



SPATIAL ANALYSIS OF SHELL PARAMETERS SUGGESTS LOW SPECIES NUMBER OF *MASTUS* (GASTROPODA: PULMONATA: ENIDAE) IN CENTRAL AND EASTERN CRETE

FRANCISCO W. WELTER-SCHULTES

Institute of Zoology and Anthropology of the University, Berliner Str. 28, D-37073 Göttingen, Germany
(e-mail: fwelter@gwdg.de)

ABSTRACT: Contrasting views in recent literature set the species number of the land snail *Mastus* in Crete (Greece) between 3 and over 17. In order to contribute to a better understanding of the spatial complexity of the genus, a biogeographical approach was employed in central and eastern Crete (6,000 km²) where distribution patterns of shell parameters of 1,600 samples totalling 5,500 specimens were analysed and evaluated at a 2 km scale. The results support grouping of the central and eastern Cretan populations in five obviously independent and genetically separated systematic entities, which are referred to as species. *M. cretensis* (Pfeiffer) and *M. sitiensis* Maassen are widely distributed in Crete. *M. abundans* Maassen, *M. gittenbergeri* Maassen and *M. violacea* Maassen occupy smaller ranges which largely conform with those of endemic species of the clausiliid *Albinaria*. The conclusions are only partly in agreement with the previous results of anatomical studies, but are consistent with predictions based on species-area relation data.

KEY WORDS: land snails, Crete, *Mastus*, shell characters, variation, biogeography

INTRODUCTION

The Aegean with its dynamic late Neogene paleogeographic history provides an excellent field laboratory for studying phylogeography, effects of isolation on paleoislands and colonisation by range expansion, particularly in slowly moving animals, such as oniscid isopods and clausiliid *Albinaria* land snails (SFENTHOURAKIS 1996, SFENTHOURAKIS & GIOKAS 1998, DOURIS et al. 1998, WELTER-SCHULTES & WILLIAMS 1999, WELTER-SCHULTES 2000). This study is devoted to the enid genus *Mastus* which, next to *Albinaria*, belongs to the most common land snails of the island of Crete.

In 430 days of field research between 1984 and 1998, some 4,200 *Albinaria* samples were collected in central and eastern Crete, including surrounding islands (WELTER-SCHULTES 1998b). During this procedure, shells of *Mastus*, *Xerocrassa* and other snails were also occasionally collected. At the end of the *Albinaria* fieldwork, 1,600 *Mastus* samples had been

collected at different localities, totalling some 5,500 empty shells, an extraordinarily valuable material for biogeographical analyses of a genus subject to extremely divergent taxonomic opinions in recent literature.

The Cretan *Mastus* material used by HELLER (1976a, b) was scarce. Based on 17 samples, the author decided to divide the genus into two species in Crete: *M. pupa cretensis* (Pfeiffer) and *M. olivaceus* (Pfeiffer). VARDINOYANNIS & MYLONAS (1988) recognised three species (*M. cretensis*, *M. turgidus* (Westerlund) and *M. olivaceus*). After studying some 200–300 Cretan samples, VARDINOYANNIS (1994) added *M. etuberculatus* (Frauenfeld) to the list, albeit without any reference to the criteria applied to separate the so called four species. Presenting a contrasting view, MAASSEN (1995) argued that the species number of *Mastus* in Crete exceeded 17, of which he described 12 as new. According to MAASSEN (1995),

species identification is possible mainly based on the genitalia and spermatophores. Having analysed shells from more than 250 localities, MAASSEN (1995) considered the shell to be of secondary importance, principally because of not providing unequivocal diagnostic characters. This is partly in agreement with the view of PARMAKELIS et al. (1997) who, without presenting their methods and results, concluded that the anatomical characters used by MAASSEN (1995) are

more reliable than conchological characters, but lose their reliability when the number of examined populations increases. To complete the record for the region of Crete, and based on conchological features, the *Mastus* populations of Gávdos (*M. claudia* Maassen et Welter-Schultes) and Gavdopoúla (*M. amenazada* Welter-Schultes) were described as endemic species (WELTER-SCHULTES 1998a, 1999).

MATERIAL AND METHODS

The present study is based on a maximum increase of the number of localities in central and eastern Crete. The study area comprised Crete between Réthimno and the eastern coast of the island, including the surrounding islands. Sampling accuracy was 1 km². Mapping was based on the UTM grid as presented in WELTER-SCHULTES (1998b). The 1,595 samples (1,465 from Crete, 130 from the small islands) are deposited at the malacological museum Haus der Natur, Cismar (Germany). The average specimen number per 1 × 1 km area was 3.5, per 2 × 2 km area – 4.5.

Shell height (H) and shell diameter (D) were measured with a micrometer (accuracy 0.005 mm, mean error determined for D ±0.035 mm, for H ±0.003 mm). The resulting mean error of the relative shell height H/D (shell shape) was ±0.7% of the sample mean. A basic knowledge of variation of *Mastus* shell parameters within a population was provided by WELTER-SCHULTES (1999). WELTER-SCHULTES (1998a, 1999) found a positive correlation between D and H and between H and H/D, but not between D and H/D (Fig. 1). For the spatial analyses, D and H/D were chosen as parameters.

The standard deviation represents a character-specific proportion of the mean (sd/μ). For H/D this

proportion is 4–8% (Fig. 2), for D it is 3–4% (WELTER-SCHULTES 1999). It should be emphasised that all the various *Mastus* species, clusters or groups show identical sd/μ proportions. Another crucial observation is that the proportion of the smallest and largest specimen (min/max) in each sample is unlikely to fall below a certain limit. The empirically determined limits were 0.70 in H/D (Fig. 2D) and 0.75 in D (WELTER-SCHULTES 1999). A min/max value below the limit indicates that the likelihood exceeds 98% that we are dealing with different species. In this sense the empirically determined min/max proportions were used to discern species, particularly north and northeast of the Dikti mountains in those cases where two specimens with extremely divergent values were collected at one locality. At some localities, the presence of two distinct species was also inferred from extraordinarily high standard deviations.

