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ZOOLOGICAL DIVERSITY OF THE AEGEAN ARCHIPELAGO

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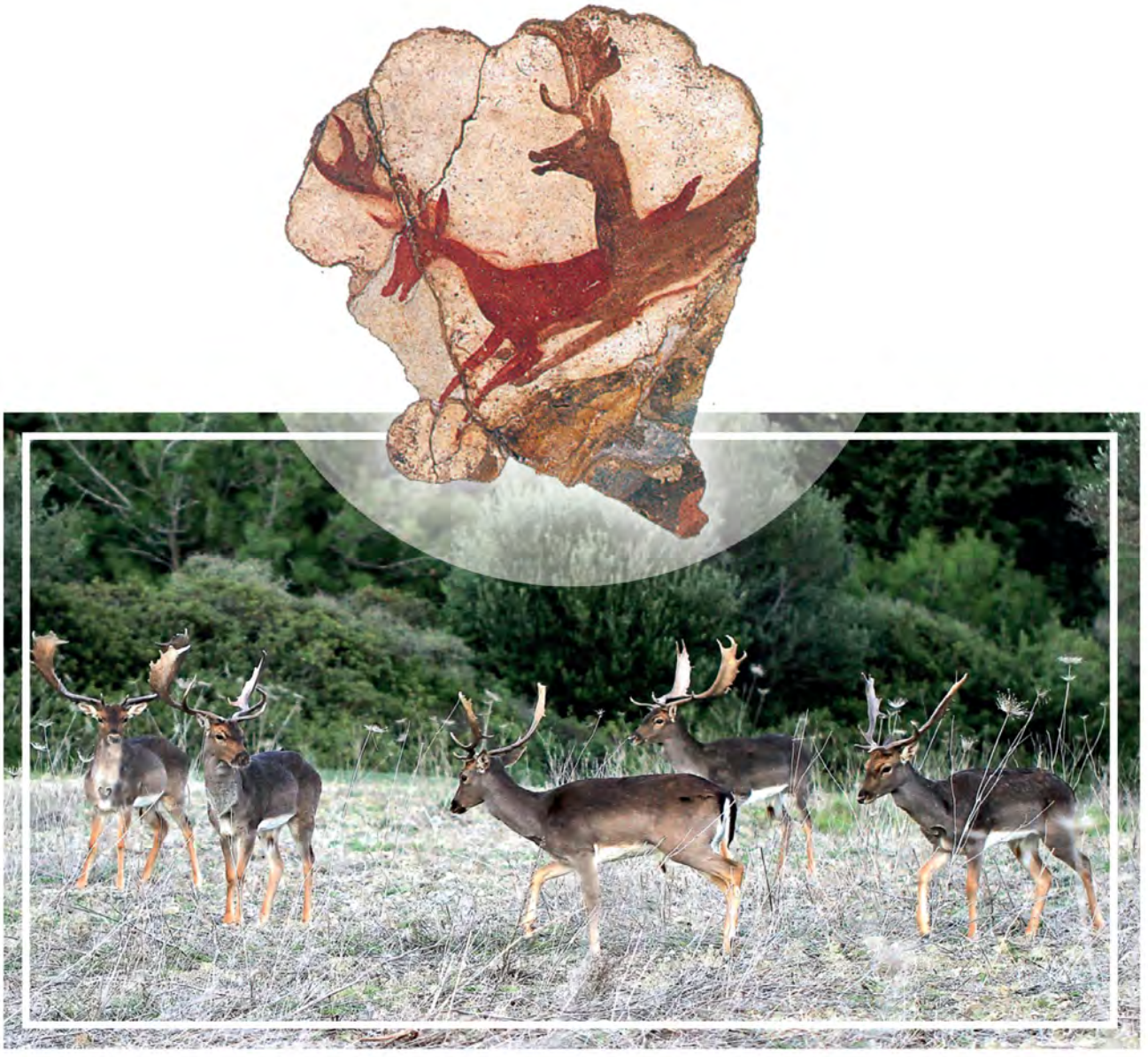

