ISSN 0022-0019

ournal of Conchology

(Established 1874)

Vol. 37, Part 4, January 2002

promoting Conservation, Biogeography and Taxonomy

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Printed by Henry Ling, The Dorset Press, Dorchester DT1 1HD

INTENSIVE SEARCHING FOR MUSSELS IN A FAST-FLOWING RIVER: AN ESTIMATION OF SAMPLING BIAS

LEE C. HASTIE[1,3] & PETER J. COSGROVE[2]

Abstract *A study was carried out in the River Kerry, north-western Scotland, in order to determine the sampling efficiencies for different size classes of endangered freshwater pearl mussels* (Margaritifera margaritifera). *An experienced worker searched 20 x 1 m² quadrats on the river bed in order to recover secretly hidden mussel samples (n = 2-74 mussels per quadrat). An overall recovery rate of 0.69 (= 269/390 hidden mussels) was achieved. A significant trend of increasing sampling efficiency with mussel size was observed. Our results suggest that the lack of juveniles observed in some, otherwise 'healthy',* M. margaritifera *populations may be explained by sampling bias.*

Key words Margaritifera, *conservation, Scotland*

INTRODUCTION

The endangered freshwater pearl mussel, *Margaritifera margaritifera* (L.), is in decline across its geographic range. During the past 50-100 years, many populations have disappeared and some others are no longer reproducing successfully (Young *et al.*, 2001). A number of factors have been implicated in this decline, including the effects of organic pollution, physical habitat degradation, over-exploitation by pearl fishermen and declining salmonid host stocks (Cosgrove *et al.*, 2000).

Margaritifera margaritifera is a long-lived species capable of reaching ages >100 y (Bauer, 1992). At present, the only practicable way of determining viability in this species is by estimating the relative abundance of juvenile mussels in overall population size/age frequency profiles (Cosgrove *et al.*, 2000; Hastie *et al.*, 2000a). Unfortunately, no size/age frequency profiles of *M. margaritifera* were reported prior to its historical decline. Hence, there are no examples of what can be described, with confidence, as data from completely undisturbed, unstressed populations available for comparison. Several populations in northern Europe still appear to be in a 'healthy' condition with some evidence of recent recruitment (Young *et al.*, 2001). However, a predominance of young mussels has never been observed in any *M. margaritifera* population (Hastie, 1999). Several *M. margaritifera* populations have been investigated (eg. Hendelberg, 1961; Stober, 1972; Bauer, 1983, 1986; Ziuganov *et al.*, 1994; Mackie & Roberts, 1995; Cosgrove *et al.*, 2000; Hastie *et al.*, 2000a), all of which are consistently reported to have lower than expected numbers of juvenile mussels. Even if recruitment varied considerably from year to year, the numbers of mussels aged 1-10 y would be expected to exceed those of older age classes.

Given the widespread decline and endangered conservation status of *M. margaritifera*, this apparent lack of juveniles in all populations is of great concern (Young, 1991). For example, it is possible that a real fall in recruitment levels has occurred, and that this may be a general feature of surviving populations (Chesney & Oliver, 1998). However, the phenomenon is by no means restricted to *M. margaritifera;* a lack of juveniles has been reported for a number of other freshwater mussel species in different parts of the world (eg. Negus, 1966; Walker, 1981; Libois & Libois, 1987; Roper & Hickey, 1994).

Some workers (al-Mousawi, 1991; Beasley, 1996) have suggested that the lack of juvenile *M. margaritifera* observed during river bed surveys may be at least partly explained by sampling bias. In other words, very small mussels may be significantly under-repre-

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sented in samples because they are extremely difficult to find. Evidence in support of this hypothesis was reported recently by Hastie (1999), who compared the age profiles of six populations observed in 1996/97 with those observed by al-Mousawi (1991) in 1984/85. Although the corresponding profiles were similar, the relative numbers of 11-20 y old mussels found in 1996/97 were consistently larger than those of 1-10 y olds found a decade earlier. It appeared that in every population, the younger age class had been less efficiently sampled (Hastie, 1999).

Newly settled freshwater mussels are very small (a size of <0.5 mm maximum length has been reported: Buddensiek, 1991). *M. margaritifera* is typically found in fine sediments trapped between large stones and boulders in fast-flowing rivers - it is extremely difficult and time-consuming to use sieves in this type of habitat, and sifting the interstitial sediments in situ, by hand, is the best technique currently available to find juvenile mussels (Hastie *et al.*, 2000a). During river bed surveys, there are bound to be degrees of under-representation of the smaller size/age classes due to sampling inefficiency. However, this has never been quantified. Given the present concern about whether surviving populations are viable in the long-term, estimates of sampling bias would be very important for future conservation strategies for this species. Hastie (1999) suggested that it may be possible to obtain these experimentally in the field.

In this paper, we aim to: (1) estimate the sampling efficiences for different size classes of a *M. margaritifera* population during river bed searches, (2) investigate their effect on observed age-frequency profiles, (3) use this information to determine if the population under investigation is viable, and (4) interpret the results in terms of the present conservation status of this species.

METHODS

SITE SELECTION

The study was carried out in July 2000, in the River Kerry, north-western Scotland. The Kerry supports a very large, 'healthy' *M. margaritifera* population with relatively large numbers of juvenile mussels (Hastie *et al.*, 2000a). A local fish farm (Inverkerry Salmon Hatchery, LandCatch Ltd.) uses gravity-fed water from the river and the facilities there were used to maintain mussels during the work.

COLLECTION OF MUSSELS

Samples of Kerry mussels (overall n<1000) were collected during standard river bed searches, using a glass-bottomed viewing bucket (Hastie *et al.*, 2000a). These were transferred, in an insulated plastic 'cool box' containing river water, to the fish farm where they were measured [maximum shell length, L (mm)], graded (5-10 mm L size class) and kept alive in large holding tanks with running river water until required. The smallest mussels (L<50 mm) were kept in small plastic containers full of river bed sediment (fine sand) within the holding tanks. After the study had been completed, all mussels were returned to the river.

SEARCH AND RECOVERY EXPERIMENT

The main practical tasks of the investigation were: (1) to hide a number of mussels within the river bed sediments of the Kerry and (2) to search for and recover the hidden mussels. It was not possible to mark the small mussels without either causing serious damage or making them more conspicuous, therefore unmarked mussels were used. The two tasks were carried out separately by the two authors; PC was responsible for concealing the mussels and LH was responsible for searching and retrieving them again.

At the fish farm, PC made up 20 different samples of graded mussels. Variable numbers of mussels (n = 1-10) in each size class were selected for each sample, noted and sealed in numbered plastic bags. Overall sample sizes ranged from 2-74 mussels per bag. LH was not present when the samples were made up and therefore had no prior knowledge of the numbers and sizes of mussels in each bag.

In the field, a $1m^2$ metal quadrat frame was placed on the river bed. Any large stones and visible mussels within the enclosed area were removed and the quadrat was then double-searched thoroughly for 10 min by both workers. The underlying fine sediments (sand/gravel) were dug out to a maximum depth of 10 cm and turned over using a trowel and sifted by hand. Any mussels found were temporarily removed and placed on the river bed nearby. LH then left the site and PC concealed a sample of mussels within the quadrat by burying them in fine sediment and/or covering them with stones. The mussels were distributed either singly or in small clusters, in similar patterns to those observed in undisturbed sediments (Hastie *et al.*, 2000b). Any large stones removed during the initial searches were returned. LH then returned and undertook a 10 min search for the hidden mussels. PC kept time with a stop watch and any mussels which LH found were returned to the empty numbered bag. Any mussels and stones which had been removed from the area before concealment were returned carefully to their approximate original positions. The entire procedure was then repeated using quadrats in different parts of the river until all 20 bags of mussels had been hidden and 'retrieved'.

DETERMINATION OF SAMPLING EFFICIENCY

The overall numbers of mussels per size class before and after recovery were compared to determine how successful the searches had been and to check for any trends in sampling efficiency relating to mussel size. Sampling efficiencies were computed as the proportions of each size class recovered. Using an age-length key constructed for the Kerry *M. margaritifera* population (Hastie, 1999), mussel ages were determined and sampling efficiency was also plotted against age in order to 'correct' two age profiles observed recently in this population (Hastie *et al.*, 2000a). The original age profiles consisted of total numbers of (visible + hidden) mussels observed for each age class during quadrat searches. 'Visible' mussels were defined as those easily seen without disturbing the river bed, whereas naturally 'hidden' mussels were those completely buried within the substrata. It was assumed that the numbers of visible mussels were recorded correctly. Therefore the numbers of mussels in each age class *(a)* was 'corrected' as follows:

where $N(a)$ = estimate of total number of mussels

$$N(a) = N_v(a) + \frac{N_h(a)}{f(a)} \qquad (1)$$

$N_v(a)$ = number of visible mussels counted
$N_h(a)$ = number of hidden mussels counted
$f(a)$ = age-specific detectability (proportion of hidden mussels found)

RESULTS

PC hid 390 mussels in the 20 quadrats. Of these, LH recovered 269, representing an overall search success rate of 0.69. This excluded two small mussels (<10 mm L) found, which did not match the sizes of those hidden by PC. Since these must have been missed during the initial (double) searches, they were not recorded as 'recoveries'. The likelihood of being found depended upon mussel size (Fig. 1).

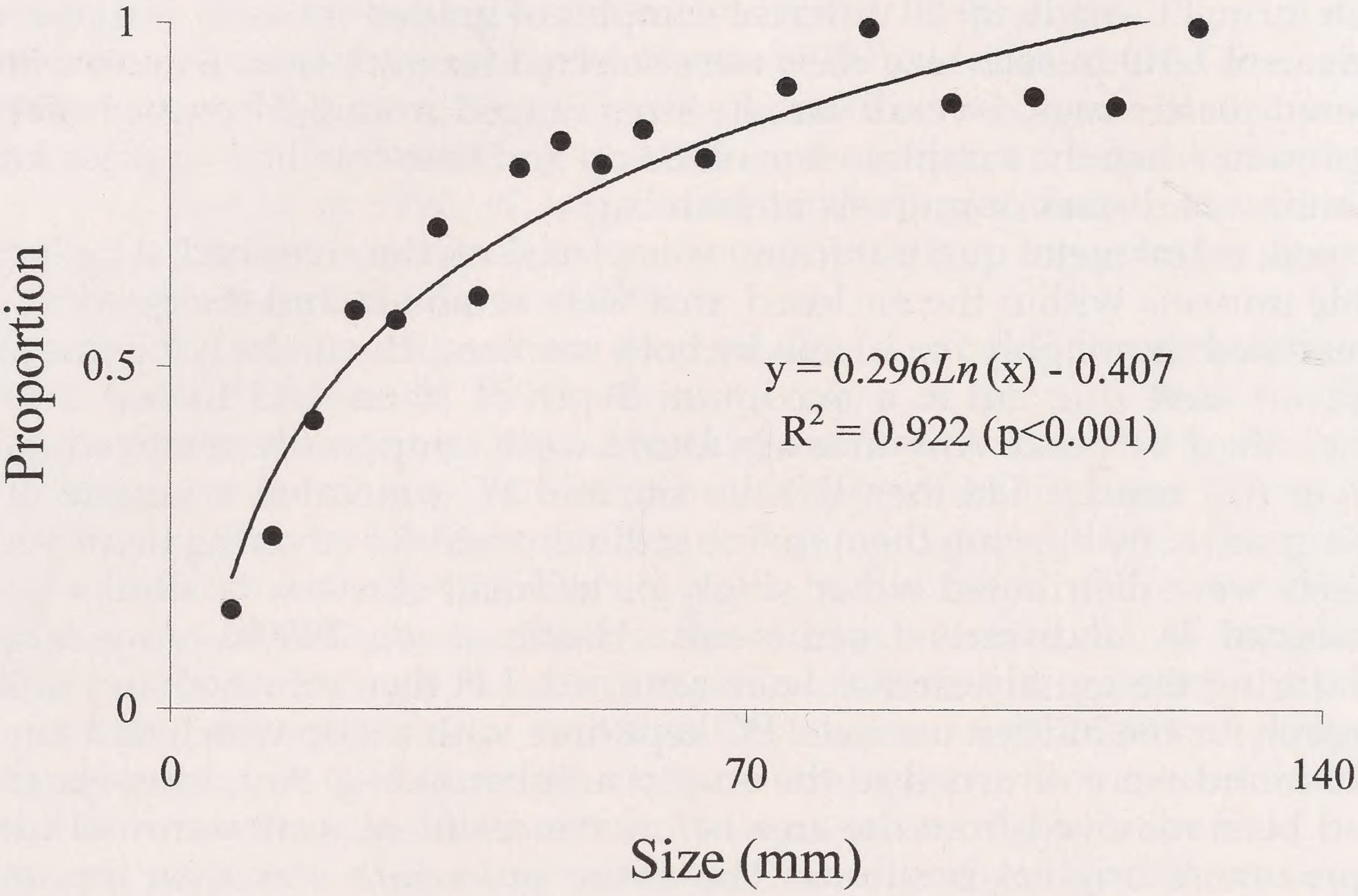

Figure 1 Plot of sampling efficiency (proportion found) against mussel size (L). The latter are plotted as size class mid-points. Fitted regression line equation and correlation coefficient are displayed.

The estimates of sampling efficiency for the different age classes of Kerry mussels are summarised in Table 1. Fig. 2 demonstrates the effects of using this data to adjust the age-frequency histograms of two Kerry mussel samples recently recorded (Hastie *et al.*, 2000a). The relative numbers of young mussels (aged <20 y) are greatly increased in both profiles, indicating considerable sampling bias towards older mussels. However, there is still an apparent lack of young mussels in the lower reach profile (Fig. 2a), whereas in

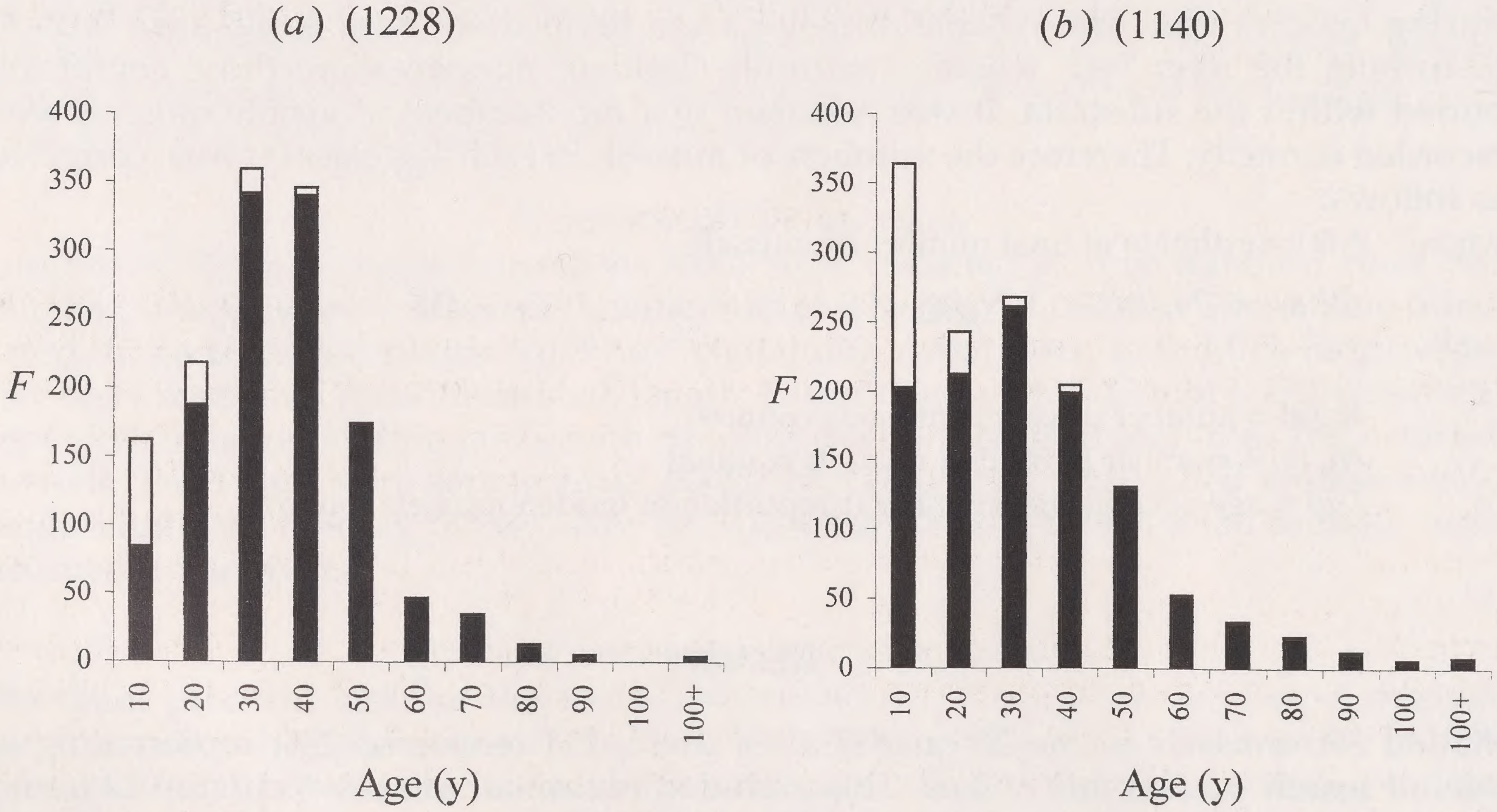

Figure 2 Mussel age-frequency histograms recorded at sites in: (a) the lower reach and (b) the middle reach of the River Kerry. Black = actual numbers of mussels-at-age observed. White = estimated numbers of mussels missed due to under-sampling. Actual sample sizes in parentheses.

TABLE 1
Estimated sampling efficiencies for different age classes of Kerry mussels. Based on the results in this study and an age-length key constructed for the Kerry *M. margaritifera* population (Hastie, 1999).

Age class (y)	Sampling efficiency[a]
1 - 10	0.50
11 - 20	0.75
21 - 30	0.83
31 - 40	0.89
41 - 50	0.93
51 - 60	0.97
61 - 70	0.99
71 - 80	1.00
81 - 90	1.00
91 - 100	1.00

a proportion of sample found.

the middle reach profile, the expected predominance of younger age classes has clearly been achieved (Fig. 2b). Following adjustments, the modal age class of the lower reach profile has remained at 21-30 y, whereas that of the middle reach profile has reduced from 21-30 y to 1-10 y.

DISCUSSION

The results of this study demonstrate that searching for juvenile *M. margaritifera* in river bed sediments (as described in this paper) is relatively inefficient, and that sampling bias towards larger adult mussels may be considerable. This corroborates recent work by Hastie (1999), who by comparing the profiles of mussel samples taken a decade apart, demonstrated that 1-10 y old mussels could be effectively under-sampled in the field. Thus, there is now strong evidence in support of the hypothesis that sampling bias may explain the lack of juveniles observed in certain, otherwise 'healthy', *M. margaritifera* populations (al-Mousawi, 1991; Beasley, 1996; Hastie *et al.*, 2000a). The fact that the expected predominance of young mussels has now been achieved in a *M. margaritifera* sample has important implications for the conservation of this species throughout its geographic range. For example, although all populations appear to lack small mussels (eg. Hendelberg, 1961; Stober, 1972; Bauer, 1986; Young, 1991; Ziuganov *et al.*, 1994; Hastie *et al.*, 2000a), it now seems likely that some of these at least have sufficient numbers of juveniles present to be considered viable.

It is interesting that, even after adjustment, the sample from the lower reach of the

Kerry still appears to lack sufficient numbers of 1-20 y old mussels (Fig. 2a), thus it appears that the mussel beds in this part of the river are not viable at present. However, there are four potential sources of error in this work that must be considered:

(1) Since unmarked mussels were used in the experiment, some error may have been introduced if additional mussels (undetected during the initial searches) were found that were the same size as those deliberately hidden in some quadrats. Although the probability of an exact size-match occurring in any quadrat was quite low (only two mis-matched mussels <10 mm L were found overall), any error associated with this would result in over-estimation of sampling efficiency and so the small mussels may be even more under-represented than figure 2 suggests.

(2) It could be argued that by hiding the mussels artificially, it was not possible to simulate accurately their natural positions in the sediment (even though this was seriously attempted). This potential error may have been reduced, for example, by leaving the hidden mussels in the quadrats for 24 h (to assume 'natural' positions) before searching for them. However, this is largely irrelevant, because the sediments (and mussel positions) are in fact routinely disturbed before proper searching begins anyway. Nevertheless, we accept that mussels may be naturally better at 'hiding themselves' than expected (by burrowing very deeply, for example – only possible in some areas). If this were the case, then sampling efficiency would again be over-estimated.

(3) There were likely to be some errors associated with estimating age-specific sampling efficiencies. Using an age-length key to convert the size-based estimates to age-based estimates introduced some bias (although this was probably very small). Owing to the non-linear relationship between shell length and age, there was a very slight tendency to over-estimate size-at-age (and age-specific sampling efficiency).

(4) It should also be noted that the field work was carried out by very experienced mussel workers (ie. >5 y research experience, >100 rivers surveyed, >500 quadrats searched), under optimal surveying conditions (generally bright weather and low river levels: Cosgrove *et al.*, 2000). Workers and surveying conditions do vary, and so our estimates of sampling bias based on optimal conditions may be conservative.

Based on these sources of error, it is possible that true sampling efficiency, particularly for the 1-10 y age class, may be significantly less than we have estimated here. In other words, there may be even more small mussels in the river bed than our adjusted profiles in figure 2 indicate. However, the observed lack of juveniles in the lower reach is markedly different from that observed in the middle reach and it seems unlikely that this can be explained fully by sampling bias.

Hastie *et al.* (2001) studied the effects of flooding on the River Kerry *M. margaritifera* population and suggested that the relative abundance of juveniles in different reaches was influenced by the hydrological stability (flood resistance) of the river bed. The mussel beds in both the lower and middle reaches are still reproducing as indicated by the presence of very small immature mussels (Hastie *et al.*, 2000a). However, much of the river bed in the lower reach is relatively unstable, resulting in higher juvenile mortality during floods (Hastie *et al.*, 2001). If there is a net loss of small mussels in the lower reaches, then this would have to be compensated for by net gains elsewhere in the river, for example in the middle reach, in order to maintain overall population viability. According to Vannote & Minshall (1982), hydrologically stable mussel beds are essential for maintaining mussel populations in fast-flowing rivers.

Most of the Kerry population (>80%) occurs in the relatively stable middle reach (unpublished data). Therefore, we conclude that there is likely to be an overall predominance of 1-10 y old mussels in the river, thus indicating that the Kerry *M. margaritifera* population is presently viable.

An observed presence and/or relative abundance of juvenile mussels is often used to determine the conservation status of *M. margaritifera* populations (eg. Bauer, 1986; Young, 1991; Chesney & Oliver, 1998; Cosgrove *et al.*, 2000). For example, in a recent national survey of historical *M. margaritifera* sites in Scotland, Cosgrove *et al.* (2000) used the following criteria: (1) presence of juveniles (<65 mm L) to determine long-term viability, and (2) presence of small mussels <20 mm L (≈ 5 y old) as an indicator of recent recruitment. Our results suggest that some individuals <65 mm L are relatively easy to find in a viable mussel bed (Fig. 1). However, it is also apparent that all individuals <20 mm L may easily be missed, particularly during large-scale surveys when sampling effort is limited, and so the second criterion is less meaningful. Perhaps the presence of mussels <30 mm L is a more realistic sign of recent recruitment in Scottish pearl mussel populations. Hastie (1999) considered an observed overall proportion of 20% mussels aged <20 y to be a critical level of recruitment in a *M. margaritifera* population. However, values of 20% and 33% were recorded in the lower and middle Kerry profiles, respectively (Fig. 2), and the former may not represent a viable mussel bed (as discussed previously). Therefore, as a precaution, we propose a critical proportion of 25% mussels aged <20 y for studies that have involved rather intensive river bed searches (eg. >10 quadrats).

It is clear that sampling bias is a major factor to consider when searching for freshwater mussels in fast-flowing rivers. Whether endangered *M. margaritifera* populations are recruiting 'normally' is fundamental to the long-term conservation of this species across its range (Chesney & Oliver, 1998) and it is vital that accurate assessments of the relative numbers of juvenile mussels in different populations are made. Those sites that were conventionally recognised as important for their relatively large numbers of juvenile mussels (Cosgrove *et al.*, 2000), almost certainly had many more juveniles than was reported. Therefore, they should still be considered to be among the most significant of the remaining viable *M. margaritifera* populations. With regard to further research, between-worker and between-river differences in sampling bias may be important and therefore these should be investigated as soon as possible.

ACKNOWLEDGEMENTS

Under the terms of the UK Wildlife and Countryside Act 1981, a special licence to work with freshwater pearl mussels was issued by Scottish Natural Heritage (SNH). LandCatch Ltd. kindly allowed us the use of their facilities at their Inverkerry salmon hatchery. We are grateful to Frances Scougall (Aberdeen University) and John Shearer (LandCatch) for technical assistance. Much of our research on *Margaritifera* would not have been possible without the much-appreciated support of Phil Boon (SNH) and Mark Young (Aberdeen University).

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LAMELLOLUCINA: A NEW GENUS OF LUCINID BIVALVE WITH FOUR NEW SPECIES FROM THE INDO-WEST PACIFIC

JOHN D. TAYLOR[1] & EMILY A. GLOVER[1]

Abstract *A new genus* Lamellolucina *is proposed for a group of Indo-West Pacific lucinid bivalves with prominent commarginal lamellae often confused under the name* Lucina dentifera *Jonas. The genus comprises seven species, four of these are newly described from the Indo-Pacific and a single species* L. reyrei *Nicklès is known from West Africa. The type species* L. pilbara *n.sp. appears to be endemic to northwestern Australia.* L. gemma *Reeve is recorded from China, Philippines and Queensland,* L. jawa *n.sp. is described from Madura, Indonesia.* L. trisulcata *n.sp. ranges from southern India to Indonesia and* L. oliveri *n.sp. is known from Arabian Sea and Gulf of Oman.* L. dentifera *appears to be restricted to the Red Sea and Gulf of Aden.*

Key words *Lucinidae, Indo-Pacific,* Lamellolucina, Lucina dentifera

INTRODUCTION

Out of the five bivalve families possessing symbioses with sulphide oxidising chemoautotrophic bacteria, the Lucinidae are by far the most diverse, live in the greatest variety of marine habitats and are geographically the most widespread. Although the biology of Lucinidae has attracted considerable attention for the probable obligate association with chemosymbiotic bacteria housed in the ctenidia and upon which the bivalves are nutritionally highly dependent (Reid, 1990; Distel, 1998; Frenkiel, Gros & Mouëza, 1996; Taylor & Glover, 2000) the systematics of the family has been relatively neglected. For some tropical Indo-Pacific species the anatomy is known and the presence of symbiotic sulphide-oxidising bacteria have been confirmed (listed in Taylor & Glover, 2000) but the majority of species are known only from dead shells and their biology unknown. The most recent generic revisions are by Chavan (1969) where the taxa were rather poorly defined and illustrated and Bretsky (1976) which was largely restricted to North American taxa. Recent systematic work has shown that there are many undescribed species and genera living in Australian coastal waters (Taylor & Glover, 1997a & b; Glover & Taylor in press). During a dredge survey of subtidal molluscs around the Dampier Archipelago, north western Australia, we collected a distinctive, but undescribed lucinid with prominent commarginal lamellae. Study of collections revealed several other species with similar sculpture and hinge characters. We unite these species into a new genus with the new Dampier taxon as the type species and also describe two other new species from the northern Indian Ocean and one from Indonesia. The genus encompasses six species from the Indo-West Pacific including the distinctive *"Lucina" dentifera* Jonas from the Red Sea, *"Lucina" gemma* Reeve from the Philippines and also a species from West Africa.

Although *L. dentifera* has for many years been referred to the genus *Lucina* (Lamy, 1920; Oliver, 1992) it differs in many characters and is clearly a member of a distinct clade from the type species (ICZN Opinion 1095), namely, *Lucina pensylvanica* Linnaeus, 1758, from the north western Atlantic. Additionally, while studying shells labelled *L. dentifera* from the Arabian Peninsula we realised that two species had been confounded together. Specimens similar to those of the original description (Jonas, 1846) and illustrations (Philippi, 1847) of *L. dentifera* appear confined to the Red Sea and Aden. The second species (new species described below) ranges from Aden around the Arabian

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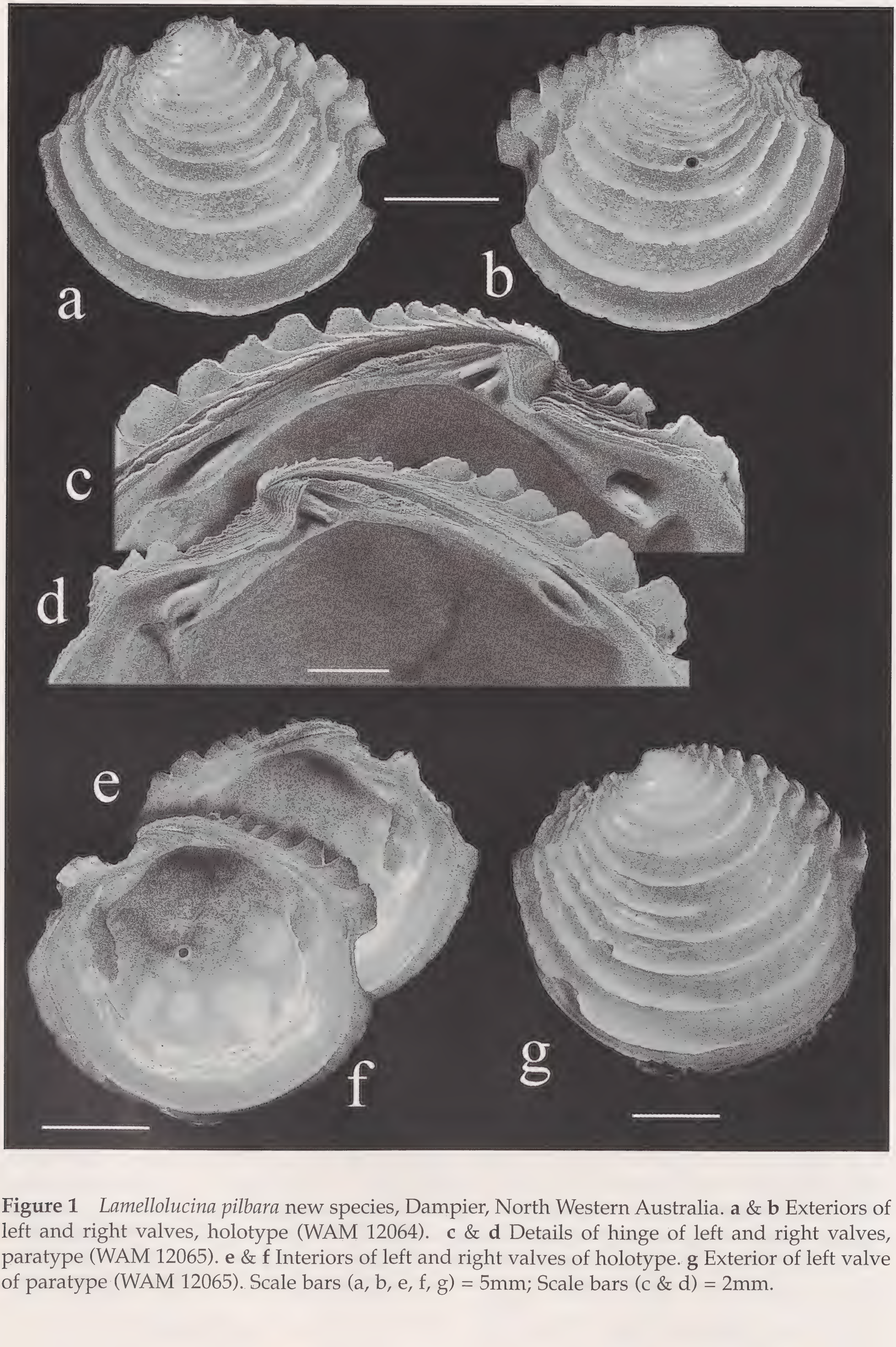

Figure 1 *Lamellolucina pilbara* new species, Dampier, North Western Australia. **a** & **b** Exteriors of left and right valves, holotype (WAM 12064). **c** & **d** Details of hinge of left and right valves, paratype (WAM 12065). **e** & **f** Interiors of left and right valves of holotype. **g** Exterior of left valve of paratype (WAM 12065). Scale bars (a, b, e, f, g) = 5mm; Scale bars (c & d) = 2mm.

Peninsula to the Arabian Sea and Gulf of Oman and this is the species illustrated as *Lucina dentifera* by Oliver (1995).

Abbreviations used in text:

BMNH	Natural History Museum, London
MNHN	Muséum National d'Histoire Naturelle, Paris
NMNH	National Museum of Natural History, Washington
NMW	National Museum of Wales, Cardiff
WAM	Western Australian Musem, Perth
ZMA	Zoological Museum, Amsterdam
ZMUC	Zoological Museum, Copenhagen
DA2/99/.	Stations of Western Australian Museum Woodside Dampier Expedition 2, July 1999. Unpublished report in Western Australian Museum

L=shell length, H=shell height, T=tumidity of single valve expressed in mm.

SEM scanning electron microscopy

SYSTEMATIC DESCRIPTIONS

LUCINIDAE

Lamellolucina new genus

Type species *Lamellolucina pilbara* new species

Fig. 1a–g

Diagnosis Shells subcircular in outline with prominent, regularly-spaced, thin, commarginal lamellae (serrated edges in some species). Interspaces smooth and radial sculpture absent. Anterior and posterior sulci present, often deeply incised. Anterior dorsal and posterior dorsal areas often bordered with imbricating flared lamellae. Lunule shallow to incised (asymmetric in some species) smooth or slightly ribbed. Ligament short and inset into shallow groove. Hinge plate robust with one or two cardinal teeth and prominent elongate lateral teeth in both valves. Anterior adductor muscle scar detached from pallial line for about 1/3 to 1/2 of its length. Inner shell margin finely beaded. Shell microstructure of composite prismatic outer layer, middle crossed lamellar layer with inner layer of prismatic structure grading to complex crossed lamellar towards hinge. Hinge of complex crossed-lamellar structure.

Derivation of name Name alludes to the prominent commarginal lamellae which are characteristic of the genus.

Geographic range Indo-West Pacific, Red Sea to Philippines, tropical West Africa.

Variation between species We recognise seven species of *Lamellolucina*, only three of which had previously been described. A key to the Indo-Pacific species is given in Table 1. Although all species possess prominent commarginal lamellae, those of *L. dentifera, L. gemma* and *L. jawa* have serrated or corrugated edges. Most species have a single anterior sulcus but *L. trisulcata* and *L. jawa* have two, separated by a narrow ridge. The form of the lunule varies considerably between species; in *L. dentifera* it is shallow but strongly asymmetric and mostly confined to the right valve, in *L. oliveri* it is similar but less asymmetric. The lunule of *L. gemma* is rounded and deeply impressed into the hinge plate, while in *L. pilbara* it is impressed but broader. In both *L. dentifera* and *L. oliveri* there are two cardinal teeth in the right valve, the anterior tooth being very small.

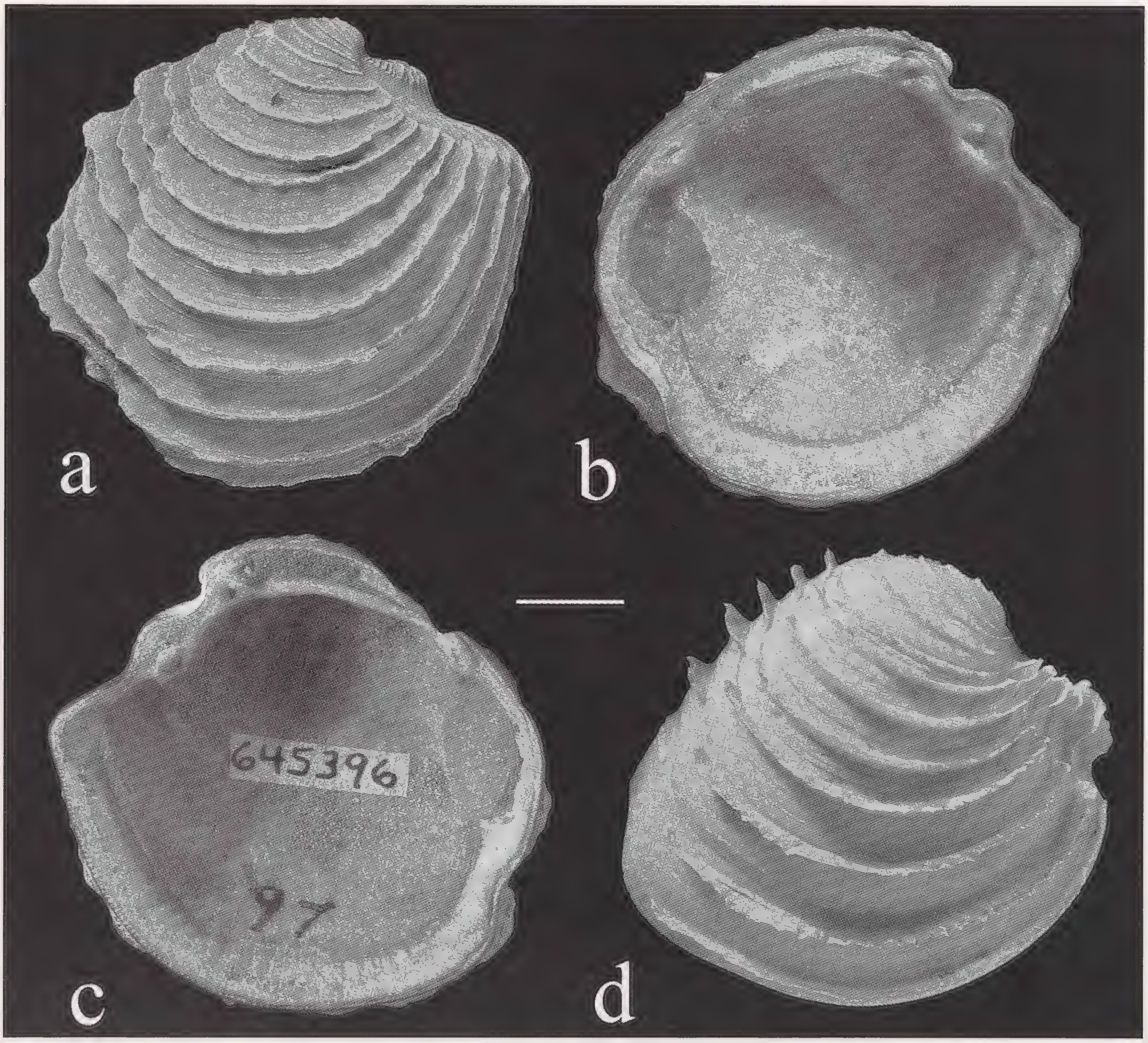

Figure 2a–c *Lepilucina gratis* Olsson, 1964, Upper Miocene, Angostura Formation, Ecuador. **a** Exterior of right valve, paratype (USNM 644097). **b** Interior of left valve paratype (USNM 644096). **c** Interior of right valve, paratype (USNM 645396). **d** *Placamen calophyllum* (Philippi, 1836), Veneridae, Dampier, NW. Australia, exterior of right valve. Scale bar = 5mm.