SIZE DISTRIBUTIONS

In 91 samples of at least ten specimens the minimum value in each sample was set to 0 and the maximum to 1, with each specimen receiving a corresponding value within this range. Given a Gaussian

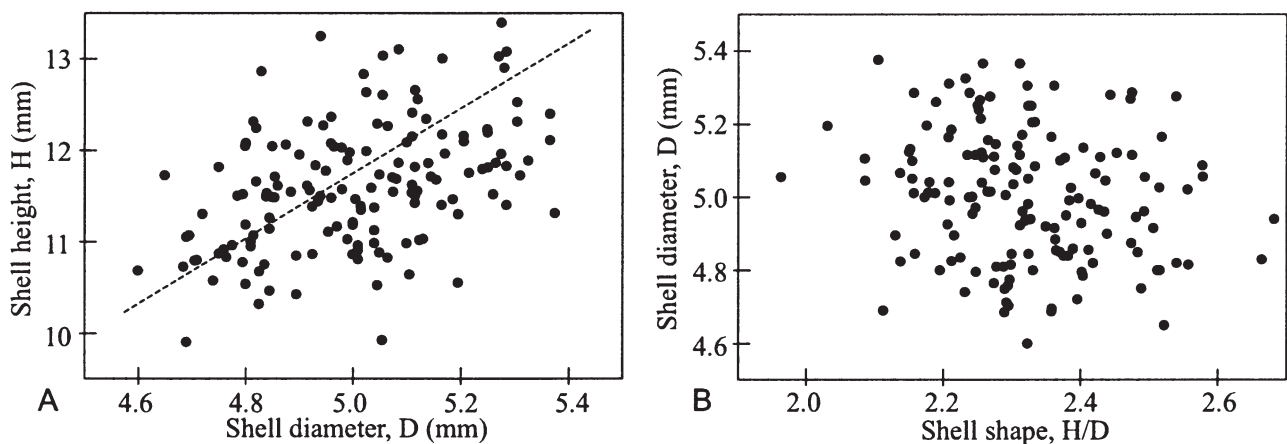


Fig. 1. Shell parameters of the largest available sample, *Mastus sitiensis* complex, UTM KU9776 near Pitsídia (n = 147): A – shell height and shell diameter, regression function: $H = 1.668D + 3.26$; $R^2 = 0.186$, correlation coefficient 0.431; B – shell diameter and relative height H/D (correlation coefficient -0.182)

