THE TERRESTRIAL MALACOFAUNA OF THE SOUTHEAST – CENTRAL AEGEAN ISLETS

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Abstract This paper studies the taxonomy, distribution and biogeographic relations of the terrestrial malacofauna on 19 islets lying in the Southeast – Central Aegean. The isolation of these islets has attracted the interest of many malacologists since the 19th century, and a total of 20 species of land snails, including seven endemics, were listed. The authors studied the malacological collections in the Natural History Museum of Crete deriving from four recent scientific expeditions to the above islets. A total of 35 species were found. Syrna, the largest islet in the group, is inhabited by 25 species. The taxonomic status and peculiarities of 14 species (Eobania vermiculata, Helix cincta, H. pronuba, Helix sp., Maltzanella godetiana, Xerocrassa ingens, Metafruticicola coartata, Mastus etuberculatus, M. unius, Orculella ignorata, Albinaria brevicollis and Lauria cylindracea) are discussed. The zoogeography of the islets is consistent with the paleogeography of the mid-Pleistocene. Biogeographically speaking they are closer to the Cyclades, though there is evidence arguing for the existence of isolated clusters of islets rather than one unique group.

Key words Southeast – central Aegean Islets, terrestrial gastropods, taxonomy, distribution, biogeography.

INTRODUCTION

The complicated geological history of the Aegean, insularity, climatic changes and the predominance of the Mediterranean type climate over the last 2.3 million years (Suc, 1984) have served as the driving forces for what is a hot spot of biodiversity (Myers *et al.* 2000). It is no exaggeration to term the Aegean "a natural laboratory of evolution, ecology and civilizations" (Sfenthourakis & Triantis, 2017). Today there are more than 7,000 islands and islets in the Aegean (Triantis & Mylonas, 2009), with a total area of 23,000km^2. These maintain one of the most diversified land snail faunas in Europe: according to Vardinoyannis & Mylonas (2019) 419 species are distributed in the Aegean, accounting for 60% of all terrestrial gastropods in Greece (695 species) (Vardinoyannis *et al.* 2018).

South of Astypalaia Island and northwest of Karpathos Island in the southeast – central Aegean, surrounded by depths exceeding 1,000m, lies a group of 19 islets (Fig. 1, Table 1). Based on the distances between them and the surrounding isobaths, 5 clusters of islets can be distinguished: the first consists of seven islets in the north, of which Syrna is the largest; then comes a chain of 6 more, where Zafora Megali is most prominent; in the southeast is a third cluster of 3 islets, chief among which is Astakida; the fourth cluster to the south is formed by the two Ounio islets; lastly, the lonely islet of Chamili lies to the southwest.

These groups of islets share many features pointing to their uniqueness in the Aegean: a) the deep sea surrounding them indicates it is unlikely they ever formed part of the nearby large islands during the eustatic changes of the Pleistocene; b) apart from Syrna islet, which was permanently settled by farmers up until the mid-20th century, all others are uninhabited, apart from occasional use by livestock breeders, fishermen and hunters; c) all islets are mainly formed of limestone, while sediments are rare; d) the climate is thermo-Mediterranean (Mavrommatis, 1978), with annual precipitation less than 400mm and a wet period lasting four months (December–March); e) the main vegetation is phrygana and herbs, except for Syrna and Plakida, where maquis is also present, while on Syrna there are abandoned fields in wind-sheltered areas; f) in most biogeographical subdivisions of the Aegean archipelago, the studied islets are placed in the Cyclades region (Strid & Tan, 1997; Vardinoyannis *et al.* 2018), while some phytogeographical studies (Rechinger & Rechinger-Moser, 1951; Strid, 1996; Kougioumoutzis *et al.* 2017) place them in the Cretan region; g) they all form part of the Natura 2000 network, not only on account of their plants and invertebrates, but also due to their

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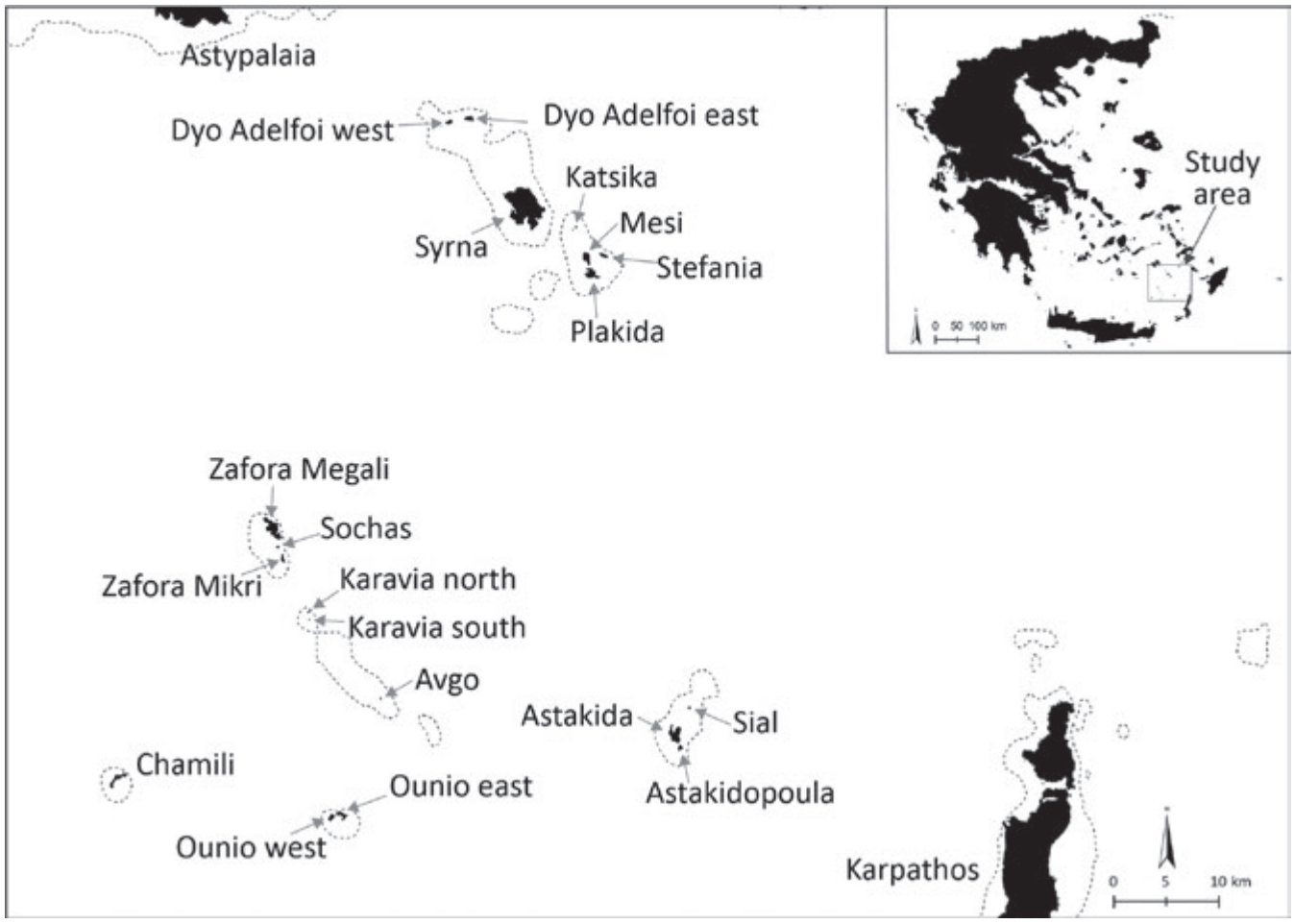

Figure 1 Map of the area studied. Dashed line: isobath of 200m.

importance for migrating birds and as nesting sites for monk seals (*Monachus monachus).*

The paleogeography of this area is not well known. Contrary to (a), Lykousis (2009) suggests that high subsidence rates during the mid-Pleistocene dramatically altered the landscape of the central Aegean. Syrna and its nearby islets were part of an extended landmass connecting continental Greece to the Cyclades and Asia Minor (Fig. 2a). Some of the other islets, e.g., from Zafora Megali in the north to the two Ounio islands in the south, formed one large, isolated island. Galanidou *et al.* (2020) present a more detailed map (Fig. 2b) for the glacial maxima over the past 500 kyr, during low sea level periods, when the islets in this study were parts of five larger islands corresponding to the aforementioned clusters.