Comparison with other genera *Lamellolucina* is most similar to *Lepilucina* Olsson 1964 (type species *Lucina (Lepilucina) gratis* Olsson 1964: 47 pl. 7 figs 1–1c) from the Upper Miocene Angostura formation, Ecuador. This species is also recorded from the Upper Miocene Gatun Formation of Panama (Woodring 1982: 615 pl. 111 figs 3, 4, 7, 9, 11). *Lepilucina gratis* (Fig. 2a–c) has prominent, thin, plain commarginal lamellae with a shallow posterior sulcus and a broad anterior sulcus which lies close to the dorsal margin of the shell and defining a prominent extension of the antero-dorsal area. The lunule is slightly impressed, short and finely ridged. In the right valve there is a single bifid cardinal tooth and short anterior and posterior lateral teeth. The left valve has two short cardinals and anterior and posterior lateral teeth. The anterior adductor muscle scar is long, fairly broad and detached from the pallial line for 4/5 of its length. The inner shell margin is finely crenulate. This genus shares with species of *Lamellolucina* the characters of prominent commarginal lamellae, the absence of radial sculpture, the anterior and posterior sulci and general features of the hinge. It differs, however, in having a much longer and more detached anterior adductor muscle and the smaller lateral teeth. The two genera are likely sister taxa.

TABLE 1

Key to Indo-Pacific species of *Lamellolucina.*

1	Commarginal lamellae serrated or corrugated.	2
	Commarginal lamellae not serrated.	4
2	Commarginal lamellae finely corrugated.	*L. java*
	Commarginal lamellae strongly serrated.	3
3	Lunule a deep round pit	*L. gemma*
	Lunule shallow	*L. dentifera*
4	Anterior sulci double	*L. trisulcata*
	Anterior sulcus single	5
5	Lunule deeply notched	*L. pilbara*
	Lunule shallow	*L. oliveri*

Furthermore, there is a complex of species and varieties named around *Dentilucina orbicularis* (Deshayes, 1836) from the Neogene of Italy and elsewhere in southern Europe illustrated by Sacco, 1901:78–80 plate 18 figs 14–22. *D. orbicularis* var. *rotundelloides* Sacco, 1901, var *sublamellata* Sacco 1901 and var. *paucilamellata* Sacco, 1901. These resemble both *Lepilucina* and *Lamellolucina* and all need detailed study. Another probably closely related species is *Phacoides micropteryx* Cossmann (1924:124, pl. 6, figs 27–30) described from the Pliocene deposits of Karikal, south eastern India. Further investigation of the Neogene faunas of Central America, southern Europe and the northern Indian Ocean is needed to clarify relationships amongst these taxa.

Although some of the species we include in *Lamellolucina* have often been referred to *Lucina* (eg. Oliver, 1993, 1995) they differ significantly from the type species *Lucina pensylvanica* (Linnaeus, 1758) and other included species (eg. *L. adansoni* (d'Orbigny, 1839), *L. carnosa* Dunker, 1858, *L. roscoeorum* Kiburn, 1974). In these species the shells are rounded and strongly inflated, globose and thick-shelled. Sculpture consists of short concentric lamellae, which in fresh specimens are extended as periostracal flaps. There is a conspicuous posterior dorsal area demarcated by a distinct groove. The anterior adductor muscle scar is medium long and although detached for about half of length lies close to the pallial line.

Prior to ICZN Opinion 1095 which established in 1977 the type species of *Lucina,* Chavan (1937, 1969) considered *L. jamaicensis* Chemnitz, 1784 = *pectinata* Gmelin, 1791 to be the type species. Within the genus he included the Recent species *L. dentifera, L. gemma* Reeve and *L. dautzenbergi* Lamy. The first two species are considered in this paper. The last species, according to the original description (Lamy, 1920: 177–179), has rounded concentric ridges and lacks the prominent projecting lamellae of *Lamellolucina.* No locality was given in the original description and the type material was not located in MNHN in 2001.

Remarks Species of *Lamellolucina* are strikingly similar in size, shape, commarginal sculpture and anterior and posterior sulci to *Placamen calophylum* (Philippi, 1836) (Fig. 2d). This species of the family Veneridae often co-occurs with lucinids in subtidal sands such as with *Lamellolucina pilbara* in the Dampier area of northwestern Australia. Little is known of the function of these shell features. Stanley (1981) provided some experimental evidence that commarginal lamellae in *Chione cancellata* might act to reduce scour

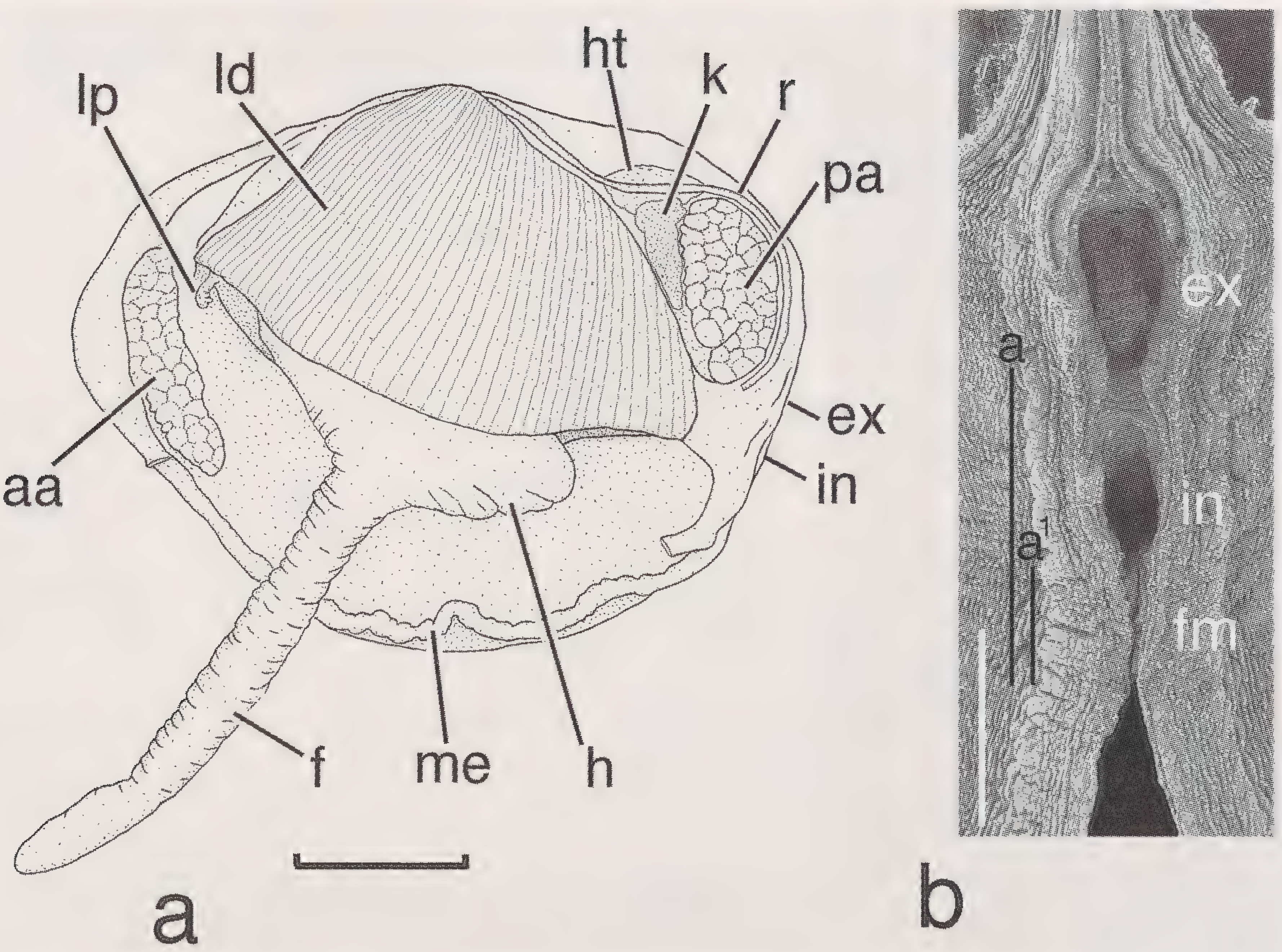

Figure 3a General anatomy of *Lamellolucina pilbara* with left mantle removed. Scale bar = 2mm. **b** Detail of posterior apertures, SEM. Scale bar = 500mm. Mantle fusion index (p. 8) is calculated as distance a1/a. Abbreviations: aa anterior adductor muscle, ex exhalant aperture, f foot, fm fused mantle, h heel of foot, ht heart, in inhalant aperture, k kidney, ld left demibranch of ctenidia, lp labial palp, me mantle edge, pa posterior adductor muscle, r rectum.

and displacement from the sediment. While Ansell & Morton (1985) showed that the commarginal lamellae of *Placamen calophylum* provide a defensive protection from some but not all shell drilling by predatory naticid gastropods. Increased predation was observed after the lamellae were experimentally removed.

Lamellolucina pilbara new species

Fig. 1, Figs 3–4, Fig. 5

Holotype One whole shell H=13.1mm, L=14.8, T=3.0mm, Mermaid Sound, Dampier Archipelago, North Western Australia, station DA2/99/2, 20°29.84'S, 110°45.04'E, depth 18m, 24 July 1999 leg J.D. Taylor and E.A. Glover, WAM 12064.

Paratypes 5 specimens. WAM 12065, locality as holotype H=13.2, L=14.0; WAM 12066, to northeast of Enderby Island, Dampier Archipelago, station DA2/99/69, 20°34.34' S, 116°34.67'E, 14m, H=16.0, L=17.0; BMNH 20001326, locality as holotype H=17.4, L=18.0; AMS C. 204856, H=21.5, L=22.1 & C. 204857, H=20.1, L=19.9, Nickol Bay, Dampier Archipelago, station DA2/99/16, 20°31.41'S, 116°52.83'E, 11m.

Other material examined Dampier Archipelago, Western Australia, dredged between 10–30m, muddy sand substrates: 8 preserved animals from 5 stations and 84 dead shells from 17 stations (BMNH).

Description Shell height to 22.8 ; length to 22.5, tumidity to 7.3 single valve. Sculpture of up to 20 widely spaced, thin, commarginal lamellae that are inclined towards the shell margin, slightly recurving at the outer edges. Interspaces between lamellae smooth except for faint growth increments. Narrow posterior dorsal area demarcated by a sulcus which runs from the umbone to the posterior shell margin where it forms a marked concavity in the shell outline. Anterior dorsal area separated by a reduction in height of the commarginal lamellae. Lamellae on both the posterior and anterior dorsal shell edge extended as imbricating scale-like folia. Lunule short, triangular, deeply impressed into the hinge plate, finely ribbed. Anterior dorsal area of right valve very slightly projecting into left valve. Umbones prominent and curved over lunule. Ligament short embedded in a narrow groove. Hinge with single bifurcate cardinal tooth in right valve, two narrow, elongate cardinal teeth in the left valve. Prominent peg-like anterior and elongate posterior lateral teeth and sockets in both valves. Anterior adductor muscle scar short, narrow, and detached from pallial line at ventral end for about 1/5 of length. Posterior adductor scar short, reniform. Pallial line distinct, narrow and continuous. Inner shell surface dull but glossy outside the pallial line. Inner shell margin finely beaded.

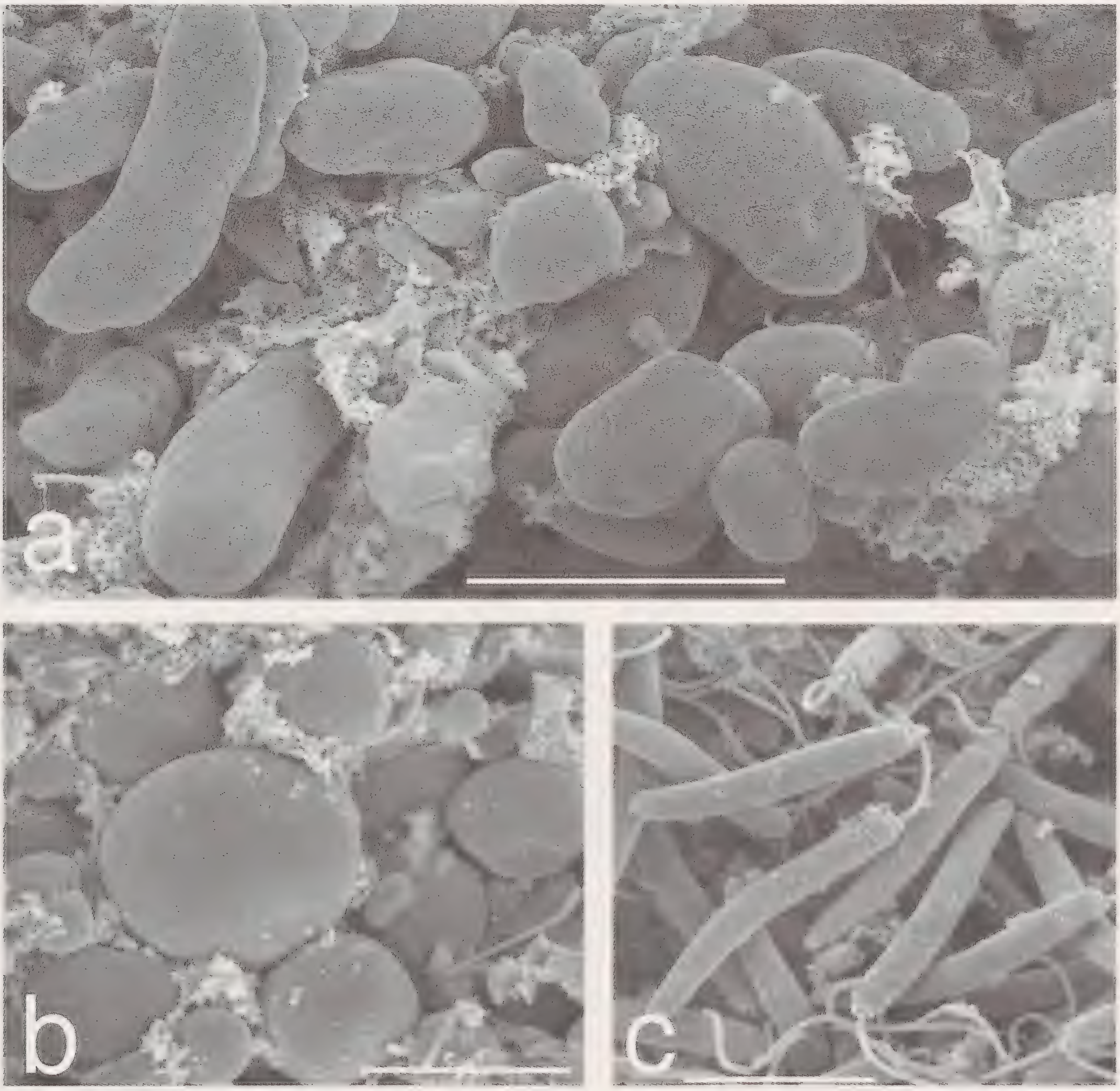

Figure 4 *Lamellolucina pilbara.* **a** Bacteria in bacteriocytes of lateral zone of ctenidial filament. **b** Granules in granule cell of lateral zone. **c** Sperm. Scale bars = 5 µm.

Shell microstructure Outer layer composite prismatic with fine first order crystals, a middle crossed lamellar layer and inside the pallial myostracum an irregularly prismatic layer grading to complex crossed lamellar under the hinge. Hinge of complex crossed lamellar structure.

Anatomy The general anatomy of *L. pilbara* is shown in Fig. 3a. In common with most lucinids (Allen, 1958) it possesses large, thickened ctenidia composed only of the inner demibranchs and an elongate cylindrical foot with a pronounced posterior heel. The labial palps are small protrusions at the edge of the lips. The posterior ends of the ctenidia join to the posterior mantle as described for *Parvilucina* (Reid & Brand, 1986). There are no mantle gills (Taylor & Glover 2000) near the anterior adductor muscle nor a mantle septum. The morphology of the posterior apertures and the extent of mantle fusion ventral to the inhalant aperture have much potential as systematic characters in Lucinidae (Allen 1958 fig. 9) and these are illustrated for *L. pilbara* in Fig. 3b. For comparison between lucinids of different sizes the extent of mantle fusion may be expressed as a ratio (see Fig. 3b for details). In *L. pilbara* the extent of mantle fusion is relatively short (ratio of 0.4) compared to 0.7 for *Anodontia alba*, but longer than *Codakia orbicularis* (0.2) and *Ctena orbiculata* (0.1) (measurements taken from Allen 1958 fig. 9). The mantle folds around the inhalant and exhalant apertures lack papillae. At the microscopic level the lateral zone of the thickened ctenidia is composed largely of bacteriocytes containing abundant potato-shaped bacteria around 3–6 µm in length (Fig. 4a). Other cells contain subspherical granules up to 6.5 µm in diameter (Fig. 4b) similar in morphology to those described as cystine-rich in *Codakia orbicularis* (Frenkiel & Mouëza, 1995). By coincidence, preparation of the gill revealed well-fixed sperm and these are illustrated in Fig. 4c. Similar in general morphology to those of *Codakia punctata* (Healy 1995: 6, fig1a) sperm of *L. pilbara* have a slender, tapering head piece 6.5 µm long and 1.0 µm wide and a mid piece of 0.7 µm long.

Derivation of name Named after the Pilbara region of northwestern Australia.

Comparison with other species *Lamellolucina pilbara* differs from *L. dentifera*, *L. gemma* and *L. jawa* in having commarginal lamellae without serrations or corrugations. It differs from *L. trisulcata* and *L. jawa* in having a single rather than double anterior sulcus. It is similar externally to *L. oliveri* but has a larger and deeper lunule and has only a single cardinal tooth in the right valve.

Lamellolucina dentifera (Jonas, 1846)

Fig. 5, Figs 6 a–d

Lucina dentifera Jonas, 1846: 17–18
Lucina dentifera Jonas. Philippi, 1847: 206, pl. 1 fig. 4
Lucina dentifera Jonas see synonomy in Oliver, 1993: 99, pl. 19 figs 6a–6b
Phacoides dentifer Jonas. Lamy, 1916: 9; Lamy 1920: 179–80; Abrard, 1942: 39 pl.4 fig 27

Material examined RED SEA: Gulf of Suez (BMNH); Gulf of Aqaba (BMNH); Gazirat Safaga (NMW); Shaab Baraia 150km N. of Port Sudan (BMNH); ARABIAN SEA: Aden (BMNH, NMW); Djibouti (NMW).

Type locality Red Sea.

Description Shell subcircular, slightly convex, H to 33.0, L to 34.5, T of single valve 8.7. Sculpture of about 20–30 evenly spaced very thin commarginal lamellae. Outer edges of

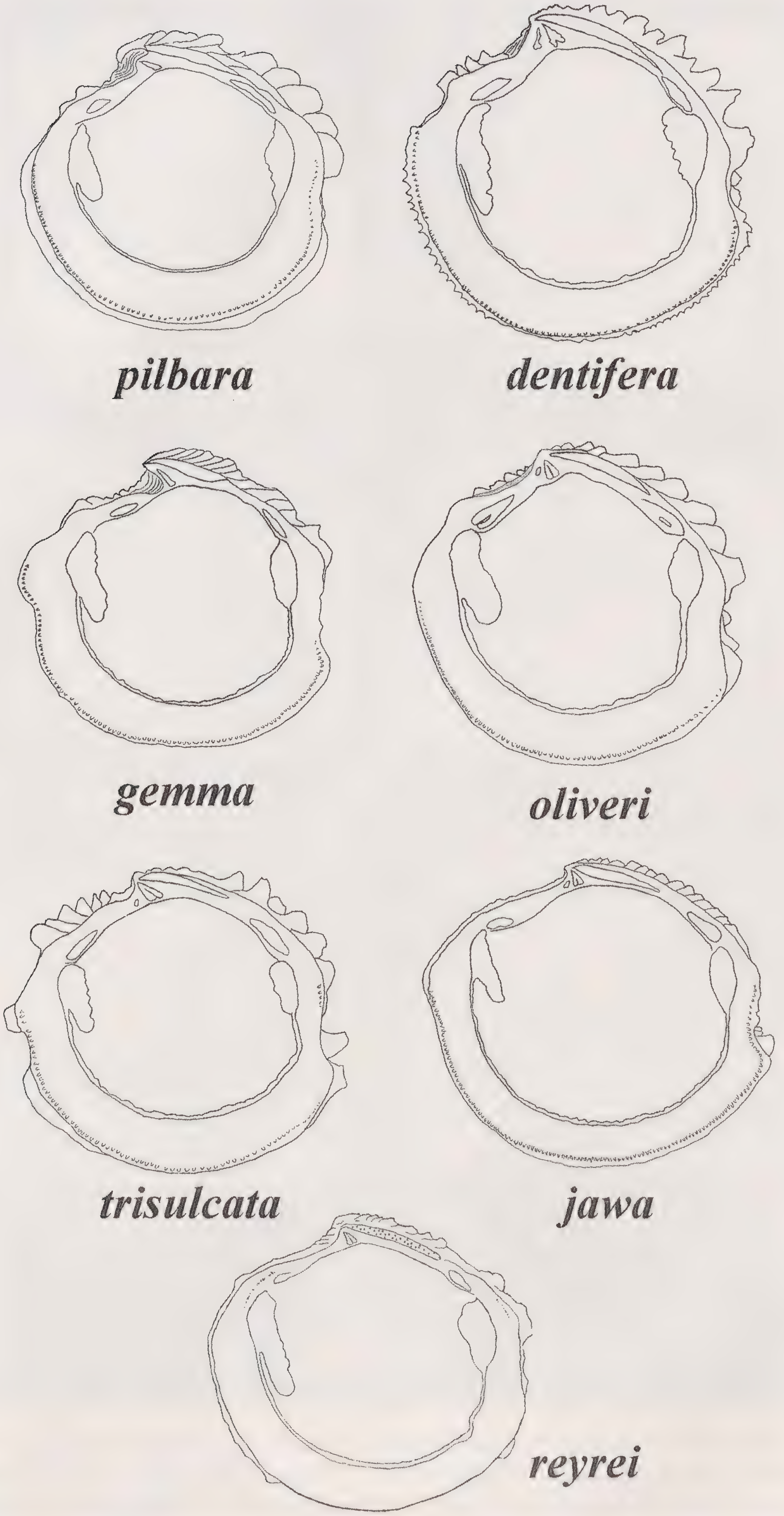

Figure 5 Outline drawings of interior of right valves of *Lamellolucina* species. Reduced to same scale.

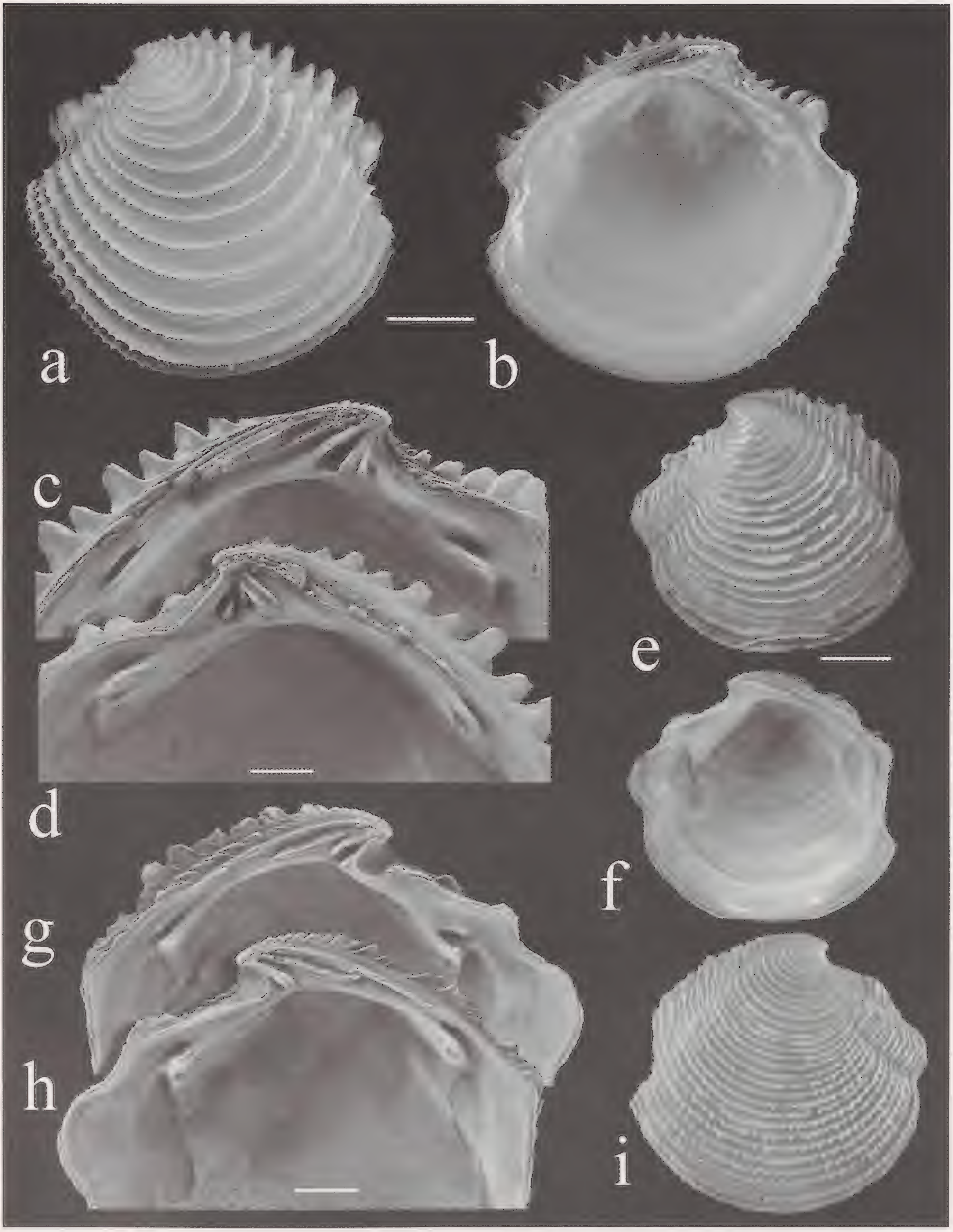

Figure 6a–d *Lamellolucina dentifera* (Jonas, 1846), Shaab Baraia, Sudan (BMNH). **a** Exterior of left valve. **b** Interior of left valve. **c** & **d** Details of hinge of left and right valves. **e–i** *Lamellolucina gemma* (Reeve, 1850). **e** Exterior of left valve of syntype, Isle of Bohol, Philippines (BMNH 1963175). **f** Syntype, interior of right valve. **g** & **h** Syntype, detail of hinge of left valve and right valve. **i** Exterior of right valve, Philippines, 11°43'N, 122º 34' E, 93-99m (MNHN). Scale bars (a & b) = 5mm; Scale bars (c, d, e, f, i) = 2mm; Scale bars (g & h) = 1mm.

the lamellae finely serrated (Fig. 6a.) although often worn in dead shells. Interspaces between lamellae smooth with low growth increments. Posteriorly, a well-defined sulcus extends from the umbones to the posterior lateral margin where there is a concave notch. Anteriorly, there is a shallow sulcus running from the umbone to the anterior margin which defines a prominent antero-dorsal area. Both anterior and posterior dorsal areas have extended folia which lack the serrations of the lamellae elsewhere on the shell. Ligament short and set in shallow groove. Lunule lanceolate, finely ribbed or almost smooth on the surface, slightly impressed, strongly asymmetric and mostly confined to the right valve. Hinge in right valve has two cardinal teeth, the posterior is larger and bifid and the anterior is a small ridge; prominent anterior and posterior lateral teeth and sockets. Left valve with two low cardinal teeth, the anterior is larger and bifid and the posterior tooth slender; prominent anterior and posterior lateral teeth. Anterior adductor elongate, lying close to pallial line and detached for about half of its length (Fig. 5). Inner shell surface dull to translucent, glossy outside the pallial line. Shell margin finely beaded.

Distribution Red Sea, Gulf of Aden.

Comparison with other species This species differs from *L. pilbara* in being larger, with prominent serrations on the commarginal lamellae and a bifurcate anterior cardinal tooth in the right valve. Distinct from all other species, the lunule is strongly asymmetric with the right valve projecting into the left and the detached ventral portion of the anterior adductor muscle lies very close to the pallial line. Although the name *L. dentifera* has been given to shells with commarginal lamellae from widely separated localities around the Indian Ocean it appears to be restricted in distribution to the Red Sea and Gulf of Aden. Records outside this area are likely to be one of the other species of *Lamellolucina* described in this paper.

Lamellolucina gemma (Reeve 1850)
Fig. 5, Figs 6e–i

Lucina gemma Reeve, 1850: pl. 11, fig. 64; 3 syntypes whole shells BMNH 1963175, H=9.6mm, 9.9mm, 8.3mm.

Material examined CHINA: NMW.Z. 1955.158.11161; PHILIPPINES: 11°43′ N, 122° 34′E MUSORSTOM 3 station DR140, 93–99m, 9 valves (MNHN); AUSTRALIA: Queensland, off Murray island, Torres St. (AMS); off Townsville Qld, 40 m, 18° 40′S, 146° 55′E (AMS)

Type locality Bohol Island, Phillipines.

Description Shell small, H to 13.5, L to 13.8, subcircular, posterior margin concave. Sculpture of 30 or more thin, closely-spaced, commarginal lamellae bearing numerous, ventrally curved, short, fine, serrations giving lamellae a crinkled appearance. Anterior dorsal area delineated by a broad, shallow sulcus across which the commarginal lamellae are confluent, although without the serrations. Within the anterior dorsal area there is a second, shallow, less well-defined sulcus which lies close to the dorsal margin. Posterior dorsal area defined by a broad sulcus with unserrated commarginal sculpture. Both anterior and dorsal edges of the shell have low, foliated extensions of the commarginal lamellae (Fig. 6e). Lunule deeply impressed, nearly symmetrical in both valves and forming a smooth, round pit beneath the umbones. Ligament short, located in a shallow groove. Hinge with a single, bifurcate, cardinal tooth in right valve and pronounced peg-like anterior and posterior lateral teeth. Left valve with two, narrow cardinal teeth

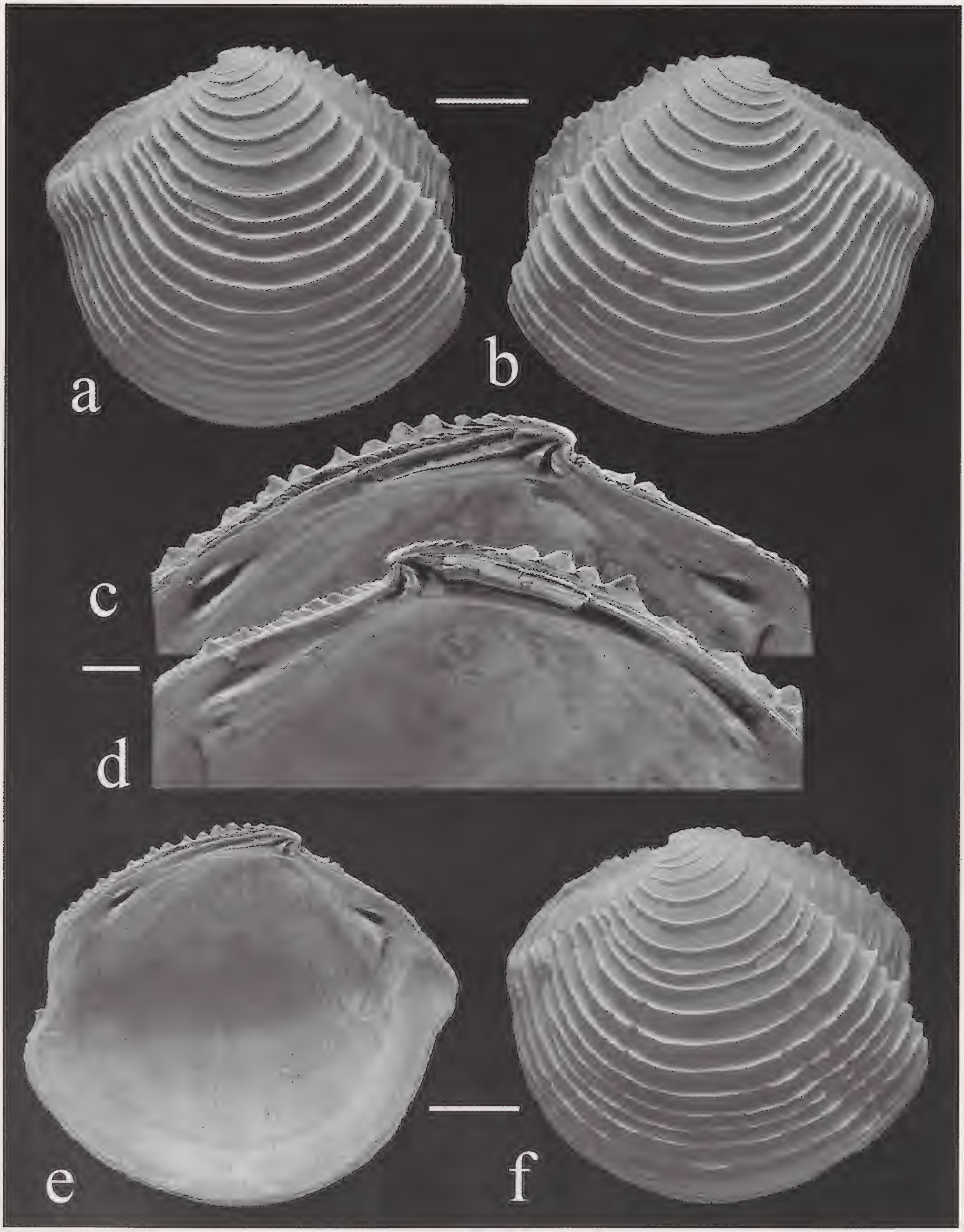

Figure 7 *Lamellolucina jawa* new species. **a** & **b** Exterior of left and right valves, Holotype ZMA 4.01.017 Madura, Indonesia. **c** & **d** Details of left and right hinges, holotype. **e** Interior of left valve of holotype. **f** Exterior of left valve of paratype ZMA 4.01.018. Scale bars (a, b, e, f) = 4mm; Scale bars (c & d) =1mm.