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A BRIEF INTRODUCTION TO THE ZOOGEOGRAPHY OF THE AEGEAN ARCHIPELAGO

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Summary: In the present work a brief introduction to the zoogeography of the Aegean Archipelago is provided. Evolutionary and speciation processes on islands in general are discussed and, in particular, some of these models are confirmed by the study of the Aegean islands. Palaeontological, climatic and human factors have contributed in shaping the fauna of these islands characterized by high level of endemism and that includes species of particular biogeographical interest. Some examples and related bibliography are provided.

Key Words: biogeography, evolution, isole greche, Mare Egeo.

Riassunto: Nel presente lavoro viene fornita una breve introduzione alla zoogeografia dell' Arcipelago dell'Egeo. Vengono discussi i fenomeni evolutivi e di speciazione nelle isole in generale e, in particolare, alcuni modelli confermati dallo studio delle isole dell'Egeo. Diversi fattori paleontologici, climatici e umani hanno contribuito a formare il popolamento zoologico di queste isole con la presenza di numerosi endemismi e di specie di particolare interesse biogeografico. Vengono citati alcuni esempi e la relativa bibliografia.

Parole Chiave: biogeografia, evoluzione, Greek islands, Aegean Sea.

As simplified ecosystems, but at the same time characterized by high levels of diversity, islands are of particular importance for the study of biogeography and evolutionary processes (Matthews & Triantis 2021).

Islands have provided fundamental insights for the development of modern biology, from the pioneering studies of Darwin (1859) and Wallace (1880) to the "theory of island biogeography", in which MacArthur & Wilson (1967) proposed for the first time that island richness is determined by an equilibrium between immigration and extinction rates.

The traditional subdivision of marine islands into "oceanic" and "continental", further distinguishing between the latter those formed by eustatic changes in sea level and those fragmented by ancient continental masses, has now been replaced by new classifications (such as shelf, shelf volcano, orogenic margin, continental arc, continental fore-arc, rifted arc-raft, isolated raft atoll, isolated block, etc.), considering as the distinctive features of each type have strongly imprinted the native biotas (Ali 2017; 2018).

The Mediterranean is a geographically circumscribed basin, and its islands can be referred to some of these different categories, but all show a substantial trait in common: a long-term history of anthropization, that played an important role in the structure and composition of their ecosystems. Especially those of the Aegean Sea were the cradle of important prehistoric cultures (Minoan, Cycladic), but also saw the civilization of classical Greece flourish.

At least within the Mediterranean context, Aegean is undoubtedly the "sea of the islands": there are more than 7000 islands, indeed, 90% of which are actually islets smaller than 10 km^2 indeed (Figs. 1-12). It is therefore hard to imagine that until 12 million years ago this area was a unique, continental landmass, which paleogeographers indicate as Ägäis.

Later (until about 5 million years ago) a slow transgression of the sea formed a biogeographic barrier between the eastern and west-central sectors, known as the Middle Aegean Trench (MAT). This latter was most likely reduced but present even during the Messinian drying phase.

Finally, tectonic phenomena and sea-level changes occurred predominantly during the Pleistocene, with alternating phases of connection and isolation between different territories and volcanic activity that originated new islands, such as Thira, Nisyros and the nearby islet of Gyali (Fassoulas 2018; Hammoud *et al.* 2021). For instance, in this phase Crete gradually emerged after being completely submerged during the Pliocene.

