B8

Zoological Journal of the Linnean Society (1995), *115*: 347–357. With 7 figures

On the development, habitat selection and taxonomy of *Helix (Jacosta) siphnica* Kobelt (Gastropoda, Helicellinae)

M. MYLONAS,[1] J. BOTSARIS,[2] J. SOURDIS[3] and E. VALAKOS[2]

[1]*Department of Biology, University of Crete, P.O. Box 1470, GR 711 10 Iraklion, Crete, Greece*
[2]*Section of Ecology and Systematics Biology Department, University of Athens, Ilissia GR 157 71, Greece*
[3]*Department of Genetics, Agricultural University of Athens, Iera Odos 75, GR 118 55, Greece*

Received September 1994, accepted for publication October 1994

The environmental factors affecting the distribution, variation, and development and taxonomy of *Helix (Jacosta) siphnica* Kobelt, 1883, an endemic landsnail of Siphnos Island (Cyclades, Greece), are examined.

Two types of populations can be distinguished due to different strategies of shell development. In the first, and more frequent, type, the keeled and depressed juvenile shells, become rounded in the later developmental stages. In the second type, in all developmental stages, only keeled shells are found. In this study changes in the allometric relationships of shell height, shell diameter and whorls are correlated with the development of the genital system and changes in habitat selection. The keeled forms are found in drier and more stony environments. The degradation of the forests to dry maquis and frygana and desertification in the Aegean insular ecosystems are probably connected with the development of keeled forms. Keeled populations of *Trochoidea siphnica* are regarded as an example of neoteny leading to paedomorphosis by retardation.

ADDITIONAL KEY WORDS:—variation – allometry – neoteny.

CONTENTS

0024–4082/95/012347+11 $12.00/0

INTRODUCTION

The problem of the peripheral angle in the terrestrial snails has been connected to selective environmental factors such as climate (Rensch, 1937; Goodfriend, 1983), soil (Gould, 1969; 1971) and predators (Cook & Pettitt, 1979).

In the Mediterranean area keeled forms of the helicid species are more frequent than those with a rounded shell periphery (Rensch, 1937; Goodfriend, 1986). This has been attributed to the dryness of Mediterranean habitats (Goodfriend, 1986), to the karstic limestone surface (Alonso *et al.*, 1985) and to other unknown, factors (Goodfriend, 1986). Gould (1969, 1971) suggested that the keeled forms of *Poecilozonites* represent a case of paedomorphy. Though this is possible in the case of the Mediterranean helicids (Goodfriend, 1986), the lack of historic and ontogenetic studies prohibits the evaluation of this possibility.

In 1989 the authors became aware of the existence of two distinct forms of the species *Trochoidea siphnica* (Kobelt), (Gastropoda:Helicellinae) which is endemic to the Cycladic island of Siphnos. All immature stages possess a depressed shell with an angular periphery. In some populations this feature is retained in the adults, but in the majority of the populations, the periphery always becomes rounded. Moreover, different habitat selection was observed in the two forms: rounded forms aestivate in the litter whilst keeled ones do so under stones.

In order to investigate the reasons for this phenomenon we studied ontogenetic change in relation to ecological requirements and habitat selection in populations belonging to the two types.

The taxonomy of the species has been unclear. In 1883 Kobelt described the species *Helix (Jacosta) siphnica* from the island of Siphnos in the Cyclades, collected by Admiral Spratt. Its depressed shell, 12–12.5 mm in diameter and 6.5–7 mm high, the five whorls and sharp keel were mentioned as the species' main characters.

Fuchs & Käufel (1936) considered it as a subspecies of *Helicella (Trochoidea) syrensis* (Pfr.), figuring its genital system for the first time (Fig. 2B), though this was based on only one individual. Mylonas (1982) classified *syrensis* in the genus *Cernuella* and kept *siphnica* in the genus *Trochoidea* without giving further details.

In the first part of this work we try to elucidate this taxonomic problem.

The species is known only from Siphnos which is in the centre of the Aegean Archipelago, with an area of 73 km^2. It is rocky and mountainous, with two main peaks: Profitis Ilias (678 m) and Agios Symeon (480 m).

MATERIALS AND METHODS

The samples that we studied were collected by M. M. in 1976 and 1978, and by all the authors in 1989. A dense network of 23 sampling stations enabled us to determine the exact distribution of the species. A number of ecological variables, such as the type of vegetation and the predominant plants, the refuges, the pH and the Ca concentration of the soil were recorded from each sampling station.

