

THE ZONITES SPECIES OF IKARIA ISLAND: REDISCOVERY AFTER OVER A CENTURY AND FIRST DESCRIPTION OF THE REPRODUCTIVE SYSTEM

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ABSTRACT: *Zonites nikariae* and *Zonites chloroticus polycrates* were previously recorded from Ikaria Island only as empty shells, collected over a century ago. Here, we report the first collection of living specimens of both taxa during a 2025 survey on the island. In the case of *Z. nikariae*, the collection of adult specimens enabled the first description of its reproductive system. Furthermore, two individuals of *Z. chloroticus polycrates* were found in Ikaria, marking the species' rediscovery on the island 138 years after it was last documented. The confirmed presence of these populations is important amid the overall decline of the genus *Zonites* across the Aegean region. However, given that both taxa were found in sparse and localised populations, targeted conservation efforts and systematic monitoring are needed to secure their survival.

KEYWORDS: Aegean Sea; islands; land snails; *Zonites*

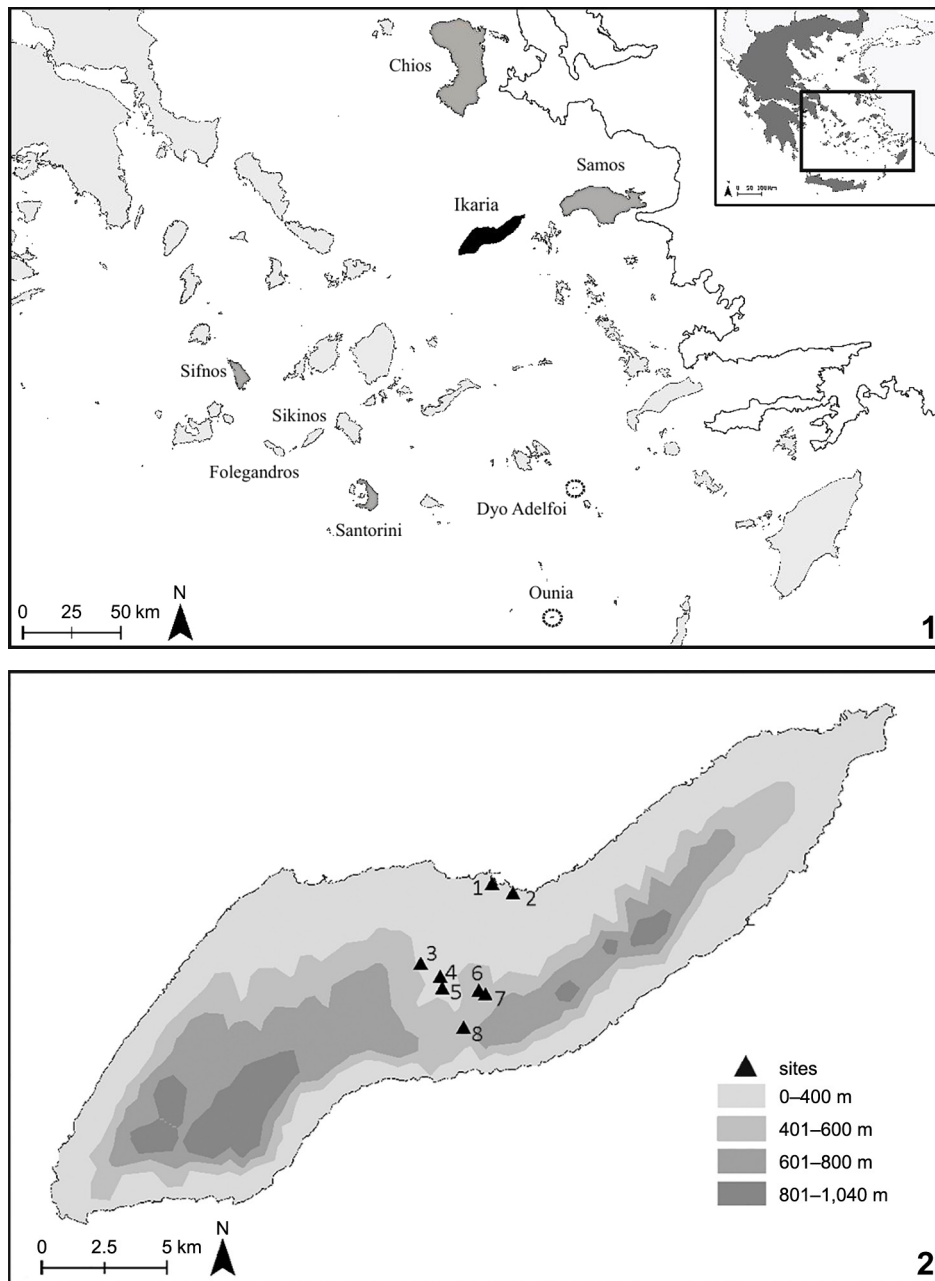
INTRODUCTION

The malacofauna of the Aegean Islands comprises 419 species (VARDINOYANNIS & MYLONAS 2019), with 51% being endemic (MYLONAS 1982, TRIANTIS al. 2008, VARDINOYANNIS & MYLONAS 2019, PROIOS et al. 2024, MAROULIS et al. 2025), representing a global biodiversity hotspot for insular land snail diversity (PROIOS et al. 2021). The genus *Zonites* Montfort, 1810 occupies a prominent position within the Greek malacofauna, as 18 of its 28 extant or recently extinct species are endemic to Greece (RIEDEL 1992, WELTER-SCHULTES 2012, BANK et al. 2025). The Aegean archipelago and Peloponnisos represent the core of the species' distribution (RIEDEL 1992, KORNILIOS et al. 2009, WELTER-SCHULTES 2012). The diversification of the genus dates to the Neogene, when it presumably expanded from Asia Minor to

Evvoia and Peloponnisos via the Cycladic land bridge (RIEDEL 1992, KORNILIOS et al. 2009).