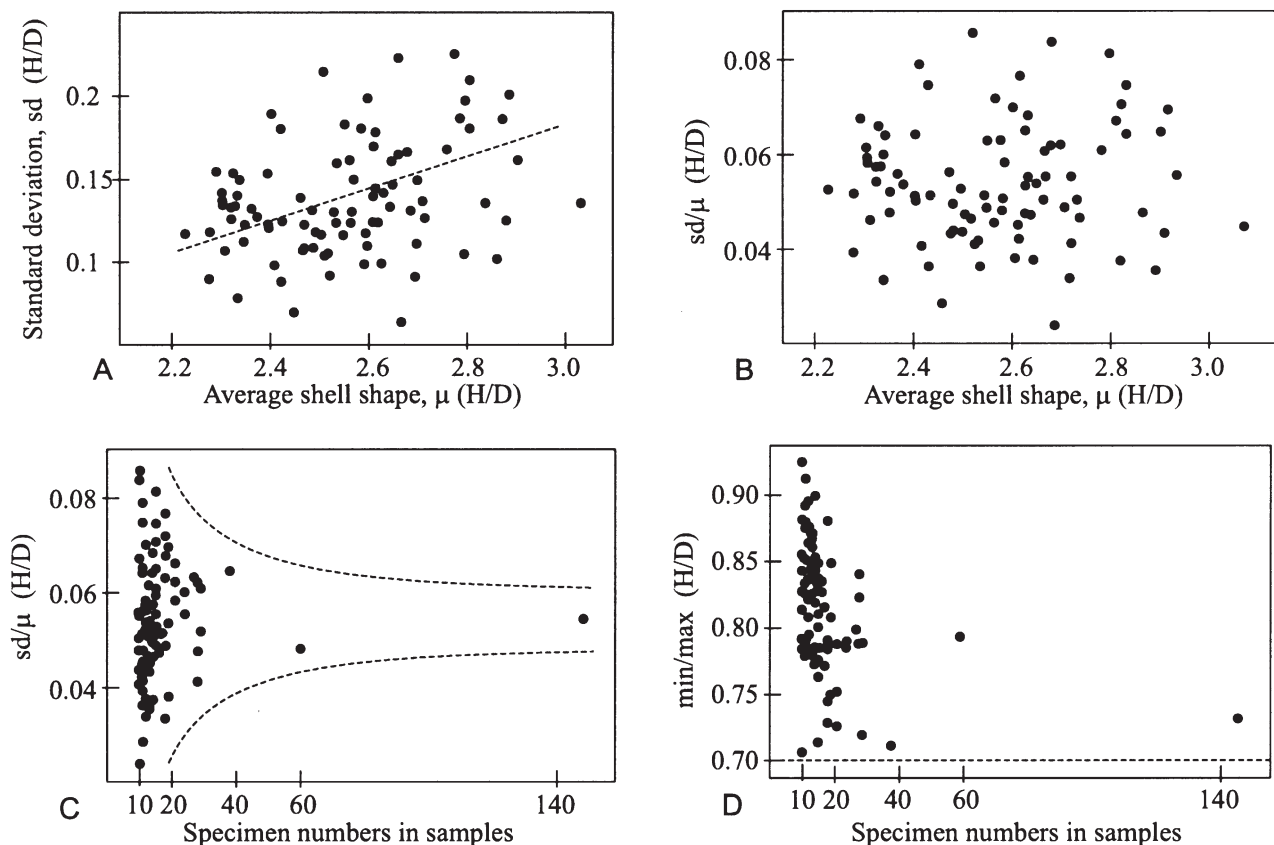


Fig. 2. Standard deviation in Cretan *Mastus* populations (H/D). Each dot denotes one of 91 samples from different regions of Crete, number of specimens ranging from 10 to 147, mean = 17.7: A – standard deviation (sd) and mean (μ). Regression line drawn by hand (the data are based on different numbers of specimens, hence different individual significances); B – proportion sd/μ and mean (μ); C – proportion sd/μ and numbers of specimens in samples. The values of larger samples range more closely around the mean of 0.5–0.6; D – proportion of sample's smallest and largest specimen (min/max) plotted against numbers of specimens in samples. In no sample a shell has a lower value than 70% of the largest value of the sample. This limit is more likely to be approached at larger specimen numbers

normal size distribution, the expected total mean of all specimens would be 0.5. The empirically determined mean values (of the total of 1,612 shells) showed skewed size distributions for the shell volume parameter $H \times D \times D$ (0.460, $p = 0.0058$). Although less pronounced, the values for H (0.475, $p = 0.0620$) and D (0.482, $p = 0.1498$) were also skewed. The shell

shape (H/D, 0.498) was regularly distributed. An average inferior to 0.5 in shell size parameters means that exceptionally large specimens are generally more frequent than exceptionally small shells. The largest *Mastus* shell was found on Dragonáda, with $D = 9.15$ mm, $H = 25.18$ mm.

RESULTS

BIOGEOGRAPHIC ANALYSIS

Two size fractions occurred sympatrically at many localities of the study area. In some regions, additional size fractions were indicated by extraordinarily low min/max values or high standard deviations of samples collected at one locality. With this method five groups were detected in central and eastern Crete, tentatively classified with the following species: *M. cretensis* (Pfeiffer) (Fig. 3), *M. sitiensis* Maassen

(Fig. 4), *M. abundans* Maassen (Fig. 5), *M. gittenbergeri* Maassen (Fig. 6) and *M. violacea* Maassen (Fig. 7).

The largest-sized *Mastus* fraction occupies an area extending from western Crete to the Sitía peninsula. It is absent from large parts of southern central Crete, the vicinity of Spinalóna, and from the eastern parts of the Sitía peninsula (Fig. 3). The group corresponds to *cretensis*, *procax* Maassen and *hemmeni* Maassen recognised in MAASSEN's (1995) paper. A widespread cluster of smaller-sized *Mastus* comprises a variety of