The syntypes of the species *Helix (Jacosta) siphnica* are kept in the British Museum of Natural History; both these and the genital system were examined in order to investigate the taxonomic status of the observed forms.

Six representative populations of the species' disjunct distribution were studied. We examined the genital system and four shell characters: shell height (SH), shell diameter (SD), number of whorls (W) and rounded periphery when present.

We then focused our attention on two populations which represent both modes of shell development (Agios Nicolas and Agios Symeon). From these populations we collected individuals at all stages of development and also recorded their position in relation to rocks, refuges and plant species. We studied the development of the shell and the genital system (fully developed, intermediate, just present) in order to determine the shell size at which reproductive maturity occurs, since it is not indicated by shell characters.

For statistical analysis of the results we used ANOVA, the Tukey test and regression analysis as described by Zar (1984).

RESULTS

Distribution and ecological requirements

Trochoidea siphnica is found in four disjunct areas (Fig. 1): the northern and southern ends of the island, and the two mountainous regions. Interestingly, the species' disjunct distribution coincides with the calcareous geological formations found on the island.

The biotopes where *T. siphnica* was found were almost identical. The pH of the soil varies between 7.4 and 7.8 and the Ca concentration between 2% and 20%. There are plenty of rocks and stones. The vegetation is dry maquis and the predominant plant species are *Juniperus phoenicea, Pistacia lentiscus, Phlomis fruticosa* and *Sarcopoterium spinosum.* A thick layer of litter is formed, especially under *P. lentiscus. T. siphnica* was never found in cultivated areas and in biotopes without calcium in the soil. The area of Profitis Ilias – Agios Nicolas – Agios Andreas is comparatively drier and more stony than the others, with *Phlomis fruticosa* predominant.

Taxonomy

We studied the genital system of individuals from populations in Agios Symeon, Agios Andreas, Agios Nicolas and Cheronisos. Its form is stable among all four populations, having the typical features of the genus *Trochoidea* (Fig. 2), i.e. two empty dart sacs on the upper part of the vagina.

Fuchs and Käufel (1936) considered *siphnica* to be a subspecies of *Helicella (Trochoidea) syrensis* (Pfr.). Our examination of the genital system of individuals from the type locality of *syrensis* (Syros Island) indicated that this species belongs, despite some peculiarities, to the genus *Cernuella* (Fig. 2E), which is characterized by a dart sac complex on one side of the vagina.

The absence of any description of the genital system of *Cernuella(?) syrensis* is responsible for many wrong determinations. Often forms belonging to