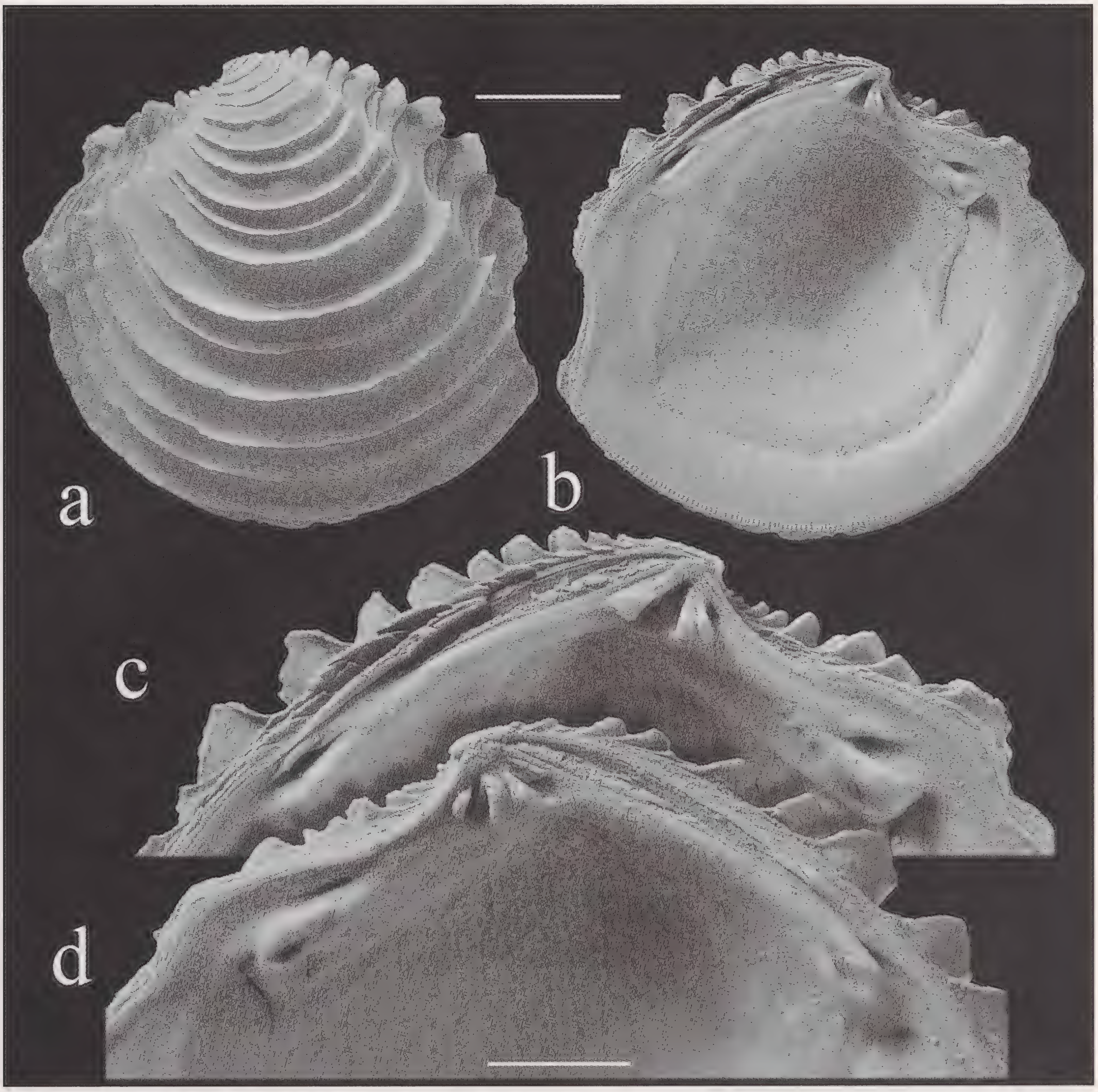

Figure 8 *Lamellolucina oliveri* new species, holotype, Gulf of Oman (BMNH 1963225/1). **a** Exterior of left valve. **b** Interior of left valve. **c & d** Detail of hinge of right and left valves. Scale bars (a & b) = 5mm; Scale bars (c & d) = 2mm.

and anterior and posterior lateral teeth and sockets. Anterior adductor scar narrow, short, detached from pallial line for about one quarter of length. Pallial line narrow, entire. Shell outside pallial line glossy, inside pallial line with small pits. Shell margin finely beaded.

Distribution Philippines, China, Queensland, Australia.

Comparison with other species *Lamellolucina gemma* can be distinguished from other species by the closely-spaced commarginal lamellae bearing numerous serrations and the deeply excavated rounded lunule. The lunule resembles those seen in a few other lucinids such as *Here excavata* (Carpenter, 1857) and *Cardiolucina eucosmia* (Reeve, 1850), (The former illustrated in Bretsky, 1976, pl.25 fig. 6 & 7 and the latter in Taylor & Glover, 1997b, fig.12).

Lamellolucina jawa new species
Fig. 5, Fig. 7

Holotype One whole shell, H=15.3, L=16.3, T single valve=3.2. Java Sea, off Madura, Indonesia 7º 07′ S 113º 29 E, Snellius Expedition II 1984 station CAD84/22, grab 50m. ZMA Moll. 4.01.017

Paratypes 3 whole shells locality as for holotype H=18.5 L=20.5 T=4.1 BMNH 20001339, H=14.6, L=16.5, T=2.9, H=15.5, L=17.1, T=5 (fused valves) ZMA Moll. 4.01.018.

Material examined INDONESIA: off Madura, Siboga Expedition 2 (ZMA).

Description Shell subcircular, slightly convex, H to 18.5, L to 22.0, T of single valve 4.1. Sculpture of about 25– 28 evenly spaced thin commarginal lamellae which are extremely finely and unevenly corrugated. Interspaces between lamellae smooth with low growth increments. Posteriorly, a well-defined sulcus extends from the umbones to the posterior lateral margin where there is a concave notch. Anteriorly, there are two shallow sulci running from the umbone to the anterior margin; the ventral sulcus is broader and less well defined and the dorsal sulcus is narrow. Between the sulci lies a narrow ridge with slightly extended lamellae. Both anterior and posterior dorsal areas have slightly extended folia. Ligament short and set in shallow groove. Lunule very small, finely ribbed. Hinge in right valve with a single bifid cardinal tooth; prominent anterior and posterior lateral teeth and sockets. Left valve with two cardinal teeth; prominent anterior and posterior lateral teeth and sockets. Anterior adductor short, narrow, detached and widely separated from pallial line for about one quarter of its length (Figs 5 & 7e) Inner shell surface pitted and striated. Outer shell margin finely beaded.

Derivation of name Named for the island of Java.

Distribution Known only from the type locality.

Comparison with other species This species differs from *L. dentifera* and *L. gemma* in having very finely corrugated rather than coarsely serrated lamellae and an extremely small lunule. It differs from *L. pilbara, L. oliveri* and *L. trisulcata* in having less prominent lamellae and from all species by the very short, narrow, anterior adductor muscle scar which is widely detached from the pallial line (Fig. 5).

Lamellolucina oliveri new species
Fig. 5, Fig. 8

Lucina dentifera Jonas: Oliver (1995): 235, fig 1019.

Holotype One whole shell H=15.8, L=16.9, T=3.5 BMNH 1963225/1, Gulf of Oman, coll. Townsend.

Paratype One whole shell BMNH 1963225/2. H=12.4 L=14.0 T=2.5); three valves, NMW 1955.158.1848 H=17.3, 16.1 16.8, Gulf of Oman, 156 fthms, coll. Townsend.

Other material examined Aden 1902.12.30.750 (BMNH); Arabian Gulf NMW.Z.1955.158. 11437.

Type locality Gulf of Oman.

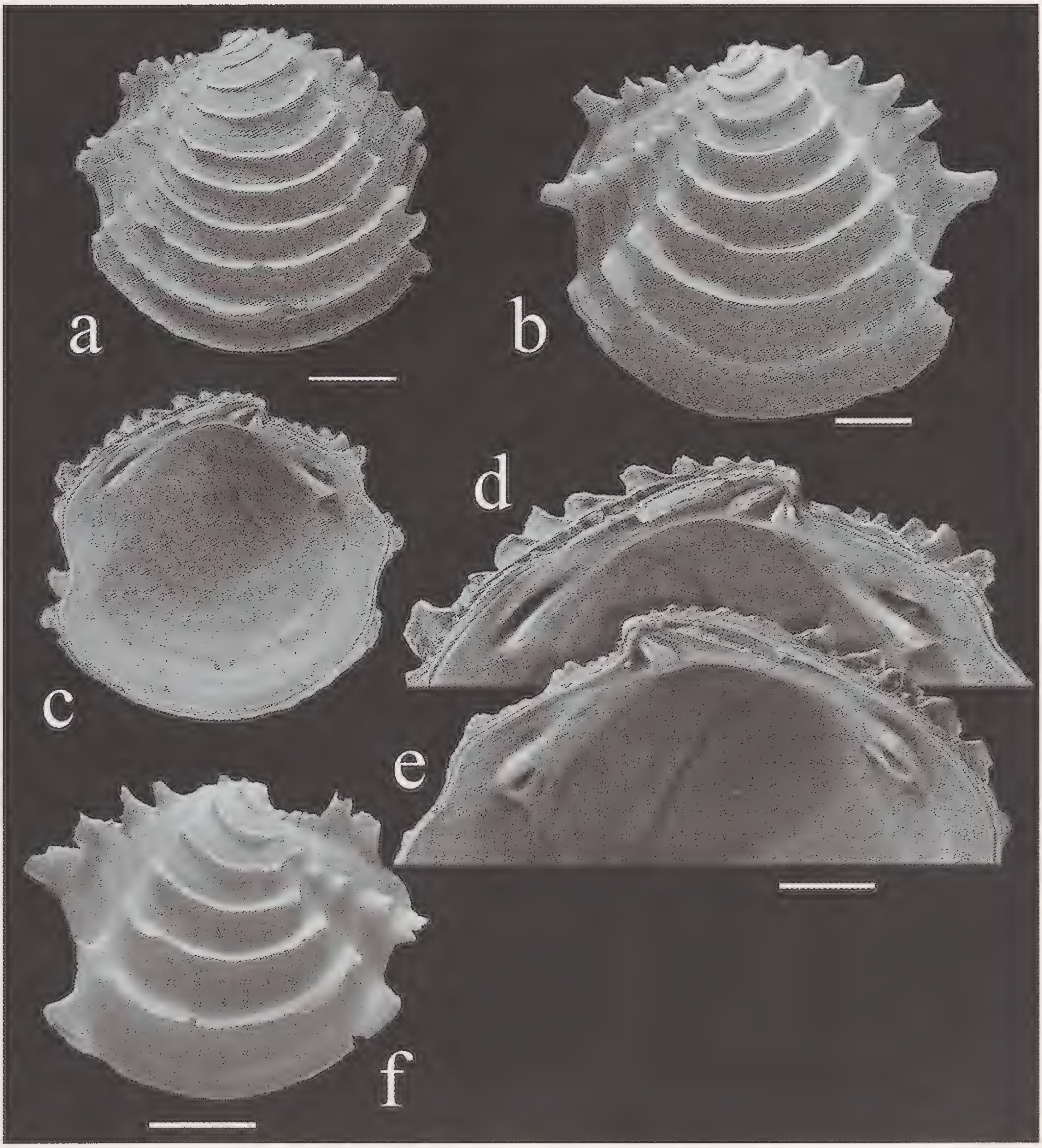

Figure 9 *Lamellolucina trisulcata* new species. **a** Exterior of left valve, holotype, Madras, (BMNH 1953.1.30.113). **b** Exterior of left valve, paratype , Jakarta Bay (ZMA 4.01.019). **c** Holotype, interior of left valve. **d** & **e** Detail of hinge of right and left vaves, holotype. **f** Exterior of right valve paratype, Jakarta Bay (BMNH 2001340). Scale bars Figs a, b, c, f = 2mm, d & e =1mm.

Description Shell subcircular, postero-lateral margin concave, H to 17.5, L to 21.0. Sculpture of about 20 more or less evenly spaced, smooth commarginal lamellae which are slightly recurved dorsally. Interspaces between lamellae smooth with low growth increments. Posteriorly, a well-defined sulcus extends from the umbones to the posterior lateral margin forming a broad groove with low commarginal lamellae. Anteriorly there is a shallow sulcus with low lamellae. Posterior and anterior dorsal areas with imbricating foliose lamellae. Ligament short and set in shallow groove. Lunule lanceolate, finely ribbed, slightly impressed, asymmetric and mostly confined to the right valve. Hinge in right valve has two cardinal teeth, the posterior is larger and bifid and the anterior is a small ridge; prominent anterior and posterior lateral teeth and sockets. Left valve with two cardinal teeth, the anterior of which is bifurcate; prominent anterior and posterior lateral teeth and sockets. Anterior adductor muscle scar narrow, and detached for about one third of its length (Fig. 5). Inner shell surface dull to translucent, glossy outside of the pallial line. Inner shell margin finely beaded.

Derivation of name Named for Graham Oliver in recognition of his work on Arabian bivalves.

Distribution Arabian Gulf and Arabian Sea, probably absent from Red Sea.

Comparison with other species Although this new species has been confused with *L. dentifera* and overlaps in range (at Aden), it is smaller, more inflated, lacks the serrations on the commarginal lamellae and the anterior adductor muscle scar is more widely detached from the pallial line. *L. oliveri* is similar to *L. pilbara* from Western Australia but in the latter the lunule is broad and excavated and there is only a single cardinal tooth in the right valve.

Lamellolucina trisulcata new species

Fig. 5, Fig. 9

Dentilucina (Dentilucina) dentifera (Jonas); Prashad 1932: 161(part).

Holotype One whole shell BMNH 1953.1.30.113, H=8.5, L=10, T=3.1. Dredged Madras, leg. R. Winckworth. 10 October 1931.

Paratypes One whole shell BMNH 1953.1.30.112, H=7.5 L=8.1 dredged Madras, India; two valves, no locality, BMNH 1854.6.30.179, H=9.2 L=11.2. Four single valves BMNH 20001340 (2v) and ZMA Moll. 4.01.019 (2v) Teluk Jakarta, off Tanjung Priok, Jakarta, Indonesia 6°02′ S 106°46′E, 10–20m.

Other material examined INDIA, Chennai (Madras) dredged (BMNH); THAILAND: Praphat Beach, Kampuan, Ranong Province (BMNH); INDONESIA: 37 lots from Teluk Jakarta, off Tanjung Priok, Jakarta, Indonesia 6°02′ S 106°46′E, 10–20m (ZMA); Madura, Siboga Expedition 2 (ZMA).

Description Shell subcircular, H to 11.3, L to 13.5 postero-lateral margin concave, tumidity of single valve to 3.9. Sculpture of about 10–12 evenly spaced, very thin commarginal lamellae. Interspaces between lamellae smooth with low growth increments. Posteriorly, a wide sulcus extends from the umbones to the posterior lateral margin forming a broad groove lacking sculpture. Anteriorly, there are two sulci separated by a narrow ridge bearing scales. The more ventral sulcus is broader and forms a concave embayment where it joins the antero-lateral margin. Posterior and anterior dorsal areas with imbricating foliose lamellae. Ligament short and set in a shallow groove. Lunule, lanceolate, shallow, slightly ribbed and asymmetric with the larger part of the lunule in the right valve. Hinge in right valve has a single cardinal tooth which is slightly bifurcate (the small projection seen in Fig. 9e may be a vestige of a second anterior cardinal tooth) and strong, peg-like anterior and posterior lateral teeth and sockets. Left valve with two cardinal teeth of which the anterior is slightly bifurcate, prominent anterior and posterior lateral teeth and sockets. Anterior adductor muscle scar short, narrow and detached for about one third of its length (Fig. 5). Inner shell surface dull to translucent, pitted, glossy outside of pallial line. Inner shell margin finely beaded.

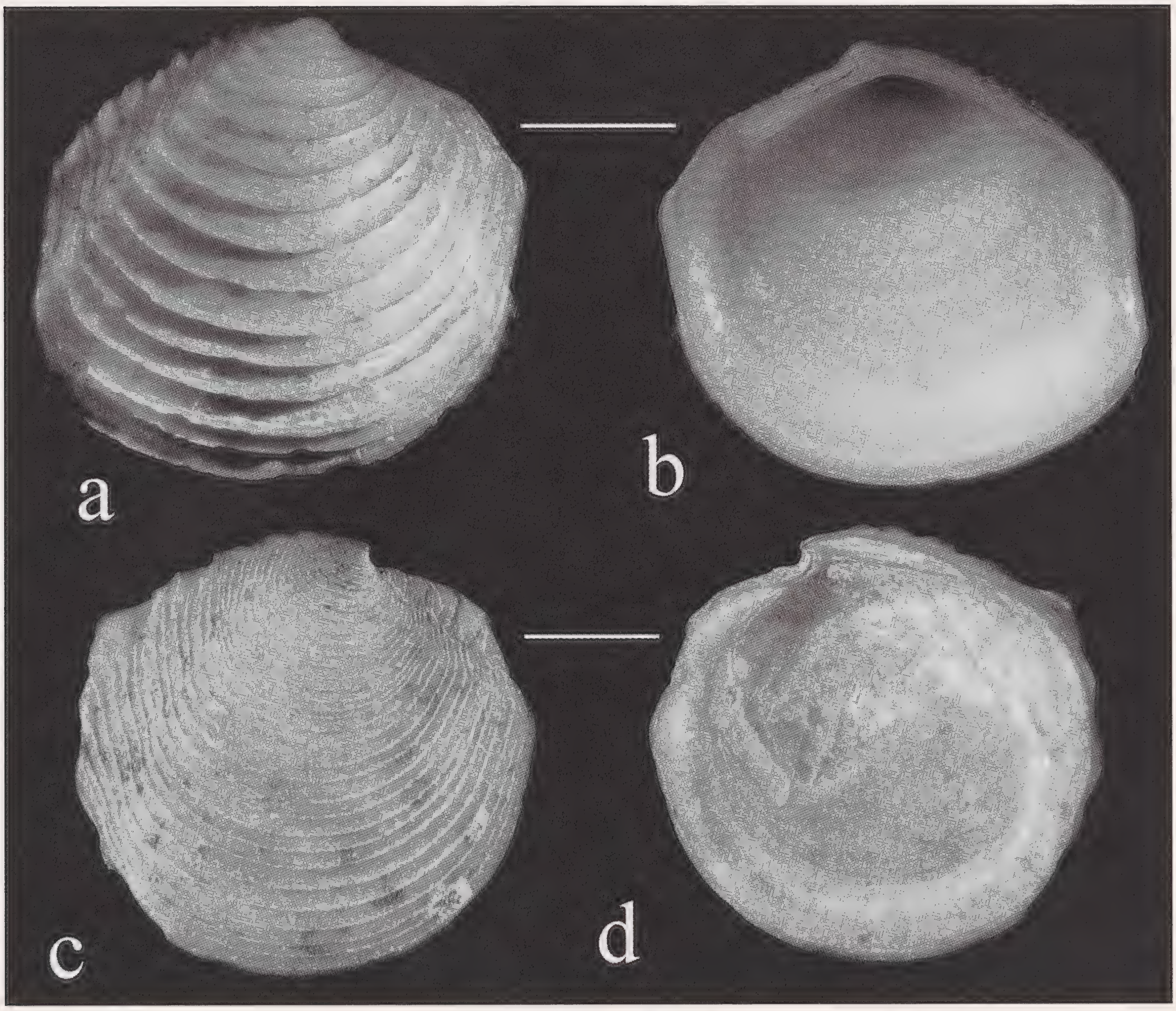

Figure 10 **a & b** *Lamellolucina reyeri* (Nicklès, 1955) 12º46.9′N, 17º29.9′ W, Casamance, Senegal, 45m. (NMHN). **a** Exterior of left valve. **b** Interior of right valve **c & d** *Phacoides gainii* Lamy, 1920, Iles Bissagos, Guinea-Bissau **c** Exterior of right valve. **d** Interior of right valve. Scale bars = 5 mm.

Derivation of name trisulcata refers to the one posterior and two anterior sulci on the shell.

Distribution Southern India to Indonesia.

Comparison with other species *Lamellolucina trisulcata* can be distinguished from other species of *Lamellolucina* by the possession of two conspicuous anterior sulci separated by a foliated ridge and the broad, smooth posterior sulcus. We have examined Prashad's (1932) material from Siboga station 2 Madura Strait and all but one of the valves which he thought were juvenile *Dentilucina dentifera* comprise *L. trisulcata* and the remaining single valve is *L. jawa* new species.

WEST AFRICAN SPECIES

We also include a species from West Africa within our concept of *Lamellolucina* and this is briefly described below.

Lamellolucina reyrei (Nicklès, 1955)

Fig. 5, Fig.10

Phacoides reyeri Nickles, 1955: 160, fig. 25.

Type material Two syntypes ZMUC. Type locality West Africa, off Sierra Leone Atlantide station 49, 7º 29′N, 13º 38′W, 74–78m.

Material examined Casamance Senegal, 12º46.9′N, 17º 29.9′W, 45m (MNHN) plus numerous samples in MNHN.

Description Shell sub-circular, L to 20. Sculpture of about 18 prominent widely spaced commarginal lamellae which become extended along the posterior and anterior dorsal margins. Broad posterior sulcus crossed by low lamellae. Anterior adductor scar detached for about 1/2 of length and lies close to pallial line. Anterior and posterior lateral teeth in both valves. Right valve with two cardinal teeth, the posterior cardinal is bifid. Left valve with two cardinal teeth. Inner shell margin finely beaded.

Distribution Found in muddy sand offshore from 40–200m from Mauritania to Ghana, Gabon to southern S. Angola, (von Cosel pers comm.)

Another species from West Africa with prominent commarginal lamellae is *Phacoides gaini* Lamy, 1920: 192, fig. d p.193. We have examined the type material (4 syntypes MNHN) of this species from Iles Bissagos, Guinea-Bissau. Although the external sculpture (Fig. 10c) resembles that of *Lamellolucina* species, the hinge lacks lateral teeth and the anterior muscle scar is elongate and detached from the pallial line for most of its length. These characters exclude *P. gaini* from our concept of *Lamellolucina.*

ACKNOWLEDGEMENTS

We are grateful to Graham Oliver NMW, Philippe Bouchet MNHN and Ian Loch AM for access to collections in their care and to Robert Moolenbeek ZMA and Tom Waller NMNH, for the generous loan of material. We thank Fred Wells and Diana Jones WAM for the opportunity to work in the Dampier Archipelago where we dredged *Lamellolucina pilbara.* Rudo von Cosel MNHN shared information on West African species. Additionally we are indebted to Harry Taylor BMNH for macrophotography and Yuri Kantor for images of *Phacoides gaini.* A grant from the Australian Biological Resources Study (ABRS) enabled some of this research.

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SOME SPECIES/AREA RELATIONSHIPS IN THE BRITISH LAND MOLLUSC FAUNA AND THEIR IMPLICATIONS

R.A.D. CAMERON[1]

Abstract *Three species/area regressions are given for the British land mollusc fauna. As expected, the slopes of these regressions are shallow; Britain is biogeographically uniform. There is, however, a latitudinal gradient in species richness that influences the slopes. When this is quantified, and area and latitude allowed for, islands around the British mainland do not have impoverished faunas relative to the mainland. This finding runs counter to theoretical expectations, and to findings on offshore island molluscs elsewhere. The regressions based on relatively large areas appear to hold good down to tiny scales (1m^2 or less); there is no consistent steepening at these scales. Quantification of such relationships at a wide range of scales will make broader European and global comparisons more rigorous.*

Key words *Species/area curves, land molluscs, Great Britain*

INTRODUCTION

Studies of the relationships between species richness and area have made significant contributions to biogeography and to the study of biodiversity (review in Rosenzweig, 1995). Such species/area relationships are usually expressed through the linear regression equation:

$$\text{Log number of species} = \mathbf{a} + \mathbf{z}(\text{log area})$$

The slope, **z**, is dimensionless, but the intercept, **a**, representing the logarithm of the number of species present when log area is zero, is dependent on the units of area used.

Four kinds of relationship are distinguished by Rosenzweig (1995), each with a characteristic range of slopes. At tiny scales, for example as between an individual quadrat and a study site, slopes are relatively steep. Within a single land-mass or biogeographic region, slopes are shallow, while when comparisons are made among such "provinces", up to global scale, the curves become much steeper. Slopes between islands of varying size are steeper than those spanning equivalent areas of a single land-mass, and islands are generally species poor relative to the same areas of equivalent mainland.

Island studies have received the most attention, largely because of the pioneering theoretical work of MacArthur and Wilson (1967). There are many published accounts of island species/area relationships for land molluscs (Cook, Jack and Pettitt 1972; Cowie 1996; Gascoigne 1994; Mylonas 1982 and 1984; Solem 1973 and 1984; Valovirta 1984; Vardinoyannis 1994; Welter-Schultes and Williams 1999), and these have made significant contributions to our understanding of island biogeography.

The other relationships have received less attention, although there are studies on birds and plants spanning the whole range from quadrats to global diversity (Shmida and Wilson 1985; Preston 1960; Rosenzweig 1995). It appears, however, that there are only two published studies involving land molluscs: the pioneering work of Lloyd-Evans (1975), based on a small part of Yorkshire, and the much more recent work of Nekola and Smith (1999), which looked at relationships from individual quadrats up to the whole State of Wisconsin.

In this paper I present three species/area relationships based on British data, and examine the extent to which they apply over the country as a whole. Area is not the only

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factor to influence species richness, but quantifying its influence makes it possible to examine other factors such as latitude more rigorously (Gaston and Blackburn, 2000). The relationships described are used as a basis for detecting latitude effects, and for examining the species richness of offshore islands. The extent to which the relationships extend to tiny scales is also examined (Cameron 1998; Nekola and Smith 1999). The relationships will also be used in making broader comparisons at European and global scales (Cameron, in prep).

MATERIAL AND METHODS

Four sources of data were used in the construction of species/area curves:

1. Lloyd-Evans (1975) gives land mollusc species lists for each of the 25 tetrads (2x2 km squares) within the Ordnance Survey 10x10 km square SE20 in west Yorkshire. His data on freshwater molluscs are not considered here.
2. Preece (1980) gives tetrad maps for all species living on the Isle of Wight (*c.* 380km^2). Every tetrad was examined, but sampling intensity was not uniform amongst them.
3. Killeen (1992) gives tetrad maps for all species in Suffolk (*c.* 3800 km^2). 26% of tetrads remained unexamined, but these were not clumped in any one part of the county; coverage at larger scales was relatively uniform.
4. The Conchological Society's *Atlas* (Kerney, 1999) gives 10x10 km square maps for all species in the British Isles. The overwhelming majority of squares have some records, but intensity of sampling varies considerably amongst them.

The first three sources have been used to construct species/area curves, starting from tetrads, and building up to the total area considered. Beyond this, each curve has been extended by taking data for larger areas up to the whole of Great Britain from Kerney (1999). Kerney (1999) is also used, together with other sources, referenced where they occur, to provide comparative data from other areas.

The correct way to construct a species/area curve for a continuous land-mass is to obtain species counts for areas of increasing size within it, up to the whole area considered, **each size of area including the results and territory of all smaller areas considered** (Rosenzweig, 1995). This usually gives a relationship which is approximately linear. This procedure, however, has certain consequences for the construction and analysis of curves:

1. The data-points are not independent, and a negative value of **z** is impossible. Estimates of variance about the regression line may give an indication of goodness of fit, but standard statistical tests are invalid.
2. The characteristics of the curve, **a** and **z**, will be influenced by the choice of starting point. In any given study, the end point is defined (the species count for the whole area). Individual, smaller equal-area patches within it will vary in the number of species they contain, and this variation will tend to increase as size gets smaller (Nekola and Smith, 1999). In an area the size of Great Britain, the geographical position of the starting point may influence species richness even at quite coarse scales. There are latitudinal gradients, and substantial blocks of land characterised by particular geological or ecological features that influence diversity. Starting in a poor site or area will give a steeper slope and a lower intercept than starting in a rich one.
3. Any area-related bias in the completeness of the species counts will affect the curve. This is clearly important when using county or national *Atlas* data where coverage is known to be uneven. In general, completeness will increase as area considered

gets larger, but some individual tetrads or 10x10 km squares will be fully recorded. Where detailed local studies are used the opposite bias may occur: it is not possible to search the whole of a 1 km^2 area at the intensity used in examining a single 1 m^2 quadrat.

Some of the problems with *Atlas* data could be solved by taking a number of starting points at random, building up areas from them, and calculating separate regressions for each; mean values for slope and intercept could be estimated. In the absence of appropriately computerised data, this would be very time-consuming, and would not eliminate bias caused by under-recording. A different approach has been adopted here, and is explained in the results section.

From data in Lloyd-Evans (1975), counts for all tetrads were obtained. Similar counts were made for smaller sets of areas of 16 km^2, 36 km^2, and 64 km^2, and for the 10x10 km square as a whole. The series was continued with data for the OS 100x100 km square in

TABLE 1

Recorded species numbers at various scales for three regions within Britain. n=number of estimates at that scale; min and max, lowest and highest numbers recorded in single areas of that size

AREA KM^2	**n**	**mean**	**min**	**max**
YORKSHIRE				
4	25	22.5	14	31
16	4	30.7	28	33
36	4	36.7	32	40
64	2	40.5	39	42
100	1	43	-	-
10,000	1	88	-	-
231,430	1	124	-	-
SUFFOLK				
4	16	25.9	14	38
16	8	38.1	30	47
36	7	46.3	38	55
100	8	54.6	48	57
196	5	60.6	59	63
400	5	63.4	56	71
900	2	71.0	70	72
1600	1	76	-	-
3800	1	81	-	-
23,000	1	102	-	-
231,430	1	124	-	-
ISLE OF WIGHT				
4	10	29.3	17	50
16	7	45.7	37	55
36	7	54.7	49	58
64	4	60	57	63
100	3	63.3	61	67
144	1	68	-	-
381	1	73	-	-
10,110	1	97	-	-
231,430	1	124	-	-

which the study area lies, and for Great Britain as a whole.

From data in Preece (1980) and Killeen (1992), a random sample of tetrads was inventoried, and smaller sets of larger areas were sampled in the same way. Overlap between areas of the same size was minimal, and restricted to the largest scales. The Isle of Wight series was extended with data for the two 100x100 km squares including and adjacent to the island, and that for Suffolk with data from four such 100x100 squares. In both cases, sea areas involved are subtracted, and a final point is provided by Great Britain as a whole.

RESULTS

THE SPECIES/AREA CURVES

Table 1 shows, for each study, the mean and range of number of species for areas with more than one example, and number of species for the rest. Although influenced by the larger number of samples available, it is noticeable that the range of species number is proportionately greater in the smallest areas. There is also a consistent difference between regions; area for area, the Isle of Wight is the richest, Suffolk is intermediate, and Yorkshire the poorest.

Figure 1 shows the log species/log area relationships for all three regions, using mean values where more than one area of that size has been sampled. Lines joining the points are drawn by eye, and serve simply to emphasise the curvilinear nature of the relationships. Also shown in the figure are estimates of species richness for ancient woodlands of varying area sampled by Wardhaugh (1996) and Cameron (1999), and the range (20–30 species) of diversity that is commonplace in semi-natural study-sites of a hectare or slightly less. It is evident that *Atlas* data, based on means, underestimate the number

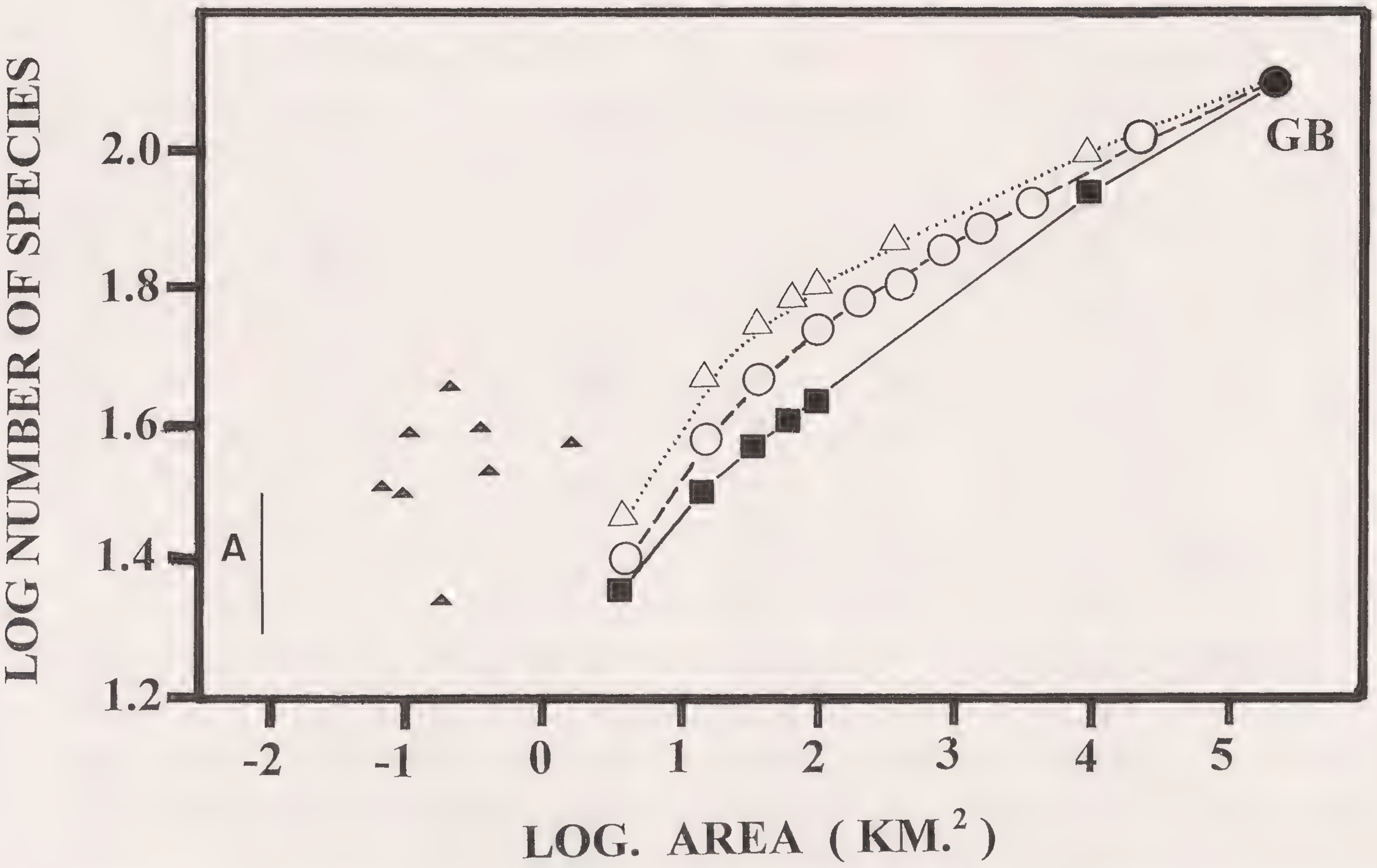

Figure 1 Species/area relationships based on the Isle of Wight (△), Suffolk (○), and Yorkshire (■), based on mean values of species richness for sampled areas (see text and table 1). Small filled triangles represent points for ancient woodlands sampled by Wardhaugh (1996) and Cameron (1999). The line A indicates the range of species richness that can be found in rich sites of *c*.1 hectare.

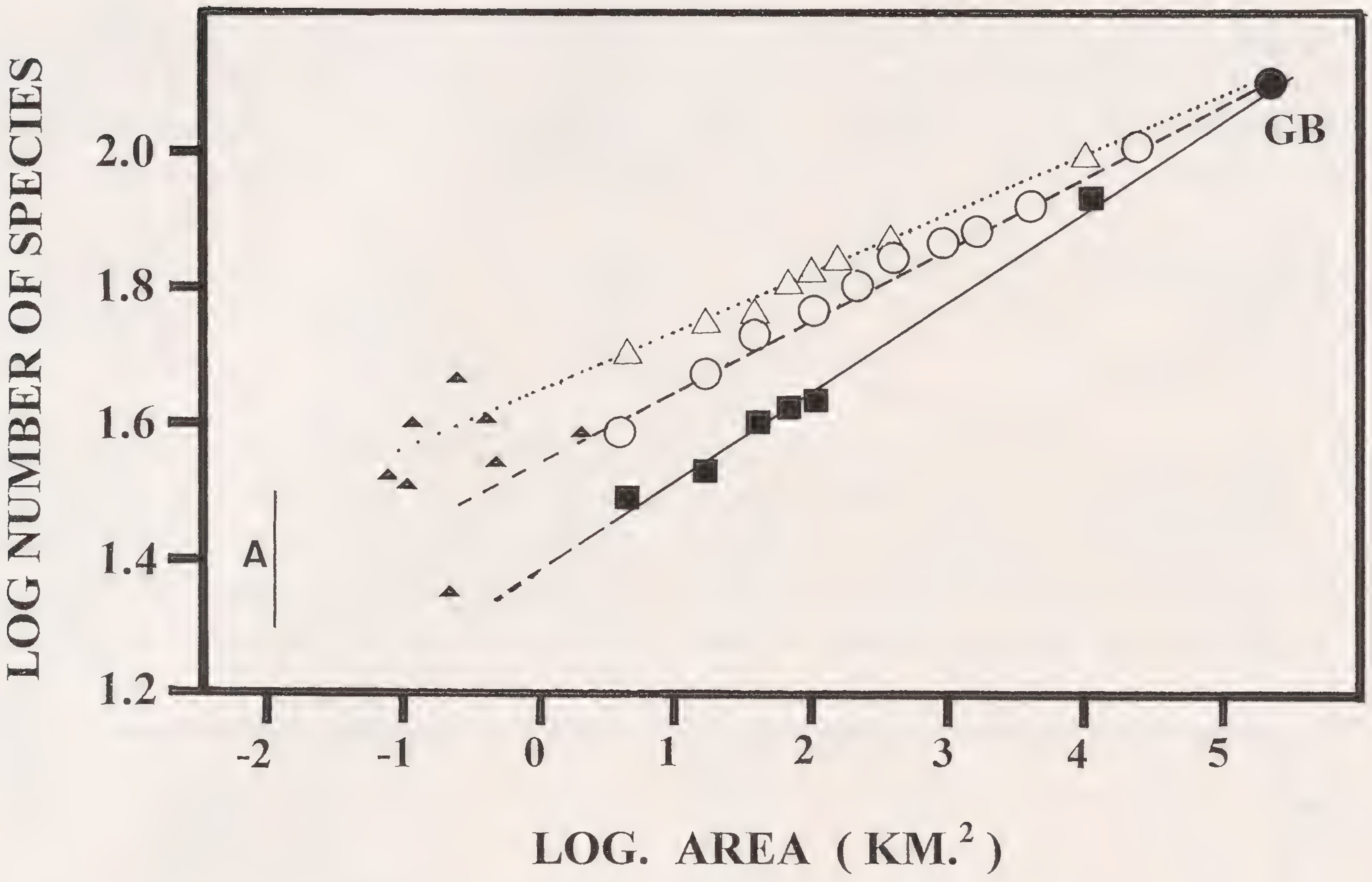

Figure 2 Species/area relationships as in figure 1, but based on maximum rather than mean species counts for any size of area. Lines represent regression equations (Table 2). Symbols as for figure 1.

of species that can be found in small areas, because not all areas have been exhaustively inventoried.