Just as old, in proportion, is the human presence on the Aegean islands. A part from a suggestive but not confirmed hypothesis about a colonization of Crete before 100,000 years ago (Howitt-Marshall & Runnels 2016), many sites (Limnos, Gioura, Kythnos) have been dated to the Paleolithic, but it is mainly during the Neolithic that a phase of significant anthropization occurs, when even islands that were not permanently inhabited were largely exploited for agriculture, pas-

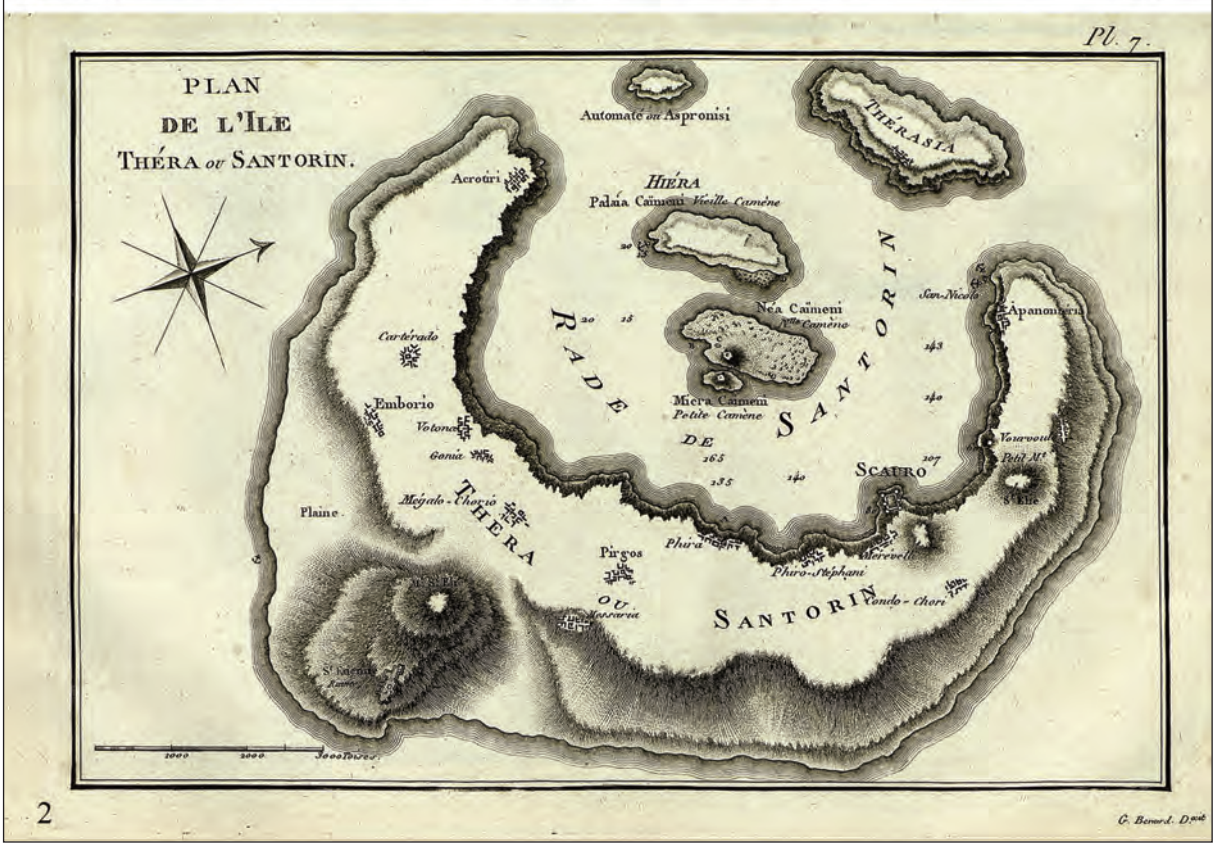

Figure 1. Greece, Aegean Archipelago and Western Turkey (Olivier 1801). Figure 2. Island of Santorini (Olivier 1801).