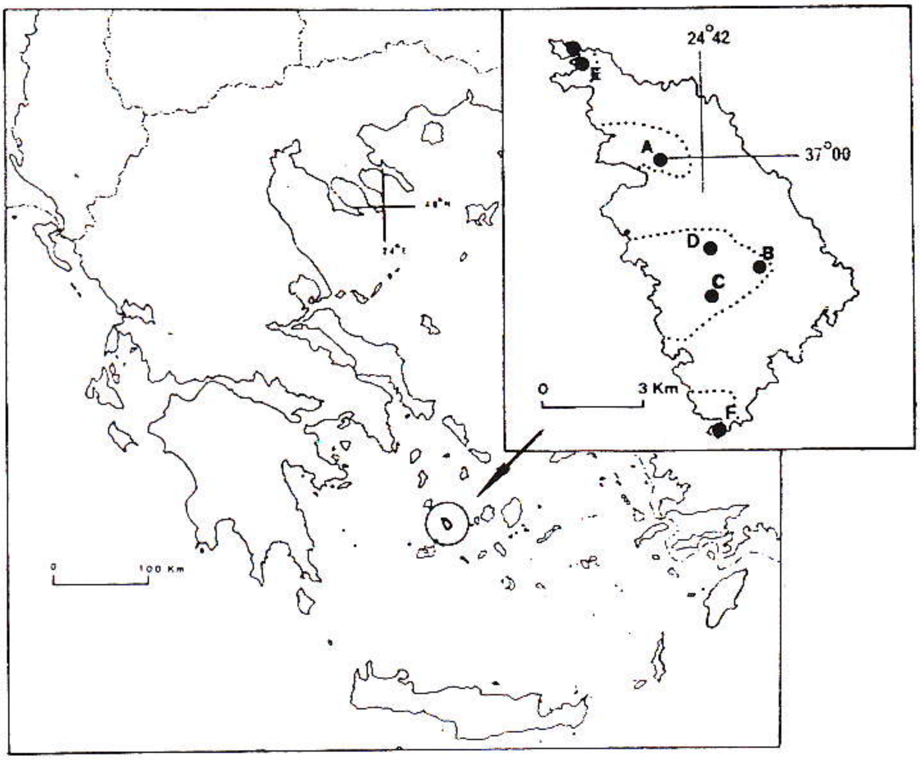

Figure 1. Siphnos island. Distribution of *T. siphnica* and the examined populations. A, Agios Symeon; B, Agios Andreas; C, Agios Nicolas; D, Profitis Ilias; E, Cheronisos and F, Agios Georgios.

Trochoidea are classified as subspecies of *syrensis* because they have similarly depressed and keeled shells.

The examined type specimens, characterized by their depressed shells and sharp keels, coincide with the populations found on Profitis Ilias. The majority of the populations found on the island, having a characteristic rounded periphery in the last developmental stages, are, until now, undescribed.

The differences found between the two forms could support a distinction at a subspecific level. We do not intend here to give a superficial description of these two forms, but to investigate, if possible, the reasons for their differentiation.

Variation among populations

The presence or absence of the rounded periphery in the last stages of shell development is a feature that by itself divides the six studied populations into two well-defined groups (Fig. 3). All adult individuals of the populations of Agios Symeon, Agios Georgios and Cheronisos (first group) are representative of the first three areas of the species' distribution, and have shells with a rounded periphery, whilst in the populations of Agios Nicolas,

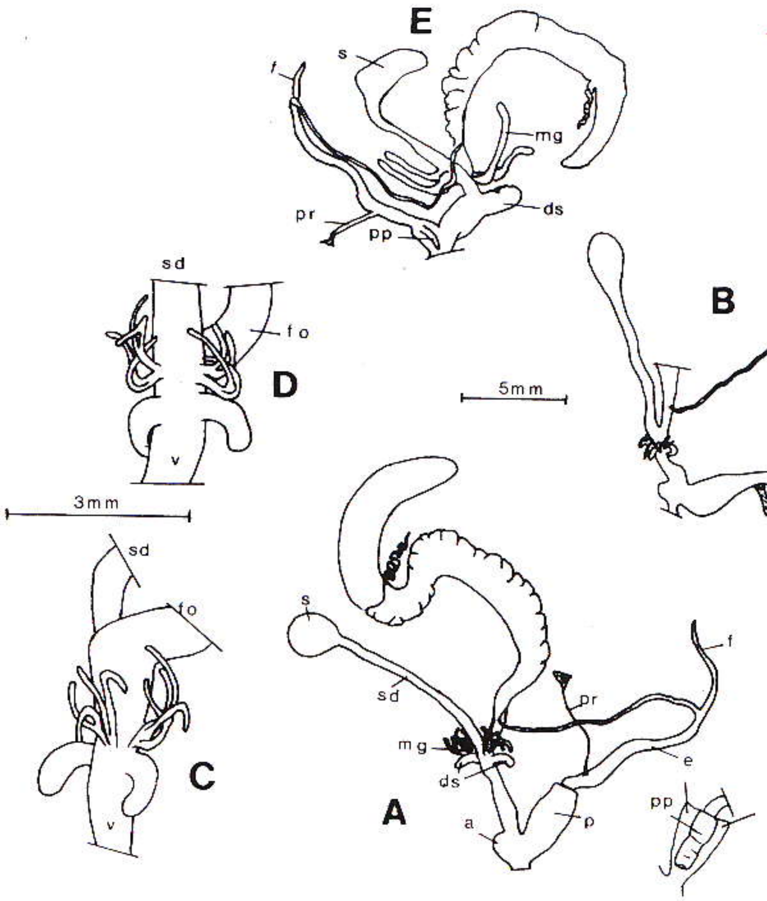

Figure 2. The genital system of *Trochoidea siphnica* (A–D) and *Cernuella syrensis* (E). A, the most common form, B, the form described by Fuchs & Käufel (1936), C and D, left and right view of mucus glands. Key: a, appendix; ds, dart sacs; e, epiphallus; f, flagellum; fo, free oviduct; mg, mucus glands; p, penis; pp, penial papilla; pr, penial retractor, s, spermatheca; sd, spermateca duct; v, vagina.