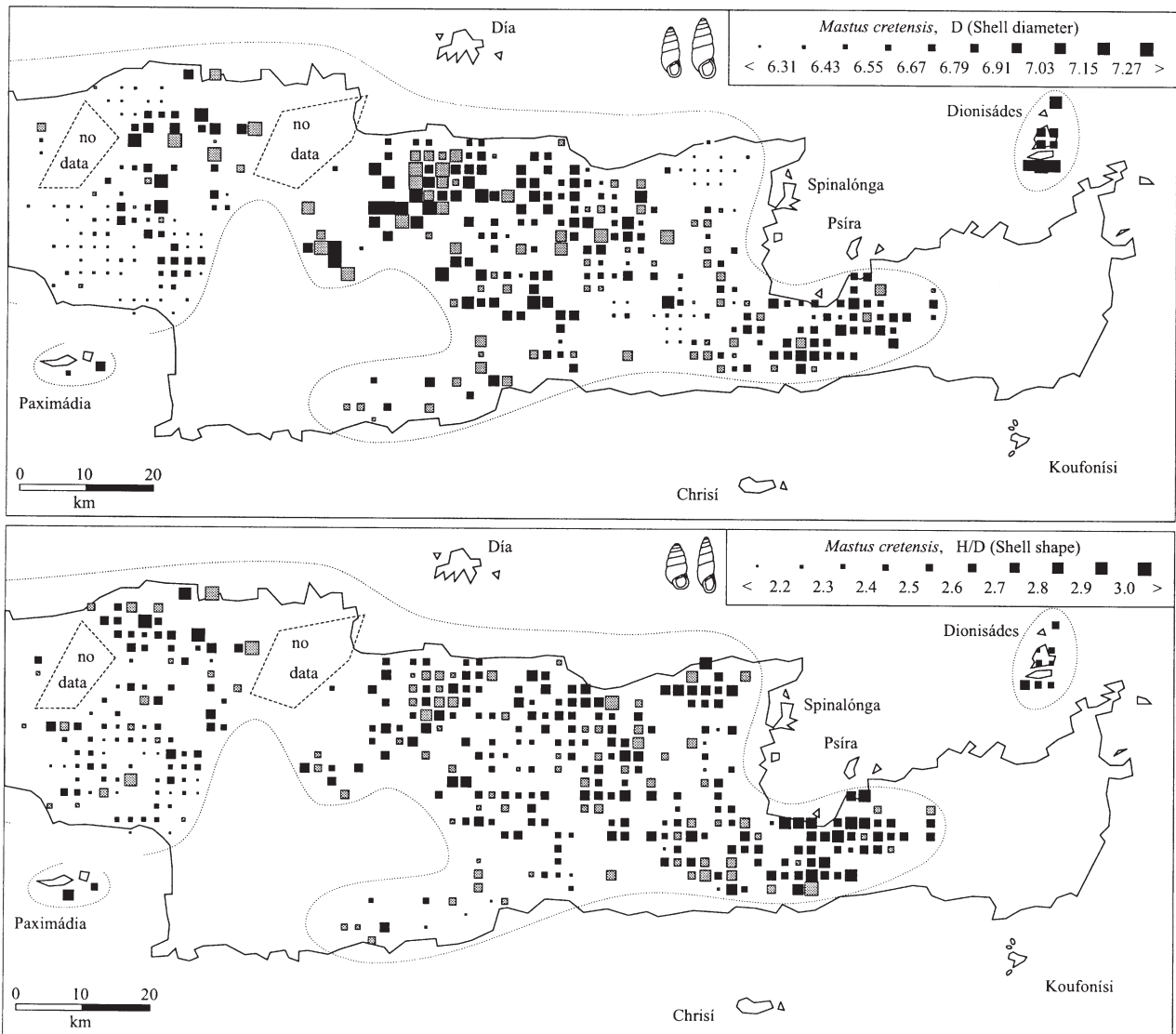


Fig. 3. Spatial variation of shell diameter (D) and shell shape (H/D) in *Mastus cretensis* from central and eastern Crete and surrounding islands based on the 2×2 km UTM grid. The cluster comprises the populations of *cretensis*, *procax* and *hemmeni* sensu MAASSEN (1995). Grey squares – data based on one specimen only; dotted line – range limit of *M. cretensis*; stippled lines – areas where the species is expected to occur but no material was available. The populations of Paximádia and the Dionisádes islands might belong to *M. cretensis* or to endemic species of these island groups

different taxa introduced by MAASSEN (1995): *sitiensis*, *itanosensis* Maassen, *ierapetrana* Maassen, *riedeli* Maassen, *subaii* Maassen, *butoti* Maassen and the undescribed species of Mátala-Festós and south of Agios Nikólaos, sensu MAASSEN (1995). The name *M. sitiensis* is selected for this complex. It occupies large parts of central and eastern Crete from Mt. Idi to the eastern coast (Fig. 4). It includes the small islands south of Crete (Koufonísi, Chrisí), but excludes the Díkti mountains and the region northeast of Díkti. Near the village of Profitis Ilías (south of Iráklío, LU2591, LU2596, LU2796), some populations with slightly smaller shells were found. Although the D values differ extremely from those of regular values of *M. sitiensis* of the region, they are classified with this species. Both forms were never found to occur syntopically.

M. abundans occupies a small range north and west of the Spinalóna peninsula (Fig. 5). The species was more common than the others (mean 4.8 specimens per 1×1 km sample, 9.0 specimens per 2×2 km sample; there was no difference in the collection method). At the southwestern range limit of *M. abundans*, the species occurs syntopically with *M. gittenbergeri*. At one of these localities (LV7304), *M. cretensis* was found as a third syntopic species. The range of *M. gittenbergeri* is located in a moderately large area of eastern Crete (Fig. 6).

M. violacea was found in three restricted areas of the Kouloúkonas range of northern central Crete (Fig. 7). The dark colour of the shell is observed only in the populations at Síses. Near Balí and Achláda, the colour is inconspicuous.