The isolation of the clusters has aroused the interest of numerous scientists and collectors since the first half of the 19th century, despite their relative inaccessibility: most of the islets lack a safe anchorage. Böttger (1883, 1885) was the first scientist to publish taxonomic studies on the land gastropods of the islets, based on the rich collection of Vice-Admiral T. Spratt. Decades later, Gambetta (1929) mentioned 8 species collected by A. Desio from Astakida. The most important contribution was by Fuchs & Käufel (1936), listing 17 taxa collected by Werner & Wettstein in 1934 and Wettstein & Rechinger in 1935. More recent studies were published in the second half of the 20th century, based on malacological material collected by H. Pieper from 1963 to 1973. Finally, Riedel & Mylonas (1995, 1997) studied the islets' zonitids on the basis of material from two scientific expeditions.

All in all, 37 papers include at least some taxonomic or distributional data concerning the land snails of the area. Most repeat data already reported by the aforementioned authors. Ten publications are focused entirely on the genus *Albinaria,* ten on the family Enidae and eight on the Zonitidae.

Table 1 Characteristics of the studied islets.

Islets	Area (km2)	Altitude (m)	Distance from the nearest larger island (km)	Vegetation	Substrate
Dyo Adelfoi East	0.22	164	7.5 from Syrna	phrygana	limestone
Dyo Adelfoi West	0.13	100	1.3 from Dyo Adelfoi East	phrygana	limestone
Syrna	7.93	322	29 from Astypalaia	phrygan, maquis, cultivations	limestone, sediments
Katsika	0.01	40	25 from Mesi	phrygana	limestone
Mesi	0.43	70	0.3 from Plakida	phrygana	limestone
Stefania	0.14	50	0.9 from Mesi	phrygana	limestone
Plakida	0.52	80	0.6 from Syrna	phrygan, maquis	limestone, sediments
Zafora Megali	1.27	227	34.4 from Syrna	phrygana	limestone
Sochas	0.03	80	0.7 from Zafora Megali	phrygana	limestone
Zafora Mikri	0.1	60	1.7 from Zafora Megali	phrygana	limestone
Karavia North	0.02	90	7.2 from Zafora Megali	phrygana	limestone
Karavia South	0.01	40	0.4 from Karavia North	herbs	limestone
Chamili	0.43	60	25.8 from Zafora Megali	phrygana	limestone, sediments
Ounio West	0.23	100	0.2 from Ounio East	phrygana	limestone
Ounio East	0.28	150	25.8 from Zafora Megali	phrygana	limestone
Astakida	0.98	200	30.5 from Karpathos	phrygana	limestone, sediments
Astakidopoula	0.14	80	0.1 from Astakida	phrygana, herbs	limestone
Sial	0.02	50	2 from Astakida	phrygana	limestone
Avgo	0.02	80	17.8 from Zafora Megali	–	limestone

The present work is the result of an extensive study of the malacological material collected during four scientific expeditions between 1989 and 2018, now held in the Natural History Museum of Crete. The rich shell collections and preserved alcohol material have enabled us to enrich our knowledge of the terrestrial malacofauna on these islets and clarify certain taxonomic uncertainties. We also discuss the biogeographic relations between the islets and the neighbouring islands in the Aegean.

Material and methods

The material we studied is the outcome of four scientific expeditions, now stored in the malacological collections of the Natural History Museum of Crete – University of Crete. The authors participated in the first three expeditions.

The first was a joint project involving scientists from the universities of Athens and Crete, supported by the Hellenic Navy. In particular, the islets of Ounio East, Ounio West, Chamili, Zafora Megali and Zafora Mikri, Sochas, Karavia North, Karavia South, Avgo, Astakida, Astakidopoula and Sial were studied over a period of 4 days (20–23/4/1989).

The second expedition was supported by the Leventis Foundation, as part of a project studying the geology, biodiversity and ecology of 50 islets in the Aegean and the Ionian archipelagoes. In this case, the Syrna cluster (Syrna, Dyo Adelfoi East, Plakida, Mesi and Stefania) was studied over the course of 4 days (26–29/10/1993).

The third expedition was organized by the North Karpathos-Saria Management Body, under the terms of a project investigating biodiversity in Natura 2000 areas. The collection (15/12/2017) took place on Astakida and Astakidopoula.

Finally, the fourth was a joint expedition by the University of Michigan and the Natural History Museum of Crete. Material from the islets of Ounio East, Ounio West, Chamili, Karavia North, Sochas, Zafora Megali, Zafora Mikri, Dyo Adelfoi East and Plakida was collected over three days (16–18/5/2018).

No material was available from Dyo Adelfoi West and Katsika islets. All of the flora and fauna on Avgo have been destroyed, as the islet was used for military exercises for many decades.

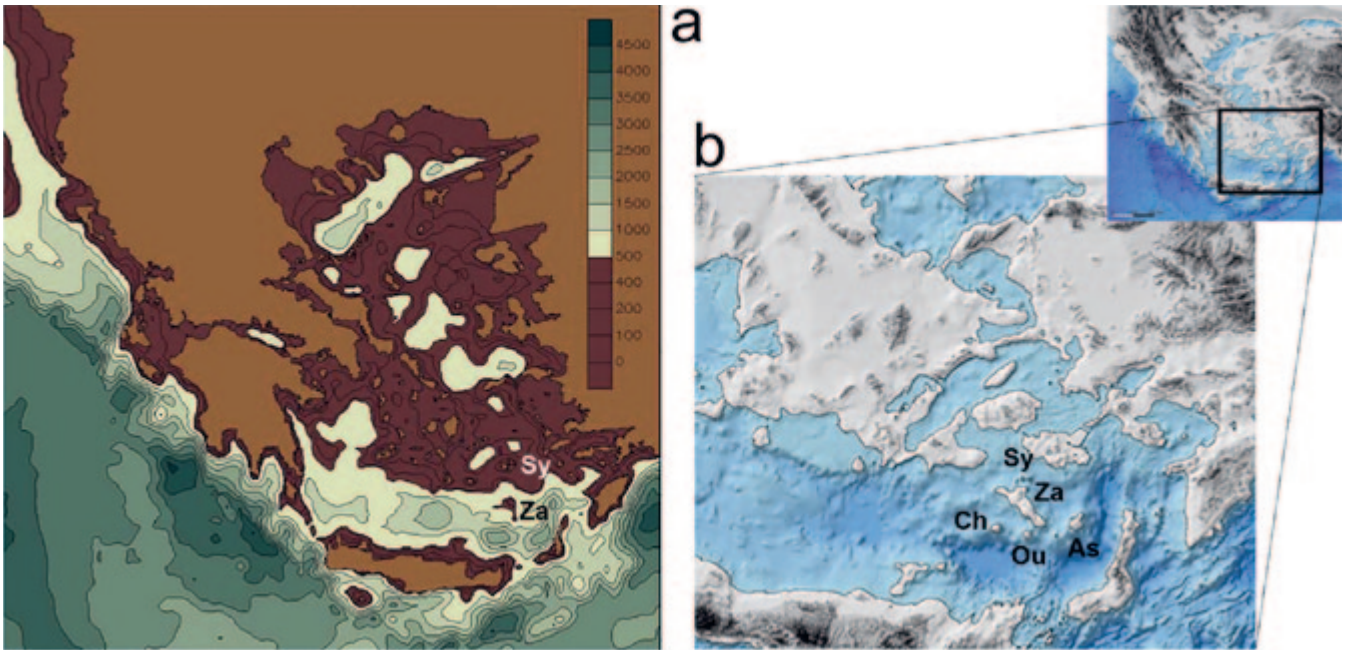

Figure 2 The paleogeography of the studied area according to a: Lykousis (2009); b: Galanidou *et al.* 2020. As: Astakida cluster, Ch: Chamili, Ou: Ounio cluster, Sy: Syrna cluster, Za: Zafora Megali cluster.