Agios Andreas and Profitis Ilias, all in the fourth region (second group), the angular periphery is always present.

Furthermore, the same grouping of the populations still holds when we consider the three measured characters, SH, SD and W (Table 1). In the first group, there are no significant differences among the three characters (SH: ANOVA $F_{2,98} = 0.195$, $P > 0.05$, SD: ANOVA $F_{2,98} = 0.297$, $P > 0.05$ and W: ANOVA $F_{2,98} = 0.259$, $P > 0.05$).

In the second group, the Agios Nicolas population is similar to the populations of Agios Andreas and Profitis Ilias as to W (ANOVA $F_{2,147} = 2.801$, $P > 0.05$) and SD (ANOVA $F_{2,147} = 0.077$, $P > 0.05$), but the populations differ as to SH (ANOVA $F_{2,147} = 9.806$ $P < 0.05$). However, there is no significant difference in SH between the populations of Agios Andreas and Profitis Ilias (Tukey test $q_{3,147} = 0.56$, $P > 0.05$).

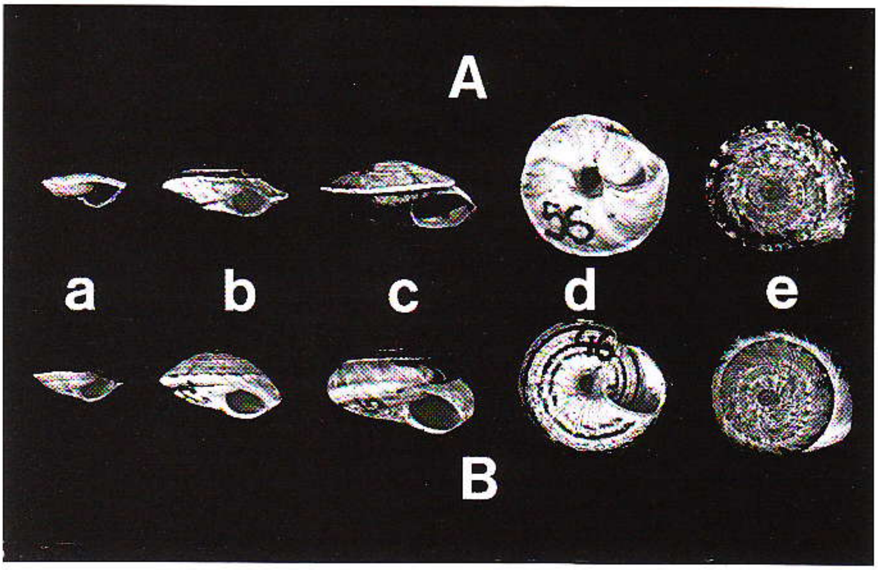

Figure 3. Shell types of *T. siphnica* (X 1). A, Agios Nicolas; B, Agios Symeon. a, b: juveniles, c, d, e: adults.

TABLE 1. Statistics of the three measured shell characters (mm) in the different populations of *T. siphica.* SH, shell height; SD, shell diameter; W, whorls

	Agios Symeon	Agios Andreas	Agios Nicolas	Cheronisos	Profitis Ilias	Agios Georgios
SH						
Mean	6.87	6.58	5.85	6.87	6.74	7.2
SD	1.48	1.12	0.81	1.71	1.62	1.77
Range	3.8–9.3	3.9–9.0	4.0–7.5	4.0–9.7	4.1–9.0	4.3–9.7
n	65	76	66	26	8	10
SD						
Mean	12.17	12.88	12.91	12.27	13.06	12.5
SD	2.27	1.37	1.07	1.63	1.73	1.47
Range	8.9–14.4	8.9–15.4	10.3–14.6	9.3–15.0	9.2–15.0	10.3–15.0
n	65	76	66	26	8	10
SW						
Mean	5.1	4.9	4.8	5.1	5.1	5.2
S.D.	0.46	0.34	0.28	0.5	0.48	1.42
Range	4.2–5.8	4.2–5.5	4.2–5.4	4.0–6.0	4.3–5.8	4.5–5.7
n	65	76	66	26	8	10

Shell development

Comparisons between the measured shell characters in the two studied populations indicate that there is a differential growth of SH versus SD and also of SH and SD versus W.

