T	4	4	4	
	Haplophthalmus G	4	2		2
	Hyloniscus	3	2		
	Libanonethes T	1			
	Minoscellus E, T	1	1	1	
	Monocyphoniscus, G	1	1		1
	Trichonethes T	1			
	Trichoniscus	13	8	2	
Styloniscidae	*Cordioniscus* T	5	5	5	
Scyphacidae	*Armadilloniscus*	2	1		
Oniscidae	*Bathytropa*	2	1		
	Rodoniscus E,G	1	1		1
Scleropactidae	*Xeroporcellio* E	1	1		
	Kithironiscus E,T	1	1	1	
Stenoniscidae	*Stenoniscus*	1			
Philosciidae	*Chaetophiloscia*	7	2		
	Lepidoniscus	1			
	Philoscia	3			
Halophilosciidae	*Halophiloscia*	2			
	Stenophiloscia	2	1		
Platyarthridae	*Platyarthrus*	4	2		
Porcellionidae	*Agabiformius*	3			
	Leptotrichus	4			
	Porcellio	9	6		
	Porcellionides	1			
	Proporcellio	2	1		
Trachelipodidae	*Nagurus*	3	3		
	Orthometopon	7	4		
	Porcellium	4	3		
	Protracheoniscus	3	2		
	Trachelipus	6	4		
Tendosphaeridae	*Tendosphaera* G	1	1		1
Cylisticidae	*Cylisticus*	1			
Armadillidiidae	*Armadillidium*	45	38		
	Echinarmadillidium	2	2		

Table 1 *continued*

Family	Genus	Total	Endemic	Troglobitic	Endogean
	Paraschizidium G	7	7		7
	Paxodillidium E	1	1		
	Schizidium	5	4	1	
	Trichodillidium E	2	2		
	Troglarmadillidium	4	4	1	
Armadillidae	*Armadillo*	2	1		
Totals:					
17	48	192	132	26	12

Trichoniscidae (4), Oniscidae (1), Armadillidiidae (2), and Scleropactidae (2). The second richest family of endemics is Trichoniscidae (29 species), which is also one of the largest Oniscidean families on a global scale, with numerous, narrowly distributed, troglobitic species, especially in the Palearctic region. In Greece, the vast differentiation of *Armadillidium* leads to a characteristic pattern, comparable to that of Italy, with Armadillidiidae being by far the richest family (58 endemic species).

Percentage of endemism is very high (69%, 132 out of 192 species) and remains high even if *Armadillidium* species are excluded (64%, 94 out of 147 species). Troglobitic species constitute a significant part of the endemics (26 species), while endogeans contribute 12 additional species. Endemism of Greek Oniscidea remains at similarly high levels even if these categories are excluded (65% without troglobitics, 63% without troglobitics and endogeans).

The OGUs with the most endemics are: DH (23), LB (22), MA (19), DJ (19), LA (18), KB (17), and EJ (16). These OGUs consist of two distinct centers of endemism, one in western Greece (Ipiros, Ionian islands—DH, DJ, EJ), and one in the central Aegean Islands (LB, MA, LA, KB).

OGU RELATIONSHIPS

For the first two steps of analysis we used the heuristic search algorithm of PAUP since data matrices were too large for an efficient exhaustive search. This procedure resulted in 582 equally parsimonious trees for the first step and 173 for the second, after more than a million topology rearrangements had been performed without changing the tree length. In the last step, the size of the data matrix permitted the use of an exhaustive search for the shortest trees (branch-and-bound algorithm). This resulted in 5 equally parsimonious trees, whose 50% majority rule consensus tree is shown in Fig. 2.

Resulting clades generally correspond to actual geographic entities. Well defined clades of the first two steps of analysis were merged during the last step as follows: M1 = DG + DH + DJ (Ionian Islands, Ipiros); M2 = EG + EH + FH + FF + FG (Peloponnisos, Sterea Ellas except Attiki); M3 = DK + EJ + EK (Pindos Mountains); M4 = FJ + FK (Thessalia, Olympos Mountains); M5 = FL + MF (Makedonia, Thraki); M6 = GE + LU + KV + KU + LV (Crete), GF (Velopoula and Falkonera islets of the western Kyklades); M8 = GG +

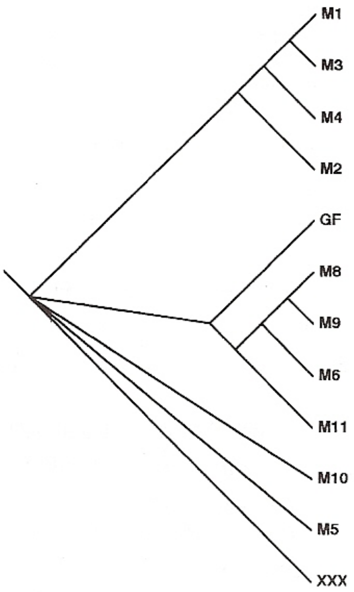

Fig. 2. The 50% majority rule consensus tree of merged OGUs during the third step of PAE (consistency index = 0.571, retention index = 0.552). See text.