Approaching the three larger islets of Syrna, Zafora Megali and Astakida is comparatively easy, as they have safe anchorages. On the other hand, landing and moving around the smaller ones is difficult, as they are semiconical, with one side almost vertical and the other steeply inclined. On the smallest islets, soil is limited to the top or to karstic crevices.

The predominant vegetation type on all the islets is phrygana and herbs. On Syrna and Plakida there are patches of maquis with *Juniperus turbinata* (Gussone) and *Pistacia lentiscus* (L.).

The collecting effort was based on the size, geomorphology and vegetation of each islet, sampling in all different types of habitat. Litter was collected from predominant shrubs on the three larger islets. Sediments and Aeolian sandstones were searched for fossils or subfossils.

The collected specimens were drowned in water for 24 h and then preserved in 75% ethanol. Some of the individuals were preserved in 96% ethanol for future molecular analysis. The collected litter was sieved through 5–0.4mm mesh and examined under a magnifying lens.

Apart from the Zonitidae from the first and second expeditions studied by Riedel & Mylonas (1995, 1997), all other identifications were carried out by the authors, based on shell characteristics and reproductive system. A digital vernier caliper was used for shell measurements, recording shell height (H), shell diameter (D), protoconch diameter (PD) and the number of whorls (W), following Kerney & Cameron (1979).

The species names of all the reported taxa verified in this study are presented in Table 2.

Based on their distributions, we classified the species found into the following five chorotypes: The Endemics of one or more islets in the area; Aegean Endemics, including those species with a restricted presence on the surrounding mainland; East Mediterranean; Mediterranean; and Palearctic. Assignment of each species to a chorotype was based mainly on the following sources: Vardinoyannis (1994); Schütt (2005); Heller (2009); Welter-Schultes (2012) and Fauna Europaea.

Results

In total, we found 35 living and extinct species of land snails on the 16 islets studied (Table 2). As no material was available from Dyo Adelfoi West and Katsika, the only known species from those two islets are those referred to by Fuchs & Käufel (1936). Furthermore, no species were found on Avgo islet.

Syrna is by far the richest islet (25 snail species), followed by Astakida with 19 species. Although Zafora Megali is the second largest islet in the area, it only hosts 12 species. The smallest islets

Table 2 List of all species found. N: new record of living population; +: presence based on bibliographic data and verified by the authors; Nex: new record of extinct population; +ex: extinct populations based on bibliographic data and verified by the authors.

Island Species	Dyo Adelfoi East	Syrna	Mesi	Stefania	Plakida	Zafora Megali	Sochas	Zafora Mikri	Karavia North	Karavia South	Chamili	Ounio West	Ounio East	Astakida isl	Astakidopoula	Sial	CHOROTYPE
Albinaria brevicollis (L. Pfeiffer, 1850)	Nex	+	N	+	N	+	N	N	+	N	N	+	+	+	N	Nex	Aegean
Caracollina lenticula (Michaud, 1831)														N	N		Mediterranean
Cecilioides acicula (O. F. Müller, 1774)		N	N	N	N									N	N	N	Palearctic
Cecilioides tumulorum (Bourguignat, 1856)		N	N		N									N	N		Mediterranean
Cochlicella acuta (O. F. Müller, 1774)		N		N													Mediterranean
Eobania vermiculata (O. F. Müller, 1774)		N	N	N	+	+	N				Nex	N	N	+	N	N	Mediterranean
Eopolita protensa (A. Férussac, 1832)	N	+															Mediterranean East
Granopupa granum (Draparnaud, 1801)	N	N	N	N	N	N	N		N		N	N	N	N	N		Mediterranean
Helix cincta O. F. Müller, 1774		N															Mediterranean East
Helix pronuba Westerlund & Blanc, 1879		Nex									Nex						Mediterranean East
Helix sp.														Nex			
Lauria cylindracea (Da Costa, 1778)	N	N			N	N		N	N			N	N	N			Palearctic
Maltzanella godetiana (Kobelt, 1878)		N												Nex	Nex		Aegean
Mastus etuberculatus (Frauenfeld, 1867)	N	+	N	+	+	+		+	+	N							Aegean
Mastus unius (O. Böttger, 1885)						N					+	+	+	+	+	+	Endemic
Mediterranea hydatina (Rossmässler, 1838)	N	N	N		N									+			Mediterranean
Metafruticicola coartata Fuchs & Käufel, 1936	+	+	+	+ex		+	N	N	+		Nex	N	N				Aegean
Monacha pseudorothii Hausdorf, 2003		N			N												Aegean
Orculella ignorata Hausdorf, 1996	N	N	N	N	N	+	N	N				N	N	N	N		Mediterranean East
Pleurodiscus balmei (Potiez & Michaud, 1838)														N	N		Mediterranean
Pyramidula chorismenostoma (Westerlund & Blanc, 1879)	N	N															Aegean
Rumina saharica Pallary, 1901		N	N	+	+									+	N	Nex	Mediterranean

Table 2 *Continued*

Island Species	Dyo Adelfoi East	Syrna	Mesi	Stefania	Plakida	Zafora Megali	Sochas	Zafora Mikri	Karavia North	Karavia South	Chamili	Ounio West	Ounio East	Astakida isl	Astakidopoula	Sial	CHOROTYPE
Rupestrella philippii (Cantraine, 1841)						N											Mediterranean
Theba pisana (O. F. Müller, 1774)		N															Mediterranean
Thiessea fuchsiana (Knipper, 1939)		N															Aegean
Vitrea clessini (P. Hesse, 1882)	N	N	N	N	N	+	+	+	N		N	+	+	+	N		Aegean
Vitrea contracta (Westerlund, 1871)		+												+	N		Palearctic
Xerocrassa cretica (L. Pfeiffer, 1841)	+	N	+	+	N									N	N	N	Mediterranean
Xerocrassa ingens Fuchs & Käufel, 1936						N	N		+		N	N	N	N			Endemic
Xeromunda candiota (Mousson, 1854)		N															Mediterranean
Zonites astakidae A. Riedel, 1985														+	+		Endemic
Zonites embolium Fuchs & Käufel, 1936	Nex	Nex						+	+			+ex	+ex				Endemic
Zonites invitus A. Riedel & Mylonas, 1995							+										Endemic
Zonites nautarum A. Riedel & Mylonas, 1995						+											Endemic
Zonites sp. (new?) A. Riedel & Mylonas, 1995											+ex						Endemic
TOTAL SPECIES FOUND	12	25	12	11	13	12	8	7	8	2	9	10	10	19	15	6	

of Karavia South and Sial have 2 and 6 species respectively. Syrna and Astakida are inhabited by the entire malacofauna of their cluster, while Ounio East and Ounio West have exactly the same species.

Three species, *Helix* sp., *H. pronuba* and *Zonites* sp. (new?) were only found as subfossils on the islets under study. The quantity and quality of *Helix pronuba* shells found on Syrna indicate a dense population that thrived until recently. Additionally, there are 6 further species (Table 2) with alive on some islets, but extinct on others. On Chamili, which is the most isolated islet in the area, 4 of the 9 species observed were found only as subfossils.

The majority of the extinct populations belong to edible species (*Helix* sp., *H. pronuba, Maltzanella godetiana, Eobania vermiculata*), which is consistent with fishermen's testimonies of repeated attempts to transport them from larger islands nearby.

Five species are the most common on almost all islets: *Albinaria brevicollis* (on all); *Vitrea clessini* (on 14); *Granopupa granum* (on 13); *Orculella ignorata* and *Eobania vermiculata* (on 12 each). On the contrary, 9 species were found only on one islet: *Helix cincta*, *Xeromunda candiota*, *Theba pisana*, and *Thiessea fuchsiana* on Syrna; *Zonites nautarum* and *Rupestrella philippii* on Zafora Megali; *Zonites invitus* on Sochas; *Zonites* sp. (new?) on Chamili and *Helix* sp. on Astakida. It is worth mentioning that no slugs were found or reported on any of the islets.