Figure 3. *Quercus infectoria* and its Gall wasp species associated (*Diplolepis* Geoffroy 1762 - familia Cynipidae) (Olivier 1801). Figure 4. Reptiles of the Aegean archipelago: *Chalcides ocellatus* Forsskål, 1775 and *Eryx jaculus* (Linnaeus 1758) = *Boa turcica* Olivier, 1801 (Olivier 1801).

toralism or mineral resources, such as obsidian (Phoca-Cosmetatou 2011; Dawson 2014).

Despite thousands of years of intense anthropic pressure, may therefore sounds surprising that this area still represents an extraordinary treasure in terms of biodiversity: for example, there is the largest percentage of endemism recorded for land snails within the Mediterranean basin. These islands are the most important breeding area for the Eleonora's falcon *Falco eleonorae* Gené, 1839, as well as for other bird species, and host the largest extant population of another iconic animal, the Mediterranean monk seal *Monachus monachus* (Hermann, 1779).

Since 1960s the islands were used as model in island biogeography studies: in his authoritative survey on the ecology and evolution of Aegean passerines, Watson (1964) found that the main factor influencing their faunal richness is habitat diversity. More recent views focused also on the vicariance processes as important factor for the evolutionary differentiation in different animal groups (Poulakakis *et al.* 2015).

The current biogeography appears to be closely related to the paleo-events that have characterized the different stages of evolution of this macro-archipelago.

During the Middle Miocene, after the breakup of the old landmass, many species invaded this area from the Eastern regions. The most representative were rhinoceros, hyenas, mastodons and small horses, that became extinct due to the successive geological and climate changes.

However, few are still occurring and displaying a relict distribution: this is the case, for instance, of the scorpion *Iurus dufoureius* (Brullé, 1832) or the terrestrial gastropod *Helicodonta gyria* J.R. Roth, 1839.

The second evolutionary phase is mainly characterized by the colonization both from European and Asiatic elements, such as lizards of the genus *Podarcis* Wagler, 1830 and amphibians of the

genus *Lyciasalamandra* Veith & Steinfarz, 2004, respectively.

However, the current distributional patterns of the island faunas seems to be more strictly related to the fluctuations of the Pleistocene glacial cycles, when animals expanded or reduced their range depending from climatic changes. The case of mammals is a good example of the influence exerted by these events: only one endemic species of the Pleistocene fauna is still surviving, the Cretan white-toothed shrew *Crocidura zimmermanni* Wettstein, 1953.

Isolation has determined generally a high level of endemism. A part from the already mentioned land snails, there are several groups of invertebrates that include a large number of endemic taxa, such as terrestrial isopods belonging to the genus *Schizidium* Verhoeff, 1901 or the darkling beetles of the genus *Dendarus* Latreille, 1829 (Schmalfuss, 2008; Anastasiou *et al.* 2018).

Of course, micro-evolutionary processes have not involved all the organisms, and even among those belonging to the same group they may be occurring in different ways: another terrestrial isopod, *Armadillo tuberculatus* Vogl, 1876, is widespread in the south-central Aegean, with morphologically divergent populations on the different islands; in contrast, those of the related *A. officinalis* Duméril, 1816, distributed in the same region, are more or less homogeneous under the morphological or molecular point of view (Kamilari & Sfenthourakis 2009).

A group of great taxonomic and ecological importance characterized by a high degree of

Figures 5-8. Landscapes of Crete Island. Figure 5. Omalós Plateau. Figure 6. Kantanos-Selino. Figure 7. Hora Sfakion. Figure 8. Paralia Elafonisi (photos by Ignazio Sparacio).