Figure 2 shows the effect of using the maximum species richness at any area sampled, rather than the mean. All three curves have straightened. The lines drawn are calculated regressions (Table 2). Most of the ancient woodland sites, and the range expected in hectare plots now lie within the range of values covered by the regressions. The Yorkshire curve, rooted in a northern and lime-deficient area is the steepest, and that for the Isle of Wight (southern and lime-rich) the least steep. The intermediate Suffolk curve, based on the most data, is taken, pragmatically, to represent a generalised British curve where there is no great change in mean latitude as area increases. It is used to correct for the effect of area in some of the analyses that follow, but use of either of the others would not give radically different results.

GENERALITIES AND DEVIATIONS

Figure 3 shows species/area points for a variety of sites within Great Britain and the Channel Islands, together with the Suffolk regression line. Areas shown are thought to be thoroughly surveyed, but are not a comprehensive set. Points for areas of less than a hectare (log value -2) are considered later (below, p. 9). The figure distinguishes Scottish points from those further south. The Suffolk line provides a reasonable fit for English data, but the more northerly points from Scotland all fall below the line, in some cases substantially.

This latitudinal effect has been quantified by taking successive east-to-west bands of 100 km north-to south depth, and obtaining species counts for each from data in Kerney (1999) (Table 3). These counts have been adjusted for the varying areas involved using the Suffolk regression, giving numbers expected if each were the size of the smallest

TABLE 2

Details of the $\log_{10}$ species/$\log_{10}$ area (km^2) regressions using maximum species counts (see text). r^2 gives the proportion of variance accounted for by the regression. Statistical tests cannot be applied; the values are given to indicate the close fit of the data to the estimated regression.

	N	a	z	r^2
YORKSHIRE	7	1.384	0.133	0.992
SUFFOLK	11	1.535	0.107	0.981
ISLE OF WIGHT	9	1.648	0.083	0.991

mainland band (12). Figure 4 shows the relationship between these adjusted values and distance south as indicated by band number. Regression lines are shown both for all bands, and for those including mainland only. Bands 1 and 2 contain only Shetland and Orkney; band 13 only the Channel Islands. The mainland slope of 0.018 represents an increase of *c.* 4% in species richness for every 100 km of movement south. Inspection of

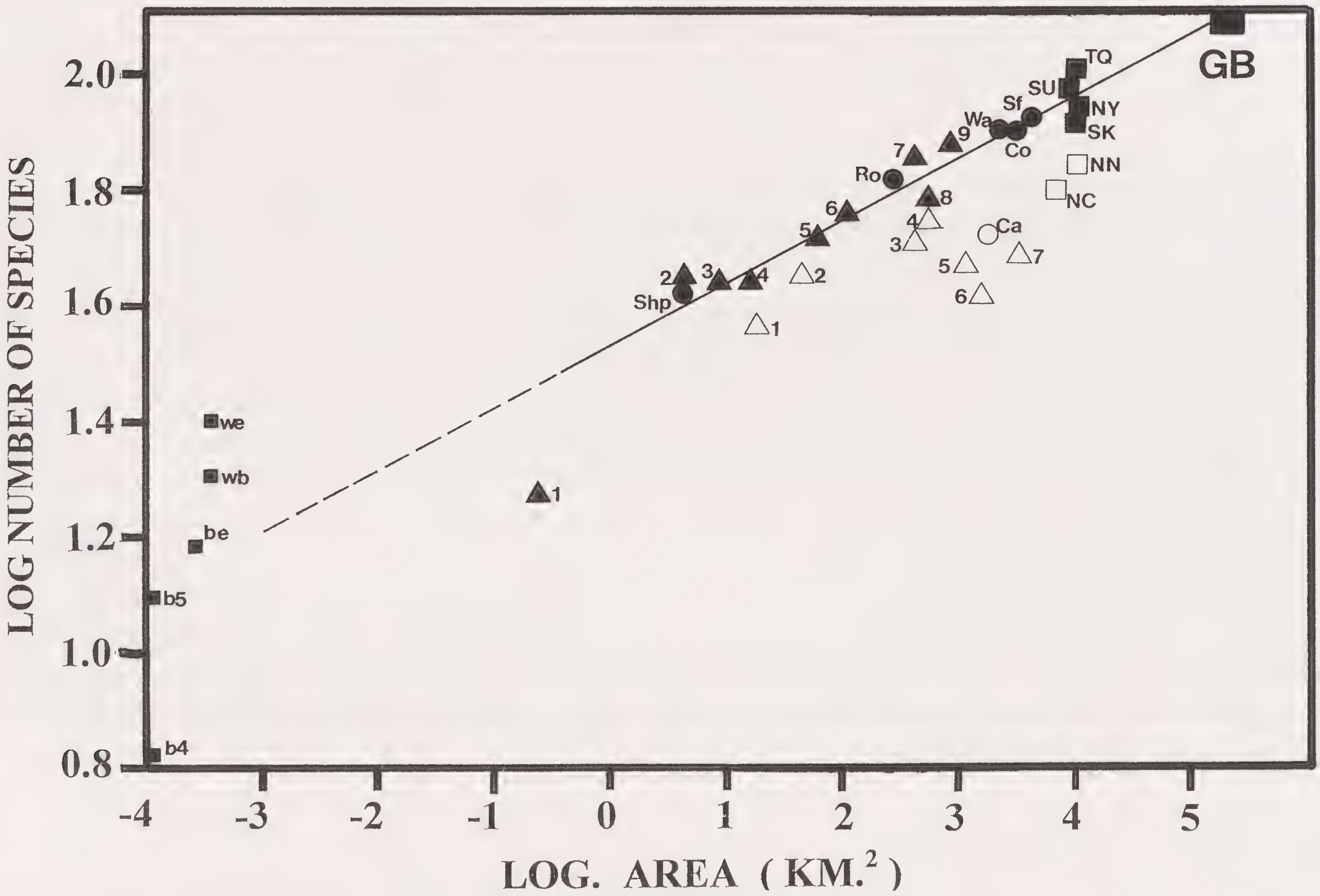

Figure 3 The Suffolk regression line, with species/area points for sites throughout Great Britain and the Channel Islands. Filled symbols represent areas from England and the Channel Islands, hollow symbols areas in Scotland.■ □ 100x100 km squares, given Ordnance Survey identification letters.● ○ Other mainland areas: **Shp** South Haven Peninsula, Dorset (Cameron, 2001b); **Ro** Rotherham borough, Yorkshire (W. Eely, pers. com.); **Ca** Caithness (Meiklejohn, 1973), **Wa** Warwickshire (Walton, 1994); **Co** Cornwall (Turk, 1984); **Sf** Suffolk (Killeen, 1992).▲ △ Islands; for **England** etc.: **1** Flatholm, Bristol Channel (Young and Evans, 1992); **2** Lundy; **3** Alderney; **4** Isles of Scilly; **5** Guernsey; **6** Jersey; **7** Isle of Wight; **8** Isle of Man; **9** Anglesey. For **Scotland**: **1** Ulva (Paul, 1992); **2** Colonsay + Oronsay (Paul, 1976); **3** Arran; **4** Islay; **5** Orkney; **6** Shetland; **7** Outer Hebrides. Data for unreferenced points comes from Kerney (1999). Small filled squares at extreme left represent points for small study sites listed in table 5 (see text, p. 9). **b4, b5** sites at Beacon Hill; **be** Benthall Edge Wood; **wb** Whiteford Burrows; **we** Waun Eurad. Species counts for these sites are slight underestimates: they do not include slugs.

TABLE 3

Log_{10} values for area, species number, and species number corrected for area (see text) for 100km deep east-west bands of Great Britian and the Channel Islands, arranged in a north–south sequence. Bands 1 and 2 contain only Shetland and Orkney respectively, and band 13 contains only the Channel Islands. All other bands contain parts of the British mainland.

100 km band	Log of land area	Log No. of species	Log species with area correction
1	3.20	1.633	1.711
2	3.03	1.681	1.777
3	3.95	1.806	1.803
4	4.30	1.875	1.835
5	4.30	1.924	1.884
6	4.23	1.919	1.887
7	4.28	1.968	1.930
8	4.25	1.977	1.939
9	4.53	1.991	1.927
10	4.62	2.025	1.951
11	4.51	2.049	1.987
12	3.93	1.964	1.964
13	2.30	1.820	1.994

Figure 4 suggests that the relationship may not be strictly linear; the trend appears steepest in the far north, and flattens out in the south.

Figure 3 includes data from a number of islands and archipelagos. Theoretical expectations, backed by numerous examples, are that continental shelf islands, where no in situ speciation has occurred, should have poorer faunas than the same areas of equiva-

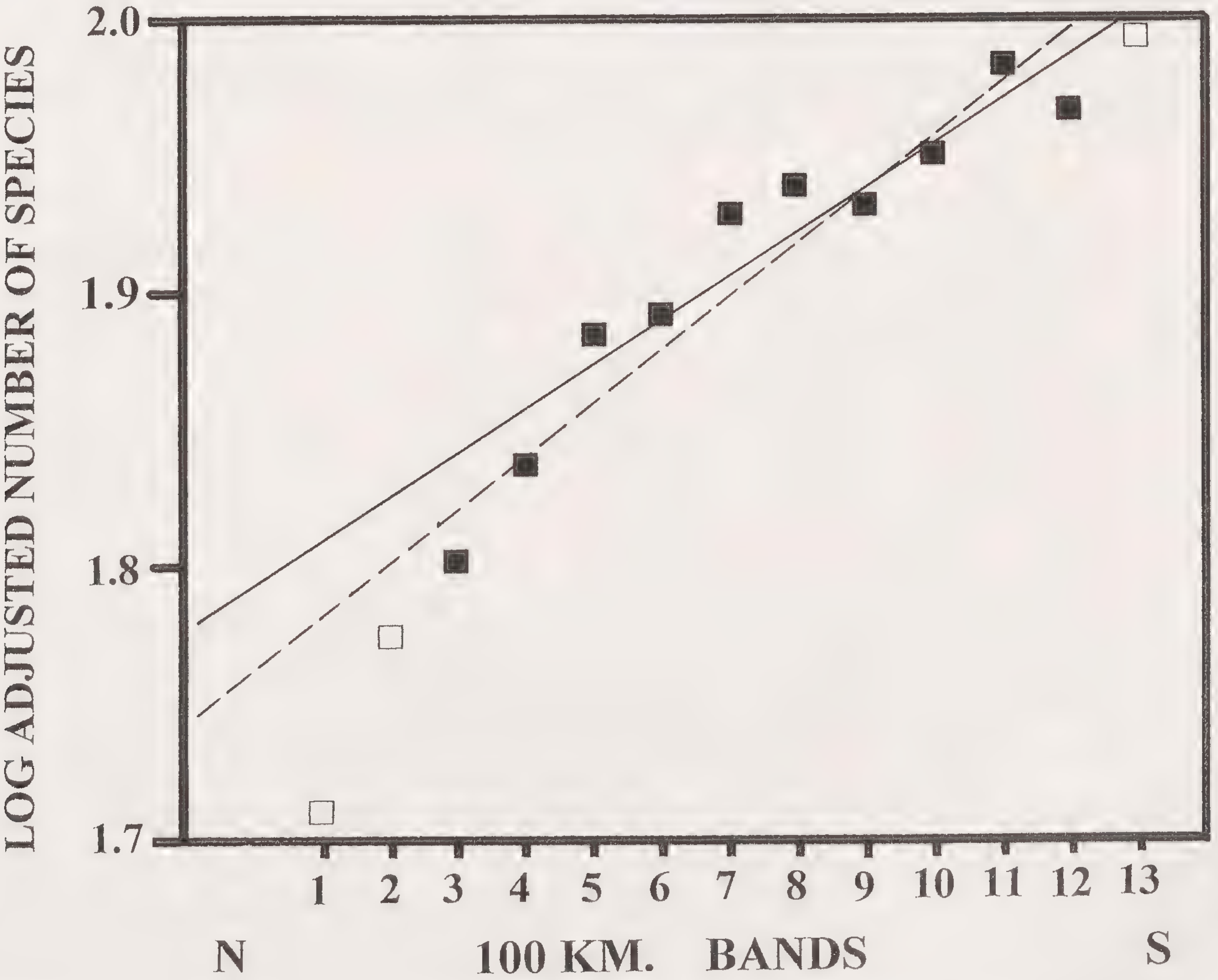

Figure 4 Variation in species richness (adjusted for area, see text and table 3) with latitude in Great Britain and the Channel Islands. Each band represents a 100 km north-south section of the country. Open symbols: bands containing only smaller islands; filled symbols: bands containing part of mainland Britain. The continuous line represents the regression based on the mainland alone, log adjusted species number = 1.78 + 0.018x band number, $P < 0.001$. The dashed line represents the regression using all data, Log adjusted species number = 1.74 + 0.021x band number.

TABLE 4

Species actually recorded for a selection of islands around Britain, and for two northern mainland areas, compared with those expected on area alone from the Suffolk regression, and with those expected after further correction for latitude, using the mainland regression shown in figure 4. Data from Kerney (1999).

ISLAND OR GRID SQUARE	LATITUDE BAND	LOG AREA KM ^{2}	RECORDED SPECIES	SPECIES EXPECTED ON AREA	SPECIES EXPECTED ON AREA & LATITUDE
Shetland	1	3.20	42	75	52
Orkney	2	3.03	47	72	52
Square NC	3	3.83	63	87	65
Square NN	5	4.00	70	92	74
Islay	6	2.78	58	68	57
Arran	6	2.63	57	66	56
Isle of Man	8	2.74	60	67	62
Anglesey	9	2.90	77	70	66
Lundy	11	0.60	47	40	42
Isle of Wight	12	2.58	73	65	70
Alderney	13	0.90	46	43	48

TABLE 5

Spot estimates (based on two values only) of **a** and **z** using data from some small-scale studies, comparing species numbers in the richest quadrat, A1, with numbers in the whole study site, A2. As elsewhere in this paper, a, the intercept, indicates the log number of species expected in 1 km^2. All sets except for the Spitzberg refer to shelled molluscs only. Beacon Hill is grassland in Sussex, Whiteford and Waun Eurad are calcareous wetlands in S. Wales and Anglesey respectively, and Benthall Edge a wood in Shropshire. Data for the Spitzberg, Tübingen, Germany, are given for comparison.

Locality	A1	A2	a	z	Source
Beacon Hill 5	0.022m^2	100m^2	1.34	0.066	Cameron and Morgan-Huws 1975
Beacon Hill 4	0.022m^2	100m^2	0.97	0.050	ditto
Whiteford Burrows	0.022m^2	300m^2	1.56	0.068	Sharland 2001
Waun Eurad	0.062m^2	300m^2	1.71	0.087	ditto
Benthall Edge	0.16m^2	216m^2	1.64	0.126	Cameron 1982
Spitzberg	1.0m^2	7km^2	1.77	0.093	Schmid 1966

lent mainland (Rosenzweig, 1995). Many of the islands represented here show no sign of impoverishment, and where they do, it appears that latitude might be a complicating factor (e.g. Shetland). This has been allowed for by applying a correction based on the results given above. To do this, the Suffolk regression has been used to estimate, for a number of islands, the species numbers expected on area alone. Suffolk lies in band 10 of the latitudinal scale shown in figure 4. This expectation has been corrected for latitude using the mainland regression shown in the figure, which adds species to the south of Suffolk, and removes species to the north (Table 4). The table also shows two northern mainland 100x100 km squares for comparison.

On the basis of area alone, the Isle of Man, and islands to the north of it, hold fewer species than expected. Correction for latitude reduces the difference between observed and expected numbers in all cases except Anglesey. In many cases the two values are very similar. Only in Shetland, and to a lesser extent in Orkney, do expected values remain considerably higher than those recorded. The two northern mainland areas are also poor relative to expectation, though not to the same degree. If the latitudinal trend is curvilinear (see above), these deviations might relate to latitude rather than to island status. Taken overall, there is no strong evidence that islands off the British coast are depauperate. Flatholm (figure 3) is a possible exception; it is much the smallest island included, and may indicate a "small island effect" (Lomolino, 2000) (see discussion).

SMALL AREAS

Observations on other organisms suggest that the species/area curve gets steeper at very small scales (Rosenzweig, 1995). Table 5 shows a variety of spot estimates (based on two points only) of **a** and **z** from detailed studies involving very small areas. The range of slopes is similar to that seen in the larger-scale studies, and values of **a**, though variable, are not in the realm of the absurd. The site totals of species numbers are shown in figure 3; it can be seen that although there is a wide scatter, the values are not grossly out of line with those expected from a downward projection of the Suffolk regression. Some would fit an even shallower slope projected down from larger areas.

DISCUSSION

Despite the failure to follow the procedure for curve construction given by Rosenzweig (1995), the species/area relationships shown here are reasonably linear, and have slopes in accord with expectation. The use of maximum richness rather than means where data from more than one area of the same size is available appears to counteract the effects of variable sampling intensity, and it reduces the effects of small-scale ecological differentiation on the results (Nekola and Smith, 1999). On this basis, the Suffolk curve is a reasonable predictor of species richness in areas from 4 km^2 up to whole counties, at least in England.

The slopes are at the low end of the range, 0.1 to 0.2, given by Rosenzweig (1995) for studies within biogeographical provinces. Some of these span considerable latitudinal ranges. In Wisconsin, Nekola and Smith (1999) found a slope of only 0.062 for land molluscs, even less steep than that for the Isle of Wight based curve reported here; the Wisconsin curve was rooted in exceptionally rich sites. If spot estimates are made comparing maximum richness sites and areas in Britain with the regional total, the Suffolk slope may be too steep. Nevertheless, the Suffolk slope (0.107) is very similar to one for British breeding birds rooted in a small wood in Berkshire (0.110, Gaston and Blackburn, 2000). For land molluscs, Britain is a very uniform region; species/area relationships are entirely as expected. Individual, rich sites of less than 1 km^2 may contain more than a third of the national fauna (Cameron, 1998). The same situation applies in Wisconsin (Nekola and Smith, 1999), which has a similar history of post-glacial recolonisation. In lower latitudes, species/area relationships may be radically different (Cameron 1995; Cameron, Mylonas and Vardinoyannis 2000; Cameron, in prep).

Even within such a uniform area, latitudinal effects are apparent. As for other organisms, interpretations of latitudinal gradients are many, various and contentious (Gaston 1996; Gaston and Blackburn 2000; Tilman and Pacala 1993). Latitudinal gradients for land molluscs across Europe are considerably steeper than within Britain, at least at large scales, suggesting a different balance of causes (Cameron, in prep.).

None of the results discussed above are unexpected. Quantification, however, makes comparisons with other faunas easier, and emphasises the importance of taking area into account when making comparisons. In the case of offshore islands, however, the results do not conform to the expectations from theory, and run counter to observations on offshore island flora and fauna generally (Rosenzweig, 1995). Most British islands, including some a considerable distance from the mainland, have faunas just as rich as those in the same areas of mainland at the same latitude. On limited evidence, this British pattern appears to be repeated for land molluscs on islands in the Great Lakes relative to mainland Wisconsin (Nekola, pers. comm.). There is scope for more intensive island studies around Britain. The figures for Orkney and Shetland may relate to latitude. They are archipelagos; although not all islands within each have been fully investigated, there is no evidence that they are under-recorded relative to nearby mainland. The apparent exception of Flatholm may indicate the "small island effect" of Lomolino (2000); below a size threshold, faunas show little relation to area, and are influenced by idiosyncratic features of each island. In the context of land molluscs, this threshold seems likely to be 1 km^2 or less. Lundy (*c.* 4 km^2) has a fauna at least as rich as that expected from the same area of mainland.

Compared with Mediterranean areas, these island data present an apparent paradox. Greece, smaller than Great Britain, may have six times as many species (Bank *et al*. 1998; Mylonas pers. com.), but the Isle of Man (550 km^2, 60 species) is richer than Naxos (428 km^2, 42 species, Mylonas, 1982) or Chios (825 km^2, 50 species, Bar and Butot 1986). At smaller scales, the disparity is greater: Alderney (8 km^2, 44 species) and Lundy (4 km^2, 47 species) are massively richer than Koufounisi (4 km^2, 14 species) or Dia (12.5 km^2, 21 species), both close to Crete (Vardinoyannis 1994; Welter-Schultes and Williams 1999). While such small Mediterranean islands may offer a narrower range of habitats than those of similar size around Britain, species/area relationships in Mediterranean islands, including those mentioned above, conform to general expectations, with slopes of *c.* 0.25, and with faunas impoverished relative to the mainland. Even there, there are anthropogenic effects which flatten the curves: some species are easily transported, and thrive in human maintained habitats (Mylonas, 1984). Such effects must be involved in the British pattern, probably to a greater extent.

The extension of a linear relationship to relatively tiny areas in the context of Britain is less unexpected (Cameron, 1998). While general regressions are of little use in predicting the species richness of individual tiny sites, which vary immensely amongst themselves (Nekola and Smith 1999; Sharland 2001), it is remarkable that individual quadrats may contain substantial proportions of a regional fauna. Nekola and Smith (1999) report a single 1m^2 quadrat containing 23 species, while Schmid (1966) reports many 1m^2 quadrats with more than 20 species, and one with 35 from a study of the Spitzberg (Tübingen, Germany), an area of 7 km^2 containing *c.* 70 species.

These quadrat data, representing some of the richest published faunas at this scale, come from temperate zones with regionally poor faunas. Apart from what they tell us about the spatial arrangement of land mollusc niches (Solem, 1984) they emphasise the need to consider studies over a very wide range of scales when attempting to make comparisons across regions and continents (Cameron, in prep.).

ACKNOWLEDGEMENTS

The data and analyses presented here have been accumulated over several years. I am grateful to Laurence Cook, Robert Cowie, Bill Ely, Ian Killeen, Moysis Mylonas, Jeff Nekola, Eva Sharland, Kostas Triantis and Katerina Vardinoyannis, who have stimulated me with comments, drawn my attention to relevant publications and provided me with data.

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CHELIDONURA AFRICANA PRUVOT-FOL, 1953 (MOLLUSCA, GASTROPODA): PROPOSED DESIGNATION OF A NEOTYPE

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Abstract Chelidonura africana *was described based on specimens belonging to two different species. References to this name in the literature are confusing and its identity is the subject of controversy. A neotype is designated to clarify the nomenclatural status of the specific name* C. africana. C. italica *Sordi, 1980 is considered a junior synonym of* C. africana.

Key words *Cephalaspidea, Aglajidae,* Chelidonura africana, *neotype.*

INTRODUCTION

The genus *Chelidonura* A. Adams 1850 (included in Aglajidae) has a narrow and elongated body, large parapodia, triangular cephalic shield and a posterior shield showing two large tapering lobes, the left usually longer than the right. There are sensory bristles on each side of the anterior end of the head. One of the most distinctive anatomical characters is the buccal mass, which is small in size (being one-fifth of the body lenght, excluding the tail) and also a relatively large, completely calcified internal shell.

According to Yonow (1994), 19 species had been assigned to the genus *Chelidonura.* Since then, some other species have been described (Ortea *et al.*, 1996). In the eastern Atlantic and western Mediterranean the following species have been described: *Chelidonura africana* Pruvot-Fol, 1953, from Morocco; *C. leopoldoi* Ortea, Moro & Espinosa, 1996 and *C. sabadiega* Ortea, Moro & Espinosa, 1996, both from Canary Islands; and *C. italica* Sordi, 1980 and *C. orchidaea* Perrone, 1990, from Italy. Another species recorded from the western Mediterranean is *C. fulvipunctata* Baba, 1938, collected in Malta (Perrone & Sammut, 1997), which has a world-wide distribution. It was previously recorded from the Mediterranean by Swennen (1961) as *C. mediterranea*, a synonym of *C. fulvipunctata.*

HISTORY OF THE PROBLEM

Pruvot-Fol (1953) described the species *Chelidonura africana* based on preserved specimens from Témara, on the Atlantic coast of Morocco, collected and figured by H. Gantès, and also based on preserved specimens from Dakar, Senegal. The original description was not very detailed, only mentioning the presence of sensitive bristles at the anterior end of the cephalic shield, and the shape of the shell. The three depicted specimens (Pl. 3, Figs. 37, 38, 39) showed a black ground colour, scattered with white spots (mainly concentrated at both the anterior and posterior ends of the cephalic shield), and an orange line bordering the parapodial lobes and the caudal processes. Specimens also had iridescent blue spots. No internal anatomy was described.

Some years later, Marcus (1976) regarded *Chelidonura nyanyana* Edmunds, 1968 (a species described from Ghana only from external characters) as a junior synonym of Pruvot-Fol's species, and discussed it with *C. evelinae* Marcus, 1955, a Caribbean species.

In a review of several genera of Aglajidae, Rudman (1974, p. 209) considered both *Chelidonura africana* and *C. nyanyana* as incertae sedis, which means that these two

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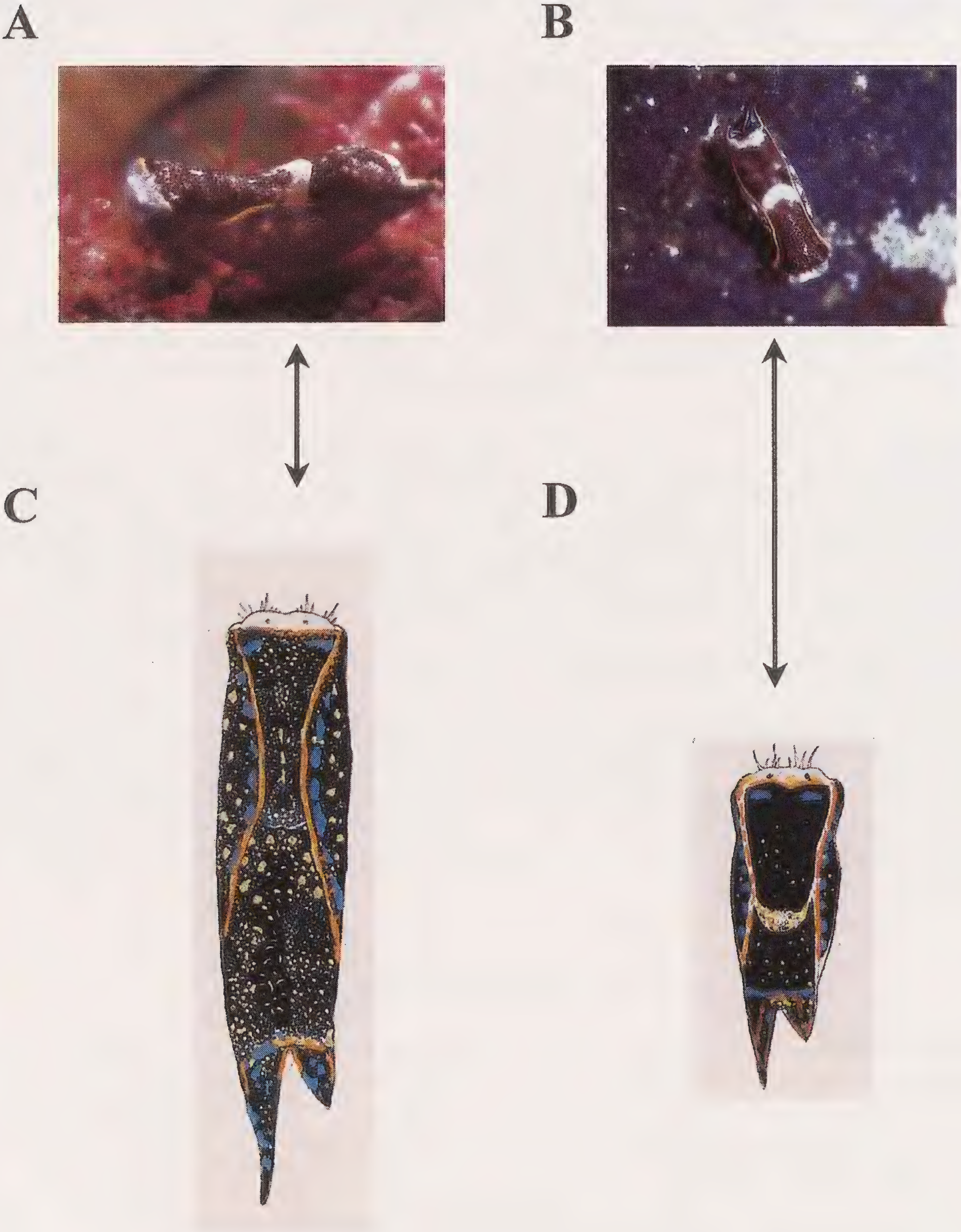

Figure 1 **A** Specimen from Tenerife, Canary Islands, designed as neotype (10 mm). **B** Specimen from Madeira Island, Madeira Archipelago (10 mm). **C** Specimen figured by Gantès in Pruvot-Fol, 1953, Pl. III, fig. 39. **D** Specimen figured by Gantès in Pruvot-Fol, 1953, Pl. III, fig. 38.

species could not be assigned to any known genus due to the absence of data.

When reviewing the systematics of the Aglajidae, Gosliner (1980: 342) noticed that the original description of *Chelidonura africana* seemed to represent two distinct species: among the three figures given by Pruvot-Fol, Figures 38 and 39 depicted "a juvenile and an adult which appear to be conspecific" (both figures are reproduced here as Figs. C and D, respectively), while figure 37 showed "an individual with very different coloration and morphology" lacking dorsally visible eyes and sensory bristles, and showing a cephalic shield emarginate at its posterior end and two reduced caudal appendages. After this review, Gosliner considered that the specimens depicted in Figures 38 and 39 should be included in the genus *Navanax* Pilsbry, 1895, whereas the specimen from Figure 37 should remain as undetermined. At the same time, Gosliner (1980) regarded *Chelidonura nyanyana* Edmunds as a synonym of *Navanax aenigmaticus* (Bergh, 1893) (a species originally described from the Pacific coast of Panama), thus part of *C. africana* became a junior synonym of *N. aenigmaticus.*

In the meanwhile, Sordi (1980) described the species *Chelidonura italica* from the Mediterranean Sea (type locality Livorno, Tyrrenian Sea), based on specimens that were very similar in colour to those of *Chelidonura africana* illustrated by Gantès in figures 38 and 39 (Pruvot-Fol, 1953).

On the east coast of the Iberian Peninsula, Templado *et al.* (1983) collected some specimens that they attributed to *Chelidonura italica,* pointing out that this species could be a synonym of *C. africana*. Later, García & García (1984) described six specimens from the Strait of Gibraltar as *Chelidonura africana,* providing a complete description of the external morphology and coloration. Both authors specified that their specimens agreed with the one depicted in Figure 39 by Gantés (Pruvot-Fol, 1953), and concluded that *C. italica* could be a junior synonym of *C. africana,* althought the latter should be considered an uncertain species, according to Gosliner (1980). García & García (1984: 81) also increased the confusion about Pruvot-Fol' s paper, suggesting that the three figures given by Gantés might represent three different species of Aglajidae.

Because of its confusing original description, Ballesteros *et al.* (1986), and later Cervera *et al.* (1988: 52), stated that *Chelidonura africana* should be considered a nomen dubium, and introduced the new name *C. italica* for the species living in the Iberian Peninsula. Subsequent authors (Martínez *et al.,* 1993; Perrone & Sammut, 1997) adopted this change.

Yonow (1990) identified some specimens from the Red Sea as *Chelidonura africana.* In a later review, she described these specimens as a new species, *C. livida* (Yonow, 1994, pp. 141–144, Fig. 1). This species has a larger body than *C. africana* (about 50 mm long), with a very dark ground colour and electric blue spots and rings along the edges of the parapodial lobes and shields, as well as white flecks on the lighter specimens. Yonow (1994: 146) stated that the type material of *C. africana* was untraceable and that this species probably was "a senior synonym of *C. italica*".

Ortea *et al.* (1996) used again the name *C. africana* for specimens collected in the Canary Islands, describing the new species *C. leopoldoi* Ortea, Moro and Espinosa (that they differentiated from *C. italica* and *C. africana* because of the absence of blue spots).

MATERIAL

Chelidonura africana The type material is untraceable, it was collected from Temara, Morocco. Neotype (here designated): Playa del Hombre, Taliarte, Tenerife, Canary Islands (May, 1998), one specimen 10 mm length collected intertidally, coll. L. Moro (MNCN 15.05/44365).

Other material examined

- Playa del Hombre, Taliarte, Tenerife, Canary Islands (August, 1997), three specimens 9 mm length collected intertidally, coll. L. Moro (MNCN 15.05/44366).
- Northern coast of Porto Santo Island, Madeira Archipelago (July, 1999), one specimen 6 mm length collected intertidally, coll. L. Moro (MNCN 15.05/44368).
- Porto do Abrigo of Porto Santo Island, Madeira Archipelago (September, 2000), one specimen 3 mm length collected intertidally (Museo Municipal do Funchal (Madeira Island), MMF31629).
- Baia do Ponta Delgada, São Miguel, Azores Archipelago (September, 1998), five specimens 1–2 mm length collected at 1 m depth, coll. L. Moro (MNCN 15.05/44367).

Discussion

There is great deal of confusion in modern literature about the identity of the species *Chelidonura africana*. When comparing the data and figures provided by Pruvot-Fol (1953, figs. 38, 39) with data of the external morphology given by Sordi (1980: 290) and with data and photographs of specimens from the Strait of Gibraltar (García & García, 1984), the eastern coast of Spain (Ballesteros *et al.* 1986; Martínez *et al.*, 1993), Malta (Perrone & Sammunt, 1997), Madeira (Malaquias *et al.*, 2001, specimen figured at the present paper in Fig. B; in press), and the Canary Islands (Ortea *et al.*, 1996), we do not find any consistent difference. The ground colour is very dark in all these specimens, scattered with white spots; there is a yellow line on the border of the parapodia and on the caudal lobes, and blue spots along the upper external border of the parapodia, as well as some on the caudal lobes and head. To illustrate the variability, Perrone & Sammut (1997, Figs. 1c and 1d) published two photographs of *C. italica* from Malta, which they called "the yellow-brown phase" and "the whitish-brown phase", respectively.

Following the Principle of Priority, Pruvot-Fol' s name *Chelidonura africana* should have preference over *C. italica* Sordi, and the latter should be regarded as a junior subjective synonym. Because of its absence from Valdés & Héros's (1998) catalogue, we can conclude that the type material of *C. africana* is lost, and it is no longer at the Muséum National d'Histoire Naturelle (Paris). In order to stabilize the nomenclature and to avoid more confusion, we propose the designation of a neotype for *Chelidonura africana,* under Article 75.3 of the Code of Zoological Nomenclature. The neotype was deposited in the Museo Nacional de Ciencias Naturales of Madrid (MNCN) and is figured in Fig. A.

Acknowledgements

We are indebted to Dr. P. Tubbs (International Commission on Zoological Nomenclature), Dr. M. Oliverio (Universitá de La Sapienza, Rome) and Dr. A. Valdés (Natural History Museum of Los Angeles) for their helpful comments and suggestions; and to Mr. L. Moro for sending us the specimen designated as neotype, as well as most of the material. This paper has been supported by the project "Fauna Iberica V" (DGESIC PB98-0532), and also was made possible by the programs "Acción Intergrada Hispano-Portuguesa HP 1999-0093" (Subdirección General de Formación y Promoción del Conocimiento del Ministerio de Educación y Cultura), Acções integradas Luso-Espanholas E91/00 (Conselho de Reitores das Universidades Portuguesas) and "NATO Grant CRG.970607" (Scientific Affairs Division of NATO).

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FIRST ANATOMIC DATA AND TAXONOMICAL CLARIFICATION OF *SUBOESTOPHORA KUIPERI* (GASULL, 1966) (MOLLUSCA, GASTROPODA: HYGROMIIDAE)

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Abstract Live specimens of Oestophora (Suboestophora) kuiperi *Gasull, 1966 (currently* Suboestophora kuiperi) *were first found in the type-locality (Cullera, province of Valencia, Spain). The shell and genitalia of this species are studied and compared with those of* Subostophora boscae *(Hidalgo, 1869), congeneric species with which the same geographic area is shared. It can be concluded that* S. kuiperi *is a junior synonym of* S. boscae.

Key words Hygromiidae, Suboestophora kuiperi, Suboestophora boscae, *synonymy, Spain.*

INTRODUCTION

Gasull (1966) described a new species, *Oestophora (Suboestophora) kuiperi,* collected at " ...macizo de Cullera. Castillo. Peñascos sobre la cantera al S..." (...massif of Cullera. Castle. Boulders on the quarry in the South...). Furthermore, Prieto (1986) elevates the subgenus *Suboestophora* to generic status, establishing the new *Suboestophora kuiperi* (Gasull, 1966) combination.