Zonites represents one of the most threatened genera of the Greek malacofauna, with nine species distributed in the Aegean islands classified under one of the three IUCN categories of threatened species (NECCA 2024), while three other species have become extinct or locally extinct (*Z. siphnicus* Fuchs et Käufel, 1936 from Sifnos, Folegandros and Sikinos, *Z. santoriniensis* Riedel et Norris, 1987 from Santorini, and *Z. embolium* Fuchs et Käufel, 1936 from Dyo Adelfoi and Ounia islets (RIEDEL 1985, 1992, MYLONAS & VARDINOYANNIS 2022).

Ikaria, an eastern Aegean island (Fig. 1), occupies a unique position regarding the genus *Zonites*, as it could serve as a land bridge across the Aegean Sea.



Figs 1–2. Collection sites: 1 – map of the Aegean Sea, highlighting Ikaria, neighbouring islands and islands from where *Zonites* species have become extinct or locally extinct; 2 – map of Ikaria with sampling sites (1 – Evdilos, 2 – Kerameio, in cultivations, 3 – Frantato 1 km to Petropouli, 4 – Petropouli to Frantato, 1.5 km after the junction, 5 – Raos tou Foutra cave, 6 – Koskina castle below, 7 – Koskina castle, below in cultivations, 8 – Kosoikia to Plagia, at col by Agios Dimitrios chapel). Shading represents altitude in meters a.s.l. (see legend)

Two taxa are known from the island: *Z. nikariae* Pfeffer, 1930 and *Z. chloroticus polycrates* Martens, 1889, both classified as Vulnerable according to the Greek Red List of Threatened Species (NECCA 2024).

Zonites nikariae was first described by PFEFFER (1930) based on three juvenile or fragmented shells, which had initially been assigned by MARTENS (1889) to *Z. smyrnensis* (Roth, 1839). The species' type locality is Raos tou Foutra (Futra Raos cave), situated near the village of Petropouli, Ikaria. Almost a cen-

tury later, RIEDEL (1985) reported the species from the same area, based on one well-preserved subfossil adult shell and several juvenile shells and fragments. In the same work, RIEDEL (1985) classified a subfossil *Zonites* shell from Delos Island as *Z. nikariae*, although he noted that the record was unexpected and of uncertain origin. BANK & MAASSEN (1998) reported the species from Ikaria, 1 km towards Frantato from the crossroad Kosoikia-Dafni-Frantato, and from Samos around Pythagorio and around Panagia



Spiliani. From both localities only shells were retrieved (RUUD BANK, personal communication).