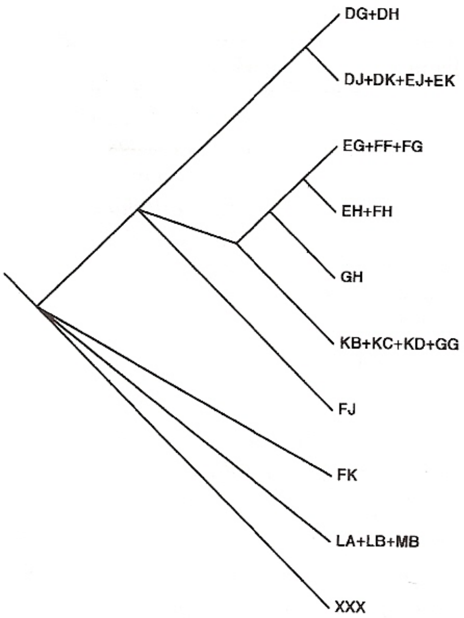

Fig. 3. The unique most parsimonious tree that resulted from the second step of PAE on *Armadillidium* endemics. Crown codes are OGUs. (Consistency index = 0.667, retention index = 0.667.)

GH + KC + KD + GJ (Attiki, Evia, and northern Sporades), M9 = KA + LA + LB + MA + MB + KB (Kyklades, Samos, Ikaria); M10 = KF + LE + LF + MC + MD (northeastern Aegean Islands and parts of Makedonia and Thraki); M11 = NA + NV + MV (Dodekanisa).

The consensus tree of the last step consists of two major clades: (1) Ionian Islands, Ipiros, and the Pindos Mountain range form a well defined group that is closely related to Peloponnisos and Sterea Ellas, and next with Thessalia-Olympos Mountain; and (2) Central Aegean Islands form a sister group with Attiki, Evia, and northern Sporades, with Crete being their closest relative. Southeastern Aegean Islands (southern Dodekanisa) are grouped next, while the small islets of western Kyklades (GF) form the sister clade of the former, probably because of the small number of endemics that are present on them. Northeastern Aegean Islands and northern Greece remain unresolved.

PAE OF ARMADILLIDIUM *SPECIES*

We applied PAE to the distribution of endemic *Armadillidium* species in two steps. First, all OGUs where some endemic *Armadillidium* spp. occur (32 OGUs) were treated independently (heuristic search). In the second step (branch-and-bound method), we merged OGUs that formed “monophyletic” units, excluding those OGUs whose relationships could not be sufficiently resolved. This procedure resulted in 9 new OGUs which define the following geographic entities: (1) southern Ionian Islands; (2) Ipiros, Pindos Mountain range, and northern Ionian Islands; (3) Peloponnisos; (4) central continental Greece (Sterea Ellas); (5) Attiki and central Evia; (6) northwestern Kyklades, southern Evia, part of northern Sporades, and Saronikos Gulf; (7) Thessalia; (8) Olympos Mountain region; and (9) central Kyklades and Samos district.

The resulting most parsimonious tree is shown in Fig. 3. This tree consists of a single partially resolved clade, while the central Aegean Islands and the Olympos Mountain region remain unresolved. Ionian Islands and Ipiros appear again as sister groups, but Peloponnisos, Sterea Ellas, and Attiki form a monophyletic clade whose sister clade is formed by the "western Aegean" group (northwestern Kyklades, southern Evia, Saronikos Gulf, and part of northern Sporades). Thessalia is also included in the same major clade, but its relationships remain unclear.

DISCUSSION

Greece, as a result of its complex topography and paleogeographic history, has been an important center of endemism for Oniscidea. The two regions richest in endemics are the mountainous Pindos plus the insular Ionian area of western Greece, and the fragmented insular central Aegean. Both regions have experienced important geomorphological changes throughout their history (Dermitzakis and Papanikolaou, 1981; Dermitzakis, 1990). The former has been directly affected by glaciations, while the latter has been affected indirectly through changes in sea level and resulting connections and disconnections of land masses. Additionally, the whole region has been subject to intensive and extensive tectonic activity from the Miocene onwards. On the other hand, these areas are among the most intensively studied of Greece. Nevertheless, it would not be premature to characterize them as the most important "centers of endemism," since no other area, with the possible exception of Crete, is expected to contain so many endemic species, judging by topographical, ecological, and historical criteria. Crete shows unexpectedly low levels of endemism considering its long period of isolation. Actually, many animal and plant groups have given rise to endemic forms on Crete. Current research on its oniscidean fauna will probably lead to a deeper understanding of this potential poverty.