Further study reveals a considerable change in the allometric relationship. This is more clear in the case SH/SD in both populations, where two

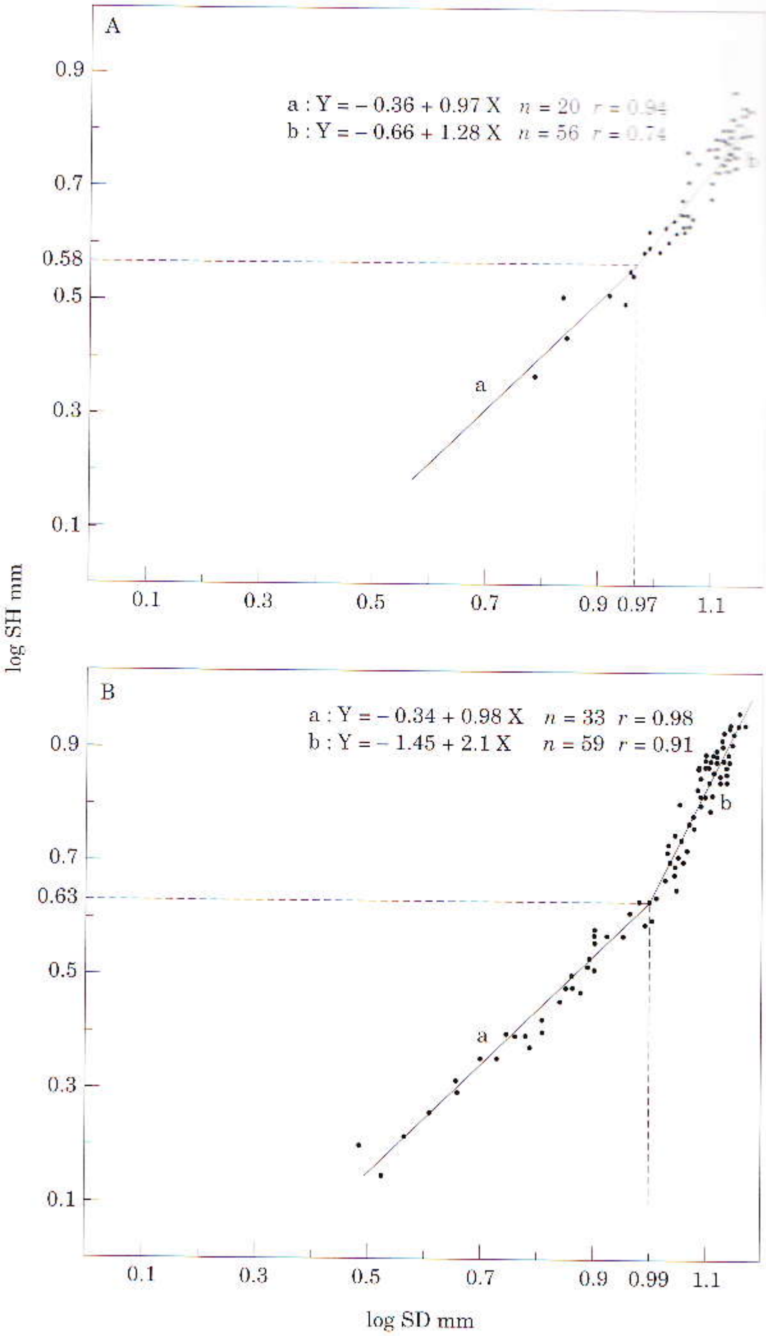

Figure 4. The change of the allometric relation of SH and SD. A, Agios Nicolas and B, Agios Symeon.

significantly different lines replace the single regression (Fig. 4). These lines and their intersection were found using the method described in Somerton & MacIntosh (1983).

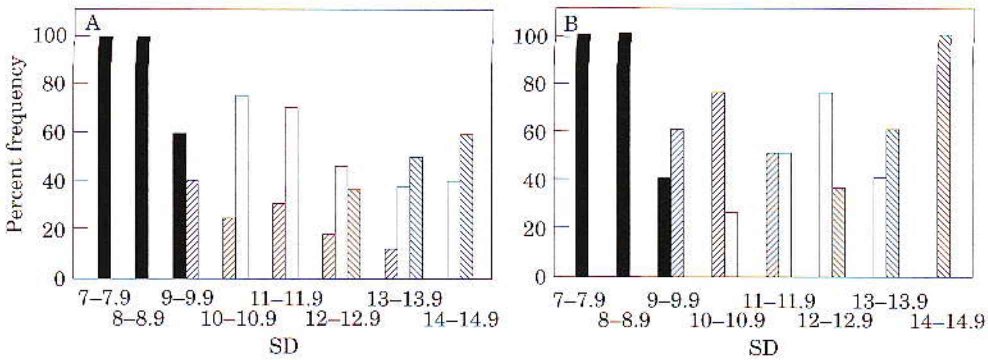

Figure 5. Development of the genital system in respect to shell diameter. A, Agios Nicolas and B, Agios Symeon. Not present (■), just formed (▨), medium (□) and adult (▧).