Zonites polycrates was first described by MARTENS (1889), distributed on the islands Chios, Samos and Ikaria. The locus typicus of the species is Marathokampos (Samos Isl.). In Ikaria, the species had been found in the area of Evdilos, but RIEDEL (1985) who studied the material of Martens reported that “the evidence from Ikaria is lacking”. RIEDEL (1985) placed *Z. polycrates* as a subspecies of *Z. chloroticus* (Pfeiffer, 1852), based on shell similarities, although its genitalia were still unknown. The nomino-

typical subspecies, *Z. chloroticus chloroticus* (L. Pfeiffer, 1852), inhabits the central part of Asia Minor, specifically the Izmir vilayet (RIEDEL 1987, BANK et al. 2025).

Both taxa, *Z. nikariae* and *Z. chloroticus polycrates*, had never been recorded alive, and consequently their reproductive system remained unknown. Here we present the results of a recent survey on Ikaria during which we collected living specimens of both *Z. nikariae* and *Z. chloroticus polycrates*. We describe the reproductive system of *Z. nikariae* and discuss the taxonomic implication of our findings.

MATERIAL AND METHODS

STUDY AREA

Ikaria is a Greek island in the eastern Aegean Sea, located approximately 19 km southwest of Samos (Fig. 1). The island has a total area of 255 km². Its terrain is rugged and predominantly mountainous, dominated by the Atheras mountain range, with its highest peak reaching 1,037 m above sea level. Geologically, Ikaria belongs to the Attic-Cycladic Massif, a crystalline belt characterised by metamorphic rocks including schists, marbles, and gneisses (LAURENT et al. 2015). The vegetation is typical-

ly Mediterranean: the northern and central slopes support evergreen oak (*Quercus ilex*) and pine forests (*Pinus brutia*) interspersed with shrublands and maquis (CHRISTODOULAKIS 1996).

SAMPLING

Land snail sampling was conducted between 14 and 17 November 2025 at eight localities (Fig. 2), including all sites where *Zonites* species had been previously reported. All samples were collected in areas with limestone substrate. At each site, sampling cov-

Table 1. Shell measurements in mm of adult *Zonites nikariae* per sampling site. Abbreviations: SD – shell diameter, SH – shell height, Wh – number of whorls, LWWhD – diameter of last whorl, PUWhD – diameter of penultimate whorl, SpH – spire height, ApH – aperture height, UmD – umbilicus diameter

Site	SD	SH	Wh	LWWhD	PUWhD	SpH	ApH	UmD
Petropouli to Frantato, 1.5 km after the junction	26.0	12.0	4.7	5.5	4.2	3.0	9.0	4.4
	26.7	12.4	4.7	5.4	3.8	2.4	10.0	5.4
	27.3	12.1	4.7	6.3	3.8	3.0	9.1	5.3
	28.4	13.4	5.0	5.7	4.3	3.5	9.9	4.5
	28.4	13.9	4.8	5.6	3.8	3.8	10.1	4.7
	29.2	14.3	5.0	6.7	4.1	3.6	10.7	5.5
	29.4	13.2	4.8	6.8	4.3	3.3	9.9	5.4
	29.9	15.3	5.0	6.8	4.6	5.0	10.3	5.5
	29.9	14.4	5.0	6.4	3.9	3.6	10.8	5.4
	30.3	14.7	5.1	5.6	4.2	4.0	10.7	5.4
	30.5	14.7	5.0	6.8	4.5	3.8	10.9	5.5
	30.6	14.3	5.0	6.3	4.4	3.8	10.5	5.7
	Koskina castle below	36.2	17.4	5.5	8.1	5.4	5.8	12.5
Mean values	27.4	14.0	5.0	6.3	4.3	3.7	10.3	5.3

Table 2. Shell measurements in mm of adult *Zonites chloroticus polycrates* per sampling site. Abbreviations as in Table 1

Site	SD	SH	Wh	LWWhD	PLWWhD	SpH	ApH	UmD
Kosoikia to Plagia, at col by Agios Dimitrios chapel	35.9	22.6	5.3	9.0	4.8	7.3	15.3	5.3
Koskina castle below	32.8	22.9	5.3	8.8	5.6	7.5	15.4	4.5
	34.1	23.0	5.2	8.7	4.8	7.6	15.4	5.3
	34.8	22.4	5.3	9.8	4.9	7.2	15.2	4.0
Mean values	34.4	22.7	5.3	9.1	5.0	7.4	15.3	4.8

ered all available biotopes, and collection of leaf litter and topsoil.

MATERIAL STUDIED

Two populations of *Z. nikariae* and two of *Z. c. polycrates* were recorded, with live individuals obtained from one population of each species.