Gasull (1966) justified the new species solely on the basis of the characteristics of the shell not having found any live samples. According to this author, *S. kuiperi* resembles *S. boscae* (Hidalgo, 1869), differentiated by its smaller size, by having one whorl less, by its tight, regular, stronger constulation, and by the shape of the aperture (angularity and callosity of the peristoma).

S. kuiperi is an extremely scarce rare species, and after an increased number of unsuccessful samplings in the type-locality in recent years, the authors have collected a live adult specimen, that allows description of the genitalia of this species for the first time ever (Martínez-Ortí, 1999). The type-series of *S. kuiperi* has been revised designating its lectotype, and thus the validity of this species is discussed from the studies of both the shell and its anatomical characteristics.

DESIGNATION OF LECTOTYPES OF *S. KUIPERI* AND *S. BOSCAE*

SELECTION OF THE LECTOTYPE OF *S. KUIPERI*

The sample with the original material used by Gasull was deposited in the Museu de Zoologia of Barcelona (MZB) with the number 84–1894 and presents a label with the following inscription: "*Oestophora kuiperi* Gas. Cullera. Castillo. (7). 16.11.66- Gasull leg. Valencia". The number 7 seems to indicate the number of specimens present in the sample at the time of its deposit. At the time of our review, the container was comprised of only 6 specimens, which must be considered as syntypes. Only two of them appear complete and in good condition. A comparison has been made between the shells and those that appear in the original photographs of Gasull (1966, p. 159) in order to identify them and select the lectotype. Only one of the two shells figured by the author has been found in the sample, selecting it as a lectotype (Figs 1a–c and 3a–c), with the number 84-1894-A. The five paralectotypes have been separated with the number 84-

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1894-B.

The dimensions of the lectotype are 9.05 mm in diameter and 4.45 mm in height, 6 whorls and an umbilicus of 1.30 mm width. The dimensions of the complete paralectotype are 8.20 mm in diameter and 4.10 mm in height, with 5 ¾ whorls and an umbilicus of 1.20 mm width.

This data differs slightly from that offered by Gasull (1966, 1975), reproduced in table 1. It must be considered that the missing specimen of the sample could not be thus measured.

OBSERVATIONS ABOUT THE TYPE OF *SUBOESTOPHORA BOSCAE*

The specimen figured by Hidalgo (1869: Plate 2, Fig. 1) is conserved in the Museé National d'Histoire Naturelle of Paris and has been designated by Fischer-Piette (1950) as the type of the species. In accordance with article 73, recommendation 73F of the ICZN, this sample must be considered as the Lectotype of the species. According to Miguel Villena, of the Museo Nacional de Ciencias Naturales of Madrid (MNCNM), who revised this sample, the locality that figures in the label is "Puebla de Rugat (now Pobla del Duc), Valencia", it must be considered as a restricted type locality. The measurements obtained by Miguel Villena are: 9 mm maximum diameter, 8.7 minimum diameter and 3.7 mm in height.

STUDIED MATERIAL

S. KUIPERI

Two live specimens, one adult and another juvenile, as well as an empty shell, were collected by the authors in the type locality of "Castillo de Cullera" (UTM 30TYJ3749) on 1/10/94, after a strong storm and under blocks of calcareous rocks of great dimensions (Martínez-Ortí, 1999). This material is deposited in the Museu Valencià d'Història Natural of Valencia (MVHN, Martínez-Ortí coll., sample nº 180V).

S. BOSCAE

For the study of *S. boscae* abundant material collected by the authors has been used. Also, consultations were made to material belonging to this species deposited at the MVHN (Siro de Fez coll.), at the MNCNM (Hidalgo and Ortiz de Zárate colls.) and at the MZB (Bofill, Chía, Gasull and Martorell colls.). The results are detailed in Martínez-Ortí (1999).

COMPARATIVE STUDY OF *S. BOSCAE* AND *S. KUIPERI*

SHELL

The differences between the shells of *S. kuiperi* and *S. boscae,* used by Gasull (1966) to base the description of the first of these species, lack content when the shell variability of *S. boscae* is studied. The first criteria used is size. Gasull (1966) indicated that *S. kuiperi* has a much smaller size than *S. boscae.* However, the shell size of *S. boscae* varies amongst broad parameters (Table 1) and specifically the lectotype of *S. boscae* is slightly smaller than the lectotype of *S. kuiperi.* Both samples find themselves near the minimum size in the variation rank for *S. boscae.*

The second criteria used by Gasull to differentiate the species is the existence of one whorl less (6) in *S. kuiperi* compared to *S. boscae* (6½–7). However, live samples of *S. boscae* examined by the authors show that the number of whorls could vary between

TABLE 1

Shell and genitalia measurements for populations of *Suboestophora kuiperi* (Gasull, 1966) and *S. boscae* (Hidalgo, 1869) (Abbreviations: **aDs** accessory Dart-sac **BC** Bursa Copulatrix **BCc** duct of Bursa Copulatrix **D** Dart **Ds** Dart-sac **Ep** Epiphallus **Fl** Flagellum **fov** free oviduct **gm** glandulae mucosae **H** height **Loc** locality **NSp** number of specimens **Ø** diameter **P** penis **Prm** Penial retractor muscle **NS** number of sample **U** umbilicus **V** vagina **W** whorls (in mm)).

	Suboestophora kuiperi			*Suboestophora boscae*					
Loc	**Gasull (1966)**	**Cullera**		**Benichembla**	**Beniarbeig**	**Orba**	**Quesa**	**Pego**	**Pobla del Duc**
NS	**84-1984 (MZB)**	**180V**	**Lectotype**	**1A**	**60A**	**66A**	**123V**	**130A**	**Holotype**
				SHELL					
NSp	?	2		7	10	12	10	12	
Ø	8.7-9.2	8.6-8.8	9.05	11.4-12.1	10.90	12.5-12.8	9.1-10.8	11.4-12.4	9
H	4.2-4.5	4.4-4.5	4.45	5.3-6.2	5.2	5.4-6.2	4.5-5.5	5.5-5.9	3.7
W	6	6	6	61/2-65/8	61/8	65/8-7	51/2-61/8	63/4-7	-
U	1.0	1.2	1.3	1.45-1.6	1.4	1.50-1.75	1.4-1.85	1.4-1.5	.
				GENITALIA					
NSp	-	1	-	1	1	1	3	1	-
Fl	-	1.00	-	1.60	1.45	1.20	1.75-1.80	1.35	-
Ep	-	1.95	-	2.10	2.50	1.50	2.40-2.85	2.45	-
P	-	4.25	-	6.80	5.00	4.25	4.75-5.10	5.00	-
Prm	-	3.05	-	3.60	2.30	-	-	3.55	-
BC	-	0.4x1.4	-	0.65x1.75	0.5x1.8	0.85x1.05	0.5-0.65x1.0-1.7	0.5x2.50	-
BCc	-	4.05	-	4.0	3.55	2.15	3.50	6.15	-
D	-	0.70	-	-	-	-	-	0.65	-
Ds	-	0.85	-	1.20	1.00	1.00	0.95-1.25	1.45	-
aDs	-	1.35	-	2.75	2.25	2.25	1.85-1.90	2.95	-
fov	-	4.00	-	3.80	4.25	4.20	3.50	5.45	-
V	-	1.40	-	4.25	2.80	1.15	2.25-2.30	1.95	-
gm	-	(4) 5.25	-	(4)10.85	(4) 6.00	(4) 6.15	(4) 7.15	(4) 12.60	-

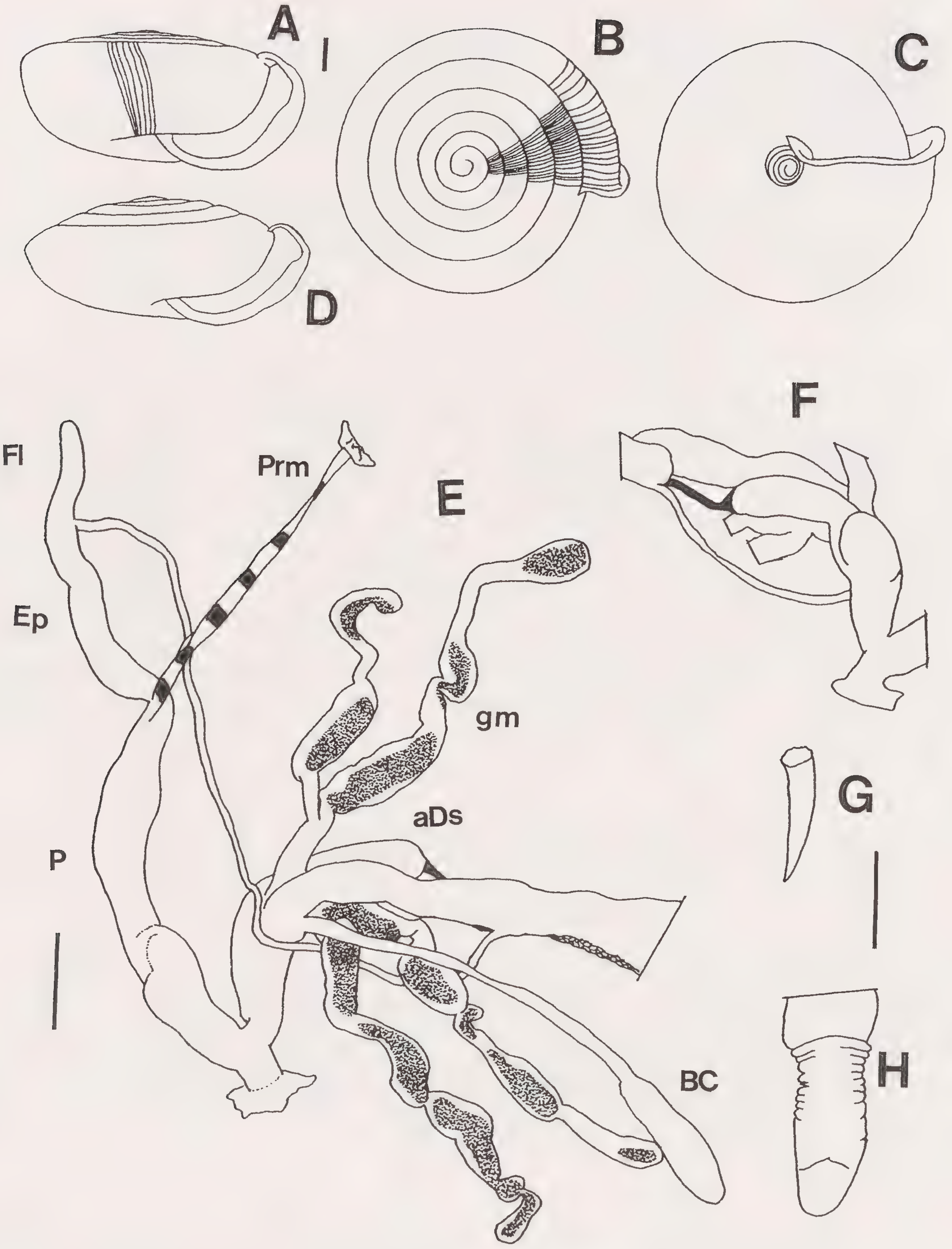

Fig. 1 *Oestophora (Suboestophora) kuiperi* Gasull, 1966 **A**–**C** Drawing of the lectotype ("Castillo de Cullera", Nº84-1894-A, MZB) **D** Shell (Cullera Nº180V, Martínez-Ortí coll., MVNH) **E** Genitalia (Nº180V); **F** Detail of the dart-sac complex **G** Dart **H** Penis. Scale bar = 1 mm.

5½ (Quesa) and 7 (Orba and Pego) (Table 1). Thirdly, Gasull (1966) indicates that *S. kuiperi* presents a stronger axial ribbing, much tighter and more regular than that of *S. boscae*. As can be observed in the samples represented in Fig. 3, the axial ribbing of *S. boscae* is very variable and samples like the ones from Orba (Fig. 3j–l), that find themselves in the upper limit of the species' size range, present an axial ribbing pattern similar to the lectotype of *S. kuiperi* from Cullera (Figs 3a–c).

The final characteristics used by Gasull (1966) to justify the validity of *S. kuiperi* refer to the morphology of the peristome. The observation of the lectotype of *S. kuiperi* indicates that it is an adult specimen that has not yet reached its growth limit, and therefore some of its features, like the angularity and callosity of the peristome's opening edge have not reached a definitive morphology. In fact, the live sample captured by the authors (Fig. 1d) presents these characteristics even more accentuatedly and within the variability of *S. boscae* (Figs 2a–c; Figs 3d–l).

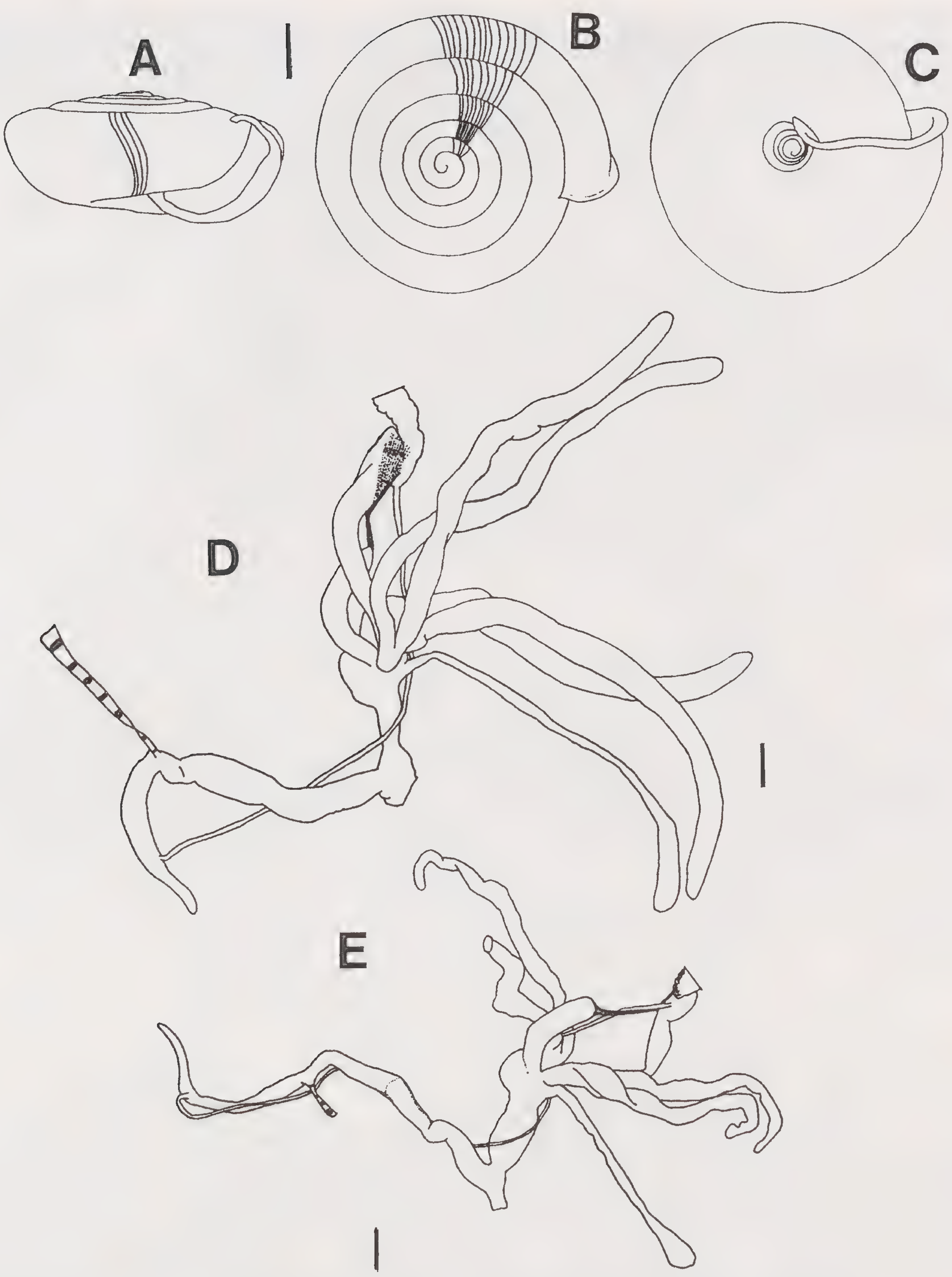

Fig. 2 *Suboestophora boscae* (Hidalgo, 1869). Martínez-Ortí coll. MVHN **A–C** Shell (Quesa, Nº123V) Scale bar = 2 mm **D** Genitalia (Pego, Nº130A) **E** Genitalia (Nº123). Scale bar = 1 mm.

GENITALIA

The genitalia of *S. kuiperi* (Figs 1e–g; Table 1) presents a similar morphology to that of *S. boscae* (Figs 2d–e) and measurements that fit in its range of variability. Given the small size of the adult sample examined, it is reasonable that the data of its genitalia appear in the inferior part of this range.

DISTRIBUTION

Fig. 4 indicates the known distribution of *S. boscae.* The map is based upon the samples collected by the authors and on the revisions of published samples by previous authors (see Puente, 1994 and Martínez-Ortí, 1999). As can be seen, the type locality of *S. kuiperi* is found included within the area of distribution of *S. boscae.*

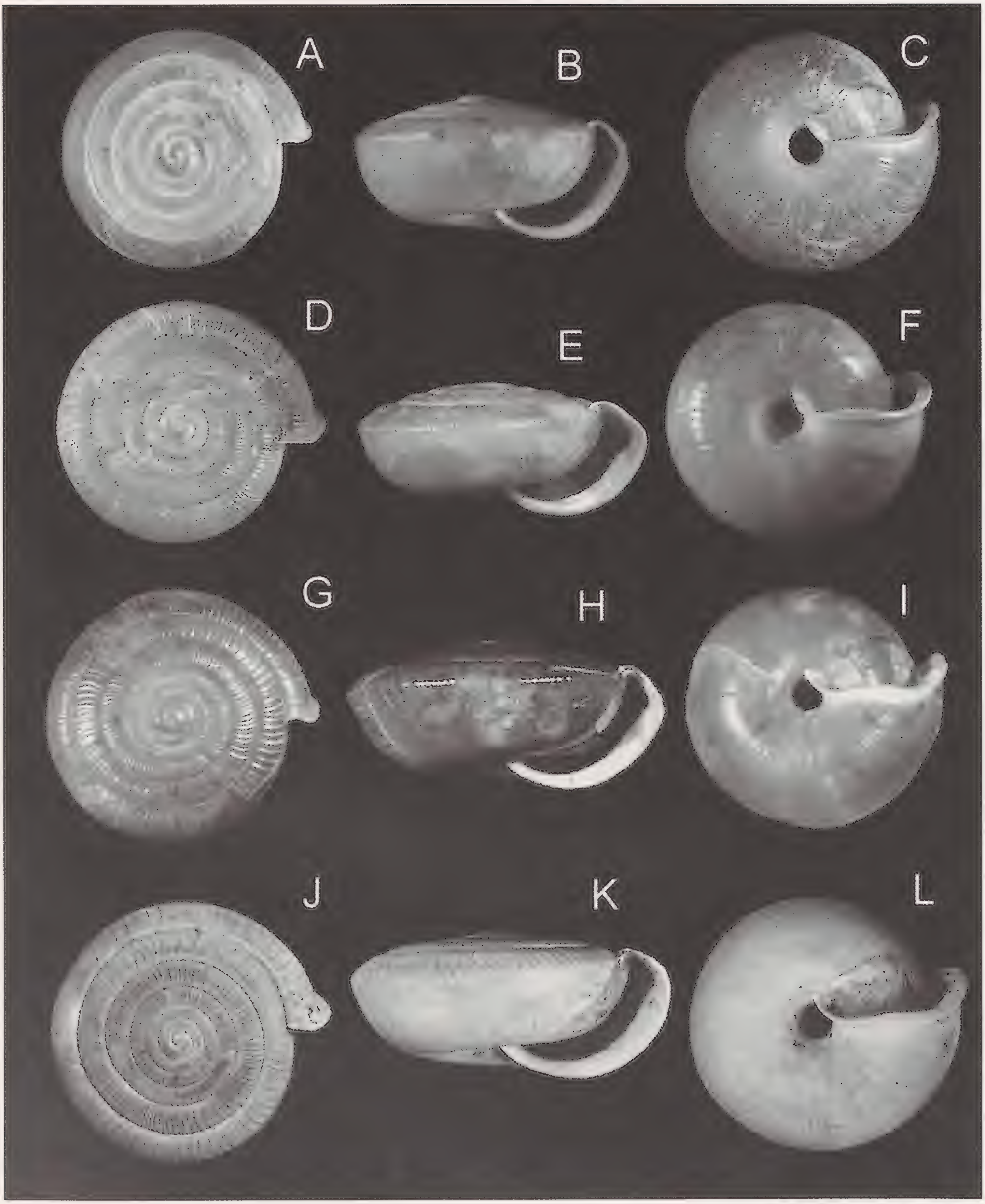

Fig. 3 **A–C** Lectotype of *Oestophora (Suboestophora) kuiperi* Gasull, 1966, 9.05 mm diameter **D–F** *S. boscae*. Martínez-Ortí coll: Quesa (Nº123V), 9.2 mm diameter **G–I** *S. boscae*. Martínez-Ortí coll: Pego (Nº130A), 11.8 mm diameter **J–L** *S. boscae*. Martínez-Ortí coll: Orba (Nº66A), 12.6 mm diameter.

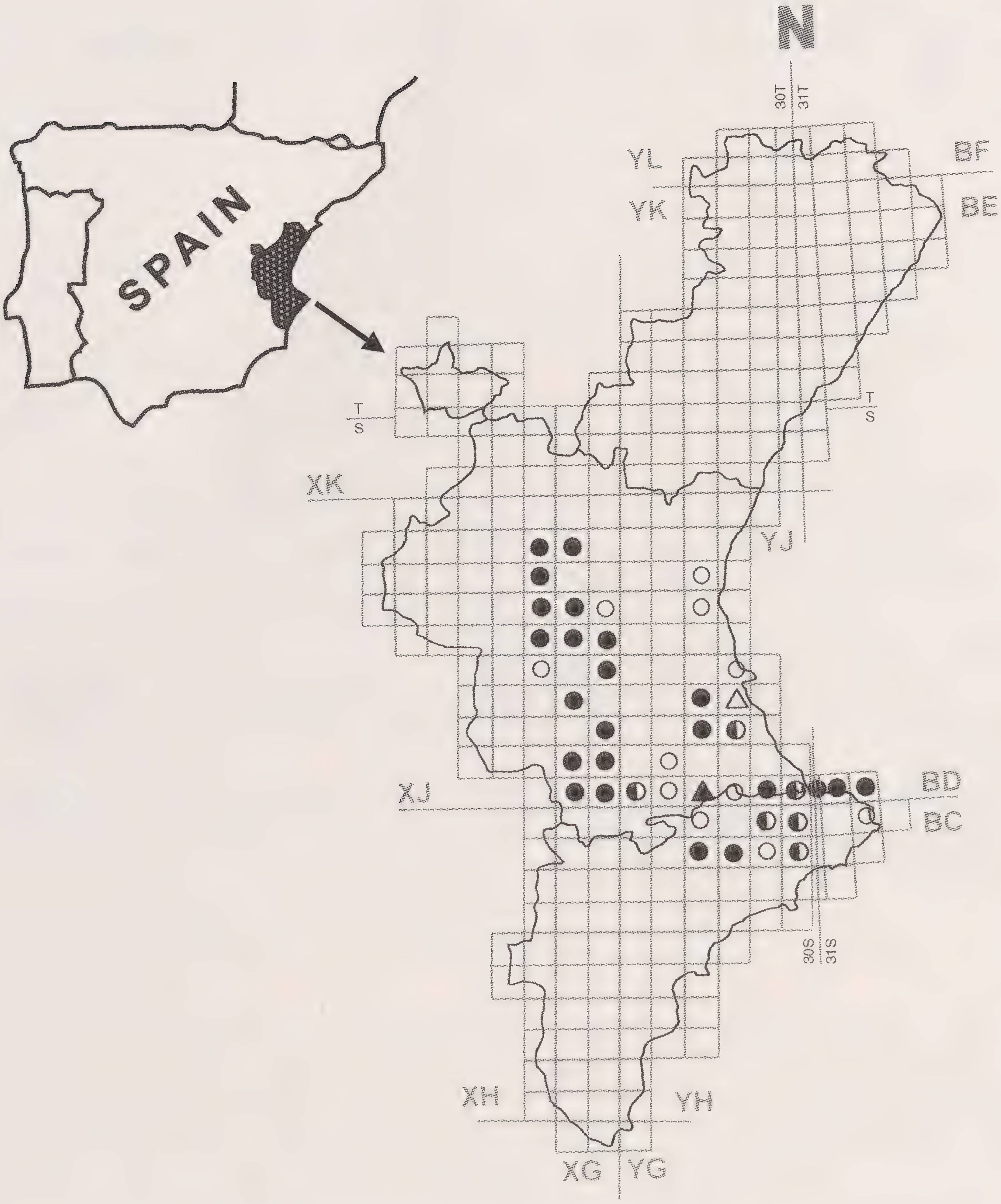

Fig. 4 Geographic distribution of *S. kuiperi* and *S. boscae* (white triangle: locus typicus of *S. kuiperi;* black triangle: locus typicus of *S. boscae;* white circle: quoted localities; black circle: new localities; half black and white circle: both).

CONCLUSIONS

Therefore, and according to our observations on the morphology of the shell and of the genitalia of *S. kuiperi* and its comparison with abundant material of *S. boscae,* we conclude that *S. kuiperi* (Gasull, 1966) should be considered as a junior synonym of *S. boscae* (Hidalgo, 1869), with which it shares the distribution area.

ACKNOWLEDGEMENTS

Thanks to Miguel Villena, curator of the Museo Nacional de Ciencias Naturales of Madrid for the information delivered on the sample type of *S. boscae,* and to Chus del Valle and Dr. Francesc Uribe of the Museu de Zoologia of Barcelona, for the loan of the samples. Also, to Ernesto Wlasiuk for the translation of this manuscript. This work has been partially financed by the Institut Valencià d'Estudis i Investigació through the CPE/086 project.

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SYLVANUS CHARLES THORP HANLEY (1819-1899) A NINETEENTH-CENTURY DILETTANTE OF THE SHELL WORLD

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BACKGROUND AND PRIVATE LIFE

Sylvanus Charles Thorp Hanley was born in Holywell Street, Oxford on the 7th January 1819, the son of William Hanley. He was admitted to Wadham College, Oxford in 1837, as a commoner, where he obtained his B.A. degree in 1841. In an obituary notice Edgar Smith (1900) tells us that Hanley subsequently became a student at law of the Inner Temple, but, after inheriting ample means from his father, he had no occasion to complete his studies. Smith also tells us that Hanley was twice married and had two sons. Unfortunately this obituary notice, the only one we have seen, leaves many other questions unanswered.

Enquiries made at Wadham College, Oxford, confirmed that he did gain a B.A., but the College authorities have no further information. The records of the Inner Temple reveal no evidence that Hanley had ever been connected with that institution, although some of the records were destroyed in a fire during the 1939-45 War. It is curious that nobody seems to have left any reminiscences concerning him. There are few surviving letters and no portrait is known to us, even though he seems to have had an early interest in photography.

The home addresses of the Hanley family, given as 7, Hanley Road, Hornsea Rise, Middlesex and 27, Hanley Road, Hornsea Rise, and Hornsea Road, in the parish of Islington, London, call for some explanation. The survey map for the Islington parish dated 1805 & 1806 shows a small group of 3 houses on the corner of Hanley Road and Hornsea Rise an extension of Hornsea Road. The plan for the parish of St Mary Islington dated 1853 shows the area labelled as the 'National Freehold Land Society's Estate'. On the same map a back lane has appeared behind the houses fronting onto Hanley Road labelled 'Sylvanus Place'. A short distance down Hornsea Road one of the original cottages shown on the earlier map is now a public house called the 'Hanley Arms'. Although the 1805/6 map indicated that the road was known as Hanley Road, the Rate Book of the period does not use that name, the area being known as the East Side. The Rate Book for Lamp, Highway & Chapel, Midsummer & Michaelmas, 1830, the first one in which the Hanley name appears in pencil under 'East Side', contains a 'Wm.Hanley, Esq', which proves he took over the property. The same book notes 'Wm.Hanley' as owning a house, Land Stables, Etc. at Newington Green. The Minute books of the Vestry of the Parish of St. Mary, Islington shows a William Lucas Hanley of Newington Green as attending the Vestry Meetings for 23rd June and 9th December 1831. In 1839 William Lucas Hanley was nominated as a trustee for the parish. Pigot's Commercial directory for London, 1832-4, lists Wm.Lucas Hanley as an Attorney at 1, Furnival's Inn. Robsons Commercial directory for 1843, lists Wm. Lucas Hanley, solicitor, 11, Angel Court, Throgmorton Street. The 1852 directory for Islington, published in 1852, shows William Hanley, Esq. as residing at 1, Park Terrace, Highbury. The 1855 directory also lists Mrs Hanley as residing at 28, Newington Green. In 1866 W. Hanley is listed as residing at 4,

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Victoria Road, Hornsea Rise.

The first reference to Sylvanus Hanley as a resident of 27, Hanley Road is for 1870. To complicate matters further it should be noted that the house numbers for Hanley Road were completely changed sometime between 1886 and 1888. The family did live in the area of Hanley Road from 1830 onwards but the name Hanley Road dates back at least to 1805. 'Sylvanus Place', however, dates from sometime just prior to 1853, after Sylvanus Hanley's family moved to this address.

Hanley died in Penzance on the 5th April 1899, aged 80, and was buried there on the 10th April the same year. His last Will and Testament, dated the 29th day of October, 1896 (fig. 5), leaves various properties, including The Hollies in Penzance and 'all my freehold houses and hereditaments situated in Hanley Road and Hornsey Road in the County of London' to his wife Eliza and two sons, Charles Ernest and Augustus Sylvanus. Smith (1900) says that only one of his sons survived him, the younger, so the elder son must have died some time between 1896 and 1900. A search through the Register of Births, Marriages and Deaths of England and Wales, however, has revealed no record of his death, and throws no light on where or when he died.

One reason for searching through the Register was to try to unravel the series of names used by Hanley's two 'reputed sons' in an attempt to resolve the probable authorship of *British marine conchology*, said to be by 'Charles Thorpe'. According to his will (a curiously worded document) he had two reputed sons. One of them, Charles Ernest Hanley, was 'formerly called and known and distinguished by the name of Charles Ernest Ward and for some time as Ernest Hanley and Ernest Thorp'. The other son, Augustus Sylvanus Hanley was 'formerly called and known and distinguished by the name of Augustus Sylvanus Ward and for some time as Augustus Hanley and Augustus Thorp'. This phraseology raises intriguing questions. Possibly Hanley married a widow, Eliza Ward, who had previously had two sons. This suggestion, however, does not take into account the given names of 'his' two sons, Charles and Sylvanus. A combination of names of this type, which would normally include parts of the father's name, would seem to indicate a father-son relationship, rather than a stepfather-son relationship. *British marine conchology*, published in 1844, contains a 'Systematic Index' with descriptions of new species, by Sylvanus Charles Thorp Hanley, a clear indication of Hanley's connection with the book. Except for the extra 'e' in Thorpe the two middle names of Hanley correspond to those of the author. In our opinion there is sufficient evidence here for including this title in the subjoined List of Hanley's Publications.

HANLEY'S PUBLICATIONS AND HIS LIBRARY

Hanley's first publication, entitled *The young conchologist's book of species*, was published in 1840 when he was just 21 years of age. In it he validly described *Haliotis sanguinea* and two other taxa. This was followed a year later by a sumptuously illustrated new edition of William Swainson's *Exotic conchology*. There followed a long series of publications in scientific journals, most of them describing new taxa. He is best remembered for the handsome four-volume *History of British Mollusca and their shells*, published between 1848 and 1853. Written in collaboration with the illustrious Edward Forbes (1814-54), it so fully occupied his time that it hindered publication of his long-awaited book about the shells of Linnaeus, *Ipsa Linnaei conchylia*. Seeing the early part of *The conchological miscellany* through the press also helped ensure that his study of the Linnaean shells, begun a dozen or more years earlier, did not appear in print until 1855. A year later there appeared his handsome edition of William Wood's *Index testaceologicus*. Between 1846 and 1863 he contributed three monographs to the *Thesaurus conchyliorum* when it was under the editorship of G. B. Sowerby (II). The *Photographic conchology*, an early experiment in the use of photography to illustrate a natural history book, appeared in 1863 (fig. 7). This was followed, in 1876, by the massive *Conchologia Indica*, illustrating the non-marine molluscan shells of the Indian peninsula, his co-author this time being William Theobald (1829-1908). His least-known publication, *Caliphs and sultans*, is a rare book having nothing to do with molluscs. An English edition of some of the lesser-known Tales from the Arabian Nights, it was published in 1868. His last publication, a short article on shipworms, appeared in 1885. By Victorian standards this was not an impressive lifetime's output but it certainly shows that Hanley was very industrious as a young man.

His own library of books about molluscs and their shells was comprehensive and included many rare titles. Books he once owned often have characteristic pencilled annotations by him scattered throughout. Occasionally he would cut out figures of shells from the plates accompanying a book and paste them close to their relevant descriptions, a practice likely to infuriate any subsequent owner of such a book. One of us (SPD) has seen - and has owned - several books formerly in Hanley's library with the name 'Bridger, Penzance' on tickets pasted inside the covers. These labels indicate that the library was acquired initially by a Penzance bookseller of that name soon after Hanley's death. Much later it seems that the library, or a large part of it anyway, was acquired by a bookseller operating out of the Farringdon Road in London who sold it to the eminent malacologist E. R. Sykes (1867-1954). Messrs Wheldon & Wesley, the natural history booksellers, bought the Sykes library after the 1939-45 War and in 1948 they issued a catalogue listing many of Hanley's books. An account of this transaction, with a verbatim copy of fifty of the choicer entries in the catalogue is given by Dance (1986).

HANLEY'S SHELL COLLECTION

Hanley built up a very large collection of shells, mainly tropical marine species, but it included a large number of North American fresh-water species many of which were described by American naturalists such as Isaac Lea (1792-1886) with whom he corresponded. Ultimately the collection contained a great deal of scientifically valuable material, including hundreds of types and figured specimens, many of them described as new to science by himself and contemporary naturalists.

The shell collection, consisting of thousands of specimens and housed in some thirteen cabinets, was left to his wife after his death. She, however, passed the collection into the care of a nephew. About this time the British Museum (Natural History) purchased many types from it. A dealer by the name of H. Harvey then acquired the collection from Hanley's nephew. In 1908 E. A. Smith examined it whilst it was still in the dealer's hands and again acquired a quantity of material for the British Museum. It was also during this time that some specimens are supposed to have found their way across the Atlantic and into some American museums. Fortunately, however, very little was dispersed in this manner. A further series of specimens was removed by the British Museum in 1921.

After this period, nothing more was heard about the collection or its whereabouts until August 1932 when it was presented to Huddersfield Museum by Mr. J. C. North of Dryclough House, Crosland Moor, Huddersfield. A small brass plate was then attached to each cabinet, bearing the legend 'The Sylvanus Charles Thorp Hanley and H. Harvey Collection', suggesting that the dealer included his name with the collection when it was sold. We have been unable to ascertain whether North bought the collection directly from a dealer but we do know that it was bought through an auction house at some point and that it had been stored for a time in the depository of T. R. Roberts Ltd. By profession North was an engineer who helped construct Aden harbour so it is likely that the collection was stored whilst North was working there. He died in 1952, his wife committing suicide shortly afterwards.

The collection was transferred to Leeds in 1957, into the care of Mr. John Armitage, the then Keeper of Zoology. It was stated at the time by people at the Huddersfield Museum that the collection was of little use as none of the shells had any data. Armitage contacted Mr I. C. J. Galbraith, of the British Museum (Natural History) in 1958 and asked for his advice about the collection. Shortly afterwards one of us (SPD), then on the staff of that museum, was sent to Leeds to examine the collection and make a report about it and its condition. He was also instructed to separate, for removal to the British Museum, all the type and figured material he could identify. As the existence of Hanley's catalogue of the collection was unknown then and relevant literature was unavailable in Leeds he was unable to identify a significant amount of type and figured material. The 203 separate lots he isolated were transferred subsequently to the British Museum (Natural History). It was then generally assumed that the Hanley collection contained little more of scientific importance and this resulted in the loss of much valuable information and the probable destruction of some type and figured material.

In 1976 one of us (AN) and Mr F. R. Woodward started working through the large Unionid collection amassed by Hanley and it soon became clear that this part of the collection still contained numerous types and figured shells (figs 2 & 4). At this stage the location of Hanley's original catalogue was unknown and its absence proved to be a major handicap. More frustrating, however, was the shortage of available literature in Leeds. For most of the first two years all publications by Hanley and his associates had to be borrowed or photocopied. Then there was the problem of analysing the coded information accompanying the shells. Hanley had marked many of his specimens or their labels in ink, the markings being in the form of letters or numbers, or both. The letter 'F' was soon recognised as meaning figured, but only a few specimens had indications of where they had been figured. Deciphering the letter 'P' was more difficult, but Hanley had produced his *Photographic conchology* in 1863, a book largely devoted to Unionids, and this proved to be the source of 'P'. A copy of this rare publication was located in the National Museum of Wales at Cardiff and, fortunately, the Leeds City Museum was allowed to borrow it. As a result it has been possible to recognise some of the specimens illustrated therein. This still leaves a small number of specimens, marked 'P', for which no illustration, published or otherwise, has been found. Also the numbers on some separate valves, particularly of the Unionids, have not been deciphered.