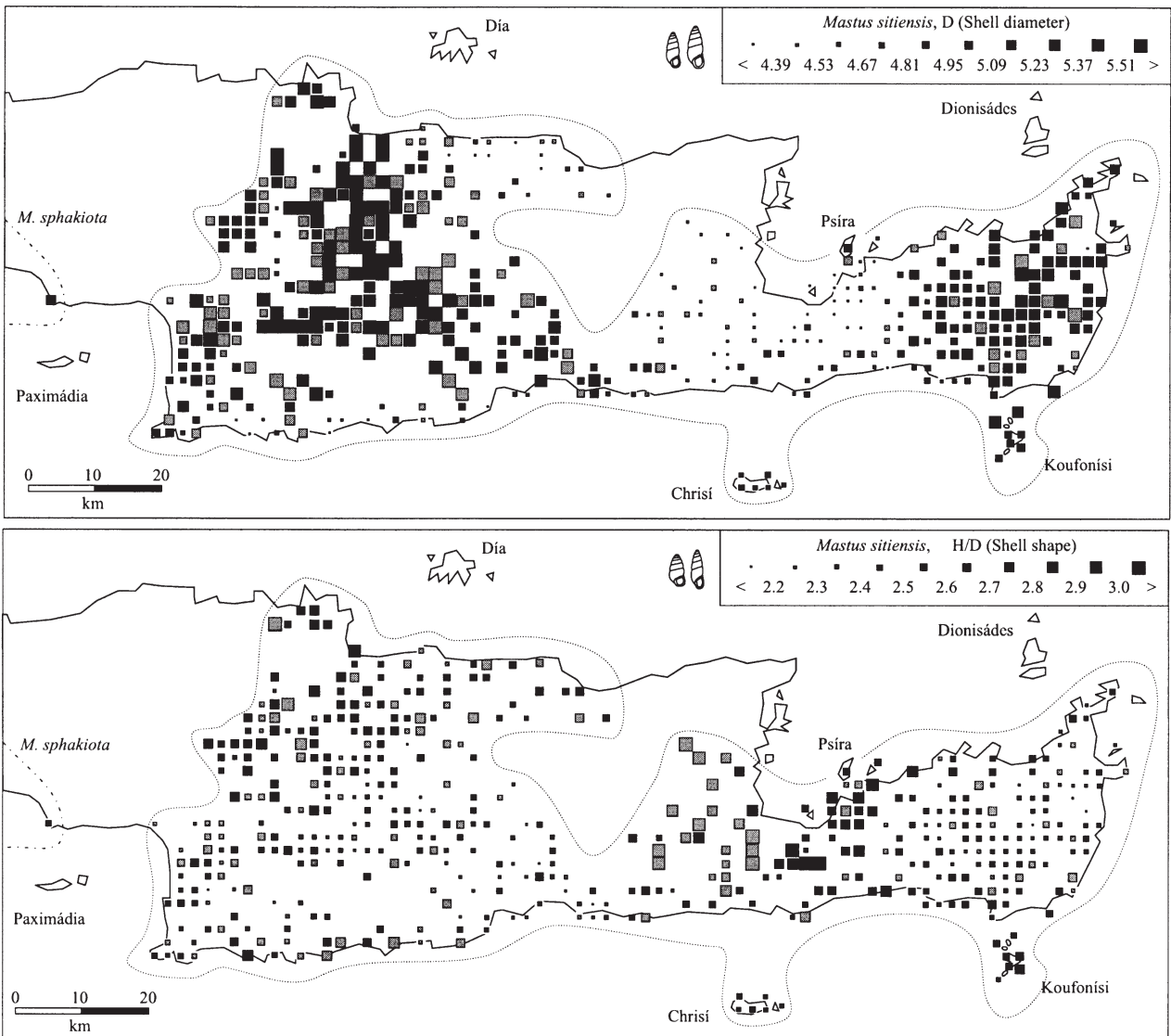


Fig. 4. Spatial variation of shell diameter (D) and shell shape (H/D) in *Mastus sitiensis* from central and eastern Crete and surrounding islands based on the 2 × 2 km UTM grid. The cluster comprises the populations of *sitiensis*, *itanosensis*, *terapetrana*, *riedeli*, *subaii*, *butoti* and the undescribed species of Mátala-Festós and south of Agios Nikólaos sensu MAASSEN (1995). Grey squares – data based on one specimen only; dotted line – range limit of *M. sitiensis*. The populations at the southwestern edge of the map belong to the western Cretan *M. sphakiota*

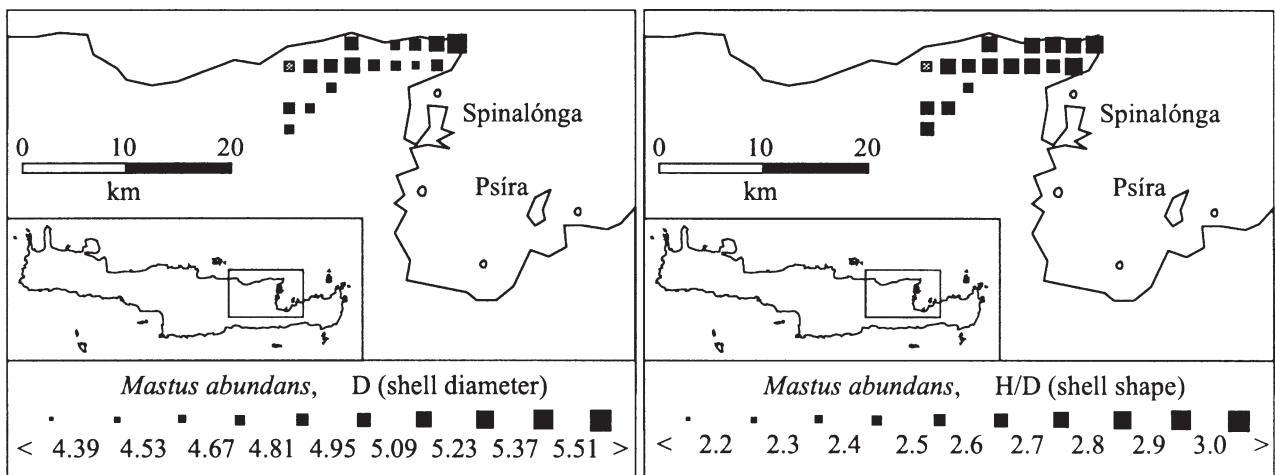


Fig. 5. Spatial variation of shell diameter (D) and shell shape (H/D) in *Mastus abundans* in central and eastern Crete and surrounding islands based on the 2 × 2 km UTM grid. Grey squares – data based on one specimen only