In both populations there is an isometric relationship of SH and SD in the first stages of shell development. But as soon as the shell exceeds 4.3 mm in height and 9.7 mm in diameter in the Agios Symeon population and 3.8 mm and 9.3 mm in that from Agios Nicolas, a positive allometric relationship alters the shell form. The allometry (slope 2.1) in the Agios Symeon population leads to more rounded shells, while in that of Agios Nicolas (slope 1.28) the change is not obvious.

The development of the genital system

Four clear stages can be distinguished in the development of the genital system: (1) juveniles before the appearance of the genital system, (2) individuals with the genital system just formed, (3) individuals with well-formed but still immature genitalia, with slender oviduct, mucus glands and penis, and (4) individuals with a fully developed adult genital system.

In Figure 5, the percentage of these stages is presented in 1 mm width-classes of the shell diameter. Figure 6 expresses the same data, but stages 2 and 3 have been merged.

The two populations have a number of noticeable similarities, as well as differences. The genital system in both populations starts its formation when SD is about 9.0–9.9 mm. In the 10.0–10.9 mm and 11.0–11.9 mm classes all specimens have an immature genital system. The first adults appear in the 12.0–12.9 mm class. The most impressive difference in the development of the genital system is the percentage of adults in the larger forms: in the Agios Symeon population, all specimens wider than 14.0 mm are adults, while in that of Agios Nicolas, only 60% are adults. In the latter population, the second 'just formed' stage is still present in larger specimens than in the former.

Habitat selection in aestivation

In general, three types of habitat are used by the individuals of *T. siphnica* for aestivation: (i) micro-cavities on the exposed surface of rocks and stones, (2) the underside of stones and (3), the thick litter layer, especially under

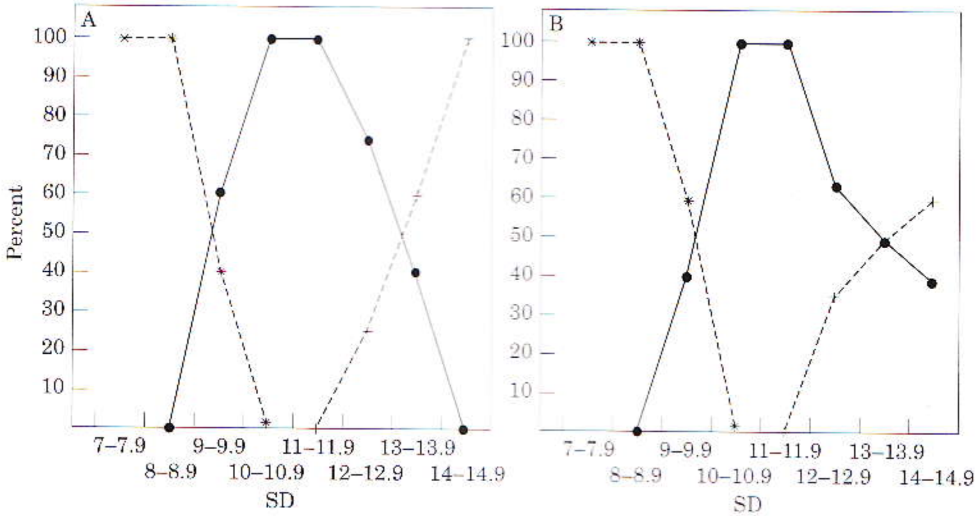

Figure 6. Development of the genital system in respect to shell diameter. A, Agios Nicolas and B, Agios Symeon. Not present (*– – –*), immature (—) adult (+– – –+).

Pistacia lentiscus and *Juniperus phoenicea.* In the population Agios Nicolas only the first two types are used.