Several years after we began this project one of the natural historians attending a meeting in York produced two manuscript volumes and asked if they were of any use or interest, as they appeared to contain information about a large shell collection. The volumes were the missing catalogue of Hanley's shells (fig. 1)! This fortuitous discovery helped to resolve many questions. To date almost three hundred possible types or figured specimens have been recognised in the Hanley Collection, currently housed in the Leeds City Museum, and there may be others unrecognised still. It will be several years yet before we can be sure that the scientific value of this collection has been assessed fully but it is reassuring to know that the time spent studying it has not been wasted.

ASSESSMENT OF HANLEY AS A SYSTEMATIST

A man of private means, Hanley could pursue the study of molluscs and their shells leisurely, could afford to buy publications on the subject, could travel when necessary, and could enjoy the luxury of doing very little or nothing if he so wished. He did all of these things. His collection is worldwide in its scope but he does not seem to have travelled widely himself to collect shells. Hanley, it would seem, was a dilettante who may not have strayed far from home, although an undated letter to J. H. Ponsonby (1848-1916), now in the archives of the Conchological Society of Great Britain and Ireland (at Leeds), shows that he dredged as far afield as Algiers (see fig. 3). We know next to nothing about his private life but we may be sure that he did not overtax himself. Latterly he seems to have been dogged by ill health. For some reason he took a special interest in bivalves. Most of his new taxa are bivalves and one of his books is entitled *An illustrated and descriptive catalogue of recent bivalve shells.* So he may be considered a specialist. His descriptions of bivalves are adequate compared with the work of his contemporaries and the same may be said of the illustrations accompanying some of them. Many of the new bivalve taxa he proposed still stand which suggests, but does not prove, that he was a good systematist. He worked in a traditional manner, offering no new insights into their relationships, content merely to have his name associated with an ever-lengthening series of so-called new species. In this respect he was no better and no worse than many other students of molluscan systematics during the middle years of the nineteenth century. That he was respected by his contemporaries is indicated by the large number of species - we list most of them - that bear his name.

Undoubtedly his best work was a major study of the British molluscan fauna, undertaken with Edward Forbes (1815-1854) This work culminated in the publication of their monumental *History of British Mollusca and their shells.* It is tempting to say that the high quality of this four-volume treatise must be due to Forbes, by far the better scientist of the two, but this would be unfair on Hanley. There is evidence throughout the work that Hanley contributed more than his fair share. Much of the text shows an acquaintance with the relevant literature that may have been expected of one whose library was so extensive. Crucially Hanley may have been closer to the collectors whose collections provided so much of the locality information in the book. Also he had time on his side, Forbes being a busy man working in various fields besides malacology. We know Forbes collected in British waters and elsewhere but less is known about Hanley's collecting activities. A close examination of their book shows that Hanley collected at many points around the English coast, especially in the south and around the Channel Islands.* It is worth repeating that he sometimes used a dredge, an implement we customarily associate with the collecting activities of Forbes. Hanley may have contributed more, possibly much more, to this splendid book than did Forbes, but that is mere speculation.

Another commendable, if lesser, piece of work was his edition of William Wood's well-known *Index testaceologicus.* Popular because of its almost 500 hand-coloured illustrations and its portability, the *Index* had been out of print for many years and Hanley was the man chosen to edit a revised, enlarged version in a larger format. The result was visually appealing and, judging from the comparatively large number of copies that were in circulation until the middle of the twentieth century, must have sold well. Such a book could only have been edited by someone with an encyclopaedic knowledge of molluscan shells and their classification. Hanley had that kind of knowledge. Apart from incorrectly denying authorship of some taxa in the book to Wood, who validly proposed scientific names for some species illustrated in an 1828 *Supplement* to it (Dance, 1972), his work on the *Index Testaceologicus* was sound.

Unfortunately he did not confine his activities to the study of shells and the writing of books about them. He meddled with shell collections made by others, thereby diminishing their scientific value. Also he had a cavalier attitude to the passage of time, one

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*It was while he was collecting around the island of Jersey that he found *Rissoa* (now *Alvania*) *lactea* (Michaud), a species rare in British waters. J.T. Marshall who seems to have known him personally, says that the species was first discovered there by the late Sylvanus Hanley, who used to related an amusing episode in connection with it. 'Just as he pounced on his first specimen he was startled by gunfire and could not realise for the moment whether it was to celebrate his discovery or to punish his excessive jubilation, but on looking up he was horrified to find that all the guns of the fort were (as he supposed) pointing at him; so they were, but it was only a coincidence that he happened to be in the line of blank fire, consequently he escaped with his life, and with his *Rissoa*' (Marshall, 1916).

of the privileges of a dilettante. In the early 1840s, when still a young man, he undertook to study and reorganise the collection of shells made by Linnaeus. The collection had been housed for many years in the rooms of The Linnean Society of London and its condition had deteriorated badly. He finished his researches in 1850 but, because he spent so much time on his work with Forbes and other studies, it was not until 1855 that he published a book about his findings, the *Ipsa Linnaei conchylia.* A year later it was discovered that the shells had been seriously disarranged during the previous five years and Hanley offered to put them in order. Apparently he had not attempted to put them in order when working on them and he now proceeded to mount representatives of the Linnaean species on wooden tablets, not necessarily utilising the same specimens mentioned in his *Ipsa.* Some 23 years and an admonishment from the Linnean Society later, he had still not finished the work. He never did finish it and, as a later study shows, it were better had he not started it (Dance, 1967).

The Linnaean collection was not the only one he misused. Through his association with the *Conchologia Indica,* published in 1876, he came to be involved with the extensive shell collection amassed by William Benson (1803-70). This collection was not only rich in species from the Indian peninsula but Benson attached great importance to precise localities, accompanying his specimens with labels giving detailed locality information. Somehow Hanley acquired Benson's collection and manuscripts, replaced the original labels with ones of his own which merely read 'India', and as if that were not enough he lost Benson's precious manuscripts! Hanley also upset his co-author, William Theobald, who was stationed in India and so was in a poor position to influence the content and progress of the book. Theobald did not wish to be associated with the errors resulting from Hanley's ignorance of Indian geography and more or less divorced himself from the book (Naggs, 1997).

It seems that Hanley was much more careful in the treatment of his own collection. As we have seen, he used different ciphers to indicate certain kinds of information; and though his labels lacked precise locality information, at least his specimens were all labelled. It is ironic that his collection has been subjected to some of the curatorial mayhem that he inflicted on the collections of others. In other respects his working methods may have been exemplary; and apart from some notable lapses he worked hard. After studying type specimens of shells belonging to the family Tellinidae, many of them belonging to species described by Hanley, A. E. Salisbury wrote: 'During my studies of the collection at the British Museum I found it impossible to say in certain instances which was the type of some of Hanley's species, where more than one shell occurs on the "type" tablet. Hanley appears to have been very casual in the way of giving measurements, and frequently these seem to be a combination, or average, taken from the type lot' (Salisbury, 1934). Conversely, as we have seen, Hanley was so meticulous about marking types and figured specimens in his own collection that it has been possible to locate many of them with relative ease.

Edgar Smith, who knew Hanley personally, said of him: 'By the death of Sylvanus Hanley conchological science has lost one of its most careful and excellent students. As far as the writer of these remarks can judge, no conchologist with whom he has been personally acquainted has devoted more care to his work than Mr Hanley. Thoroughness being his motto' (Smith, 1900). Was the obituarist being truthful - or merely polite? Perhaps we should leave judgement to a higher authority.

ACKNOWLEDGMENTS

We take this opportunity to thank all those who have given us help and advice with research into the history of Hanley and his shell collection. In particular we wish to thank Mr Fred R. Woodward without whom this project may not have got off the ground. We are indebted to staff members at various institutions, especially the following: Islington Central Library and Archives; the Royal Museum (part of the National Museums of Scotland), Edinburgh; the National Museum of Wales, Cardiff; the Manchester Museum. Finally, we wish especially to thank members of the staff of the Mollusca Section at the Natural History Museum, London, past and present, for all their help and patience when dealing with the many queries directed to them over the years.

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SMITH E.A. 1915 Note on *Tellina splendida* of Anton. *Journal of Conchology* **14:** 339–340.

LIST OF MOLLUSCAN TAXA PROPOSED BY HANLEY

This list, should be used in conjunction with the following list of Hanley's publications. F. & H. *Hist. Brit. Moll.* refers to Forbes and Hanley's *A history of British Mollusca and their shells*, 4 vols, 1848-53. There are six taxa in Hanley and Theobald's *Conchologia Indica*, 1876, that are attributed to "Thorp" or "Thorpe" MSS. We have already given our reasons for considering "Thorp" and "Thorpe" to be Hanley pseudonyms. We have ignored many other scientific names associated with illustrations in the *Conchologia Indica* because they are not validly proposed. We may have overlooked some names occurring in the *Catalogue of recent bivalve shells* (1842-56) but we are reasonably confident about the validity of those we have culled from this confusing publication.

Readers should also be aware that many names have been erroneously or carelessly attributed to Hanley in subsequent publications. A typical example is *Tellina splendida* cited as of Hanley in Salisbury (1934) but was clearly stated by Hanley (1856) to be the *T. splendida* of Anton 1839. The confused systematics of this taxon was resolved by Smith (1915) and Salisbury should have referred to Hanley's taxon as *T. splendida* Anton *in* Hanley 1856 non Anton, 1939.

abyssicola Forbes & Hanley, 1850 ***Rissoa*** F.& H. *Hist. Brit. Moll.* **3**: 86, **4**: pl.78 figs 1,2.
acinaces, 1843 ***Solen*** *Proc. zool. Soc. Lond.* **11**:101.
acuminatus, 1842 ***Solen*** *Proc. zool. Soc. Lond.* **10**:122.
ala, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:165.
ancilla, 1859 ***Pseudoliva*** *Proc. zool. Soc. Lond.* **27**:429.
ancilla, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:148.
andamanicus, 1876 ***Bulimus*** ex Thorp MSS, *Conch. Indica* pl. cxlviii fig.10.

antipodum, 1860 ***Nucula*** *Proc. zool. Soc. Lond.* **28**:441.
arcuatula, 1844 ***Modiola*** *Proc. zool. Soc. Lond.* **12**:16.
ascia, 1856 ***Unio*** 'Benson MS' *Cat. rec. biv. shells* p. 385 fig. 20.
asper, 1845 ***Donax*** *Proc. zool. Soc. Lond.* **13**:14 -15.
asperrima, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:59-60.
assimilis, 1845 ***Donax*** *Proc. zool. Soc. Lond.* **13**:17.
assimilis, 1858 ***Pinna*** *Proc. zool. Soc. Lond.* **26**:255.
assimilis, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:144.
aurora, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:147.
beddomeae, 1876 ***Helix (Plectopylis)*** *Conch. Indica* pl. cl figs 1,2.
belcheri, 1858 ***Siphonaria*** *Proc. zool. Soc. Lond.* **26**:153.
bicolor, 1845 ***Ostrea*** *Proc. zool. Soc. Lond.* **13**:107.
biradiata, 1844 ***Modiola*** *Proc. zool. Soc. Lond.* **12**:15.
blainvillei, 1858 ***Siphonaria*** *Proc. zool. Soc. Lond.* **26**:153.
bonanni, 1885 ***Chama arcinella*** var. *J. Linn. Soc. Zool.***18**:292.
britannica Forbes & Hanley, 1852 ***Ianthina*** F. & H. *Hist. Brit. Moll.* **4**: 260, pl.133 fig. 1. Apparently the first published appearance of this name, taken from a manuscript by W. E. Leach and mentioned by J. G. Jeffreys to Forbes and Hanley (who introduce it under *Ianthina communis*).
brookii, 1860 ***Leda*** *Proc. zool. Soc. Lond.* **28**:440.
bruguieri, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:142.
bruguieri, 1845 ***Venus*** *Proc. zool. Soc. Lond.* **13**:21.
brunnea, 1858 ***Siphonaria*** *Proc. zool. Soc. Lond.* **26**:24.
calathus, Forbes & Hanley, 1850 ***Rissoa*** F. & H. *Hist. Brit. Moll.* **3**: 82, **4**: pl.78 fig. 3.
callichroa, 1845 ***Ostrea*** *Proc. zool. Soc. Lond.* **13**:107.
canaliferus, 1844 ***Lithodomus*** *Proc. zool. Soc. Lond.* **12**:16-17.
carbo, 1858 ***Siphonaria*** *Proc. zool. Soc. Lond.* **26**:24.
carinata, 1843 ***Donax*** *Proc. zool. Soc. Lond.* **11**:5-6.
carnicolor, 1844 ***Amphidesma*** *Proc. zool. Soc. Lond.* **12**:162.
carolinensis, 1858 ***Pinna*** *Proc. zool. Soc. Lond.* **26**:225.
carpenteri, 1858 ***Bulla*** *Proc. zool. Soc. Lond.* **26**:543-544.
casta, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:63.
celticum Forbes & Hanley, 1852 ***Onchidium*** F.& H. *Hist. Brit. Moll.* **4**:3, **1**: pl. F.F.F.* fig. 6.
chemnitzii, 1845 ***Ostrea*** *Proc. zool. Soc. Lond.* **13**:106.
chemnitzii, 1858 ***Pinna*** *Proc. zool. Soc. Lond.* **26**:136.
chemnitzii, 1844 ***Venus*** *Proc. zool. Soc. Lond.* **12**:160-161.
chinensis, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:165.
clarkii Forbes & Hanley, 1852 ***Cerithiopsis*** F.& H. *Hist. Brit. Moll.* **3**: 368, **4**: pl.103 fig. 6.
cochinensis, 1858 ***Cyrena*** *Proc. zool. Soc. Lond.* **26**:543.
coluber, 1876 ***Neritina*** ex Thorp MSS, *Conch. Indica* pl. clvii fig.10.
columbiensis, 1845 ***Ostrea*** *Proc. zool. Soc. Lond.* **13**:107.
columbiensis, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:71.
conradi, 1860 ***Leda*** *Proc. zool. Soc. Lond.* **28**:440.
coquimbensis, 1856 ***Montacuta*** *Proc. zool. Soc. Lond.* **24**:340.
cor, 1844 ***Cytherea*** *Proc. zool. Soc. Lond.* **12**:110.
corbis, 1856 ***Unio*** 'Benson MS' *Cat. rec. biv. shells* p. 386 pl. 23 fig. 43.
corbuloides, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:70.
costata, 1842 ***Psammobia*** *Proc. zool. Soc. Lond.* **10**:122-123.
culter, 1845 ***Donax*** *Proc. zool. Soc. Lond.* **13**:14.
culter, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:69-70.
cumingii, 1856 ***Cyrenoida*** *Cat. rec. biv. shells* p. 353 pl. 15 fig. 5.

cumingii, 1861 ***Pandora*** *Proc. zool. Soc. Lond.* **29**:272.
cumingii, 1858 ***Pinna*** *Proc. zool. Soc. Lond.* **26**:254-255.
cumingii, 1862 ***Solaria*** *Proc. zool. Soc. Lond.* **30**:204.
cumingii, 1860 ***Solenella*** *Proc. zool. Soc. Lond.* **28**:441.
cumingii, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:59.
cuspis, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:72.
cycladiformis, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:70.
cygnus, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:144.
cylindricus, 1843 ***Solen*** *Proc. zool. Soc. Lond.* **11**:101.
cyrenoidea, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:64.
decipiens, 1844 ***Venus*** *Proc. zool. Soc. Lond.* **12**:162.
dentifera, 1843 ***Donax*** *Proc. zool. Soc. Lond.* **11**:6.
deshayesii, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:148.
diana, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:147-148.
diemenensis, 1844 ***Cytherea*** *Proc. zool. Soc. Lond.* **12**:110.
discus, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:63-64.
dohrni, 1861 ***Leda*** *Proc. zool. Soc. Lond.* **29**:242.
dombei, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:144.
dorbignyi, 1858 ***Pinna*** *Proc. zool. Soc. Lond.* **26**:228.
dunkeri, 1859 ***Dolium*** *Proc. zool. Soc. Lond.* **27**:431.
dunkeri, 1862 ***Solaria*** *Proc. zool. Soc. Lond.* **30**:204.
eburnea, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:61.
effossa, 1842 ***Cytherea*** *Proc. zool. Soc. Lond.* **10**:123.
elongata, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:144.
euglypta, 1858 ***Pinna*** *Proc. zool. Soc. Lond.* **26**:228.
eulimoides, 1844 ***Odostomia*** *Proc. zool. Soc. Lond.* **12**:18.
excavata, 1842 ***Cytherea*** *Proc. zool. Soc. Lond.* **10**:123.
exulum, 1858 ***Siphonaria*** *Proc. zool. Soc. Lond.* **26**:25.
favannii, 1859 ***Dolium*** *Proc. zool. Soc. Lond.* **27**:430.
felix, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:71.
fimbriata, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:149.
flavidus, 1883 ***Donax*** *J. Linn. Soc. Zool.* **16**:540-541, pl.12 fig. 3.
formosa, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:142.
fragilis, 1840 ***Scalaria*** *Young conch. book of species*, p. 63, text fig.
frigida, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:143-144.
fumata, 1858 ***Pinna*** *Proc. zool. Soc. Lond.* **26**:227.
globularis, 1844 ***Cingula*** in Thorpe, *Brit. mar. conch.* pp. viii, xlii and fig. 87.
gouldii, 1858 ***Pinna*** *Proc. zool. Soc. Lond.* **26**:255.
gouldii, 1846 ***Tellina*** in G.B.Sowerby, *Thes. conch.* **1**:(6):272.
gracilior, 1844, ***Lacuna*** in Thorpe, *Brit. mar. conch.* p. xxxviii and fig. 86.
gracilis, 1845 ***Donax*** *Proc. zool. Soc. Lond.* **13**:15.
grandis, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:141-142.
granulatus, 1844 ***Mytilus*** *Proc. zool. Soc. Lond.* **12**:17.
gravida, 1879 ***Leptomya*** *J. Linn. Soc. Zool.* **14**:580-581.
gubernaculum, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:142.
guildingii, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:60.
hiberna, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:148.
hilaris, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:140.
hindsii, 1844 ***Cytherea*** *Proc. zool. Soc. Lond.* **12**:110.
hindsii, 1860 ***Leda*** *Proc. zool. Soc. Lond.* **28**:440-441.
hystrix, 1858 ***Pinna*** *Proc. zool. Soc. Lond.* **26**:226.
imbellis, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:143.

impar, 1883 ***Donax*** *J. Linn. Soc. Zool.* **16**:541 pl.12 f.4.
inaequalis, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:71.
incarnata, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:68.
inornata, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:144.
insculpta, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:70.
involutus, 1856 ***Unio*** 'Benson, MS' *Cat. rec. biv. shells* p. 385, pl. 23 fig. 19.
irus, 1844 ***Tellina*** *Proc. zool. Soc .Lond.* **12**:166.
isis, 1875 ***Achatina (Glessula)*** *Proc. zool. Soc. Lond.* **43**:606.
jeffreysii Forbes & Hanley, 1850 ***Spirialis*** F. & H. *Hist. Brit. Moll.* **2**: 386, **4**: pl. 57 fig. 8.
jubar, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:60.
juvenilis, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:140-141.
kraussii, 1858 ***Pinna*** *Proc. zool. Soc. Lond.* **26**:226.
lacerata, 1845 ***Ostrea*** *Proc. zool. Soc. Lond.* **13**:106.
lacerata, 1844 ***Venus*** *Proc. zool. Soc. Lond.* **12**:161.
laceridens, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:61-62.
lilium, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:147.
limborgi, 1879 ***Melania*** *J. Linn. Soc. Zool.* **14**:580.
listeri, 1883 ***Donax*** *J. Linn. Soc. Zool.* **16**:540 pl.12 f.2.
listeri, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:69.
lubricus, 1845 ***Donax*** *Proc. zool. Soc. Lond.* **13**:17.
lucerna, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:147.
lux, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:140.
lyra, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:68-69.
lyra, 1844 ***Venus*** *Proc. zool. Soc. Lond.* **12**:161-162.
macandrei, Forbes & Hanley 1850 ***Spirialis*** F.& H. *Hist. Brit. Moll.* **2**: 385, **4**: pl. 57 figs 6, 7.
mactroides, 1856 ***Pythina*** *Proc. zool. Soc. Lond.* **24**:340.
magnifica, 1845 ***Venus*** *Proc. zool. Soc. Lond.* **13**:21-22.
malabarica, 1860 ***Nucula*** *Proc. zool. Soc. Lond.* **28**:441.
mars, 1846 ***Tellina*** in G.B.Sowerby, *Thes.conch.* **1**:(6):273.
m'andrewii, 1860 ***Nucula*** *Proc. zool. Soc. Lond.* **28**:441-442.
mazatlanica, 1856 ***Meleagrina*** *Cat. rec. biv. shells* p. 388 pl. 24 fig. 40. ***megodon***, 1845 ***Ostrea*** *Proc. zool. Soc. Lond.* **13**:106.
megotara, Forbes & Hanley, 1848 ***Teredo*** F. & H. *Hist. Brit. Moll.* **1**: 77, **4**: pl.1 fig. 6, pl.18 figs 1, 2.
melanostoma, 1876 ***Paludomus*** ex Thorpe MSS, *Conch. Indica* pl. cxxi figs 8, 9.
menkei, 1858 ***Pinna*** *Proc. zool. Soc. Lond.* **26**:228-229.
mesodesmoides, 1883 ***Donax*** *J. Linn. Soc. Zool.* **16**:539-540, pl.12 fig.1.
metcalfei, 1844 ***Modiola*** *Proc. zool. Soc. Lond.* **12**:14.
metcalfei, 1844 ***Parthenia*** in Thorpe, *Brit. mar. conch.* p. xlvi.
metcalfii, 1860 ***Leda*** *Proc. zool. Soc. Lond.* **28**:370.
micans, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:72.
miles, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:146-147.
minax, 1858 ***Pinna*** *Proc. zool. Soc. Lond.* **26**:227.
monile, 1876 ***Paludomus*** ex Thorpe MSS, *Conch. Indica* pl. cviii fig.10.
multistriata, 1845 ***Ostrea*** *Proc. zool. Soc. Lond.* **13**:106.
nassoides, 1859 ***Pseudoliva*** *Proc. zool. Soc. Lond.* **27**:430.
navicula, 1845 ***Donax*** *Proc. zool. Soc. Lond.* **13**:15.
niveus, 1856 ***Solen*** *Cat. rec. biv. shells* p. 336 pl. 12 fig. 40
nobilis, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:165.
nuculoides, 1856 ***Pythina*** *Proc. zool. Soc. Lond.* **24**:341.
nux, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:62-63.

obliquata, 1844 **Cytherea** *Proc. zool. Soc. Lond.* **12**:109.
oblonga, 1856 **Cyrenoida** *Cat. rec. biv. shells* p. 353, pl. 15 fig. 6.
ophis, 1875 **Cyclophorus** *Proc. zool. Soc. Lond.* **43**:605.
ovum, 1845 **Cytherea** *Proc. zool. Soc. Lond.* **13**:21.
owenii, 1844 **Tellina** *Proc. zool. Soc. Lond.* **12**:164.
parma, 1858 **Siphonaria** *Proc. zool. Soc. Lond.* **26**:24-25.
perplexa, 1844 **Tellina** *Proc. zool. Soc. Lond.* **12**:149.
pes-tigris, 1845 **Ostrea** *Proc. zool. Soc. Lond.* **13**:106-107.
pharaonis, 1844 **Tellina** *Proc. zool. Soc. Lond.* **12**:148.
phidias, 1876 **Helix** ex Thorp MSS, *Conch. Indica* pl. cxlix fig.4.
philippinarum, 1844 **Cyrena** *Proc. zool. Soc. Lond.* **12**:159-160.
philippinarum, 1844 **Cytherea** *Proc. zool. Soc. Lond.* **12**:110.
philippinarum, 1844 **Modiola** *Proc. zool. Soc. Lond.* **12**:15.
philippinarum, 1843 **Solen** *Proc. zool. Soc. Lond.* **11**:101.
philippinarum, 1844 **Tellina** *Proc. zool. Soc. Lond.* **12**:69.
pinguis, 1844 **Tellina** *Proc. zool. Soc. Lond.* **12**:63.
placens, 1844 **Cyrena** *Proc. zool. Soc. Lond.* **12**:160.
planum, 1843 **Mesodesma** *Proc. zool. Soc. Lond.* **11**:102.
plebeia, 1844 **Cytherea** *Proc. zool. Soc. Lond.* **12**:109-110.
plebeia, 1844 **Tellina** *Proc. zool. Soc. Lond.* **12**:147.
plumula, 1844 **Lithodomus** *Proc. zool. Soc. Lond.* **12**:17.
ponderosa, 1858 **Oniscia** *Proc. zool. Soc. Lond.* **26**:255, pl.42 figs 9,10.
princeps, 1844 **Tellina** *Proc. zool. Soc. Lond.* **12**:62.
prora, 1844 **Tellina** *Proc. zool. Soc. Lond.* **12**:61.
proxima Forbes & Hanley, 1850 ***Rissoa*** F. & H. *Hist. Brit. Moll.* **3**: 127, **4**: pl. 75 figs 7,8.
psittacus, 1882 **Leptomya** *Proc. zool. Soc. Lond.* **50**:576.
pudica, 1844 **Tellina** *Proc. zool. Soc. Lond* **12**:62.
puella, 1844 **Tellina** *Proc. zool. Soc. Lond.* **12**:165.
pulchella, 1843 **Donax** *Proc. zool. Soc. Lond.* **11**:6.
pumila, 1844 **Tellina** *Proc. zool. Soc. Lond.* **12**:69.
punctostriata, 1843 **Donax** *Proc. zool. Soc. Lond.* **11**:5.
pygmaea, 1856 **Corbula**, *Cat rec. biv. shells* p. 344, pl. 12 fig. 34
radiata, 1844 **Cyrena** *Proc. zool. Soc. Lond.* **12**:159.
radula, 1856 **Unio** 'Benson, MS' *Cat. rec. biv. shells* p. 382, pl. 23 fig. 41.
rastellum, 1844 **Tellina** *Proc. zool. Soc. Lond.* **12**:59.
redimiculum var. 1858 **Siphonaria** *Proc.zool. Soc. Lond.* **25**:25.
reevei, 1862 **Solaria** *Proc. zool. Soc. Lond.* **30**:204-5.
regia, 1858 **Pinna** *Proc. zool. Soc. Lond.* **26**:227.
regia, 1844 **Tellina** *Proc. zool. Soc. Lond.* **12**:61.
regium, 1862 **Solaria** *Proc. zool. Soc .Lond.* **30**:205.
rissoides, 1844 **Odostomia** *Proc. zool. Soc. Lond.* **12**:18.
roborata, 1844 **Venus** *Proc. zool. Soc. Lond.* **12**:161.
robusta, 1844 **Tellina** *Proc. zool. Soc. Lond.* **12**:63.
rodon, 1844 **Tellina** *Proc. zool. Soc. Lond.* **12**:140.
rostellum, 1858 **Pinna** *Proc. zool. Soc. Lond.* **26**:227-228.
rota Forbes & Hanley, 1850 ***Skenea*** F. & H. *Hist. Brit. Moll.* **3**:160, **4**: pl. 73 fig. 10, pl. 88 figs 1,2.
rubescens, 1844 **Tellina** *Proc. zool. Soc. Lond.* **12**:60.
rumphii, 1858 **Pinna** *Proc. zool. Soc. Lond.* **26**:136.
rumphii, 1858 **Siphonaria** *Proc. zool. Soc. Lond.* **26**:153.
sanguinea, 1840 **Haliotis** *Young conch. book of species,* p. 60, frontisp. fig. 5.
scabra, 1844 **Venus** *Proc. zool. Soc. Lond.* **12**:161.

scabrum, 1844 ***Amphidesma*** *Proc. zool. Soc. Lond.* **12**:17.
scalariformis, 1844 ***Cingula*** in Thorpe, *Brit. mar. conch.* p. viii, p. xlii (as *Rissoa scalariformis*)
scalpellum, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:147.
scobina, 1856 ***Unio*** 'Benson, MS' *Cat. rec. biv. shells* p. 382, pl. 23 fig. 40.
sculpta, 1845 ***Artemis*** *Proc. zool. Soc. Lond.* **13**:12.
semen, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:164.
semistriata, 1843 ***Mya*** *Proc. zool. Soc. Lond.* **11**:6-7.
semisulcata, 1843 ***Donax*** *Proc. zool. Soc. Lond.* **11**:5.
senator, 1875 ***Achatina (Glessula)*** *Proc. zool. Soc. Lond.* **43**:606.
senegalensis, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:68.
serratizona, 1876 ***Cyclophorus*** ex Thorp MSS, *Conch. Indica* pl. cxliv fig. 7.
simplex, 1845 ***Artemis*** *Proc. zool. Soc. Lond.* **13**:11.
sincera, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:68.
sol, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:142-143.
sordida, 1844 ***Cyrena*** *Proc. zool. Soc. Lond.* **12**:159.
sordida, 1844 ***Modiola*** *Proc. zool. Soc. Lond.* **12**:16.
sordidus, 1845 ***Donax*** *Proc. zool. Soc. Lond.* **13**:15-16.
souleyeti, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:71-72.
sowerbii, 1862 ***Solaria*** *Proc. zool. Soc. Lond.* **30**:206.
sowerbii, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:62.
spectabilis, 1882 ***Leptomya*** *Proc. zool. Soc. Lond.* **30**:576-577.
spectabilis, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:141.
spinosa, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:148-149.
strangei, 1858 ***Pinna*** *Proc. zool. Soc. Lond.* **26**:254.
striatula, 1844 ***Modiola*** *Proc. zool. Soc. Lond.* **12**:14.
strigata, 1844 ***Modiola*** *Proc. zool. Soc. Lond.* **12**:15-16.
subnodulosa, 1844 ***Venus*** *Proc. zool. Soc. Lond.* **12**:160.
subquadrata, 1845 ***Artemis*** *Proc. zool. Soc. Lond.* **13**:11-12.
subramosa, 1844 ***Modiola*** *Proc. zool. Soc. Lond.* **12**:14-15.
subtruncata, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:149.
taylori, 1860 ***Leda*** *Proc. zool. Soc. Lond.* **28**:370.
taylori, 1862 ***Solaria*** *Proc. zool. Soc. Lond.* **30**:205.
tellinoides, 1856 ***Kellia*** *Proc. zool. Soc. Lond.* **24**:340.
tennentii, 1858 ***Cyrena*** *Proc. zool. Soc. Lond.* **26**:23.
tennentii, 1861 ***Parmacella*** ex Templeton MSS in J. E. Tennent, *Sketches of the natural history of Ceylon*, p. 391.
tennentii, 1876 ***Unio*** nom.nov. for ***Mya corrugata*** Wood, *General conchology* 1815, p.108 pl.12 figs 1,2,3. (non Müller,17—) *Conch. Indica* pl.11 fig. 6.
theobaldi, 1875 ***Ampullaria*** *Proc. zool. Soc. Lond.* **43**:605-6.
theobaldi, 1876 ***Achatina*** *Conch. Indica* pl. xvii fig. 5.
ticaonicus, 1845 ***Donax*** *Proc. zool. Soc. Lond.* **13**:14.
triquetrum, 1843 ***Mesodesma*** *Proc. zool. Soc. Lond.* **11**:101-102.
trirostris, 1863 ***Unio*** *Photographic conch.* pl. 2 fig. 9.
tuba, 1868 ***Clausilia*** *Ann. Mag. nat Hist.* (Series 4) **1**:343.
tulipa, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:148.
turrita, 1844 ***Odostomia*** *Proc. zool. Soc. Lond.* **12**:18.
turrita, 1844 ***Parthenia*** in Thorpe, *Brit. mar. conch.* pp. viii, xliv, fig. 91.
umbilicatulus, 1840 ***Nautilus*** *Young conch. book of species*, p. 145, text fig.
undulata, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:72.
valtonis, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:143.
varians, 1844 ***Cytherea*** *Proc. zool. Soc. Lond.* **12**:109.

velaris, 1856 ***Unio*** 'Benson MS' *Cat. rec. biv. shells* p. 385 pl. 23 fig. 42.
vernalis, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:141.
verrucosa, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:60.
vestalis, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:141.
virens, 1844 ***Glauconome*** *Proc. zool. Soc. Lond.* **12**:18.
virgo, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:143.
virgulata, 1844 ***Tellina*** *Proc. zool. Soc. Lond.* **12**:164.
vulcanus, 1875 ***Unio*** *Proc. zool. Soc. Lond.* **43**:606-607.
walpolei, 1871 ***Monocondylaea*** *Proc. zool. Soc. Lond.* **39**:587-588.
woodwardi, 1860 ***Yoldia*** *Proc. zool. Soc. Lond.* **28**:370-371.
zebuense, 1844 ***Amphidesma*** *Proc. zool. Soc. Lond.* **12**:17-18.

LIST OF HANLEY'S PUBLICATIONS

The shells of Margate, Ramsgate & Broadstairs, with figures of nearly all the species. Published by R.C. Osborne, Margate. 28pp.

1840 *The young conchologist's book of species. Univalves, &c.* Pp. viii, 146; col. frontisp. London. A second, slightly enlarged edition appeared in 1842.

1841 *Exotic conchology or figures and descriptions of rare, beautiful, or undescribed shells … by William Swainson.* Second [i.e. Third] edition, edited by Sylvanus Hanley. Pp. 39; 48 col. pls. London.

1842-43 *An illustrated, enlarged, and English edition of Lamarck's species of shells &c.* London. This work appeared in instalments and has a complicated history. It should be noted that the first three plates of this issue of the work were not included in the reissue of 1846 and do not appear in the same form in the completed work (see next item). For fuller bibliographic details see *Catalogue of the books … in the British Museum (Natural History)* **6** (Supplement): 432 (1922). Both editions are very rare and may be described as 'work in progress'. They were the forerunners of the following publication.

1842-56 *An illustrated and descriptive catalogue of recent bivalve shells…with 960 figures by Wood and Sowerby, forming an appendix to the "Index Testaceologicus"*. Pp. xviii, 392, 24; pls ix-xxiv. London. We regard this as the definitive text of the preceding rare and complicated publication. The 'Appendix' (pp. 335-389) contains full descriptions of several new taxa, accompanied by references to figures in accompanying plates. We give 1856 as the publication date of all the taxa included in this 'Appendix'.

1842 Descriptions of four new species of bivalve shells. *Proc. zool. Soc.Lond.* **10**:122-123.

1843a On five new species of *Donax. Proc. zool. Soc. Lond.* **11**:5-6.

1843b & Reeve, L. Descriptions of five new species of bivalve shells, from the collection of W. Metcalfe, Esq. *Proc. zool. Soc. Lond.* **11**:101-102.

1844a Descriptions of new species of Mytilacea, *Amphidesma*, and *Odostomia. Proc. zool. Soc. Lond.***12**:14-18.

1844b Descriptions of new species of *Tellina* collected by H.Cuming, Esq. *Proc. zool. Soc. Lond.***12**:59-64; 68-72; 140-144; 146-149; 164-166.

1844c Descriptions of new species of shells belonging to the genus *Cytherea. Proc. zool. Soc. Lond.* **12**:109-110.

1844d Descriptions of new species of *Cyrena, Venus* and *Amphidesma. Proc. zool. Soc. Lond.***12**:159-162.

1844e 'Thorpe, Charles' [presumed pseudonym of Hanley; see above, Background and Private Life]. *British marine conchology…illustrated…by G. B. Sowerby and W. Wood.* Pp. l, 267; 8 pls (1 col.). London.