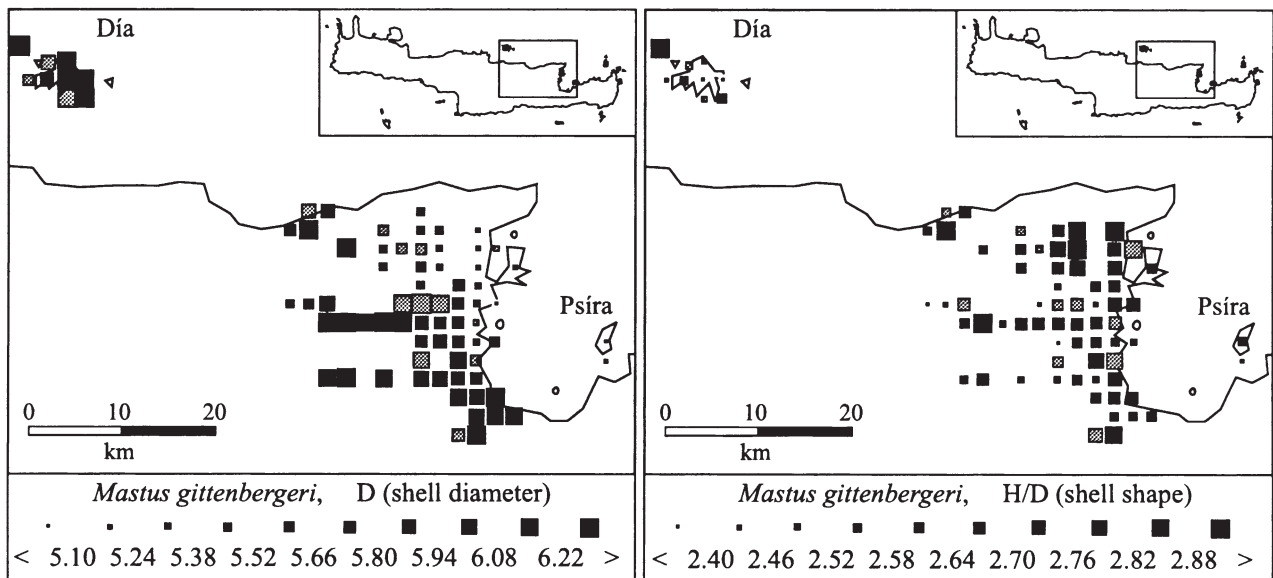


Fig. 6. Spatial variation of shell diameter (D) and shell shape (H/D) in *Mastus gittenbergeri* from central and eastern Crete and surrounding islands based on the 2×2 km UTM grid. Grey squares – data based on one specimen only. The form of Día is more likely to belong to an endemic species

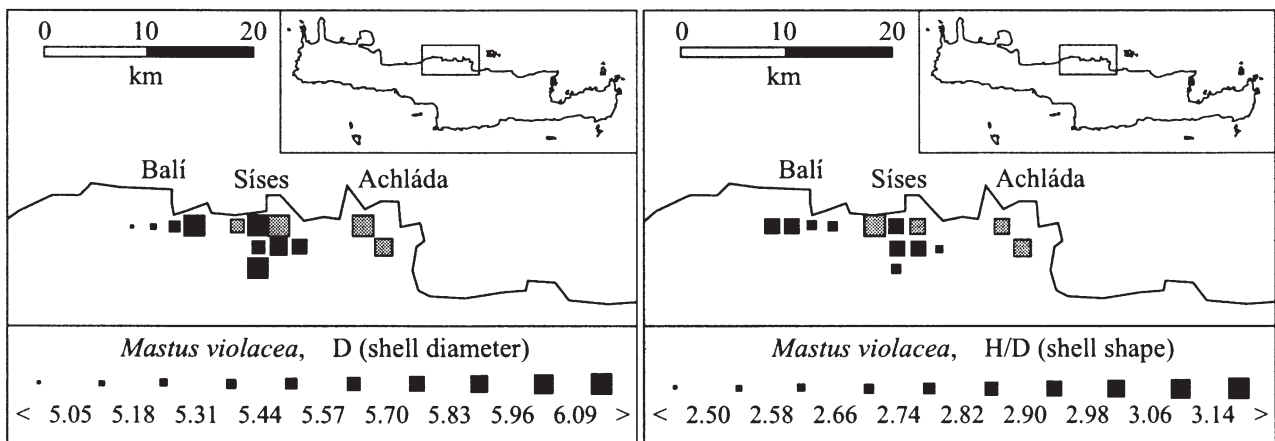


Fig. 7. Spatial variation of shell diameter (D) and shell shape (H/D) in *Mastus violacea* from central and eastern Crete and surrounding islands based on the 2×2 km UTM grid. Grey squares – data based on one specimen only

SHELL VARIATION AND GEOLOGY

Regarding the geological substratum of the localities, it was observed that *Mastus* samples collected on pre-Neogene terrain were slightly more variable than those found on Neogene substrata (Table 1). With respect to most characters the populations of pre-Neogene substrata showed slightly though not

significantly higher degrees of variation than those living on Neogene/Quaternary deposits. Among populations inhabiting late Cenozoic substrata, those living on younger terrain (Messinian and younger) were slightly less variable than those from older Neogene deposits (Serravallian and Tortonian). This analysis yielded no difference among species or size fractions.

DISCUSSION AND CONCLUSIONS

GENETIC ENTITIES?

The main question concerns the classification of the five groups detected by the morphological

method. The results presented in MAASSEN (1995), based on anatomical data, provided some reasons for supposing that the groups detected in this study do not represent species. However, MAASSEN's (1995)



Table 1. Standard deviation of *Mastus* shell parameters of populations of selected geological substrata (n – number of samples, sd – standard deviation, μ – mean). All samples consisted of at least 10 specimens. Effects of different number of specimens in samples were neglected

	D	H	H×D×D	H/D
Pre-Neogene: n	58	58	58	58
sd/ μ	0.0380	0.0607	0.119	0.0546
Serravallian, Tortonian: n	13	13	13	13
sd/ μ	0.0362	0.0579	0.111	0.0530
Messinian and younger: n	18	18	18	18
sd/ μ	0.0345	0.0539	0.102	0.0530

conclusions were not accepted by other researchers working on *Mastus*; they argued that the differences in anatomical characters were not easy to read (PARMAKELIS et al. 1997). Extremely divergent views on such features as the absence of bursa (MYLONAS & VARDINOYANNIS 1989, MAASSEN 1995), expression of the bursa diverticulum (VARDINOYANNIS & MYLONAS 1988, MAASSEN 1995) or morphology of the spermatophores characterize the discussion. Although MAASSEN's (1995) study was based on solid methods and results, it has not been established that all species are reproductively isolated from each other and hence represent species in the sense of most accepted species concepts.