Zonites nikariae was found at: a) Petropouli to Frantato, 1.5 km after the junction Kosoikia – Dafni – Frantato (Fig. 2, site 4), where 6 adult and 8 juvenile shells were found, along with 6 adult and 8 subadult live specimens, that were later preserved in alcohol. This locality lies within 1 km of all previously known records of *Z. nikariae*; b) Koskina castle below (Fig. 2, site 6), where 1 adult and 5 juvenile fresh shells were collected. *Zonites c. polycrates* was found at: a) Koskina castle below (Fig. 2, site 6), where 4 adult and 12 juvenile shells were collected, along with 1 subadult

and 1 juvenile preserved in alcohol; b) Kosoikia to Plagia, at col by Agios Dimitrios chapel (Fig. 2, site 8), where 1 fresh adult shell was found.

Soft tissues were first transferred to absolute ethanol for molecular analyses. All living specimens were drowned for 24 hours in water and subsequently preserved in 75% ethanol. Shell measurements of *Z. nikariae* were obtained from 12 of the largest specimens (Table 1) and of *Z. c. polycrates* from 5 specimens (Table 2), using a vernier calliper. We measured: shell diameter (SD), shell height (SH), number of whorls (Wh) following KERNEY & CAMERON (1979), diameter of the last and penultimate whorl (LW_hD and PUW_hD, respectively), spire height (SpH) and aperture height (ApH), and umbilicus diameter (UmD). All material is deposited in the malacological collection of the Natural History Museum of Crete, Heraklio, Greece.

RESULTS

Zonites nikariae Pfeffer, 1930

DESCRIPTION OF THE SHELL

Shell slightly elevated with a blunt apex, flat whorls regularly increasing, without deep sutures (Fig. 3). Immature specimens always with a sharp keel whereas in adult shells the keel disappears over the last

quarter of the body whorl (Fig. 3a). Measurements of 12 adult specimens collected from the sampling station towards Frantato, are given in Table 1. A diagnostic character of the species is that the aperture height is nearly three times the spire height. The adult specimen from Koskina castle is considerably larger (36.2 mm SD) and, in this specimen, the keel