According to bibliographical data, 25 species were reported in the islet clusters investigated here. Five were not confirmed in the present study: two from Zafora Megali [*Zebrina fasciolata* (Olivier, 1801) and *Albinaria olivieri* (Roth, 1839)] and three from Astakida [(*Metafruticicola pellita* (Férussac, 1832), *Cernuella virgata (Da Costa, 1778) (=C. arcuata* (Kobelt, 1878) and *Albinaria moreletiana* (Böttger, 1878)].

Fuchs & Käufel (1936) recorded *Zebrina fasciolata* on Zafora Megali, based on a single shell. On the same islet *Albinaria olivieri* was first recorded by Böttger (1883) as *Clausilia privigna* (Böttger, 1878), followed by reports from several authors (Kobelt, 1892; Wagner, 1923; Zilch, 1977; Seidl, 1978). Since thorough sampling during the first and fourth expeditions failed to locate these species, we do not include them in the terrestrial malacofauna of Zafora Megali.

Gambetta (1929) is the only scientist to have reported the three other species for Astakida. However, neither *Metafruticicola pellita* nor any other *Metafruticicola* species have since been observed there, even though it is the most intensively studied islet of all. The record of *Cernuella virgata* (=*C. arcuata*) is probably a misidentification of *Xerocrassa cretica* or *X. ingens* as found by us on Astakida. *Albinaria moreletiana* has a restricted distribution on eastern Crete (Welter-Schultes, 2010) and is thus also excluded from the present species list.

Gambetta (1929) reported the species *Xeromunda candiota* from Astakida. Although it was never found there, the present study did locate it on Syrna. It is noticeable that 5 out of 8 species listed by Gambetta (1929) for Astakida turned out to be incorrect (*Metafruticicola pellita, M. grelloisi* (Bourguignant, 1857), *Xeromunda candiota, Cernuella arcuata and Albinaria moreletiana*).

On Syrna we found *Thiessea fuchsiana*, a species that was recorded from Katsika islet by Fuchs & Käufel (1936).

Despite the islets' isolation and inaccessibility, bibliographic records for them are adequate when compared to those for other more easily accessible islands in the Aegean, such as Skyros, Kalymnos, Astypalaia (Triantis *et al.* 2008) or Kastellorizo (Mylonas *et al.* 2019). Zafora Megali, Karavia North and Astakida were the best studied islets in the area, with 7, 5 and 8 species reported respectively. Despite being the largest islet in the area, Syrna was one of the least studied.

Taxonomic, ecological and distributional remarks.

1. *Eobania vermiculata*. Both living and subfossil populations were found on 12 of the 16 islets studied. The richest living populations occur on Astakida and Astakidopoula. Especially on the smaller islets, most of them show remarkable variability in shell height, shell diameter and thickness of apertular lip (H=17–22mm, D=22–30mm, lip thickness=1–5mm). On Plakida islet there are exceptionally small adult individuals, less than 15.5mm in height and 20mm in diameter (Fig. 3D).
2. *Helix cincta*. A dense population of large to very large *Helix* with a brown aperture was found on central and on northwest part of Syrna, where phrygana and maquis vegetation predominate. Seven of the 19 specimens in our sample have a high conical

spire (H=45–47.9mm), with the five spiral bands characteristic of *H. valentini* Kobelt, 1891, which is endemic to Kalymnos Isl. and certain nearby islets (Triantis *et al.* 2008; Welter-Schultes, 2012; Neubert, 2014). In the same sample, 5 specimens had a more spherical shell with fused spiral bands, as in *H. cincta*, which is distributed in most of the East Aegean islands and further east in the Levant (Neubert, 2014). All the other specimens have intermediate characters. The shell measurements and mean of the 19 specimens from Syrna are: H: 42.4mm (39.0–47.9), D: 40.5mm (35.9–44.2), W: 4.9 (4.7–5.1). In contrast to intra-population shell variability, the distal genitalia do not differ either from *H. cincta* or *H. valentini* from Pserimos Island (Dodecanese). Given the population variability in shell characteristics and stability of the genitalia as well as the molecular similarity of both species (Psonis *et al.* 2015a), we suggest that these two taxa belong to the same species, namely *Helix cincta* Müller, 1774 (Fig. 3B).

3. *Helix pronuba*. On south and southwest part of Syrna, with phrygana vegetation, we found a dense population of small, spherical shells with a brown aperture that we assigned to *H. pronuba* [n=24, H: 25.6mm (24–27.9), D: 26.8mm (24.8–29.5), W: 4.0 (3.7–4.2)]. According to these measurements, the Syrna population is closer to specimens from the islands of Crete and Karpathos (Dodecanese) than Anafi (Cyclades). All specimens found were subfossil shells that presumably died some years ago. On Chamili we found two broken subfossil shells of *Helix.* Based on the protoconch and shell sutures, we assume that they also belong to *H. pronuba.*

   The species is distributed in SE Mediterranean coastal areas and on several islands and islets of the south Aegean (Crete and its adjacent islets, Karpathos, Kasos and neighbouring islets, Chalki and Anafi) Mylonas (1982); Vardinoyannis (1994); Welter-Schultes (2012); Neubert (2014).
4. *Helix* sp. In loose sediments on Astakida we found numerous subfossil shells, though only 5 adult specimens were intact. Their surface was corroded, without obvious riblets, granulation or spire bands (Fig. 3C). The only helpful characteristic was their brown aperture. Shell measurements are: H: 33.7mm (31.2–36.1), D: 35.3mm (33–37.1), W: 4 (3.7–4.2). The possibility of their being *H. cincta* was rejected, as the known populations of this species (Neubert, 2014) from the Aegean and Asia Minor differ in terms of shell height / diameter ratio, the number of whorls and protoconch. On Astakida, shell diameter is always bigger than shell height, there are 4 rather than 5 whorls and the protoconch is bigger. These parameters are close to *H. pronuba*, but the latter is at least 10mm smaller in all dimensions. The location where these shells were found, close to the only safe anchorage on Astakida, and the coexistence of subfossil *Maltzanella godetiana,* support the idea of human transportation from an unknown population.
5. *Maltzanella godetiana*. (Fig. 3A) On central and on northwest part of Syrna there is a dense living population of *M. godetiana*, sympatric with *H. cincta*. Subfossil shells of this species were also found on Astakida and Astakidopoula; all were broken except for one adult on each islet. The measurements of 9 adult shells from Syrna are: H: 28.4mm (27.4–29.7), D: 31.3mm (30.3–33), W: 3.6 (3.4–3.8), Dprot: 8.5mm (7.2–10.4), while from Astakida H: 33.5mm, D: 34.3mm, W: 3.9, Dprot: 9.5 and from Astakidopoula H: 35.8mm, D: 37.3mm, W: 3.9, Dprot: 9mm. The dimensions of populations from Anafi, Amorgos, Naxos and Astypalaia islands indicate the existence of two distinct groups: one of relatively smaller dimensions (Syrna, Astypalaia), and a second (Naxos Amorgos, Astakida, Astakidopoula) with larger shells. However, we found no differences in the genitalia of the groups.
6. *Xerocrassa ingens*. Fuchs & Käufel (1936) first reported *Helicella (Trochoidea) syrensis ingens* from Karavia North Islet. In the same work they named several subspecies of *H. syrensis* Pfeiffer. 1846 from the Aegean islands that were subsequently classified in the genera *Xerocrassa* and *Candidula*. We studied the genitalia of 5 adult specimens from Karavia North, which is the locus typicus of the species, all of which belong to the genus *Xerocrassa*. The species is clearly different from *X. cretica*, which is the predominant species of the genus in the Aegean. *X. ingens* has a smaller flagellum than *X. cretica* and its