An important insight into the differences between our and MAASSEN's (1995) results may be provided by reflections on the significance of *M. gittenbergeri*. The anatomical differences between *M. gittenbergeri* and other *Mastus* populations are greater than those found among the other species sensu MAASSEN (1995). *M. gittenbergeri* is characterized by a flat penis papilla, a unique character expression in Cretan *Mastus*. It was detected as a well characterized unit in the shell analysis, but other species sensu MAASSEN (1995), particularly those within the *M. sitiensis* complex, where the anatomical differences are less pronounced, could not be discerned morphologically. This needs an explanation.

If environment- or climate-related factors influenced or determined the shell character expressions, then *M. gittenbergeri* and the members of the *M. sitiensis* complex should be subject to the same effects. In the region west and south of Agios Nikólaos, *M. gittenbergeri* and populations of the *M. sitiensis* complex live sympatrically. This is clearly visible in the morphological record, indicating that environment is not responsible for a general absence of shell differences between small *Mastus* species. The region does not exhibit obvious particularities in its landscape when compared with other areas of Crete, and assuming an invisible difference to be responsible for the shell character divergence would be highly speculative.

Examples for such speculations are provided in literature concerning *Albinaria*. Ecological features

have often been suspected to determine *Albinaria* shell parameters (LOOSJES 1955, AYOUTANTI et al. 1987, MYLONAS et al. 1987), but thorough analyses designed to substantiate these speculations provided very poor results against the alternative hypothesis of random-based spatial variation of shell size and shape (GITTEBERGER 1991, KEMPERMAN 1992, WELTER-SCHULTES in press). We may at least assume that the *Mastus* shell parameters are not completely induced by environment, and that two sympatric and reproductively isolated units should produce distinct shell sizes and shapes, at least at some localities.

To conclude, our grouping is somehow consistent with the findings of MAASSEN (1995), who seems to have applied a less restrictive species concept. Some anatomical characters in *Mastus* could be subject to spatial variation, like the morphological characters, so that not all the groups detected by MAASSEN (1995) would represent reproductively isolated units. The *M. sitiensis* complex, consisting of anatomically closely related units, could not be separated in our study and might represent a polytypic species. The anatomically more distinct *M. gittenbergeri* was clearly separated in the shell analysis. MAASSEN's (1995) results are generally confirmed, except the species classifications.

SPATIAL VARIATION OF SHELL

Spatial aggregations of large and small values in all species suggest that D and H/D are not randomly distributed. The values of both characters vary gradually from one site to another, supporting the view that we are dealing with polytypic species. The best example is the *M. sitiensis* complex. MAASSEN (1995) rarely examined samples of the areas between populations identified as different species. This applies particularly to the transition zones of *itanosensis/sitiensis*, *sitiensis/ierapetrana*, *sitiensis/small species* south of Agios Nikólaos, *riedeli/small species* south of Agios Nikólaos, *riedeli/butoti*, *butoti/species* of Mátala-Festós and *riedeli/species* of Mátala-Festós. One of the few analyses of transition zones (*riedeli/ierapetrana*) resulted in obvious difficulties in the interpretation of the combined anatomical and conchological data.

This substantiates the conclusions of PARMAKELIS et al. (1997) that the anatomical characters used by MAASSEN (1995) are less reliable at an increased number of analysed populations.

The *Mastus* species with smaller ranges seem to have equivalents in *Albinaria*. *M. violacea* lives exclusively in the Kouloúkonas mountain range, occupying nearly the same ranges as *Albinaria violacea* Schilthuizen et Gittenberger and *A. v. ulrikae* Schilthuizen et Gittenberger. This species complex is divided into three geographic populations: near Balí (west), near Síses (central) and near Achláda (east). Such a splitting is also observed in *Mastus violacea*. In *Albinaria* as well as in *Mastus*, the dark colour of *violacea* is only observed in the central populations (near Síses) whereas near Balí and Achláda the shell colours are typical. The range of *M. gittenbergeri* conforms largely with the eastern Cretan range of *Albinaria praeclara* (Pfeiffer). *M. abundans* has an equivalent in *A. maltzani* (Boettger). The evolution and phylogeography of *Albinaria* and *Mastus* had the same dynamic paleogeographic background, so parallelisms are not surprising.

ISOLATED POPULATIONS

Outside a continuous terrain, statements on systematic position of isolated populations, such as the ones of the small neighbouring islands of Crete, remain difficult. Anatomical and molecular analyses could shed light on these populations. The population of the island of Psíra (Figs 4, 6) could belong to either *M. sitiensis* or *M. gittenbergeri*. The presence of the eastern Cretan *Albinaria teres* (Olivier) on Psíra indicates that we might be dealing with *M. sitiensis*. The species of Día could be an endemic island species or belong to *M. gittenbergeri* (Fig. 6). The populations from the Dionisádes islands, classified with *M. cretensis* (Fig. 3), could represent an endemic species. The presence of several endemic *Albinaria* species on Día (WELTER-SCHULTES 1992) and the Dionisádes (SCHULTES & WIESE 1991) indicates that also the *Mastus* populations of these islands are likely to represent endemic species. The presence of an endemic *Albinaria* subspecies and a possibly endemic *Xerocrassa* species (WELTER-SCHULTES & WIESE 1993) allows similar conclusions for the species of the Paximádia islands, classified with *M. cretensis* (Fig. 3). The conspicuous *M. sitiensis* populations of Profitis Ilías might represent relict forms in the same way as has been suggested for populations of *Albinaria hippolyti* (Boettger) from the same locality (WELTER-SCHULTES 2000). The values of shell parameters (particularly D) of the conspicuous *Mastus* form conform with the values of the Idi mountain populations, the same region where the closest relatives of the *A. hippolyti* populations from the vicinity of Profitis Ilías are located (SCHILTHUIZEN et al. 1993).