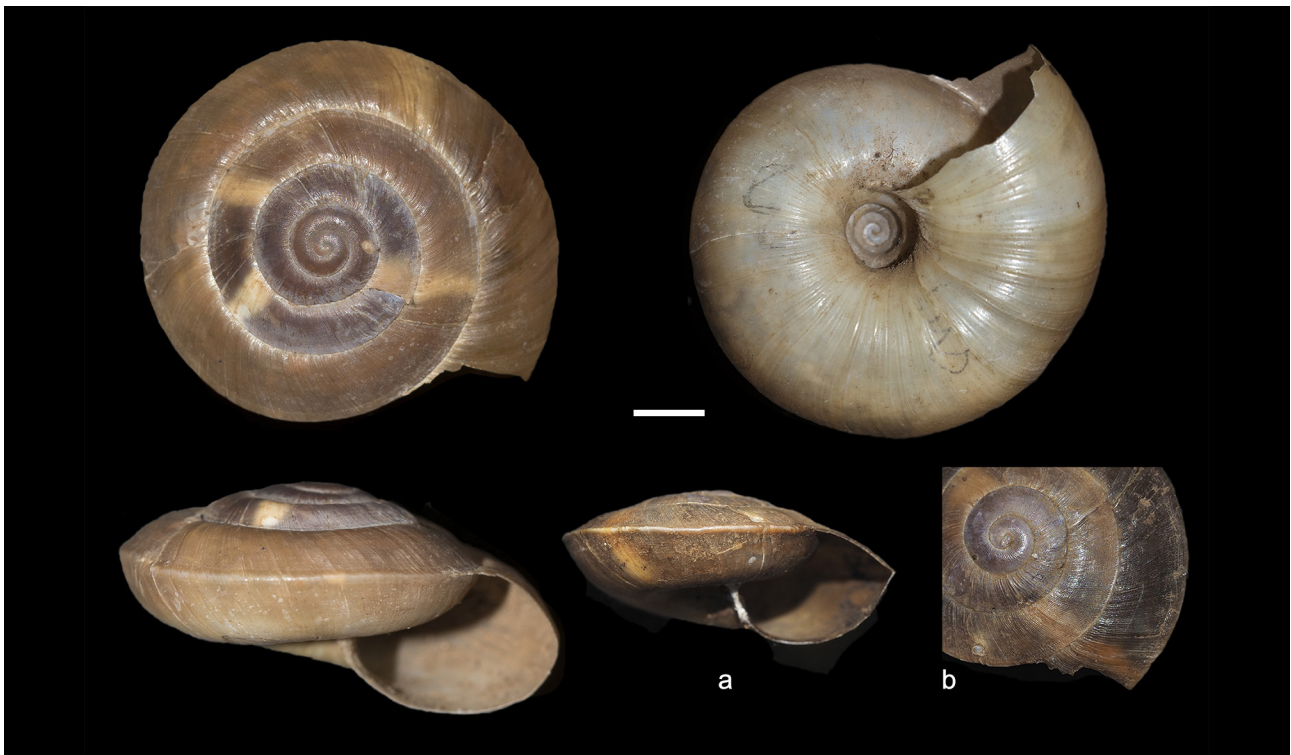


Fig. 3. Shells of *Zonites nikariae*, a – juvenile; b – shell granulation. Scale bar 5 mm

disappears along the entire last whorl. The umbilicus is broad, perspective, measuring approximately one fifth of the shell diameter. Shell colour of upper part brown, in basal part light brown. The protoconch has dense, discontinuous radial wrinkles, which gradually give rise to radial rows of minute granules (Fig. 3b). Granulation becomes weaker on the last whorl; its surface becomes smoother and only irregular radial folds remain, while the basal surface is smooth.

REPRODUCTIVE SYSTEM

Penis long and cylindrical, with a small swelling in its proximal part, internally, it has one or two axial pilasters and numerous folds (Fig. 4). The penial sheath is thin and covers the distal two thirds of penis; its upper edge is connected to the proximal one third of the epiphallus by muscular fibres. The penial retractor is strong and attached to the penis at the top of an almost pear-shaped or spherical caecum, according to SCHILEYKO (2003) or flagellum according to RIEDEL (1985). The epiphallus is very long, more than twice the length of penis; it opens laterally into the caecum. The junction of epiphallus – vas deferens is not clear as there is a gradual decrease of epiphallus diameter. The vagina is long, equal in length to penis, covered by a well-developed perivaginal gland. The free oviduct is very long, longer than the vagina. Spermathecal stalk is shorter but thicker than the free oviduct. Spermatheca is very large with attenuated apical part.

HABITAT

Zonites nikariae was found in two different habitats. The first site, Petropouli to Frantato, 1.5 km after the junction Kosoikia – Dafni – Frantato, is located on a northeastern, almost permanently shaded, steep torrent slope, with large limestone cliffs, stone walls and piles of stones. The vegetation consists of trees and shrubs of *Quercus ilex*, *Q. coccifera*, *Pistacia lentiscus*, ferns and many herbaceous plants. Living individuals were collected while active under piles or large stones. The second site, Koskina castle, is much drier than the previous, located 30 m below the summit (700 m above sea level). There are many limestone rocks and stones. The vegetation consists of phrygana with *Thymbra capitata*, *Sarcopoterium spinosum* and *Pistacia lentiscus*.

Zonites chloroticus polycrates Martens, 1889

DESCRIPTION OF THE SHELL

The shell characteristics of the specimens from the two populations found on Ikaria (Fig. 5) generally agree with RIEDEL's (1985) description of *Z. c. polycrates*, which was based on samples studied by MARTENS (1889), FUCHS & KÄUFEL (1934, 1936), as well as his own from Chios and Samos. The measurements from the Ikaria specimens (Table 2) are very



Fig. 4. Reproductive system and the internal structure of penis of *Zonites nikariae*. Scale bar 5 mm

close to that of [MARTENS \(1889\)](#) for *Z. polycrates* with respect to shell diameter and number of whorls.

The three characters that, according to [RIEDEL \(1985\)](#), differentiate *Z. c. polycrates* from the nominotypical subspecies – namely a more curved, non-scalariform spire, a blunter apex, and a smoother shell surface – fall within the range of interspecific variability observed in the populations of Ikaria and therefore its taxonomic distinction from the nominotypical subspecies is questionable. The only consistent differences found concern shell diameter and the ratio between the diameter of the last and the penultimate whorl. In the typical subspecies, shell diameter is greater reaching up to 43.3 mm ([RIEDEL 1987](#)) and the last whorl is approximately as wide as the penultimate one. In contrast, in *Z. c. polycrates* the shell diameter does not exceed 35.6 mm and the ratio of the last to the penultimate whorl ranges from 1.5 to 2. Regarding the reproductive system, comparison with

that of the nominotypical subspecies as described by [RIEDEL \(1987\)](#) cannot be made, as the Ikaria specimens are subadult and juveniles.