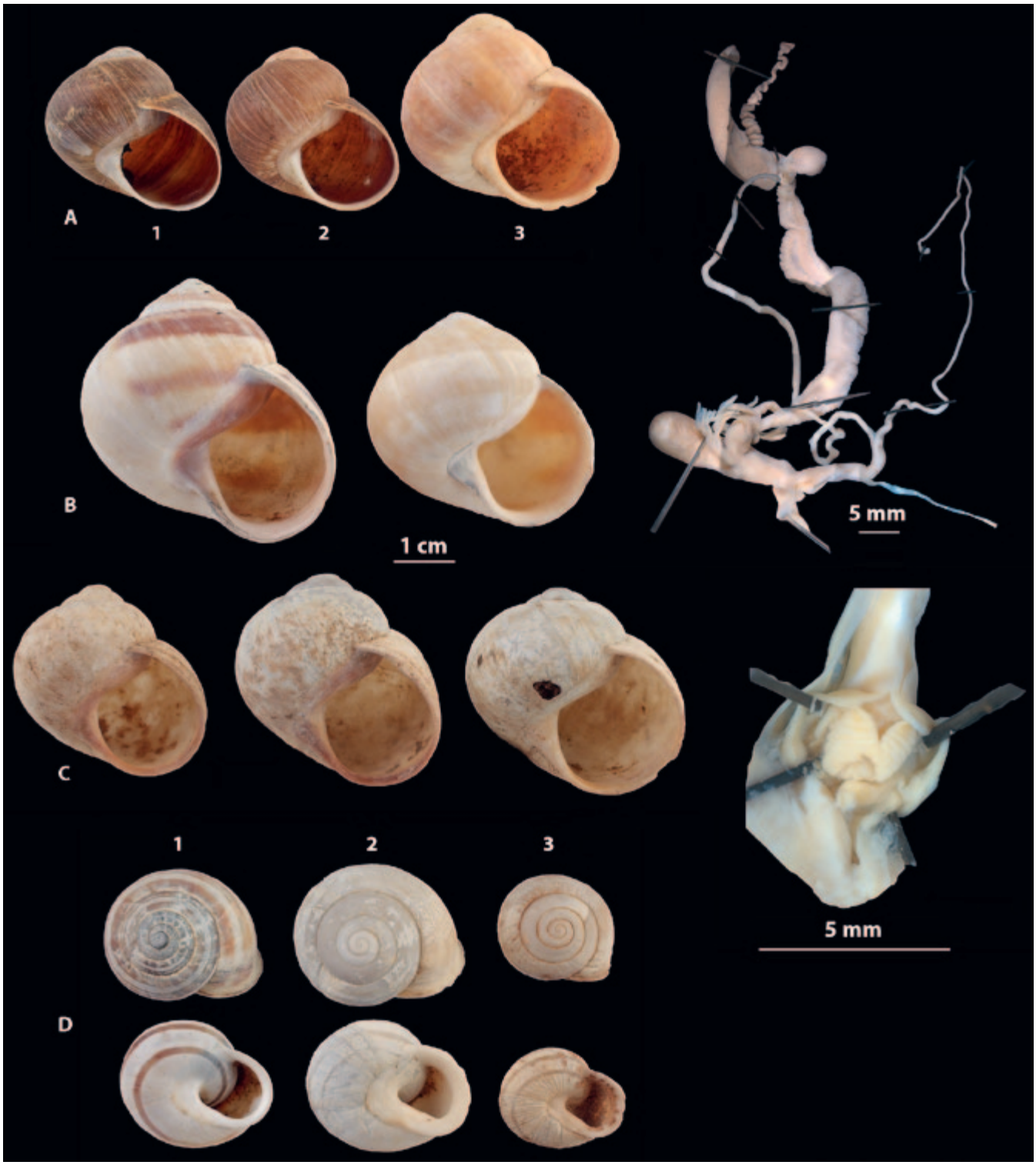

Figure 3 **A** Shell variability of *Maltzanella godetiana*, 1–2: Syrna, 3: Astakida. **B** Two shells from Syrna of *Helix cincta* – left shell closer to "*valentini*", right shell closer to *cincta*. On the right side its genitalia and penis papilla. **C** Subfossil shells of *Helix* sp. from Astakida. **D** *Eobania vermiculata,* 1: Syrna, 2: Astakida, 3: Plakida. Scalebar for all shells is 1cm.

penis is globular. We found the species on 6 other islets, always smaller in size than on Karavia North (Figs 4 A, B). On Astakida it was found sympatric with *X. cretica*. A few specimens from the islets of Ounio East, Sochas and Zafora Megali have a shell shape

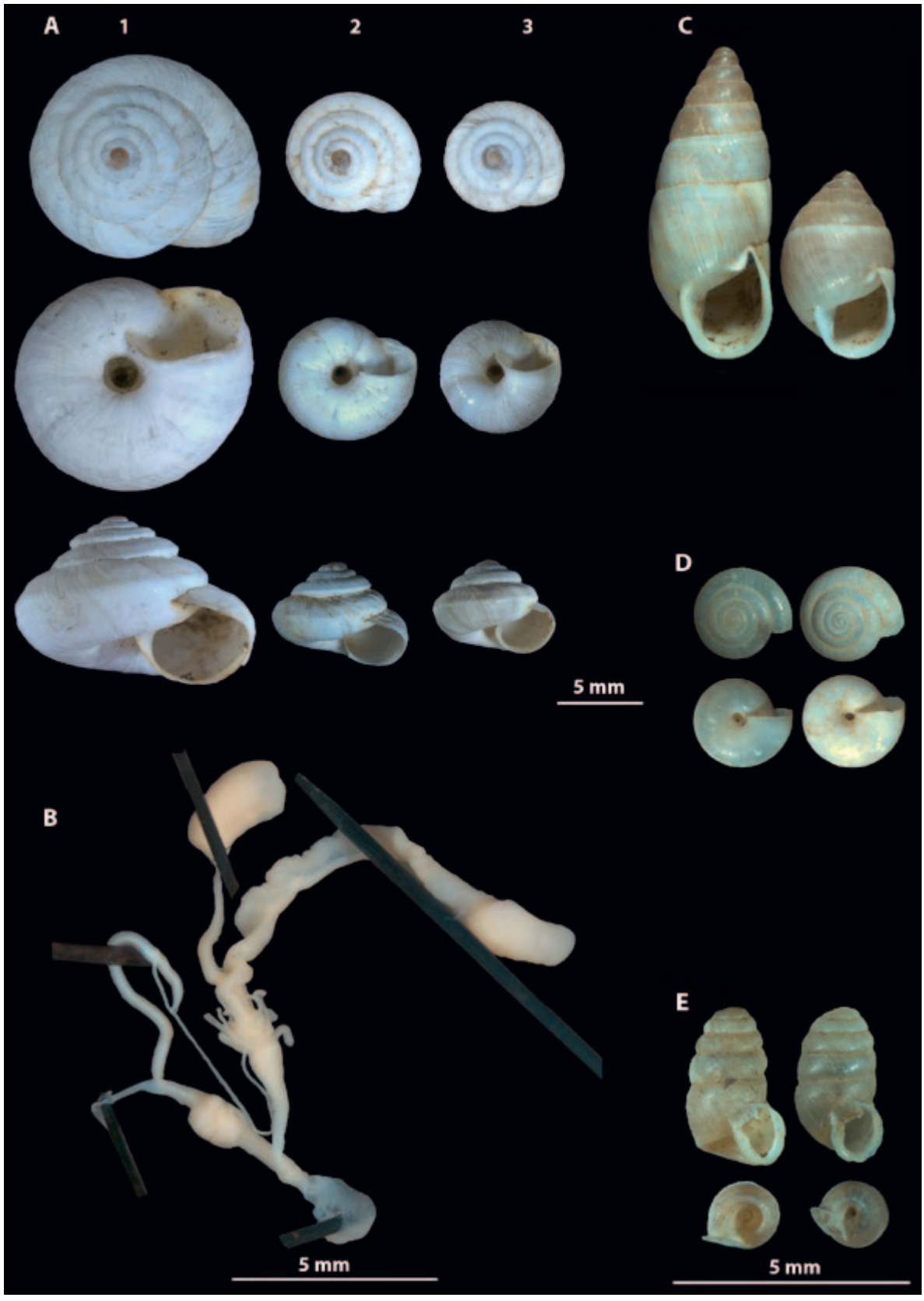

Figure 4 **A** shell variability of *Xerocrassa ingens* on 1: Karavia North, 2: Astakida, 3: Chamili. **B** genitalia of *X. ingens* from Karavia North. **C** *Mastus etuberculatus* left Syrna, right *Mastus unius* Astakida. **D** shell variability of *M. hydatina*, left Syrna and right Astakida. **E** *Lauria cylindracea* Syrna (left), Zafora Megali (right). Shells A, C, D same scale.

similar to *X. cretica*, but their reproductive system is clearly that of *X. ingens*. By contrast, on Syrna, Plakida and Astakida there are specimens with shell characteristics of *X. ingens*, but genitalia typical of *X. cretica*.