Some populations northeast of the Díkti mountains are classified with *M. cretensis*, though they might belong to an endemic species of the area northeast of Neapoli (Fig. 3). An additional endemic species in this region, next to *M. gittenbergeri* and *M. abundans*, would not be surprising. The endemic *Albinaria maltzani* (Boettger) occupies nearly the same area, *A. hippolyti arthuriana* (Boettger), *A. wiesei* Gittenberger and *A. corrugata moreletiana* (Boettger) are other endemic snails of the region (WELTER-SCHULTES 1998b).

WESTERN CRETE

The few Cretan samples from localities situated west of the study area were not sufficient for analyses based on the biogeographical method applied in central and eastern Crete. According to MAASSEN (1995), *M. cretensis* is widely distributed in the northern regions of western Crete. *M. olivaceus*, with its type locality near Omalós, is possibly an endemic species of the Lefká Ori. Another group from western Crete, *M. sphakiota* Maassen, could be endemic or conspecific with either *M. olivaceus* or *M. sitiensis*. The anatomical characters suggests a close relationship to forms of eastern Crete (MAASSEN 1995). The ranges of *M. sphakiota* sensu MAASSEN and *M. sitiensis* sensu WELTER-SCHULTES are separated by more than 10 km (Figs 3, 4). It has to be mentioned that the neighbouring islands of Gávdos (*Mastus claudia*) and Gavdopoúla (*Mastus amezazada*) host endemic species, probably closely related to *M. sphakiota*. More research on the forms of western Crete is necessary.

MASTUS AND GEOLOGY

The results suggest that populations living on older substrata are slightly more variable than those found on younger substrata. This could be explained by older substrata providing more variable habitats, but there is no evidence in support of this hypothesis. In view of a more recent colonisation of the geologically younger habitats (WELTER-SCHULTES 2000), a slightly lower degree of diversity can be explained by a smaller gene pool of the younger populations.

This alternative is in agreement with many studies of genetic and morphological diversity of populations subject to range expansions, for example in populations of areas that were colonised after the Pleistocene (KOMMA & SEITZ 1984, LAGERCRANTZ & RYMAN 1990, WESTERBERGH & SAURA 1994, ADEPO-GOURENE et al. 1997, GULLBERG et al. 1998, SINCLAIR et al. 1999) or after the Oligocene (COOPER & COOPER 1995). Colonisation by range expansion may involve only few individuals, and consequently a low number of genotypes. When new areas are colonised by pe-



ripheral populations, the effect of genetic drift may be enhanced (DURKA 1999). Peripheral populations expanding their range are at a high risk of losing large parts of their genetic diversity during expansions (HEWITT 1996). *Mastus* is a multiple-mating hermaphrodite, but if gene flow and the degree of inbreeding are low, the effects of historical range expansions on genetic diversity and differentiation may be enhanced (JARNE 1995, HEWITT 1996, DURKA 1999). In Crete these prerequisites were established for *Albinaria* (SCHILTHUIZEN & LOMBAERTS 1994).

At the moment it would be premature to present a well-resolved late Neogene colonisation scenario for *Mastus* in Crete, as has been attempted for *Albinaria*, to understand the present-day distributional ranges of the species (WELTER-SCHULTES 2000).

ENIDAE AND SPECIES-AREA RELATIONS

The present study revealed the presence of five *Mastus* species on Crete, plus the western Cretan *M. olivaceus*. *M. sphakiota* and the form occupying the range of *Albinaria maltzani* in eastern central Crete are two other candidates for the list of species. According to our results Crete hosts 7 ± 1 *Mastus* species. MAASSEN (1995) concluded that there were at least 18 species, VARDINOYANNIS (1994) and earlier authors listed 3–4 species.

The Cretan number of enid species can be compared with the proportion of Enidae on other islands (species-area relations). One Cretan *Turanena* species has to be added to the list Cretan enids. In Kíthira the proportion of Enidae is 8% of the total autochthonous land snail species number (3/37), in Kárpáthos 6% (2/36), in Ródos 10% (5/50) (WELTER-SCHULTES & WILLIAMS 1999). The conti-

ental Albania (29,000 km²) hosts approximately 200–250 autochthonous land snail species, of which 13–14 (5–7%) belong to Enidae (DHORA & WELTER-SCHULTES 1996, 1999, WELTER-SCHULTES & WILLIAMS 1999). In Crete (8,300 km²) the number of autochthonous land snails is 120 (WELTER-SCHULTES & WILLIAMS 1999). Assuming a proportion of Enidae for Crete as 6–9% yields an expected number of *Mastus* species between 6 and 10. This number fits well with our results. It is in agreement neither with the statements of VARDINOYANNIS (1994) and earlier authors nor with the conclusions of MAASSEN (1995).

PROSPECTS OF SHELL MORPHOLOGY

Collecting thousands of land snail shells for biogeographical studies, as has been done in the present study, or with *Albinaria* (WELTER-SCHULTES 1998b) implies no ethical problem. Undertaking a biogeographically equivalent study in anatomy or molecular biology would imply killing and dissecting thousands of animals, an objectionable procedure when equivalent results can be obtained with morphological methods. Besides ethical and species protection problems, the work would be far more time-consuming and expensive. One of the major advantages of shell studies is the possibility to analyse large numbers of specimens from numerous localities and thus obtain relatively well-resolved multi-dimensional data. Given a well-analysed spatial variation, the shells do not necessarily have to possess unequivocal diagnostic features to be of considerable value in taxonomical studies. The remaining questions can be then tested with anatomical or molecular methods in smaller study areas serving as model systems.

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