In Figure 7, the percentage of aestivating individuals in the three types of habitat, is presented in 1 mm width classes of the SD. All juveniles narrower than 9.0 mm, in both populations, aestivate in micro-cavities. Their depressed shells, sharp keels and colour make them almost invisible. Individuals wider than 9.0 mm start aestivating under stones. In Agios Symeon, forms wider than 11.0 mm penetrate the litter, sometimes deeper than 25 cm. Almost all specimens wider than 13.0 mm use this type of habitat for aestivation. Conversely, in Agios Nicolas, the larger forms still use the underside of stones.

DISCUSSION

Sharp breaks in allometry have mostly been observed in crustacean growth and are usually associated with sexual maturity (Teissier, 1960). Cain (1981)

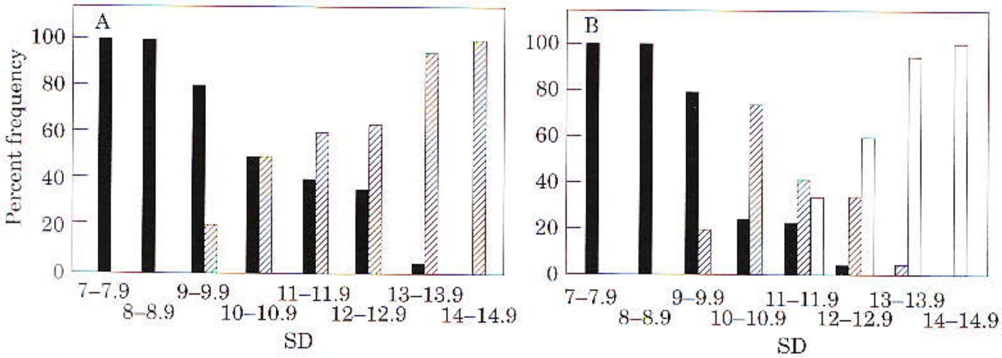

Figure 7. Habitat selection in respect to shell diameter. A, Agios Nicolas and B, Agios Symeon. Rocks (■) stones (▨) and litter (□).

supported the adaptive value of allometric changes, correlating the different developmental forms with their environments. This is true in the case of *T. siphnica*. Moreover, there is a striking coincidence of shell changes with the development of the genital system.

In the first developmental stages, all individuals from the examined populations have an angular periphery and aestivate in micro-cavities on the surface of rocks. Their flat form, colour and angular periphery offer them, in respect of the substrate, good camouflage and physical protection against predators, chiefly birds, rodents (*Rattus*, *Apodemus*) and beetles (Carabidae).

With the appearance of the genital system, which occurs when the SD exceeds 9.0 mm, the SH accelerates its development, so that gradually the shell becomes more rounded. At this stage the individuals change their aestivating habits and rest in fissures of rocks, under stones, or in piles of stones.

Sexual maturity in the Agios Symeon population is connected with the 12.0–12.9 mm class of the SD and the complete formation of the fifth whorl; the shell periphery becomes completely rounded and individuals aestivate in the litter. This change in habitat selection can be attributed to the connection of thermoregulation with the formation of the genital system.

Cowie (1985) mentioned that in Mediterranean habitats both adults and juveniles are forced off the ground to avoid lethal temperatures. This does not totally fit with the case of *T. siphnica*, as we found that on the ground and the surface of the rocks, where juveniles aestivate, the temperature during the warm summer days exceeds 50–55°C, while at the same time in the litter it does not exceed 25–30°C. Cowie also found that juveniles of *Theba pisana*, near the species' northern limits in South Wales, are less affected by high temperatures on the ground than the adults. This is the same pattern of reaction as the one we observed in *T. siphnica*.

Changes in shape, maturity and habitat in keeled or rounded forms of *T. siphnica* are associated with climatic or microclimatic conditions and avoidance of enemies. In this it is similar to other Mediterranean helicids (Alonso *et al.*, 1985; Goodfriend, 1986).

Keeled adults in the population of Agios Nicolas are probably connected with the stony and dryer conditions of this biotope. The predominance of *Phlomis fruticosa*, which creates a thin litter layer, does not provide suitable shelters for aestivation. This is probably linked to the observation that 40% of the bigger individuals remain immature. In contrast, in Agios Symeon the predominance of *P. lentiscus* and *J. phoenicea*, with their thick litter layers, creates cooler resting sites for the adults.