7. *Thiessea fuchsiana*. This species is known from Astypalaia and the islet of Katsika (Knipper, 1939). Subai (1996) reported it from Astypalaia, and Triantis *et al.* (2008) from Astypalaia and its satellite islets. On Syrna we found many shells, some of which were very fresh, but no living specimens. Their dimensions are H: 8.5–11.1mm, D: 16.3–20mm, W: 3.9–4.4. According to Psonis *et al.* (2015b) *T. fuchsiana* and *T. amorgia* (Westerlund, 1889) from Naxos and Amorgos respectively are very close on the basis of mtDNA.
8. *Metafruticicola coartata*. Two species of *Metafruticicola* have been recorded on the islets (Bank *et al.* 2013): *M. coartata* with the subspecies *M. c. coartata* and *M. c. gemina* Fuchs & Käufel (1936) and *M. pellita* from Astakida. As we argued earlier, the latter must be regarded as an incorrect reference. *M. coartata* is one of the most common species on the studied islets; on Stefania and Chamili we only found subfossil shells. The two subspecies differ in terms of the relatively flatter shell, wider umbilicus and wider last whorl of *M. c. gemina*. Although the above differences are obvious on Karavia North, which is the locus typicus of *M. c. gemina*, intermediate shells are found on Sochas and Zafora Mikri. The dimensions of the more variable *M. c. coartata* are H: 7.1–11.1mm, D: 12–16.4mm, W: 5–6.1 and of *M. c. gemina* are H: 8.5–9.3mm, D: 14.3–15.3mm, W: 5.5–5.8. The reproductive system of both subspecies, including the internal form of penis, is the same.
9. *Mediterranea hydatina*. (Fig. 4D) On Astakida, Riedel & Mylonas (1995) reported a typical form of the species with a narrow, deep umbilicus. We also found the species on Dyo Adelfoi East, Syrna, Mesi and Plakida, but always with a wide umbilicus. Samples from the south Cyclades and Astypalaia in the malacological collections of the Natural History Museum of Crete include some shells with a wide umbilicus, classified by A. Riedel as *Mediterranea* aff. *hydatina*. The opposite phenomenon is observed on Ikaria Isl. and some other northern Aegean islands, where there are populations with an entirely closed umbilicus; Riedel (1983) named these *M. h. ikaros* Riedel, 1983. However, a north – south geographic trend featuring closed – open umbilicus is obvious.
10. *Mastus etuberculatus & Mastus unius* (Fig. 4C). *Mastus* is one of the most common genera throughout the Aegean islands, with dense populations and many species. According to Bank (1997), taxonomy within the genus is chaotic. The use of spermatophores by Maassen (1995) as a reliable taxonomic character for the species on Crete was very promising, but difficulties locating and studying spermatophores and contradictions with molecular analyses (Parmakelis, 2003) have resulted in an unreliable taxonomy. Böttger (1885) first mentioned the species *Mastus unius* from the two Ounio islets. Fuchs & Käufel (1936) later recorded the subspecies *M. pupa anaphiensis* Fuchs & Käufel, 1936 from Dyo Adelfoi West and Karavia North, *M. pupa euberculatus* from Plakida and Stefania, and *M. p. unius* from Zafora Megali and the two Ounio islets. Heller (1976) considered *M. anaphiensis* a synonym of *M. etuberculatus* and *M. unius* a synonym of *M. pusio* (Broderip, 1836). Finally, in a preliminary work based on shell characteristics, Bank (1997) cited the species *M. anaphiensis* from Dyo Adelfoi East, Dyo Adelfoi West, Syrna, Plakida, Mesi and Stefania, and *M.unius* from Chamili, Ounio East, Ounio West, Zafora Megali, Karavia North, Karavia South, Sial, Astakida and Astakidopoula.

    We studied samples from all islets except Sochas, where the genus is absent. Two sympatric forms were observed on Zafora Megali. We examined the genitalia in all populations, but found no clear taxonomic characters and no spermatophores. Based mainly on shell characteristics, we consider that the populations from the 6 southern islets plus one of the two forms from Zafora Megali belong to the species *M. unius* and not *M. pusio*, as they invariably have an angular tooth (absent in *M.pusio*). Furthermore, the bursa copulatrix has a duct, whilst in *M. pusio* (Syros and Naxos populations) the bursa copulatrix opens directly to the pedunculus. On the islets in the Syrna cluster, we agree with Heller (1976) that the species present is *M.*

etuberculatus, as there are no shell or genitalia differences between *M. etuberculatus* and *M. anaphiensis*. Shells in the Zafora Megali cluster are closer to *M. etuberculatus*, but have a relatively larger diameter and show significant population variability.

11. *Orculella ignorata*. Fuchs & Käufel (1936) recorded *Orcula doliolum turcica* (Letourneux, 1884) from Cyclades and Zafora Megali. According to Gittenberger & Hausdorf (2004), this is a synonym of *Orculella critica*. We found the genus on most of the studied islets. Based on shell form, the populations were closer to *O. critica*, having cylindrical shells and no narrowed lower whorls like *O. ignorata*. Study of the genitalia from all populations showed that the penial appendix -the main specific characteristic of *O. ignorata* (Gittenberger & Hausdorf, 2004) - is simple. Thus, based on genitalia rather than shell characteristics, we assign our samples to *O. ignorata*.
12. *Albinaria brevicollis*. (Fig. 5) The genus *Albinaria* is one of the most diversified and problematic genera in the Aegean. Böttger (1883) was the first to publish three endemic taxa from the studied islets: *A. sculpticollis* (Böttger, 1883) from Zafora Megali, *A. s. unia* (Böttger, 1883) from Ounio, and *A. privigna* from Zafora Megali. Wagner (1923) placed *A. privigna* as a subspecies of *A. olivieri*. From the Desio collection, Gambetta (1929) recorded the species *A. moreletiana* and *A. rhodia* (Pollonera, 1916) from Astakida. Fuchs & Käufel (1936) added three more taxa in this area: *A. brevicollis casia* (Böttger, 1883) from Syrna and Stefania, *A. karavica karavica* Fuchs & Käufel, 1936 from Karavia North, and *A. k. sica* Fuchs & Käufel, 1936 from Zafora Megali. Pfeiffer (1955) placed all the above taxa in two species: *A. brevicollis* with the subspecies *casia*, *karavica* and *sica*, and *A. sculpticollis* (Böttger, 1883) with the subspecies *unia*. Finally, Nordsieck (1977) and Zilch (1977) recorded the species *A. brevicollis* with the subspecies *casia*, *karavica*, *sica* and *sculpticollis*, and *A. olivieri* with the subspecies *privigna*. The report of *A. moreletiana* by Gambetta (1929) from Astakida must be incorrect, as this species is endemic to a restricted area of Crete and has never been found on Astakida by anyone else. The species *A. rhodia* also mentioned by Gambetta (1929) is regarded as a synonym of *A. brevicollis* by Nordsieck (1977).