differentiation is the land snail genus *Albinaria* Vest, 1867 (Fig. 13), which has become a model for various ecological, systematic and evolutionary studies. Different hypotheses have been proposed to explain the high rate of endemism of these populations, currently fragmented into numerous species and subspecies. Phylogenetic analysis by Dimopoulou *et al.* (2017) on populations from the island of Dia (Crete) shows a complex phenomenon of speciation and diversification. Only in Crete, for instance, about 150 taxa of *Albinaria* are reported with a high proportion of endemics (Kittel & Hirschfelder 2018). A large number of endemic populations are moreover exclusive to larger islands, such as *A. klemmi* Paget, 1971 and *A. rechingeri* Paget, 1971 known from Rhodes, *A. rollei* (Boettger, 1896), *A. greeni* Tomlin, 1935, *A. mavromoustakisi* Brandt, 1961 and *A. alajana cypria* H. Nordsieck, 1993 from Cyprus or even small ones, such as *A. fuchskaeufeli* H. Nordsieck, 1977 endemic to Kinaros Island, *A. jaeckeli* Wiese, 1990 and A. *torticollis* (Olivier, 1801) from Dìa Island (Crete), *Albinaria pondika* Welter-Schultes, 2010 from Isola Pondikonísi (Crete).

Probably the differentiation within this genus reflects a pattern of divergence with non-adaptive radiation (Gittenberger 1991; Parmakelis *et al.* 2005 in the genus *Mastus* Beck, 1837).

This does not mean that selective processes have not been completely involved in the radiation. Schilthuizen (2018), for example, studied the roles of natural selection imposed by the biotic and abiotic environment and of sexual se-

Figures 9-12. Crete Island. Figure 9. *Julodis pubescens ivenii* Mannerheim, 1837: Hora Sfakion. Figure 10. *Purpuricenus desfontainii desfontainii* (Fabricius 1793): Zaros. Figure 11. *Albinaria eburnea samariae* (H. Nordsieck 2004): Omalós, upper part of Samariá Gorge. Figure 12. *Potamon potamios* (Olivier, 1804): Vamvakades (photos by Ignazio Sparacio).