Paleoclimatic evidence (Grove *et al.*, 1991) for the last 40 000 years supports the hypothesis of a cooler and wetter climate in the area, which was covered with forests or wet maquis until the beginning of the historical period 5000 years ago (Runemark, 1971). These environmental conditions would have favoured rounded forms of *T. siphnica*.

The degradation of the forests to dry maquis or phrygana, which gradually became the dominant type of vegetation in the Aegean, and the desertification associated with human environmental impact (Runemark, 1971), forced the selection of more thermophilous and xerophilous forms. Keeled populations of *T. siphnica* probably arose as a result of this pressure. The mechanism of this selection could be what Gould (1977) termed "a case of neoteny causing paedomorphy by retardation". The cost of this change to neotenic populations is very high, as 40% of the larger individuals remain immature, or at least reach maturity later than the rounded forms.

The establishing process of keeled populations of *T. siphnica* that we have observed, based on habitat selection, allometric development and paedomorphy due to climatic changes and desertification, could also be the reason that led to the dominance of keeled helicids in the Mediterranean region.

ACKNOWLEDGEMENTS

We would like to thank Prof. A. J. Cain for his comments on the manuscript and Dr L. M. Cook for his constructive comments on earlier drafts. Special thanks are given to K. Vardinoyannis for her assistance.

REFERENCES

Alonso MR, Lopez Alcantara A, Rivas P, Ibanez M. 1985. A biogeographic study of *Iberus gualtierianus* (L.) (Pulmonata: Helicidae). *Soosiana* **13:** 1–10.

Cain AJ. 1981. Possible ecological significance of variation in shape of *Cerion* shells with age. *Journal of Conchology* **30:** 305–315.

Cowie RH. 1985. Microhabitat choice and high temperature tolerance in the land snail *Theba pisana* (Mollusca:Gastropoda). *Journal of Zoology, London* (A) **207:** 201–211.

Cook LM, Pettitt CWA. 1979. Shell form in *Discula polymorpha*. *Journal of Molluscan Studies* **45:** 45–51.

de Bartolome JFM. 1982. Comments on some Mediterranean rockdwelling helicids. *Journal of Conchology* **31:** 1–6.

Fuchs A, Käufel F. 1936. Anatomische und Systematische Untersuchungen an Land- und Süsswassermollusken aus Griechenland und von den Inseln des Aegäischen Meeres. Archiv für Naturgeschichte, (N.F.), 5: 441–662.

Goodfriend GA. 1983. Clinal variation and natural selection in the land snail *Pleurodonte lucerna* in western St. Ann Parish, Jamaica. Ph. D. Dissertation, Univ. Florida, Gainesville.

Goodfriend GA. 1986. Variation in land snail shell form and size and its causes: A review. *Systematic Zoology* **35**(2): 204–223.

Gould SJ. 1969. An evolutionary microcosm: Pleistocene and recent history of the land snail *P. (Poecilozonites)* in Bermuda. *Bulletin Museum of Comparative Zoology* **138**(7): 407–532.

Gould SJ. 1971. Precise but fortuitous convergence in Pleistocene land snails from Bermuda. *Journal of Paleontology* **45:** 409–418.

Gould SJ. 1977. *Ontogeny and Phylogeny*. Cambridge, MA: Harvard University Press.

Grove AT, Moody J, Rackham O. 1991. Crete and the south Aegean Islands: Effects of changing climate on the environment. Robinson College, Cambridge.

Kobelt W. 1883. Diagnosen Neuer Arten. *Jahrbucher des deutsches Malacologisches Gesellschaft* 15: 181–183.

Mylonas M. 1982. Zoogeography and Ecology of the terrestrial Molluscs of Cyclades. Ph. D thesis. University of Athens.

Rensch B. 1937. Untersuchungen über Rassenbildung und Erblichkeit von Rassenmerkmallen bei sizilischen Landschnecken. Z. *Indukt. Abstamungs-Vererbugsl.* **72:** 564–588.

Runemark H. 1971. The phytogeography of the Central Aegean. *Opera Botanica* **30:** 20–28.

Somerton DA, MacIntosh RA. 1983. The size at sexual maturity of Blue King Crab, *Paralithodes platypus* in Alaska. *Fisheries Bulletin* **81**(3): 621–628.

Teissier G. 1960. Relative growth. In: Waterman TM, ed. *The physiology of Crustacea*, vol. 1, 537–60.

Zar HJ. 1984. *Biostatistical Analysis*. Englewood Cliffs, NJ: Prentice-Hall.