    We observed living *Albinaria* populations on all the studied islets except for Dyo Adelfoi East and Sial, where we found one empty shell on each. Although the variability among populations from the different islets is great in terms of shell size, colour (from shining white to dirty white), surface (ribbed or slender) and suture (deep or not), we believe that only *A. brevicollis* is present. Chamili, Karavia South, Karavia North, Zafora Mikri, Zafora Megali, Sochas, Syrna, Mesi and Stefania have monomorphic populations, whilst Astakida, Astakidopoula, Ounio East, Ounio West and Plakida have slender and ribbed forms with intermediates. The slender forms on Astakida were found on the top of the islet on calcareous rocks, while the ribbed ones under stones much lower down. On Zafora Megali we did not find *A. olivieri privigna.*
13. *Lauria cylindracea*. (Fig. 4E) The genus *Lauria* is represented in the Aegean by two species, namely *L. cylindracea*, distributed in most of the Aegean islands, and *L. umbilicus* (Roth, 1839) from Syros (Welter-Schultes, 2012). According to Roth (1839), the latter is easily identifiable mainly by its triangular aperture, formed by a keel at its base and a wide umbilicus. *Lauria* was found on 9 of the studied islets. All populations from Astakida, Ounio East, Plakida, Syrna and Dyo Adelfoi East have the characteristics of *L. umbilicus*. Specimens on Ounio West, Karavia North, Zafora Mikri and Zafora Megali either have intermediate features or are typical *L. cylindracea*. The two forms and their intermediates are also found on many Aegean islands, e.g. Amorgos, Astypalaia, Naxos, Paros and Kalymnos. We consider that there is only one species in the Aegean, *L. cylindracea*, with two ecomorphs and their intermediates.

Zoogeographic relations

Table 3 reports the number of extant species and percentage of chorotypes for all islets and each cluster. Looking at the entire group of islets, it is evident that more widespread chorotypes (Mediterranean, E. Mediterranean, Palearctic) prevail, while those with a more restricted distribution (Endemic, Aegean) constitute the minority. This is also the case for the Syrna and Astakida

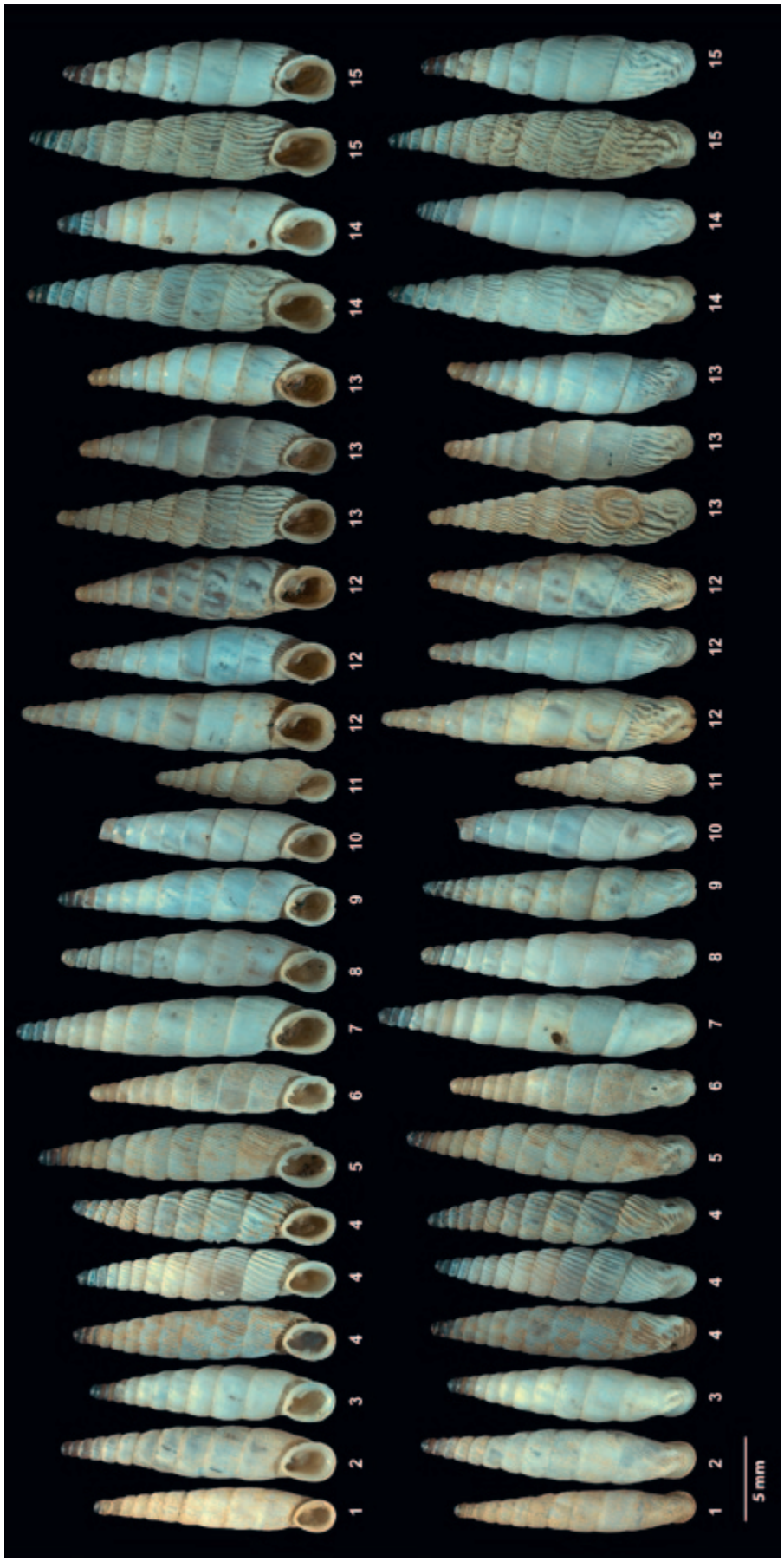

Figure 5 *Albinaria brevicollis* variability on the islets (shells are placed from north to southeast): 1: Dyo Adelfoi East; 2: Syrna; 3: Stefania; 4: Plakida; 5: Mesi; 6: Zafora Megali; 7: Sochas; 8: Zafora Mikri; 9: Karavia North; 10: Karavia South; 11: Chamili; 12: Ounio West; 13: Ounio East; 14: Astakidopoula; 15: Astakida. Scalebar for all shells is 5mm.

Table 3 Extant species number (N) and percentage of chorotypes in all the studied islets and in each islet cluster.

Islet Cluster	All islets		Syrna		Zafora		Chamili		Ounio		Astakida	
Chorotype	N	%	N	%	N	%	N	%	N	%	N	%
Endemic	6	18.7	0	0.0	5	35.8	2	40.0	2	22.2	3	17.6
Aegean	8	25.0	8	34.8	4	28.6	2	40.0	3	33.3	2	11.8
Mediterranean East	3	9.4	3	13.0	1	7.1	0	0.0	1	11.1	1	5.9
Mediterranean	12	37.5	9	39.1	3	21.4	1	20.0	2	22.2	8	47.1
Palearctic	3	9.4	3	13.0	1	7.1	0	0.0	1	11.1	3	17.6
Total number of species	32		23		14		5		9		17	

clusters, which are relatively closer to the inhabited islands of Astypalaia and Karpathos respectively, and consequently more affected by man. By contrast, chorotypes with a restricted distribution form the majority of species on the more isolated clusters of Zafora, Ounio and Chamili, accounting for over 55% of the total.

The majority of the 7 endemic species belong to the genus *Zonites* (5), and one species each to the genera *Mastus* and *Xerocrassa*. Three are single island endemics, while one, *Z. astakidae*, is distributed only on Astakida and Astakidopoula, which are very close to each other. The three remaining endemics are found on more than one islet cluster: *Z. embolium* on the Syrna, Zafora and Ounio clusters; *X. ingens* on all clusters except for Syrna, and *M. unius* on the three southern clusters of Chamili, Ounio and Astakida.

Based on their entire distribution, the eight Aegean species form three groups. The first consists of three species (*Thiessea fuchsiana, Monacha pseudorothi*, *Metafruticicola coartata*) distributed mainly on SE Cyclades and Astypalaia. The first two of these were found only on the Syrna cluster, while the third on all clusters except for Astakida. Three species (*Mastus etuberculatus, Albinaria brevicollis, Maltzanella godetiana*) are distributed on the Cyclades and the Dodecanese, but not on Crete. Finally, two species (*Vitrea clessini, Pyramidula chorismenostoma*), are found on many Aegean islands including Crete. *V. clessini* and *A. brevicollis* were found on all clusters, *M. godetiana* on the Syrna cluster and Astakida, *M. etuberculatus* on the Syrna and Zafora clusters and *P. chorismenostoma* on the Syrna cluster.