HABITAT

At the Koskina castle, *Z. c. polycrates* occurs sympatrically with *Z. nikariae*, but was found approximately 20 m lower, in an area with fewer shelters yet similar phrygana-type vegetation to that of the *Z. nikariae* habitat. At Kosoikia to Plagia at col by Agios Dimitrios chapel, it was found in phrygana with *Thymbra capitata*, *Sarcopoterium spinosum*, *Genista acanthoclada* and *Salvia fruticosa*, close to patches of *Quercus ilex* forest. During the present survey, it was not found in Evdilos, where it had previously been reported by [MARTENS \(1889\)](#).



Fig. 5. Shells of *Zonites chloroticus polycrates* from the site Koskina castle below (Ikaria Island). Adults and juveniles (bottom right). Scale bar 5 mm



DISCUSSION

Our survey on Ikaria documented the first records of living populations of both *Z. nikariae* and *Z. chloroticus polycrates*, whereas all previous surveys spanning more than a century (MARTENS 1889, PFEFFER 1930, FUCHS & KÄUFEL 1934, 1936, RIEDEL 1985, BANK & MAASSEN 1998) had only reported subfossil or empty shells.

The discovery of sufficient individuals and shells of *Z. nikariae* allowed us to provide a more detailed description of the shell compared to those available to date (PFEFFER 1930, RIEDEL 1985), including shell colouration and dimensions. Regarding shell diameter and height, specimens from the population Petropouli to Frantato, 1.5 km after the junction Kosoikia – Dafni – Frantato are smaller than the subfossil specimen measured by RIEDEL (1985), whereas the adult individual from the Koskina castle is clearly larger.

Although, according to RIEDEL (1985), *Z. nikariae* is conchologically close to *Z. smyrnensis*, which is distributed in Asia Minor and Chios, there are remarkable differences in their reproductive systems. The main distinguishing features of *Z. nikariae* relative to *Z. smyrnensis* include the perivaginal gland, which in *Z. nikariae* envelops the entire vagina; the shape of the caecum, which is spherical to pear-shaped and lacks an appendix; the mode of attachment of the penis retractor to the caecum, occurring apically rather than laterally; and the comparatively much shorter penis and longer epiphallus. In addition, the reproductive system of *Z. nikariae* differs markedly from that of all other Aegean species of the genus, primarily in the absence of an appendage on the caecum (Fig. 4). Therefore, the taxonomic validity of *Z. nikariae* is also confirmed by features of the reproductive system.

The rediscovery of living *Z. chloroticus polycrates* on Ikaria, 138 years after its collection by Örtzen from Evdilos in 1887 (MARTENS 1889), is particularly noteworthy given the species' apparent absence from the island throughout the entire 20th and early 21st century. This extended temporal gap raises important questions about population persistence and

detectability, reflecting the cryptic nature of these land snails in Mediterranean island ecosystems and the challenges of surveying them outside optimal sampling periods (TRIANSTIS et al. 2008, MAROULIS et al. 2022). Based on shell characters, RIEDEL (1985) placed *Z. polycrates* as a subspecies of *Z. chloroticus*. Our observations suggest that the diagnostic characters proposed by RIEDEL (1985) for separating the two subspecies fall within the overall variability of the species, at least for the Ikaria population. Unfortunately, the material collected did not include sexually mature individuals, precluding the first description of the reproductive system of *Z. c. polycrates* and its comparison with the nominotypical subspecies. Further comparisons with populations of the species from other islands and the study of the species' reproductive system will resolve its taxonomic status.

Given the broader decline of the genus *Zonites* across the Aegean, where several taxa have become extinct, persisting only as subfossils (RIEDEL 1985, RIEDEL & MYLONAS 1995, 1997, MYLONAS & VARDINOYANNIS 2022), and with nine species listed under the IUCN categories of threatened species (NECCA 2024), the confirmed survival of viable populations of two *Zonites* taxa on Ikaria is encouraging. However, their populations are scarce and highly localised, making them particularly susceptible to habitat degradation and anthropogenic disturbance, and their current classification as Vulnerable in the Greek Red List of Threatened Species (NECCA 2024) is unlikely to change in light of our findings. Therefore, targeted conservation measures and systematic monitoring are needed to ensure the long-term survival of these threatened Aegean endemics.

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