1845a Description of three species of shells, belonging to the genus *Artemis*. *Proc. zool. Soc. Lond.* **13**:11-12.
1845b Descriptions of six new species of *Donax*, in the collection of H.Cuming. Esq. *Proc. zool. Soc. Lond.* **13**:14-16.
1845c Description of two new species of *Donax*. *Proc. zool. Soc. Lond.* **13**:17.
1845d Descriptions of three new species of bivalves of the genera *Cytherea* and *Venus*. *Proc. zool. Soc. Lond.* **13**:21-22. See also *Ann. Mag. nat. Hist.* **16**:356-357.
1845e A description of new species of Ostreae, in the collection of H.Cuming, Esq. *Proc. zool. Soc. Lond.* **13**:105-107.
1846 Monograph of the family *Tellina*. In G.B.Sowerby's *Thesaurus conchyliorum* **1**:221-336; pls 56-66.
1848-53 Forbes E. & Hanley S. C. T. *A history of British Mollusca and their shells*. 4 vols. London. The book was issued in parts and the dates of issue have been worked out by A. Reynell (1918). Briefly, the dates of issue of each volume are as follows: vol. 1, 1 Jan. to 1 December 1848; vol. 2, 1 Jan. 1849 to 1 Feb. 1850; vol. 3, 1 March 1850 to 1 Sept. 1851; vol. 4, 1 Jan. 1852 to 1 May 1853. Refer to Reynell's article for more detailed information about the dates of issue of the text and plates.
1849 & Forbes E. On the geographical distribution and uses of the *Ostrea edulis*. *Edinb. new phil.Journ.* **47**:239-248.
1854-58 *The conchological miscellany of Sylvanus Hanley illustrative of* Pandora, Amphidesma, Ostrea, Melo, *the Melaniadae,* Ampullaria *and* Cyclostoma *in Forty Plates*. London & Edinburgh. This publication contains no pagination, the following compilation is taken from two copies in the Tomlin library in the National Museum of Wales, Cardiff. *Pandora*. 1 pl. legends shared on page with Melo. *Amphidesma*. 3 pls. legends, 1pp. *Ostrea*. 3 pls. legends, 1pp. *Melo*. 14 pls. legends shared on page with Pandora. Melaniadae. 8 pls. legends, 3pp. *Ampullaria*. 4 pls. legends, 1pp. *Cyclostoma*. 7 pls. legends, 4pp.
1855 *Ipsa Linnaei conchylia. The shells of Linnaeus, determined from his manuscripts and collection, &c.* Pp. 556; 5 col. pls. London.
1855-56 *Index testaceologicus, an illustrated catalogue of British and foreign shells, by W. Wood … a new and entirely revised edition*. Pp. xx, 234; pls 38+8. London.
1856 Descriptions of four new species of Kelliadae in the Cuming collection. *Proc.zool.Soc.Lond.* **24**:340-341.
1858a Description of a new species of *Cyrena* from Ceylon, and of new Siphonariae. *Proc. zool. Soc. Lond.* **26**:23-25.
1858b Descriptions of two new species of *Pinna*. *Proc. zool. Soc. Lond.* **26**:136.
1858c On *Siphonaria*. *Proc. zool. Soc. Lond.* **26**:151-153.
1858d Description of new Pinnae. *Proc. zool. Soc. Lond.* **26**:225-229.
1858e Description of new Pinnae. *Proc. zool. Soc. Lond.* **26**: 254-255.
1858f Description of a new *Oniscia*. *Proc. zool. Soc. Lond.* **26**:255-256.
1858g Description of a new *Cyrena* and *Bulla*. *Proc. zool. Soc. Lond.* **26**:543-544.
1859a Description of new univalve shells from the collections of H. Cuming and Sylvanus Hanley. *Proc. zool. Soc. Lond.* **27**:429-431.
1859b Systematic list of the species of *Dolium* restricted. *Proc. zool. Soc. Lond.* **27**:487-493.
1860a On the Linnean manuscript of the *'Museum Ulricae'*. *J. Linn. Soc. Zool.***4**:43-90.
1860b On some new species of Nuculaceae in the collection of Hugh Cuming, Esq. *Proc. zool. Soc. Lond.* **28**:370-371.
1860c Descriptions of new Nuculidae. *Proc. zool. Soc. Lond.* **28**:440-442.
1860d Monograph of the family Nuculidae, forming the Lamarckian genus *Nucula*. In G.B.Sowerby's *Thesaurus conchyliorum* **3**:105-168; pls 226-230.
1861a Description of a new *Leda*. *Proc. zool. Soc. Lond.* **29**:242.
1861b Description of a new species of *Pandora*. *Proc. zool. Soc. Lond.* **29**:272.

1861c List of Ceylon shells. In Tennent, J.E., 1861, *Sketches of the natural history of Ceylon*. Pp.388-95. London.

1862 Description of new *Solaria*, chiefly in the collection of H. Cuming, Esq. *Proc. zool. Soc. Lond.* **30**:204-206.

1863a Monograph of the recent species of the genus *Solarium*. In G. B. Sowerby,'s *Thesaurus conchyliorum* **3**:227-248 pls 250-254.

1863b *Photographic conchology, a second, or photographic series of the Conchological miscellany &c.* 3 Pts. Pp. 3; 7 hand-col. photo. pls. London.

1868a, Description of a rare Indian *Clausilia*. *Ann. Mag. nat. Hist.* (Series 4) **1**:343

1868b *Caliphs and sultans, being tales omitted in the usual editions of the Arabian nights entertainments.* London.

1871 Description of a new species of *Monocondylaea*. *Proc. zool. Soc. Lond.* **39**:587-588.

1875 Descriptions of new land and freshwater shells from India. *Proc. zool. Soc. Lond.* **43**:605-607.

1876a & Theobald W. *Conchologia Indica: illustrations of the land and freshwater shells of British India*. Pp. xviii, 65; 160 col. pls. London. According to R.T. Abbott, *Compendium of land shells*, 1989, p. 204, this was published 1870-76. He also gives 1875 as the date for *Theobaldius anguis* Hanley and Theobald, but this name does not occur in *Conchologia Indica*. We regard 1876 as the correct publication date for this book.

1876b Description of new land and freshwater shells from India. *J. Conch.* **1**:152.

1879 Description of two new shells. *J. Linn. Soc. Zool.* **14**:580.

1882 On the Genus *Leptomya* (A.Adams). *Proc. zool. Soc. Lond.* **50**:576-577.

1883 Description of a new species of *Donax* in the collection of the author. *J. Linn. Soc. Zool.* **16**:539-541.

1885a On a new variety of *Chama*, allied to the *C. arcinella* of Linnaeus. *J. Linn. Soc. Zool.* **18**:292.

1885, On the *Teredo utriculus* of Gmelin, with remarks upon other ship-worms. *Ann. Mag. nat.Hist.* **16**:25-31.

PARTIAL LIST OF TAXA NAMED AFTER HANLEY

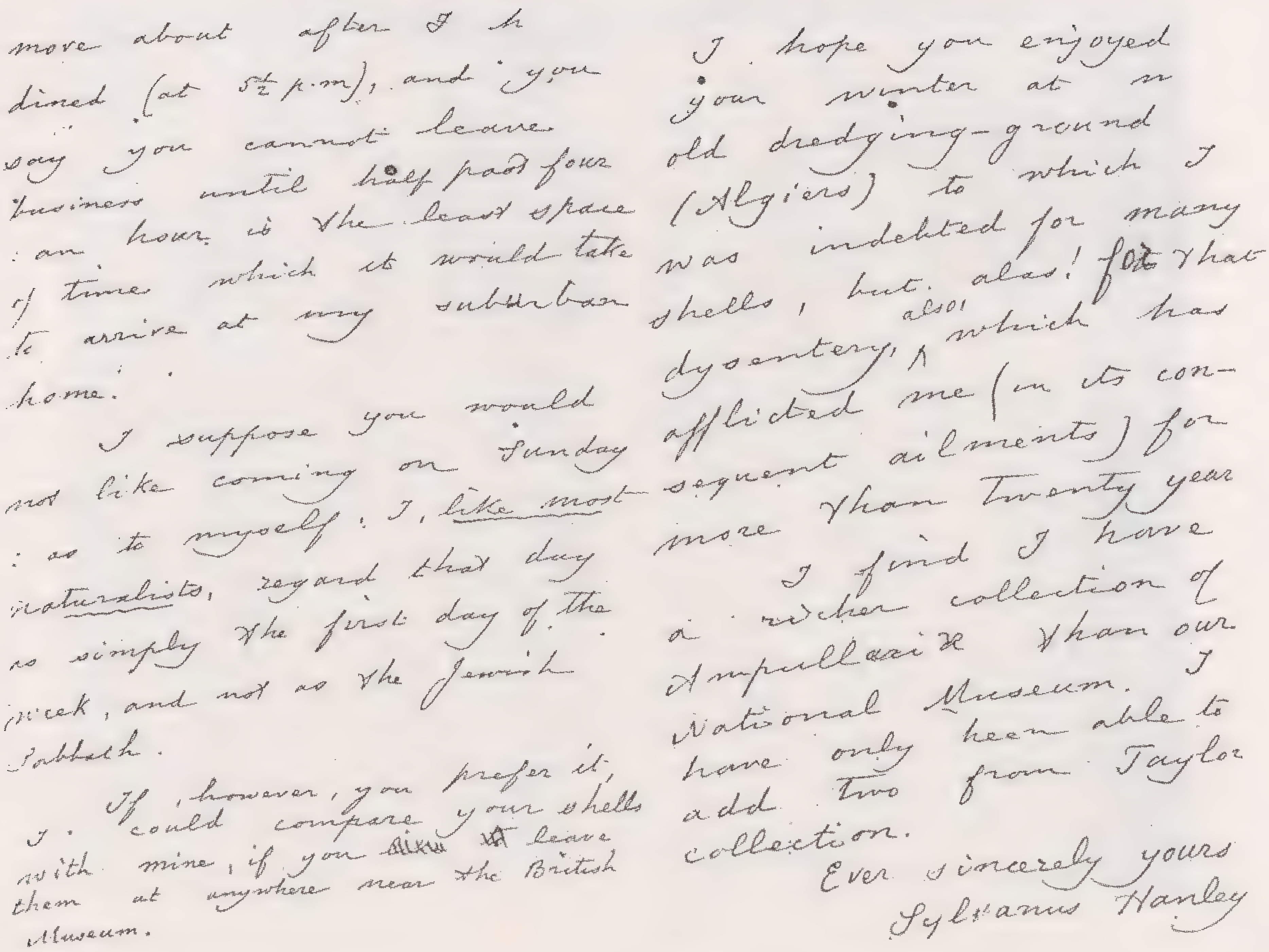
hanleyana	*Achatinella*	Pfeiffer, 1855
hanleyana	*Auricula*	Gassies, 1869
hanleyana	*Castalia*	G.B.Sowerby, 1869
hanleyana	*Cerithidea*	G.B.Sowerby, 1866
hanleyana	*Cytherea*	G.B.Sowerby, 1851, Reeve, 1864
hanleyana	*Dosinia*	H. & A. Adams, 1857
hanleyana	*Nassa*	Marrat, 1880
hanleyana	*Turritella*	Reeve, 1849
hanleyana	*Wilkinsonaea*	Chitty, 1857
hanleyanum	*Buccinum,*	Dunker, 1847
hanleyanum	*Clausilia*	L.Pfeiffer, 1850
hanleyanum	*Cyclostoma (Leptopoma)*	L.Pfeiffer, 1856
hanleyanum	*Cylindrella*	L.Pfeiffer, 1847
hanleyanum	*Donax*	Philippi, 1847
hanleyanum	*Helicina*	L.Pfeiffer, 1849
hanleyanus	*Trochus*	Reeve, 1843
hanleyanus	*Lithodomus*	Reeve, 1857
hanleyanus	*Unio*	G.B.Sowerby, 1866

hanleyanus	*Unio*	Lea, 1852
hanleyi	*Ampullaria*	Reeve, 1856
hanleyi	*Bulimus*	L.Pfeiffer, 1846
hanleyi	*Bulla*	A.Adams, 1850
hanleyi	*Cerithium*	G.B.Sowerby, 1855
hanleyi	*Chiton*	Bean, 1844
hanleyi	*Columbella*	Deshayes, 1863
hanleyi	*Cultellus*	Dunker, 1861
hanleyi	*Cyclostoma*	L.Pfeiffer, 1847
hanleyi	*Drillia*	Carpenter, 1856
hanleyi	*Fusus*	G. B. Sowerby, 1880
hanleyi	*Helix*	L.Pfeiffer, 1845
hanleyi	*Leptochiton*	(Bean) J.E.Gray, 1847
hanleyi	*Mitra*	Dohrn, 1861
hanleyi	*Nucula*	Winckworth, 1931
hanleyi	*Paludomus*	Dohrn, 1858
hanleyi	*Planaxis*	E. A. Smith, 1872
hanleyi	*Pinna*	Reeve, 1858
hanleyi	*Rissoina*	Schwartz von Mohrenstern, 1860
hanleyi	*Scintilla*	Deshayes, 1855
hanleyi	*Tapes*	G.B.Sowerby, 1852
hanleyi	*Tellina*	Dunker, 1853
hanleyi	*Tellina*	Bertin, 1878
hanleyi	*Trophon*	Angas, 1867
Hanleyella	Sirenko,1973	(Polyplacophora)
Hanleya	Gray, 1857	(Polyplacophora)
Hanleyidae	Bergenhayn, 1955	(Polyplacophora)

Fig. 1 Two pages from Hanley's original collection manuscript catalogue Vol. 2 pages 238-9, No's 132–168, listing part of his collection of *"Unio"*.

Unio Opalinus Anthony
Michigan
(male & female)
rarely sent — only one which has
ever gone to Europe —

Fig. 2 *Ligumia opalinus* (Anthony, 1866). Acc.No. LEEDM.C.1957.173.26517. Michigan, North America. Forwarded to Hanley by Anthony, syntype *Unio opalinus* Anthony, 1866.



more about after I h dined (at 5½ p.m), and you say you cannot leave business until half past four: an hour is the least space of time which it would take to arrive at my suburban home.

I suppose you would not like coming on Sunday: as to myself, I, like most naturalists, regard that day as simply the first day of the week, and not as the Jewish Sabbath.

If, however, you prefer it, I could compare your shells with mine, if you ~~[illegible]~~ ~~at~~ leave them at anywhere near the British Museum.

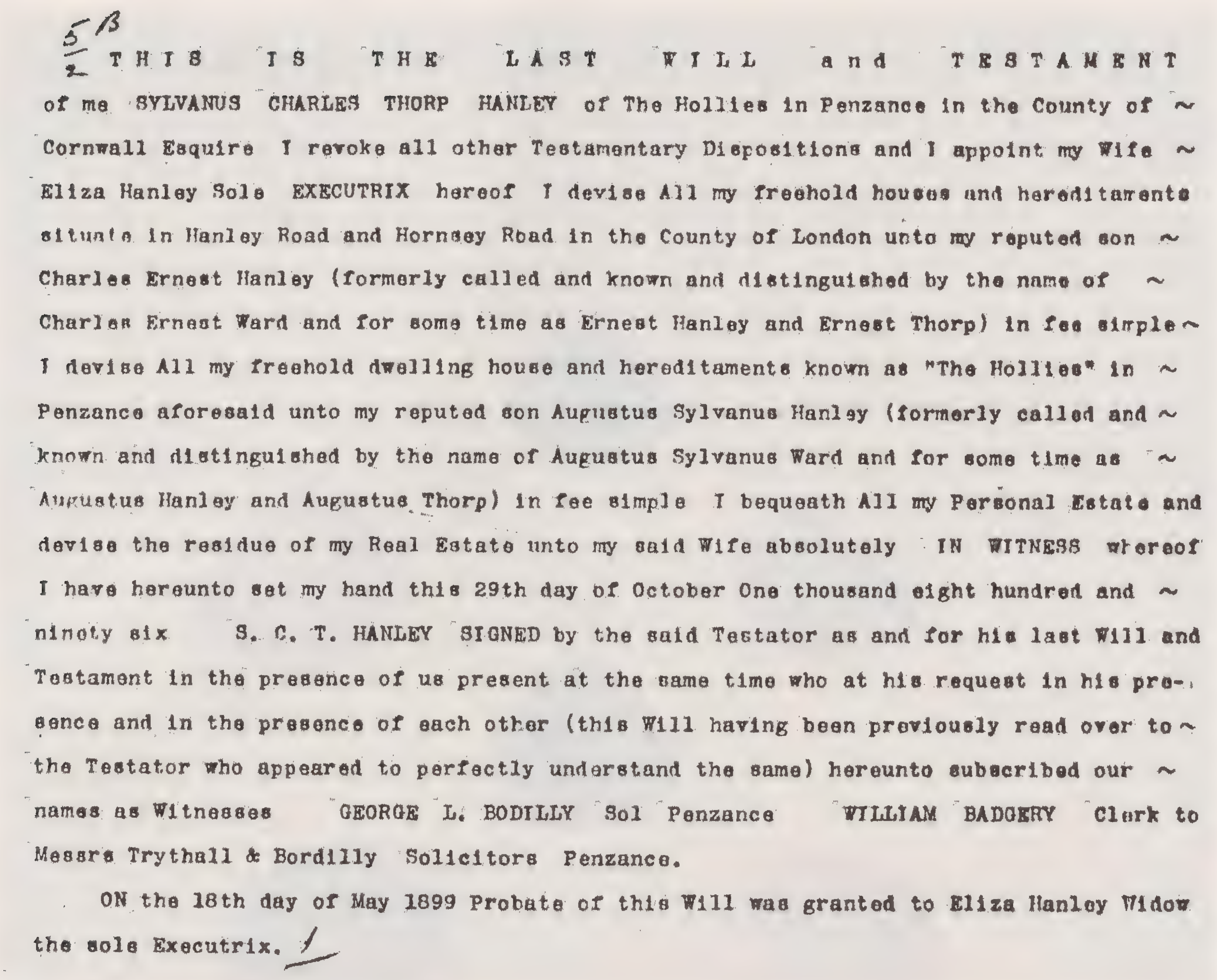
I hope you enjoyed your winter at n old dredging-ground (Algiers) to which I was indebted for many shells, but, alas! for that dysentery, also! which has afflicted me (in its consequent ailments) for more than twenty year.

I find I have a richer collection of Ampullariæ than our National Museum. I have only been able to add two from Taylor collection.

Ever sincerely yours
Sylvanus Hanley

Fig. 3 Part of an undated letter from Hanley to J.H.Ponsonby.

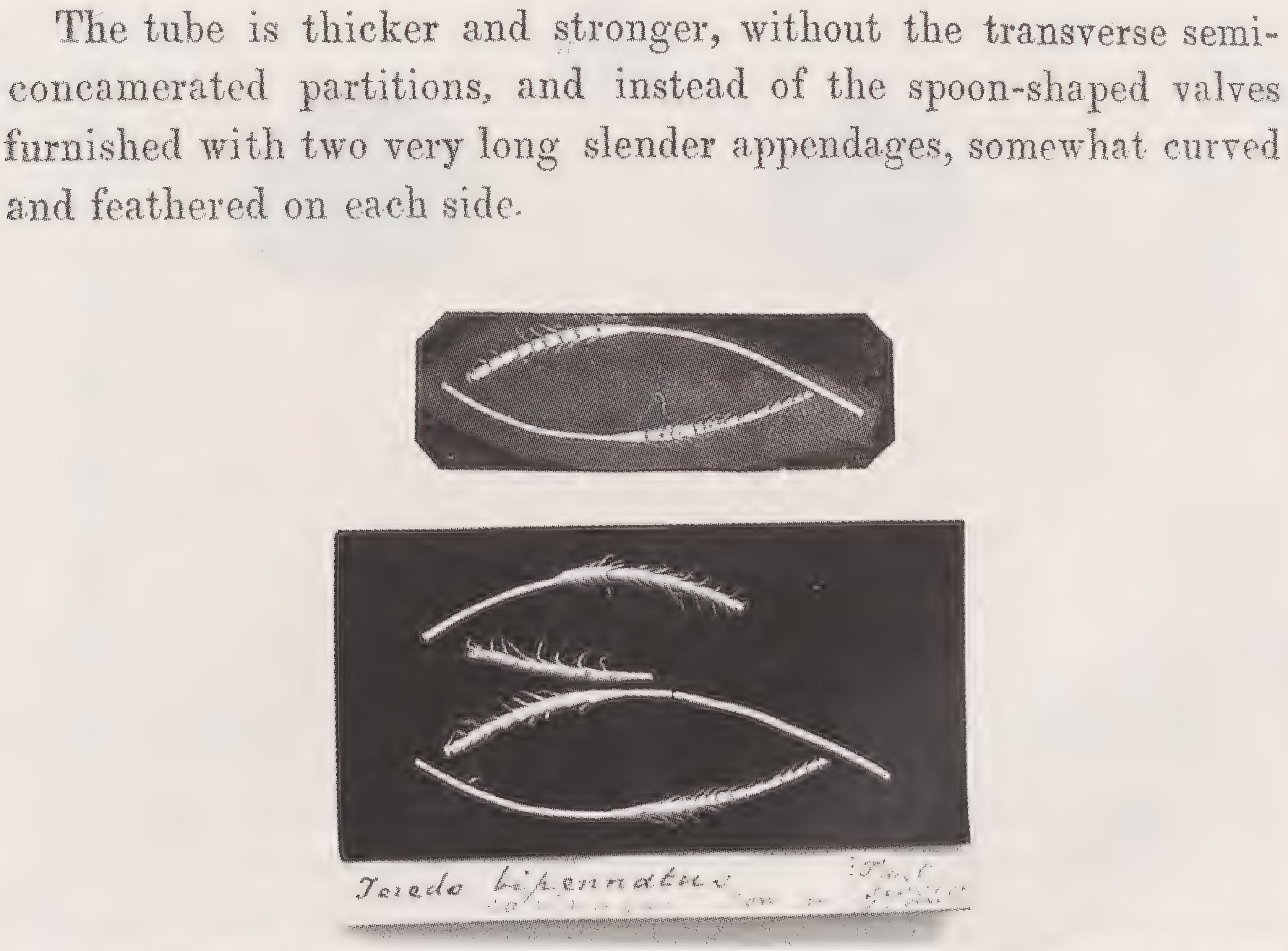
Fig. 4 *Fusconaia flava* (Rafinesque, 1820). Acc.No. LEEDM.C.1957.173.10779. Hanley MSS Catalogue Vol. 2 page 240, No. 175 as *Unio trigonis* Lea, 1831. Figured Reeve *Conch. Icon.* Pl.



5B/2 THIS IS THE LAST WILL and TESTAMENT
of me SYLVANUS CHARLES THORP HANLEY of The Hollies in Penzance in the County of ~
Cornwall Esquire I revoke all other Testamentary Dispositions and I appoint my Wife ~
Eliza Hanley Sole EXECUTRIX hereof I devise All my freehold houses and hereditaments
situate in Hanley Road and Hornsey Road in the County of London unto my reputed son ~
Charles Ernest Hanley (formerly called and known and distinguished by the name of ~
Charles Ernest Ward and for some time as Ernest Hanley and Ernest Thorp) in fee simple ~
I devise All my freehold dwelling house and hereditaments known as "The Hollies" in ~
Penzance aforesaid unto my reputed son Augustus Sylvanus Hanley (formerly called and ~
known and distinguished by the name of Augustus Sylvanus Ward and for some time as ~
Augustus Hanley and Augustus Thorp) in fee simple I bequeath All my Personal Estate and
devise the residue of my Real Estate unto my said Wife absolutely IN WITNESS whereof
I have hereunto set my hand this 29th day of October One thousand eight hundred and ~
ninety six S. C. T. HANLEY SIGNED by the said Testator as and for his last Will and
Testament in the presence of us present at the same time who at his request in his pre-
sence and in the presence of each other (this Will having been previously read over to ~
the Testator who appeared to perfectly understand the same) hereunto subscribed our ~
names as Witnesses GEORGE L. BODILLY Sol Penzance WILLIAM BADGERY Clerk to
Messrs Trythall & Bordilly Solicitors Penzance.

ON the 18th day of May 1899 Probate of this Will was granted to Eliza Hanley Widow
the sole Executrix.

Fig. 5 Hanley's Last Will and Testament Dated May 18 1899.



The tube is thicker and stronger, without the transverse semi-concamerated partitions, and instead of the spoon-shaped valves furnished with two very long slender appendages, somewhat curved and feathered on each side.

Fig. 6 Part of page from Turton's *Conchylia Dithyra Insularum Britannicarum* 1848, with 131 extra photograph's by Hanley, showing original specimen below, from the Hanley collection at Leeds. *Teredo pedicellata* Quatrefages, 1849. Acc.No. LEEDM.C.1957.173.24649. Guernsey.

Fig. 7 Plate VII from Hanley's "Photographic Conchology" of 1863. From copy in Tomlin Library, National Museum of Wales, Cardiff.

THYASIRA POLYGONA (JEFFREYS) (BIVALVIA: LUCINOIDEA), AN ABANDONED TAXON WITH A POSSIBLE AMPHI-ATLANTIC DISTRIBUTION

IAN J. KILLEEN[1] & P. GRAHAM OLIVER[1]

Abstract Thyasira polygona *(Jeffreys) previously regarded as a variety of* T. flexuosa *(Montagu) is considered to be a distinct species. It is confirmed from British waters on the west of Scotland and the North Sea. Similar taxa have been recorded from the Mediterranean* [Ptychina biplicata *Philippi*], *Caribbean* [T. trisinuata *(d'Orbigny)] and north-western Atlantic* [T. obesa *(Verrill)*] *but shell and anatomical study is required to confirm the relationships of these. It is surmised that the British and north-western Atlantic material is conspecific and represents an additional amphi-Atlantic* Thyasira *species.*

Key words Thyasira, Thyasira polygona, *British distribution, amphi-Atlantic, Mediterranean.*

INTRODUCTION

The bivalve *Thyasira flexuosa* var. *polygona* (Jeffreys, 1864) was described from material collected 40 miles east of Whalsey Skerries (Shetland) at a depth of 87 fathoms (161m). Jeffreys (1881) subsequently gave a number of other locations from the north-eastern Atlantic, Vigo Bay (Spain), and Mediterranean Sea. It was later recorded from Gairloch (west of Scotland) at 30 fathoms (65m) by Marshall (1897) but subsequently has not been thought worthy of separate status. It is not recognised as a distinct part of the British fauna by Bowden & Heppell (1968) or by Smith & Heppell (1991) but is cited as a variety in a European context by Nordsieck (1969). Within the Mediterranean it is treated as a junior synonym of T. *flexuosa* (Parenzan, 1974) and is not cited in Sabelli *et al* (1990) Dall (1901) included *T. f.* var. *polygona* in his synonymy of the American taxon *T. trisinuata* (d'Orbigny, "1846", 1853 see Appendix) along with *T. obesa* (Verrill, 1872). This synonymy was repeated by Abbott (1974) but Payne & Allen (1991) in describing *T. trisinuata* cast doubt on the inclusion of *T. f.* var. *polygona* in its synonymy. The type locality of *T. trisinuata* is in the Caribbean and that of *T. obesa* off Marthas Vineyard. Lamy (1920) also follows Dall's (1901) synonymy but gives north of Spain as a recorded location.

Warén (1980) records that no type specimens of *T. f.* var. *polygona* were present in the Jeffreys collection, but in the National Museum of Wales, Marshall's cited specimen from Gairloch is extant. Marshall and Jeffreys collaborated and it is with reasonable certainty that Marshall's specimen does represent Jeffreys' concept of var. *polygona*. This shell is indeed polygonal in outline and quite distinct from typical *T. flexuosa*.

In the preparation of an identification guide to British Thyasiridae (Oliver & Killeen, in prep.) the authors were obliged to investigate the status of the variety *polygona* because if Dall's (1901) synonymy was correct then *T. trisinuata* would be part of the British fauna. Also during this study a number of specimens of the var. *polygona* were located including some with preserved internal anatomy which allowed comparison with the observations made by Payne & Allen (1991) on American examples of *T. trisinuata* from the north-west Atlantic.

This paper reports on our observations but due to the small amount of material available stops short of a final solution. However, we urge all those involved in benthic sampling to look out for strongly trisinuate thyasirids in samples from North Atlantic shelf depths.

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Thyasira polygona (Jeffreys, 1864)

Material examined **Preserved animals** 10 specimens, Forties oil field, North Sea, 57°45′N 00°50′E, NMW.Z. 2001.049. 1 specimen, Sleipner Vest oil field, North Sea, 58°30′N 01°42′E, 110m, NMW.Z. 2001.047. 2 specimens, Block 21/1b, North Sea, 57°52′N 00°08′E, 115m, NMW.Z. 2001.048. 1 specimen Fladen Ground, North Sea, ex environmental assessment survey station PMG1/4.1, May 2001, NMW.Z. 2001.046. **Shells only** 1 shell, Gairloch, west of Scotland, *c.* 57°43′N 05°44′W, Leg. Marshall, NMW 1953.183. 1 shell, Firth of Lorn, west of Scotland, 56°28′N 05°36′W, 61m, Leg. S. M. Smith private collection. 1 shell, Sound of Jura, west of Scotland c. 56°N 05°45′W, NMS. 1977.105.337.

Institutional abbreviations NMS, National Museums of Scotland; NMW, National Museum of Wales (pre 1970); NMW.Z National Museum of Wales (post 1970).

Description The shell (Figs 1, 5–8). Shells to 9mm in height. Outline polygonal, umbos narrow, pointed. Posterior margin strongly trisinuate, first sinus (sn^1) formed by slope of umbo and auricle, second (sn^2) by the auricle and first posterior fold (pf^1) and third (sn^3) by the posterior sulcus. Anterior angulate, lunule margin (lm) very long, reaching almost to the mid-point and sloping steeply, anterior ventral margin curved, some individuals slightly angulate at ventral extremity. Auricle (au) prominent, raised posteriorly. Submarginal sulcus (sms) and posterior sulcus (ps) very strong and demarcated by sharply angled folds, narrow anterior slope (as) flattened, demarcated by a faint ridge (ar).

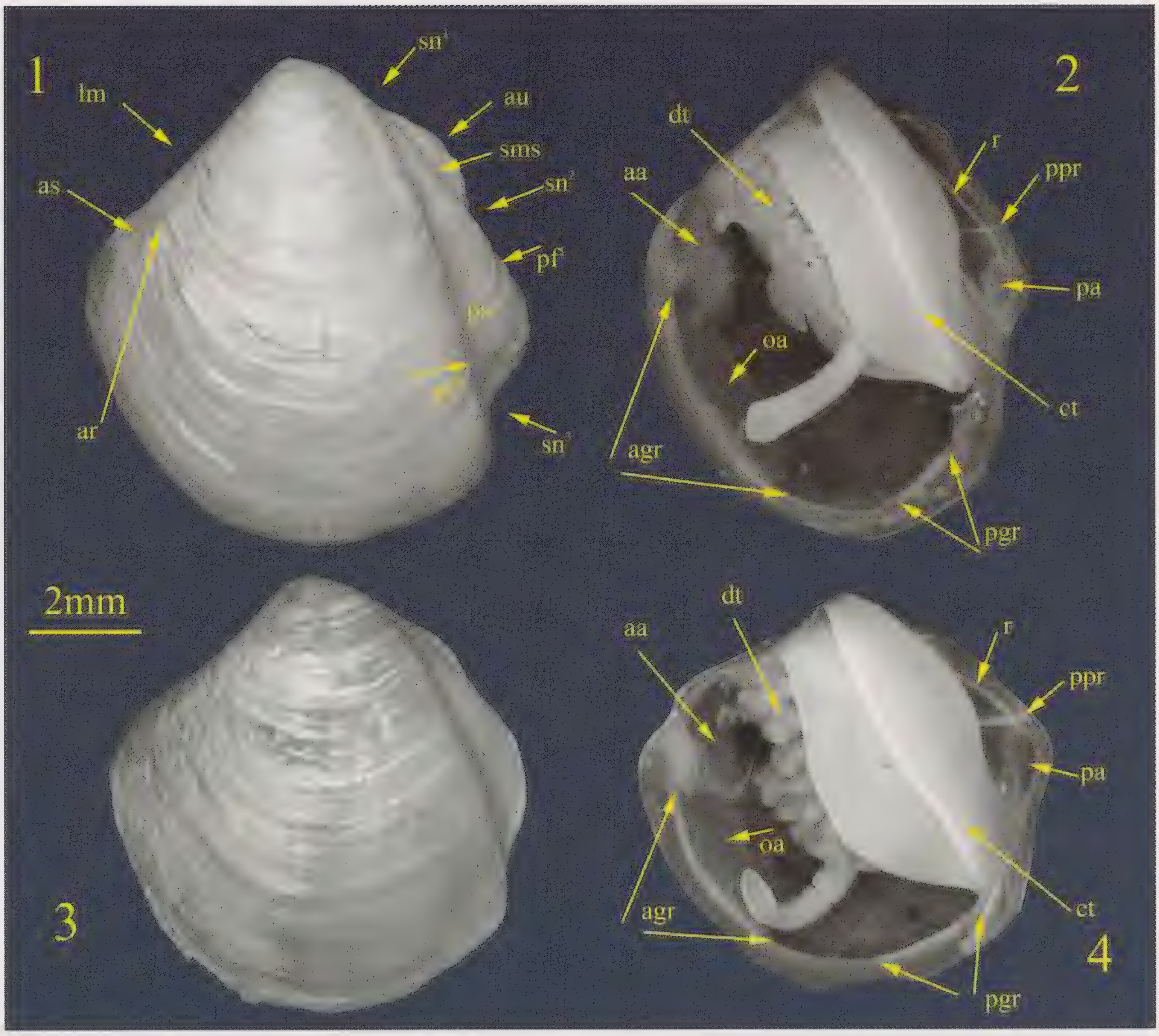
Hinge weak with a single peg like cardinal tooth in the RV and a corresponding indentation in the margin of the LV. Ligament mostly sunken, inserted in a shallow depression and extending one half the length of the auricle. Muscle scars indistinct, posterior adductor placed on inner side of the first posterior fold.

Internal anatomy (Fig. 2). Adductor muscles strongly discrepant in size, anterior elongate (aa), posterior small and rounded (pa). Pedal retractor muscles very weak, the posterior (ppr) almost thread like and attached dorsal to and seperated from the adductor. Anterior inner mantle edge with a narrow thickened glandular ridge (agr) extending to a point in line with the beak; to its inside a weakly opaque area (oa) is present; also a small but less developed posterior glandular ridge (pgr) is present. The gills are composed of both inner and outer demibranchs (od), the outer half the size of the inner, neither are especially thick and with the filaments clearly visible. The digestive tubules (dt) are deeply divided and terminate in pointed finger like tips.

Comparisons with T. flexuosa *Thyasira polygona* has been compared with typical *T. flexuosa* from localities throughout its British range (3, 9–11). The type locality of *T. flexuosa* is Falmouth and figure 9 represents a shell from this locality. All of these typical *T. flexuosa* shells illustrate the key differences from *T. polygona*. The auricle is much weaker and there is no first sinus. The submarginal sulcus is stronger and the associated first fold is more acute. The posterior sinus is deeper and the posterior fold sharper. The lunule margin is not as long nor as steeply sloping and is concave rather than straight. There is no narrow flattened anterior slope.

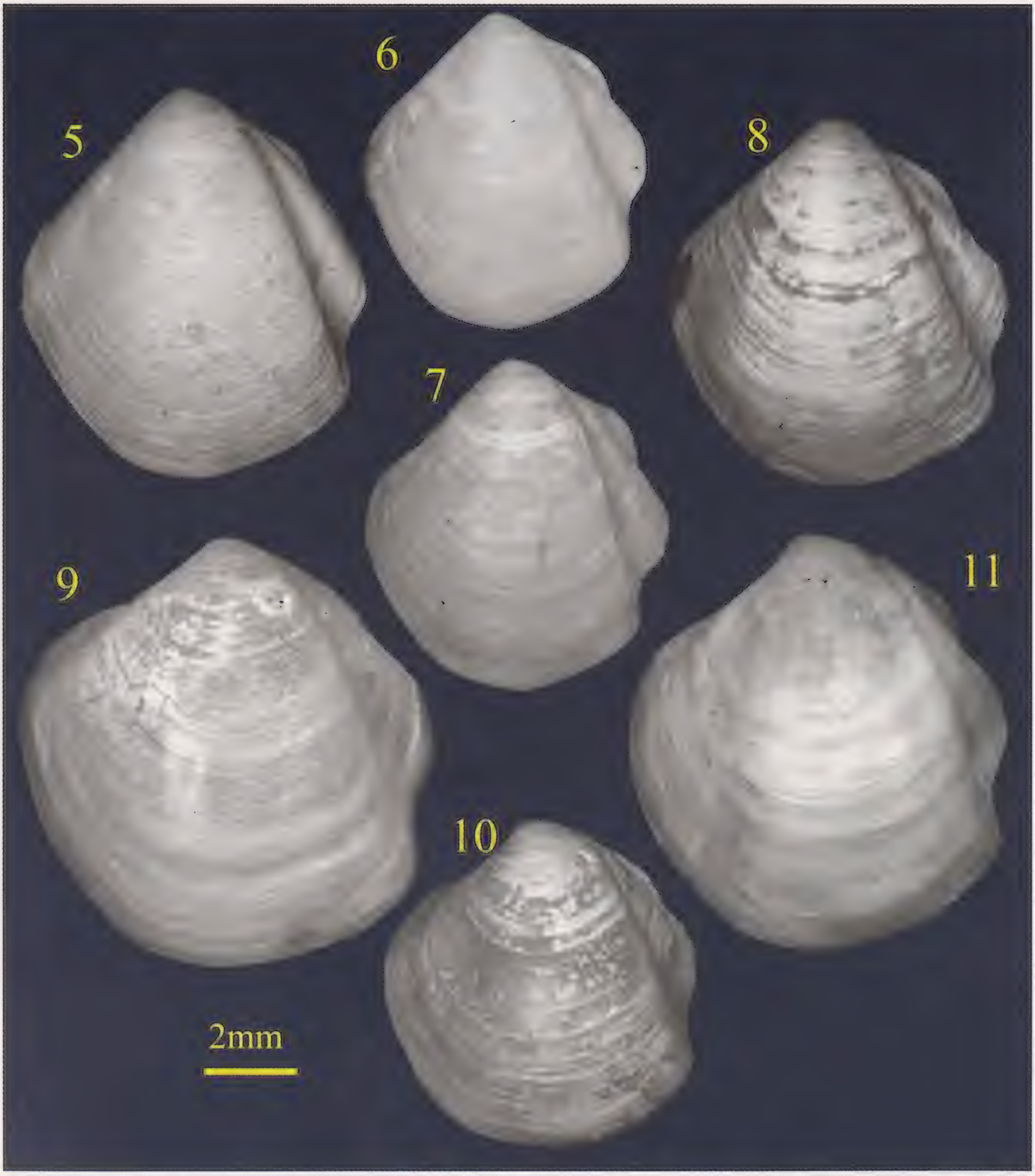
Anatomical comparisons are illustrated using a specimen of *T. flexuosa* from the Murdoch gas field (Fig. 4). The key differential characters of *T. flexuosa* are as follows.