The sum of Endemism and Aegean Endemism on the studied islets varies from 31% to 100%, following a pattern whereby the southern islets have more endemics than the northern ones, and the western ones more than those in the east. The most isolated and inaccessible islets have the highest percentage of Aegean endemics (Karavia South 100%, Karavia North 75%, Zafora Mikri 71%, Chamili 67%).

DISCUSSION

One of the thorniest issues involved in studying the terrestrial land snails of the Aegean is the taxonomic uncertainty surrounding most of the most species rich genera, such as *Albinaria*, *Mastus*, *Xerocrassa*, *Orculella* etc. Repeated revisions are full of corrections not always accepted by other taxonomists. For *Albinaria* see among others Wagner (1923, 1924); Nordsieck (1977), Welter-Schultes (2010); for *Mastus* Heller (1976), Maassen (1995), Parmakellis *et al.* (2005); for *Xerocrassa* Hausdorf & Sauer (2009) and for *Orculella* Gittenberger & Hausdorf (2004).

The enormous population diversity of the Aegean caused by vicariance and/or dispersal, plus a gradual change in the use of taxonomic characters—from shell to reproductive system, and more recently to genetic distances by using molecular techniques—has led to problematic taxa, as most of the publications are based on insufficient data sets (Cameron & Pokryszko, 2005; Triantis *et al.* 2008).

Based on the rich malacological collections at the Natural History Museum of Crete, consisting of shells, alcohol material and frozen tissue not only from the studied area, but also from most of the islands and islets of the Aegean, our own observations have successfully solved some of the lasting taxonomic problems surrounding Aegean land snails, while simultaneously highlighting others that remain unsolved due to missing data.

According to this work, *Xerocrassa ingens* has distinct features in its genitalia that leave no doubt as to its generic and specific status. However, the scalariform shell cited as its main subspecific character according to Fuchs & Käufel (1936) turns out to be insufficient, as the islets under study host scalariform shells with genitalia of *X. cretica*, or typical *X. cretica* shells with genitalia of *X. ingens*.

Based on the latest revision of the genus *Helix* by Neubert (2014), *H. valentini* is endemic to Kalymnos and its surrounding islets; in fact, the IUCN has characterized this species as endangered (Neubert *et al.* 2019). Nevertheless, the shell variability of the Syrna population, ranging from typical *H. valentini* shells to typical *H. cincta* shells and their intermediates, plus the similarities of their genitalia and the small genetic distance between them (Psonis *et al.* 2015a), leave no doubt that there is only one species, *H. cincta*. The populations of Kalymnos and nearby islets must thus be reassigned to the subspecies *H. cincta valentini*.

The case of *Lauria* is also informative. Existing data support the appearance of two species in the Aegean: *L. umbilicus* and *L. cylindracea* (Welter-Schultes, 2012). Our findings on the populations of the studied islets and also in the Cyclades and the Dodecanese show that there is a mixture of distinct and intermediate populations. We observed an ecological pattern of differentiation but no distributional one, whereby the characters of the "umbilicus" form are related to drier habitats on the islands.

In the taxonomic remarks we argued that *Mastus unius* is not a synonym of *M. pusio*, as claimed by Heller (1976), since we found shell differences. We agree with Parmakellis *et al.* (2005) that a new taxonomic approach is needed for the genus *Mastus* in general, based on spermatophores and DNA analysis.

Despite the generally accepted taxonomy for *Thiessea fuchsiana* and *Zonites astakidae*, the molecular approach taken by Psonis *et al.* (2015b) and Kornilios *et al.* (2009) suggest that they are closely related to *T. amorgia* and *Z. pergranulatus* respectively. Further studies on both genera might realign the existing taxonomy.

The genus *Albinaria* was the object of numerous specific and subspecific revisions on the islets studied here (Böttger, 1883; Wagner, 1923; Gambetta, 1929; Fuchs & Käufel, 1936) up until 1977, when the dominance of *A. brevicollis* with a number of subspecies was established by Nordsieck (1977) and Zilch (1977). As we stressed in the remarks, no other *Albinaria* species is distributed in the area. The presence of *A. olivieri* must be regarded as doubtful, since it was not found during the most recent expeditions to Zafora Megali. The isolation, small population size and severe environmental conditions of the islets have led to morphological differences and peculiarities. It is not clear whether shell differences suffice to argue for the polytypic status of *A. brevicollis* in the area, or whether the species should only be regarded as morphologically variable. In the remarks we related some shell variables (smooth vs. ribbed) to certain ecological preferences (rocks-soil).

If we compare the total species richness of the studied islets with other island groups in the Aegean, we can see a striking similarity to two of them. The first is the nearby island group of Astypalaia, where 33 species of land snails (Triantis *et al.* 2008) were found, even though Astypalaia is almost 8 times bigger than the studied islets. The second is the Kastellorizo island group, with 31 species (Mylonas *et al.* 2019), which is almost the same area as the studied islets, but very close to the enormous source area of the Turkish mainland.

Triantis *et al.* (2008) compared the structure of the malacofauna on three island groups in the Aegean. The Astypalaia and Skyros island groups lie far from the surrounding mainland and have highly nested malacofaunas. The two larger islands hold the entire diversity of their group. On the other hand, the Kalymnos group is very close to the Turkish mainland and shows a higher disorder of species, as smaller islands in the cluster keep extant species not found on larger islands, but on the mainland of Turkey. The same pattern was found in the Kastellorizo island group (Mylonas *et al.* 2019). Syrna and Astakida host also the entire diversity of their cluster, but not Zafora Megali. The species that cause disorder in this cluster are not dispersers from bigger areas, as in the Kalymnos or Kastellorizo groups, but local endemics or relicts.

Existing data on the chorotypes of Aegean land snails (Mylonas, 1982, Vardinoyannis, 1994; Botsaris, 1996, Triantis *et al.* 2004, 2008) and other invertebrates (Simaiakis *et al.* 2005) argue for the predominance of the Mediterranean chorotype,

and of widespread (Palearctic – Mediterranean) chorotypes in general, rather than more restricted (Endemic – Aegean) ones. The closer to the surrounding mainland the islands are, the higher the percentage of widespread species found, and vice versa (Triantis *et al.* 2008). The chorotypes on the islets studied here tell us a different story: the predominant chorotype for all the malacofauna of the studied islets is Mediterranean. Widespread chorotypes outnumber restricted ones (56% – 44% respectively), even though the studied islets lie far from mainland coasts. This is more obvious for the Syrna and Astakida clusters, which are closer to larger inhabited islands and more affected by man. For the three more isolated clusters Zafora, Ounio and Chamili the predominant chorotypes are Endemic and Aegean. We argue that the predominance of restricted chorotypes is related to isolation and restricted human presence, and that of widespread ones to proximity to larger islands, the mainland and the influence of man.

There is a general congruence between the Pleistocene paleogeography of the area as resented by Lykousis (2009), Sakellariou & Galanidou (2017) and Galanidou *et al.* (2020) and the observed differentiation and distribution of land snails in the area. There are no species pointing to the unity of all the studied islets. The Syrna cluster is closer to that of Astypalaia and the south Cyclades, the three southern clusters have their own endemic species, and while the islets in the Zafora Megali cluster do have their own endemics, they also serve as a corridor between the Syrna cluster and the three southern ones. In general, all islets are biogeographically closer to the Cyclades than to the Dodecanese or Crete, a finding which tallies with Strid & Tan (1997) and Vardinoyannis *et al.* (2018). The proximity of the Syrna and Astakida clusters to Astypalaia and Karpathos respectively, and the consequent increase of anthropochorous species on them mask the isolation of the two clusters and increase their similarities to the surrounding islands.

Although some of the islets in the south – central Aegean presented here suffer from human influence, in common with most Aegean islands they preserve many endemic species and forms and are potential fields for studying patterns of isolated snail communities and isolated communities in general. The terrestrial malacofauna justifies the protection afforded to the islets as parts of the Natura 2000 network, and their characterization as "the Galapagos of the Aegean".

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