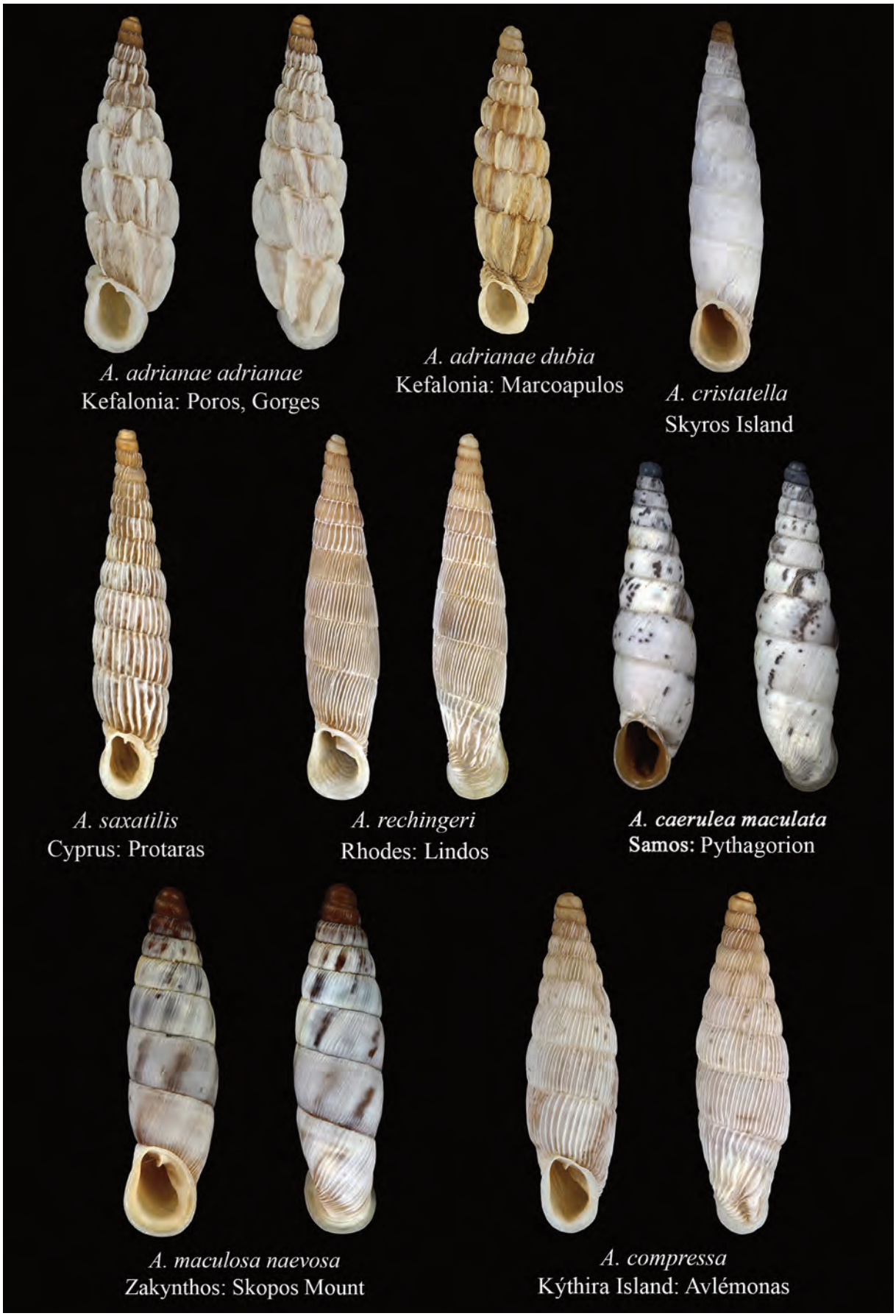

Figure 13. Some *Albinaria* species from Greek islands (photos by Ignazio Sparacio).

lection, Giokas *et al.* (2014) made a comparative studies on the morphological variations driven by selection.

The distribution and differentiation patterns of the dragonfly *Platycnemis pennipes* (Pallas, 1771) in the Aegean are the result of an interaction between dispersal and vicariance, also influenced by the ecological characteristics of the species (Battin, 1992).

Among vertebrates, it is remarkable that four of the five *Podarcis* species found in the Aegean, namely *P. gaigeae* (Werner, 1930), *P. levendis* Lymberakis *et al.*, 2008, *P. milensis* (Bedriaga, 1882) and *P. cretensis* (Wettstein, 1952), are island endemics, and some of them have a narrow distribution and a very small population size.

As already said, the Aegean archipelago is an ideal model for research on evolutionary, ecological and biogeographic phenomena – with particular reference to speciation and geographical isolation.

The complex geo-paleontological history of all these islands – sometimes even very small in size – and the presence of man since ancient times have contributed to the creation of the multiform natural history of the Aegean archipelago.

As summarized by Sfenthourakis & Triantis *et al.* (2017), the prevailing factors that have contributed to the development and diversification of the animal communities present in the Aegean islands are: the heterogeneity of the habitat; geographical and climatic factors; adaptive and non-adaptive radiation phenomena, often realized in a short time; vicariance and dispersal phenomena; very high turnover rates of species in a short time with fairly stable community characteristics. Despite the numerous works carried out on these animal communities, they can, and should, still be subjects of further study and research.

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Εὕδουσι δ' ὀρέων κορυφαί τε καὶ
φάραγγες πρώονές τε καὶ χαράδραι φῦλά
τ'ἑρπέτ' ὅσα τρέφει μέλαινα γαῖα θῆρές τ'
ὀρεσκῴοι καὶ γένος μελισσᾶν καὶ κνώ
δαλ' ἐν βένθεσσι πορφυρέας ἁλός εὕδουσι
δ' οἰωνῶν φῦλα τανυπτερύγων

"end the mountain-peaks are asleeep and the ravines,
the headlands and the torrent-beds,
all the creeping tribes that the black earth nourishes,
the wild animals of the mountains, the race of bees
and the monsters in the depths of the surging sea;
and the tribes of long-winged birds are asleep".

(Alcman, 7th century B.C.)

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