The analyses of OGU relationships lead to the recognition of two major biogeographic units. One contains the continental mountainous part of Greece (plus Ionian Islands), and one contains the Aegean part (Fig. 4). PAE is supposed to provide historically resolved patterns, and we might perceive its results as hypotheses on the relative timing of OGU separation. Such an interpretation, though, would mean that: (1) Attiki, Evia, and northern Sporades share a more recent common history with the central, eastern, and southern Aegean Islands than they do with continental Greece; (2) Crete was more recently connected to the central Aegean Islands than to the rest of Greece; and (3) endemics of the Dodekanisa diverged before the separation of Crete from the Kyklades. All these hypotheses are in contrast to the established paleogeography of the area (Dermitzakis, 1990). On the other hand, it is important to note that the resulting groups are similar in respect to several ecological factors, such as climate and

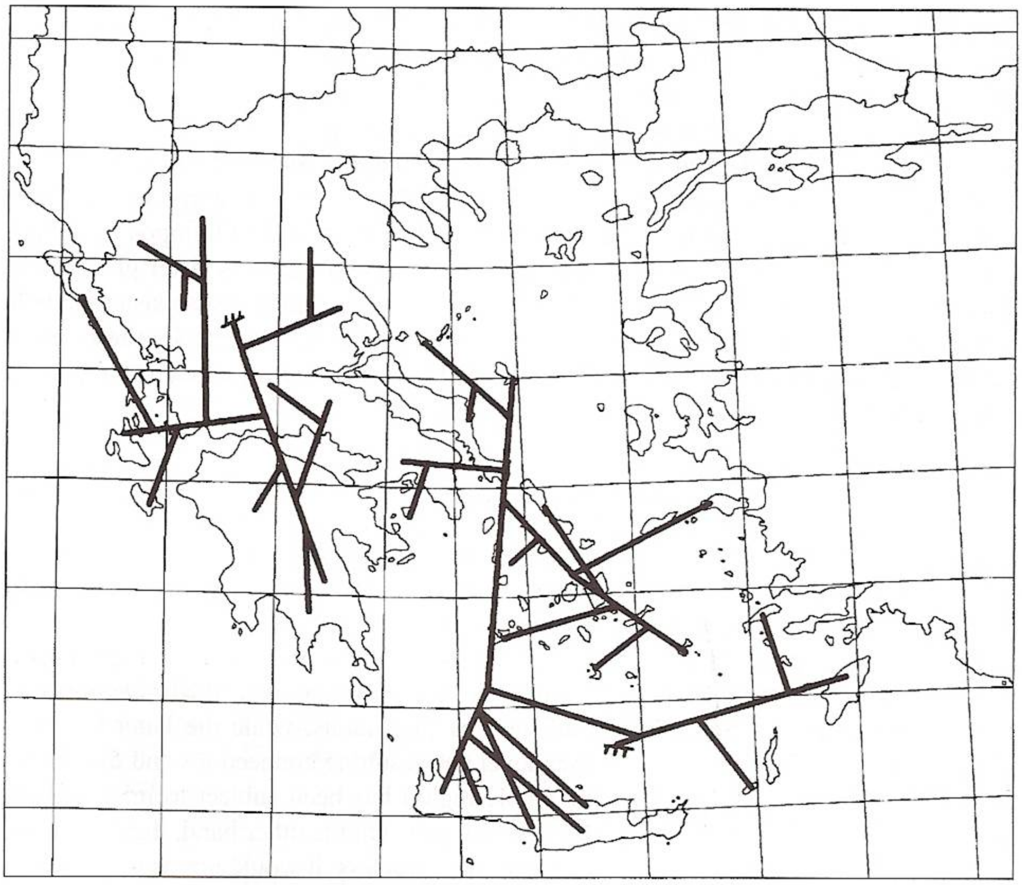

Fig. 4. The two major biogeographic entities that have resulted from the present analysis. The cladograms show the relationships within OGUs of each major entity as revealed by PAE.

vegetation. These must have played an important role in the shaping of modern patterns, especially during the Pleistocenic glacial periods, when the circum-Aegean lands were much less affected by climatic change. Hence, the existing data cannot justify a purely vicarianistic interpretation of Oniscidean differentiation. A more complex explanation that involves ecological factors is required.

This view is supported by the results of the separate analysis of *Armadillidium* species. This genus has largely differentiated in the continental part of Greece (including Evia and northern Sporades that were part of continental Greece until very recently). The separation of the two major clades coincides with the topographical separation of western continental Greece (to the west of the Pindos Mountains) and southern-south-eastern continental Greece (Peloponnisos and to the east of Pindos). These regions are also ecologically distinct (the western part is much more humid than the eastern parts) and were affected differently by glaciations. Additionally, inside the eastern clade, OGU relationships correspond to ecological similarities (the Aegean coastal and insular areas diverge first, followed by the climatically similar Attiki, while the mountainous Peloponnisos and central Greece remain as the more recent sister clades).

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