The posterior pedal retractor is broader and attaches close to the posterior adductor scar. The anterior glandular ridge is more pronounced but does not extend so far around the ventral margin and the adjacent opaque area is wider and more strongly developed. The posterior glandular ridge is more pronounced and longer. The digestive tubules terminate in blunt, rounded apices.



Figs 1–2 *Thyasira polygona*, Jeffreys; Forties oil field; **1** external of left valve with structures indicated: ar, anterior ridge; as, anterior flattened slope; au, auricle; lm, lunule margin; pf^1, 1st posterior fold; pf^2, 2nd posterior fold; ps, posterior sulcus; sms, submarginal sulcus; sn^1, 1st posterior sinus; sn^2, 2nd posterior sinus; sn^3, 3rd posterior sinus. **2** soft parts seen after removal of shell and left mantle with structures indicated: aa, anterior adductor muscle; agr, anterior glandular ridge; ct, ctenidium; dt, digestive tubules; oa, opaque area of mantle; pa, posterior adductor muscle; pgr, posterior glandular ridge; ppr, posterior pedal retractor muscle; r, rectum.

Figs 3–4 *Thyasira flexuosa*, Montagu; Murdoch gas field, 54°17′N 01°18′E, 32m, NMW.Z. 2001.102; **3** external of left valve. **4** soft parts seen after removal of shell and left mantle with structures indicated, abbreviations as Fig. 2.



Figs 5–8 *Thyasira polygona* Jeffreys: **5** Gairloch, cited specimen in Marshall, 1897; **6** Sound of Jura; **7** Firth of Lorn; **8** Block 21/1b, North Sea.

Unresolved Taxonomic Issues Illustrations of *T. trisinuata* (d'Orbigny, "1846") given by Dall (1901) and subsequent N. American authors (Abbott, 1974) as well as those by Payne & Allen (1991) are all based on specimens from the north-east coast of the USA. These are therefore all indicative of *T. obesa* (Verrill, 1872) rather than *T. trisinuata,* which is Caribbean in origin. From comparisons with these descriptions its is apparent that *T. obesa* and *T. polygona* are similar in shell form and Dall's (1901) synonymy is understandable. The anatomy of *T. trisinuata* as illustrated by Payne & Allen (1991) is based on a very small and partially dissected individual (3mm) but their description, especially that of the pointed digestive tubules compares well with the present British material.

We have compared the type figures of *T. trisinuata* and they show a trisinuate and strongly inflated shell but the illustrations are small and the description scant.

Jeffreys (1881) gives Lusitanian and Mediterranean localities for *T. polygona* but he gives no descriptions or illustrations. Recent illustrations from the Mediterranean and Moroccan literature (Parenzan, 1974, Pasteur-Humbert, 1962) show strongly sinuate and deeply plicate forms with a short high auricle. Consequently it would appear that *T. polygona* can be recognised in these regions but as with the western Atlantic we would wish to confirm this with anatomical comparisons.

Of further potential nomenclatural significance is *Ptychina biplicata* Philippi, 1836, which was described from Sicily. This taxon has long been regarded as a synonym of T. *flexuosa* (Lamy, 1920, Sabelli et al, 1990) but even the small original illustrations show a shell much more similar to *T. polygona.* If this taxon is conspecific with *T. polygona* then this has the earliest available name. We are currently trying to aggregate a large series of relevant material from the Mediterranean Sea to solve this issue. It also predates *T. trisinuata* and would have to be considered in the review of that taxon.

PRELIMINARY CONCLUSIONS

Although the shell of *Thyasira* species can show considerable variation (Ockelmann, 1958, 1961; Oliver & Killeen in prep) the differences between typical British *T. flexuosa* and *T. polygona* are both large and consistent. The anatomical data from the North Sea material gives the strongest indication that *T. polygona* is a separate species from *T. flexuosa.*

This study has also indicated that *T. polygona* may range south to north-west Africa and the Mediterranean. It may also be present in the Caribbean and north-west Atlantic. Further study is required to confirm this range and the results will alter the final nomenclature.

Concerning the relationship with the American counterparts we remain unconvinced that the tropical *T. trisinuata* and boreal, *T. obesa* are indeed conspecific and this needs to be clarified to stabilise the nomenclature. Our initial suspicions are that *T. polygona* and *T. obesa* are most likely synonymous but we have some doubt about *T. trisinuata.*

The addition of another amphi-Atlantic species would not be problematic as in the Thyasiridae this distribution is common with *T. flexuosa, T. gouldi, T. sarsi, T. obsoleta, T. equalis, T. ferruginea* and *T. pygmaea* all having similar amphi-Atlantic ranges in waters of shelf depth. Currently the American fauna includes the three taxa, *T. flexuosa, T. trisinuata* and *T. gouldi* and thus a similar situation in the western Atlantic should not be a surprise.

We believe that the likely outcome of a full review of Mediterranean material will be the confirmation of *T. polygona* in that region. This would have the likely nomenclatural implication of the taxon taking the name of *Thyasira biplicata* (Philippi, 1836).

APPENDIX

The date of publication of *Lucina trisinuata* d'Orbigny is most frequently cited as 1846 (Dall, 1901, Abbott, 1974, Payne & Allen, 1991). The name however does not appear in Sherborn (1922) for names published before 1850 and does not appear in Ruhoff (1980) for names published between 1850 and 1870. This confusion can be traced to the imprecise dates of publication of the livraisons but the catalogue of the British Museum (Natural History) (1913) states that for Tome II, pages 113–330 probably appeared in 1853, despite the application of the date 1846 by d'Orbigny to the newly described taxa from page 149 onwards. In this paper we follow the BM(NH) catalogue and apply the date 1853 to taxa described in pages 113–330. This conclusion has been confirmed by Gary Rosenberg, Academy of Natural Sciences, Philadelphia, from his unpublished research.

ACKNOWLEDGEMENTS

The authors wish to thank all those who kindly lent material for this study; Sankurie Pye (NMS), Shelagh Smith, Environmental Resource and Technology, Edinburgh, Cordah Ltd, Aberdeen. To BP/Amoco (UK) for initial sponsorship and particularly to John Hartley of Hartley Anderson Consultants for his continuing support and enthusiasm.

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THE TAXONOMIC AND CONSERVATION STATUS OF *THYASIRA GOULDI* (PHILIPPI, 1844), THE NORTHERN HATCHET SHELL, IN BRITISH WATERS

IAN J. KILLEEN[1] & P. GRAHAM OLIVER[1]

Abstract Thyasira gouldi *is shown to have a wider British distribution than previously thought. It is confirmed to range along the west coast of Scotland from Loch Sween in the south to Loch Etive, Loch Eil and "Cape Wrath" in the north. Additionally it is a frequent component of the fauna of Sullom Voe, Shetland and has recently been found on the east coast of Scotland in the Firth of Forth.* T. gouldi *is not recorded from the open North Sea and appears to be confined to inlets and sea lochs The discrimination of* T. gouldi *and* T. flexuosa *is reviewed and the prodissoconch size is considered to be the most reliable character. Variation and growth changes in* T. gouldi *are illustrated. The conservation status is reviewed but any change is not recommended until there is a greater understanding of the ecology and population genetics.*

Key words Thyasira gouldi, *British distribution, biodiversity action plan, conservation.*

INTRODUCTION

Thyasira gouldi was named by the German malacologist, R.A. Philippi (1845), based on the description of a variety of *T. flexuosa* described by A.A. Gould (1844) in his *"Invertebrates of Massachusetts"*. It was subsequently recognised as an amphi-Atlantic species by Ockelmann (1958) who recorded it from Greenland, Jan Mayen, Iceland, Faeroes and Norway. It may have a circum boreal-subarctic distribution as it has been recorded from across the subpolar regions of Russia (Miloslavskaja, 1970) and the Pacific west coast of America (Bernard, 1983).

Throughout the history of *T. gouldi* there has been frequent comment on its similarity and consequent confusion with *T. flexuosa;* indeed as recently as 2000, Coan, Scott & Bernard synonymised *T. gouldi* with *T. flexuosa*. Despite this there has been little published on the discrimination of these species with only Ockelmann (1958) stressing the large prodissoconch size of *T. gouldi* as definitive. Blacknell (1973) in his unpublished thesis gave a set of both conchological and anatomical characters but this work has not been widely available and confusion has remained in the eyes of British and other workers.

The earliest record of *T. gouldi* in the British Isles is based upon specimens in the United States National Museum labelled "Shetland" and confirmed by Ockelmann (Bowden & Heppell, 1968). This material is most likely from the Jeffreys collection. Marshall (1897) records *T. flexuosa* var *gouldi* Phil. between the Hebrides and Faeroes. However, his comment that the species was smaller, rounder, and flatter, without the longitudinal furrow suggests that he may have been referring to *T. equalis* (Verrill & Bush, 1898). In 1971 Blacknell (1973) found a dense population of *T. gouldi* from a site at the head of Loch Etive, west Scotland. He subsequently re-examined material identified as *T. flexuosa* from Pearson's (1970, 1972) Loch Eil surveys and showed that *T. gouldi* was present before the fauna was influenced by discharge of pulp mill effluent (Blacknell & Ansell 1974). However, material, dated 1980, in the Shelagh Smith collection indicates that it was still present later than 1974. Blacknell & Ansell (1975) also recorded *T. gouldi* from Loch Sunart and Loch Linnhe although there appears to be no extant material from these locations. Smith & Nunn (in prep.) report *T. gouldi* living in

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outer Loch Carron collected by the British Geological Survey but, again, there is no extant material. Since the mid 1970s there have been further reports of *T. gouldi* from Shetland, in particular Sullom Voe, and the North Sea oilfields arising from environmental monitoring surveys. These records have almost all appeared only in 'grey literature' and have hitherto, remained unconfirmed. *Thyasira* material from these surveys has been deposited in both the National Museums of Scotland and the National Museum of Wales, yet none is labelled *T. gouldi.*

Southward & Southward (1991) revisited Blacknell's upper Loch Etive sites in September 1989. However, twelve 0.1m^2 grab samples yielded just 3 living individuals of *T. gouldi,* from where Blacknell & Ansell (1974) had reported hundreds to thousands per square metre. Southward & Southward (1991) suggested that the presence of virus-like particles on the bivalve's gill bacteria as a possible reason for the population's decline. In April 1992, Killeen, Light and Smith collected *Thyasira gouldi* (*c.* 100 specimens from one dredge haul of mud and organic detritus) from Loch Etive, at Sailean Ruadh, some 15-20 km further south-west of Blacknell &Ansell's sites.

As a result of this reported decline in Loch Etive and believed disappearance from Loch Eil, *T. gouldi* was added (in 1992) to Schedule 5 of the UK Wildlife and Countryside Act, 1981. Subsequently it was included on the short-list of priority species on the UK Biodiversity Action Plan under the common name of the Northern Hatchet Shell (English Nature, 1999).

The authors in preparing a review and identification guide to British Thyasiridae (Oliver & Killeen in prep.) decided that the unconfirmed nature of many of the records of *T. gouldi* necessitated a more detailed examination. This paper presents the results of a re-examination of material from the British Isles.

MATERIAL EXAMINED

The material in the first list includes all material that initially carried *T. flexuosa* and *T. gouldi* identifications. Only localities are given but all material is available through the National Museum of Wales, National Museums of Scotland and the private collection of Dr. Shelagh Smith. The second list gives details of *T. gouldi* material from outside the British Isles which is used for comparisons.

List 1
West Scotland: Firth of Clyde, Loch Fyne, Loch Sween & Loch na Cille, Firth of Lorn & Loch Spelve, Loch Etive, Loch Eil, Loch Creran, Loch Ailort, Loch Torridon, Loch Laxford, Loch Eriboll, *Northern & Western Isles:* Isle of Lewis; Orkney, Water Sound; Shetland, Sullom Voe. *East Scotland:* Cromarty Firth, Firth of Forth. *North Sea:* from Magnus oil block (61°35′N) to Caister gas block (54°12′N), 50+ samples. *Irish Sea and South West England:* Weymouth, Salcombe Falmouth, Milford Haven, St. Georges Channel, Cardigan Bay, Morecambe Bay.

List 2
Greenland: Ella Island, 5–24m, ZMC, det. Ockelmann; Fiskerness, 70 fathoms, NMW.1955.158.11391. *Iceland:* Havnefjord, 64°04.2′N 21°58.6′W, 15m, ZMC; Seydisfjord, 83m, ZMC; Isafjordur, 40m, ZMC. All det. Ockelmann. *Faeroes:* Sørvåg, 24m; Fundingfjord, 43m, ZMC. All det Ockelmann. *Norway:* Varanger, 125–150fathoms, NMW.1955.158.11390. *Spitzbergen:* Green Harbour, Icefjord, 30 fathoms, NMW.1955.158.11392. *North-west Atlantic:* Casco Bay, Maine, NMW.1955.158.11387. Wiscasset, Maine, NMW.1955.158.11388.

Institutional abbreviations NMS, National Museums of Scotland; NMW, National Museum of Wales (pre 1970); NMW.Z National Museum of Wales (post 1970). RSMNH, Royal Museum of Scotland = National Museums of Scotland. SMS, private collection of Dr. Shelagh M. Smith. ZMC, Zoological Museum, Copenhagen.

DISCRIMINATION OF *T. GOULDI* AND *T. FLEXUOSA*

Ockelmann (1958) gave the major characteristic separating *T. gouldi* from *T. flexuosa* as the size of the prodissoconch, 210–260µm as opposed to 160–190µm, (Compare figs 20–25) but also stated that in general the shell outline is "rather evenly rounded but some are somewhat pyriform". Blacknell (1973) tabulates both shell and anatomical differences and for the shell adds to Ockelmann's characters, a well defined ligament and weak hinge tooth. Anatomical characters of *T. gouldi* cited by Blacknell are: a thick – compact rejection area, thicker gill filaments, more widely spaced interfilamental junctions, deeper palps, no dark line on the mantle edge, characters of the sperm in that the acrosome is poorly defined and the tail is long (60µm).

Given this array of characters there is no doubt that *T. gouldi* is distinct from *T. flexuosa* but from the material examined by us *T. gouldi* has been consistently recorded as *T. flexuosa*.

We have reviewed the shell characters with the aim of facilitating recognition of *T. gouldi* on the shell alone and make the following conclusions.

The prodissoconch size is the most consistent shell character and is not only larger but has a prominent rim that gives a pin-head appearance (Fig. 4) to the beaks under low magnification. The horizontal diameter (parallel with hinge plate) of the prodissoconch was measured from SEM images on shells from a range of Scottish sites (Figs 22, 23–25) and ranged from 205–250µm with most in the range of 220–240µm.

The shell outline is variable although those shells from Shetland, Jura, Loch Sween and the Firth of Forth are rounded with a longer auricle and weaker posterior sulci (Figs 1, 11–14). Some shells from Loch Etive and many of those from Loch Eil were by contrast more polygonal especially in that the lunule margin is long and steeply sloping (Figs 4, 5, 9, 10). Shells from the Faeroes (Fig. 18) were also more polygonal in outline.

Shells of *T. flexuosa* (Figs 2, 8) in contrast have a more angular outline with a more concave lunule margin and more pointed anterior. The auricle is shorter often more raised and the posterior sulci are more prominent and develop earlier in ontogeny. However the typical *flexuosa* form can be easily confused with the polygonal form of *T. gouldi* and furthermore in many samples of *T. flexuosa* the auricle although always short can be so weakly elevated as to be almost obsolete. Consequently although in broad terms the shells of these species can be distinguished the variation is such that there may often be doubt as to their identity and thus the need to examine the larval shell.

The ligament is less sunken in *T. gouldi* and its prominence is related to the proportion visible in dorsal view. This has been measured and calculated as a ratio of shell length. Figure 28 shows that these ratios are significantly different ($p< .0001$) for *T. flexuosa* (mean = 36) and *T. gouldi* (mean = 42), and also *T. sarsi* (Philippi, 1845) (mean = 52), with the exposed ligament increasing in length accordingly.

The weaker expression of the hinge teeth was not verified across the range of *T. gouldi* and *T. flexuosa* examined.

The periostracum of *T. gouldi* is more persistent and gives a silky sheen to the external appearance, whereas in *T. flexuosa* the surface is either chalky or matt.

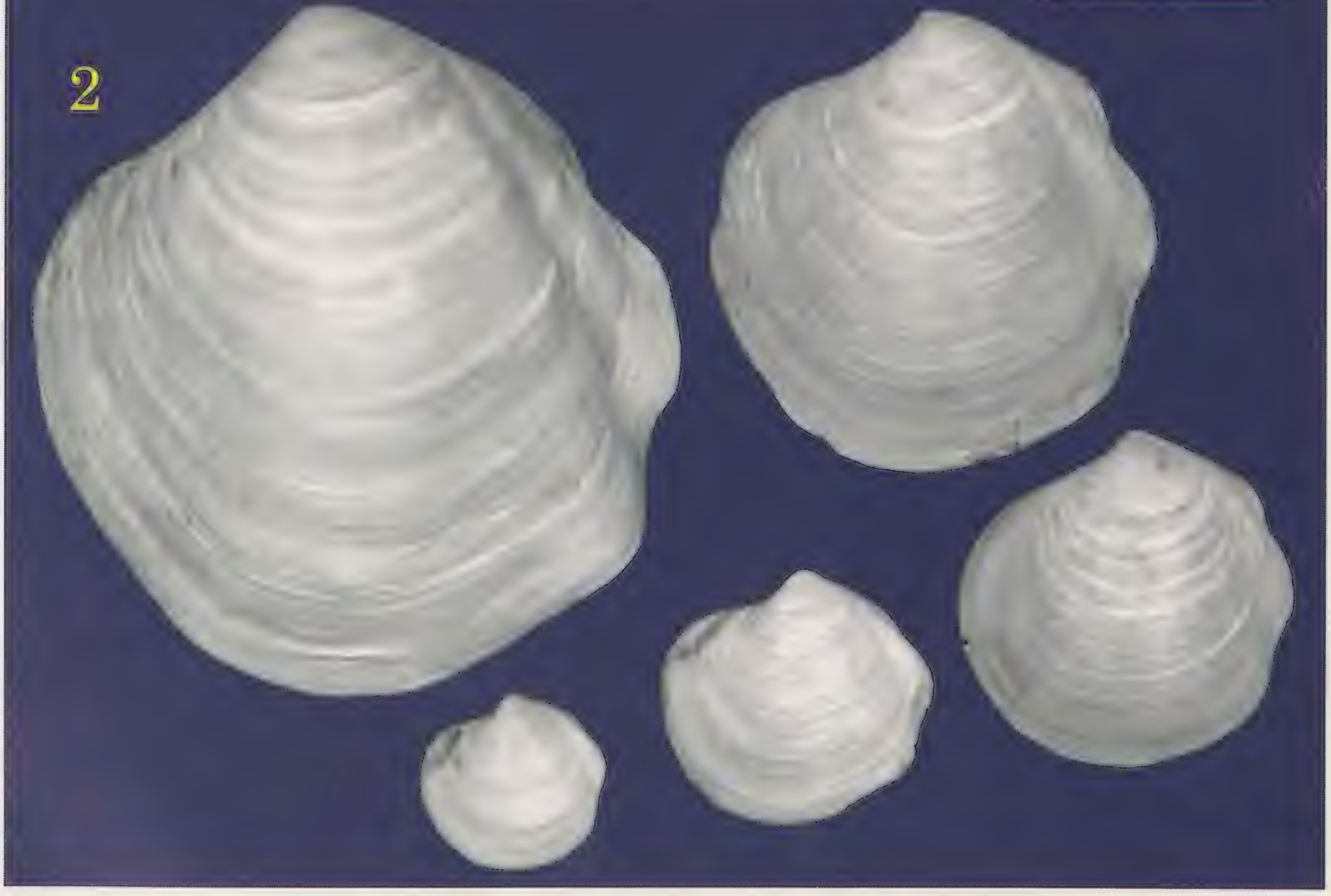
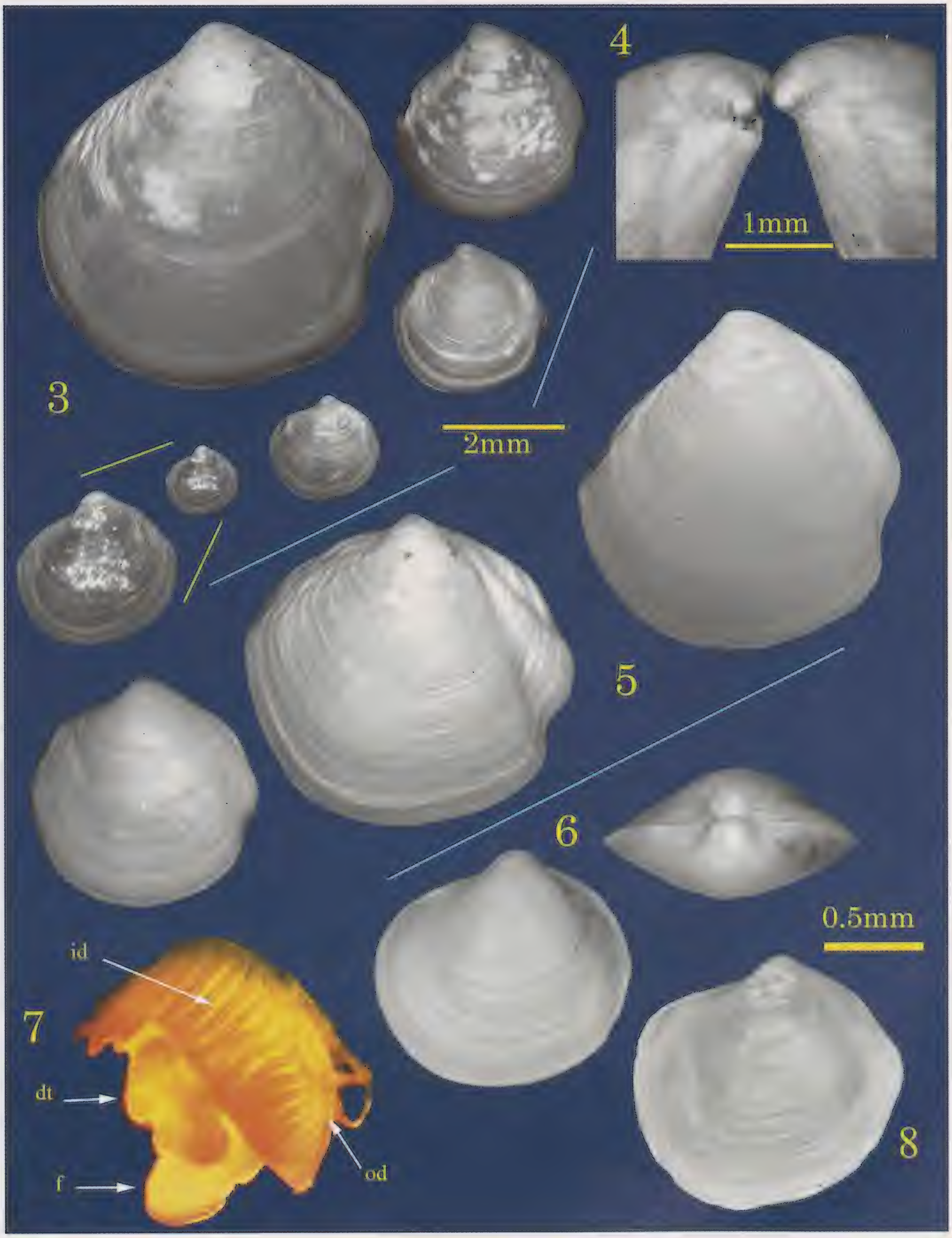
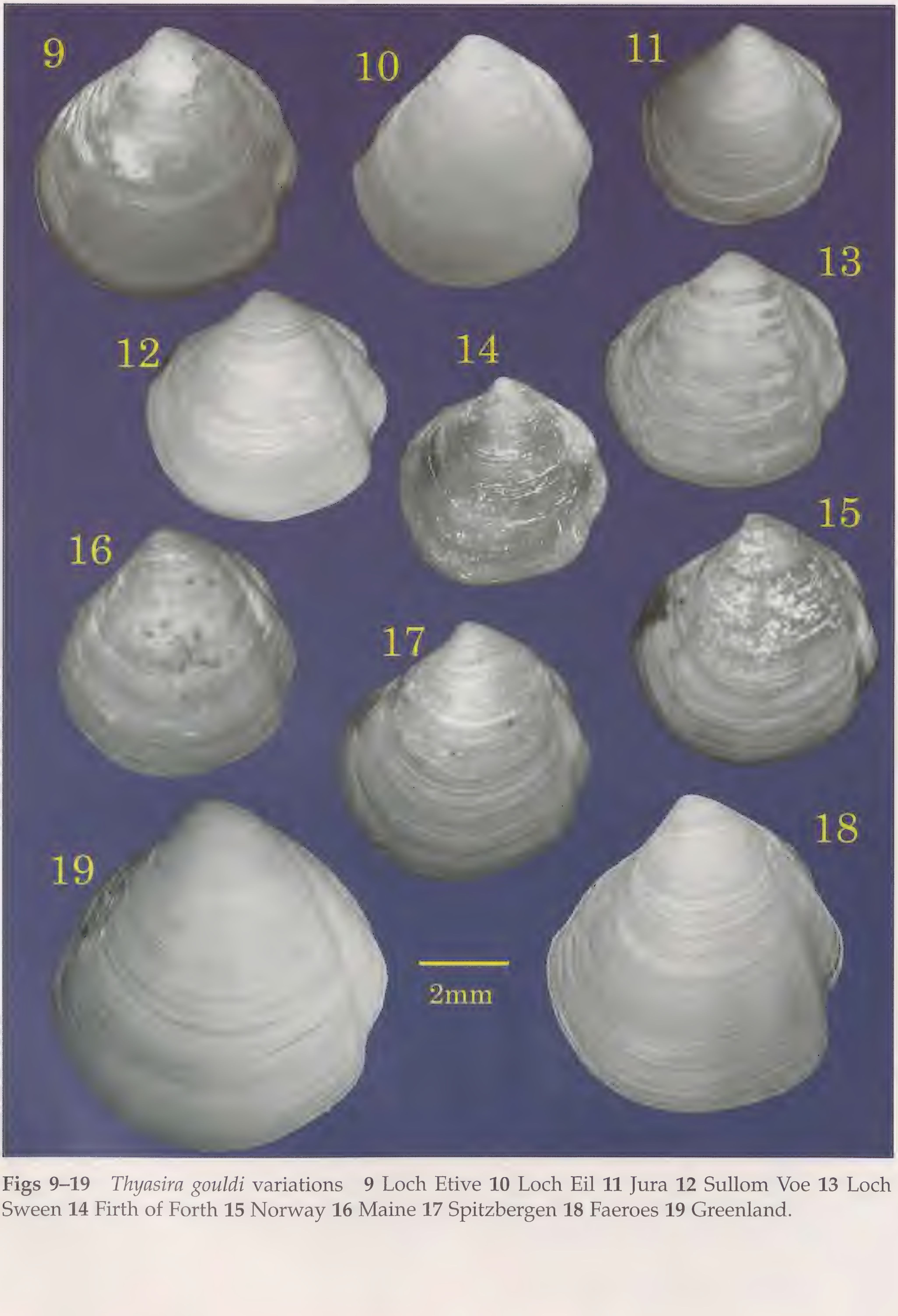


Fig. 1 *Thyasira gouldi* size series, Sullom Voe, Shetland.
Fig. 2 *T. flexuosa*, size series, Sullom Voe, Shetland.

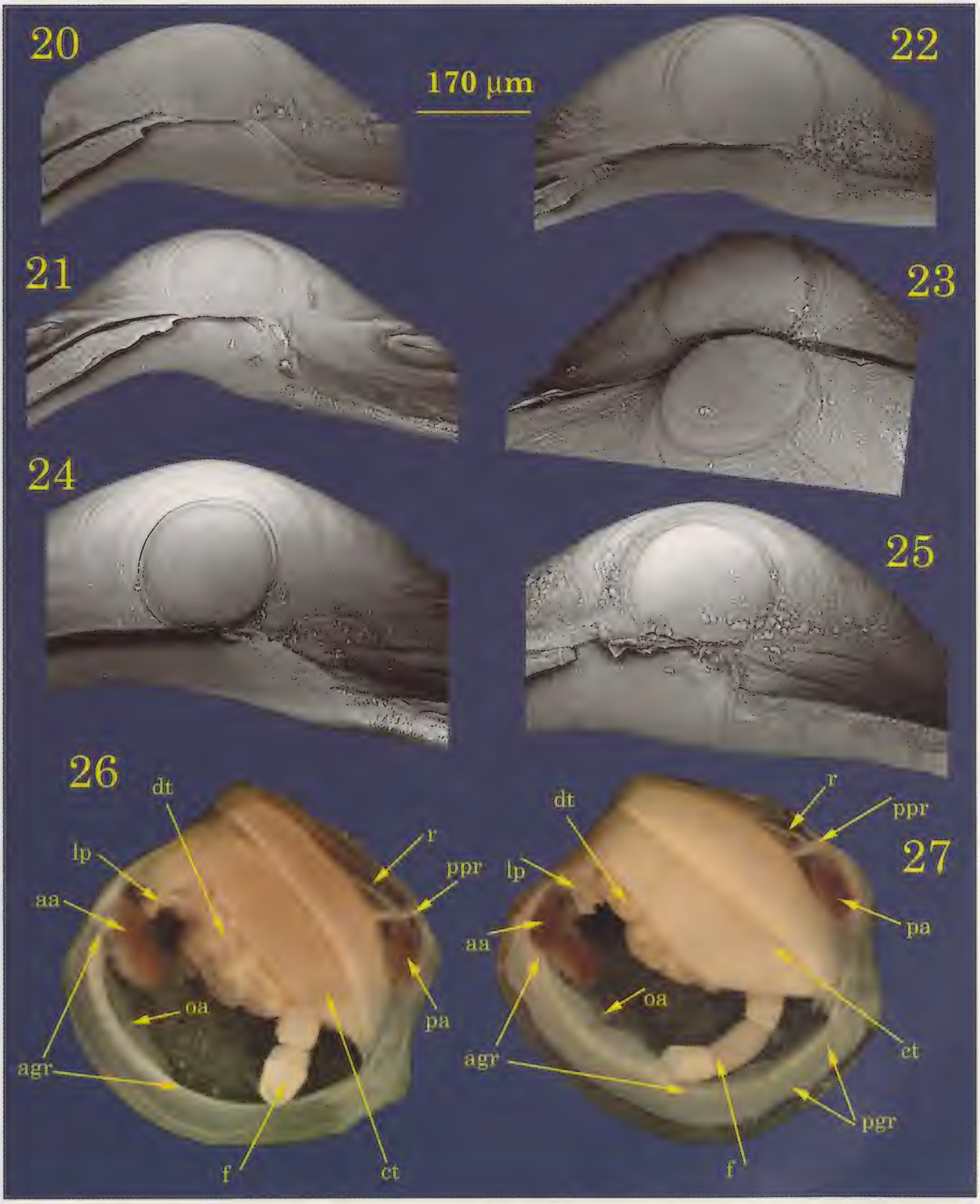


Figs 3–7 *Thyasira gouldi* **3** size series, Loch Etive **4** pin head larval shell in normal light, L. Etive. **5** variations from Loch Eil **6** dorsal and lateral views of juvenile, "Cape Wrath" **7** gross anatomy of juvenile, "Cape Wrath"; dt - digestive tubules, f - foot, id - inner demibranch, od - outer demibranch.

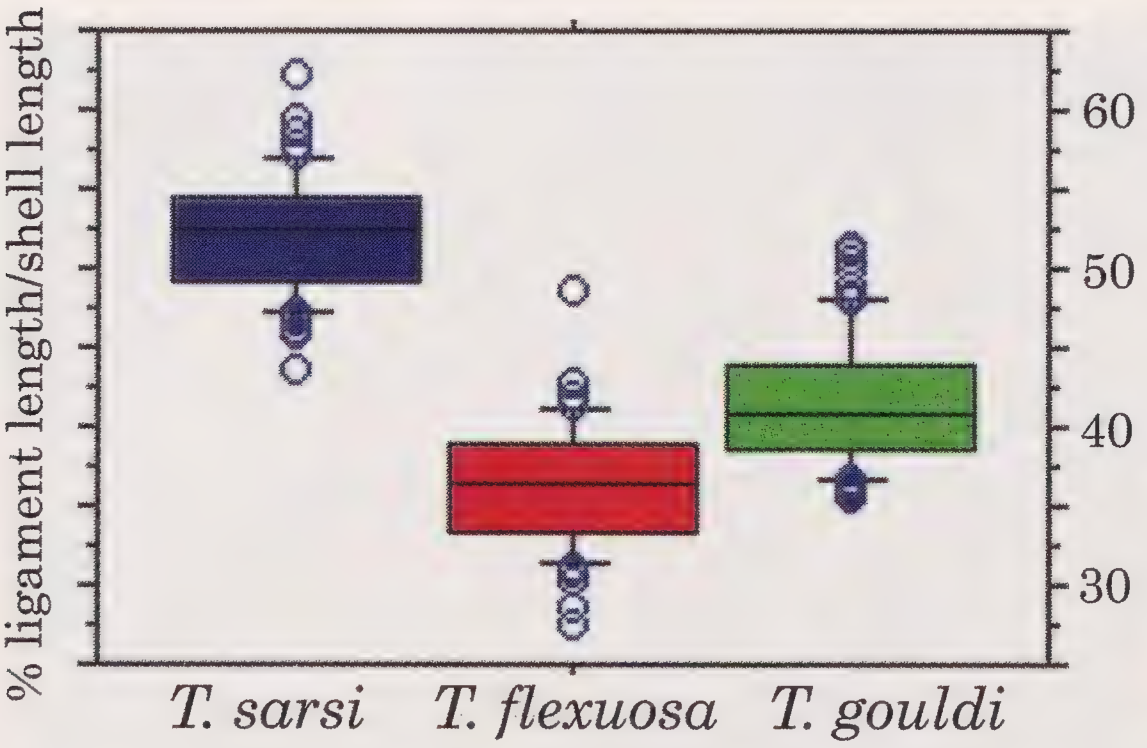
Fig. 8 *T. flexuosa*, juvenile, Cape Wrath".



Figs 9–19 *Thyasira gouldi* variations **9** Loch Etive **10** Loch Eil **11** Jura **12** Sullom Voe **13** Loch Sween **14** Firth of Forth **15** Norway **16** Maine **17** Spitzbergen **18** Faeroes **19** Greenland.



Figs 20–27 SEM images of prodissoconchs **20–21** *T. flexuosa* **20** Sullom Voe **21** Cape Wrath. **22–25** *T. gouldi* **22** Sullom Voe **23** Cape Wrath **24** Loch Eil **25** Loch Etive **Figs 26–27** gross anatomy viewed from the left side with left mantle removed, both from SullomVoe **26** *T. gouldi* **27** *T. flexuosa* aa, anterior adductor, agr - anterior glandular ridge, ct - ctenidium, dt - digestive tubules, f - foot, lp - labial palps, oa - opaque glandular area, pa - posterior adductor, pgr – posterior glandular ridge. ppr - posterior pedal retractor.



Scheffe for Lig/Lth
Effect: species
Significance Level: 5 %

	Mean Diff.	Crit. Diff.	P-Value	
sarsi, flexuosa	15.800	1.531	<.0001	S
sarsi, gouldi	10.529	1.459	<.0001	S
flexuosa, gouldi	-5.272	1.459	<.0001	S

Means Table for Lig/Lth
Effect: species

	Count	Mean	Std. Dev.	Std. Err.
sarsi	75	52.095	3.681	.425
flexuosa	75	36.295	3.746	.433
gouldi	92	41.566	3.952	.412

Fig. 28 Box plot indicating 10th, 25th, 50th, 75th and 90th percentiles of the ratios of ligament length/shell length expressed as percentages for three species of *Thyasira*; *T. sarsi*, *T. flexuosa* and *T. gouldi*. Tables showing means and results of f-test.

The micro-anatomical characters given by Blacknell have not been reviewed but we confirm those characters that can be easily observed by simple removal of the shell (compare figs 26 & 27). The ctenidia have thicker filaments and the 'rejection area' (= anterior glandular ridge and opaque area) is more compact in *T. gouldi*.

VARIATION IN FORM OF *T. GOULDI*

Growth changes

Many lucinoids show rather large changes in shell outline through their ontogeny but thyasirids generally show this to a lesser degree. However the smallest shells (0.5 to 1.5mm) of *T. gouldi* differ significantly from the mature shell Figs 1, 3, 6). At this small size specimens of *T. gouldi* have characteristics of the subgenus *Mendicula* and the authors admit to being initially confounded by them. The proportions are distinctly longer than high and the anterior part more extended. The posterior sulcus is not yet developed and the auricle is not defined. The prodissoconch is very prominent. Interestingly in similar sized shells of *T. flexuosa* the sulcate posterior is already apparent.

The internal anatomy was also examined (Fig. 7) and the ctenidium was found to undergo development at this stage. Initially the outer demibranch is barely visible and is present as a series of small bud like filaments, the adult arrangement becomes apparent at about 2mm.

Variations

Variation in the form of the adult shell is apparent both within and between populations. Most Scottish populations display the rounded outline with a long prominent auricle. The Loch Eil and, to a lesser extent, the Loch Etive material contained shells where the lunule margin is steeply sloping and much longer. This pyriform extreme graded into the typical form and all had the large prodissoconch (Figs 3, 5).

In samples from beyond Britain we found that those from north-east USA (Fig. 16), Spitzbergen (Fig. 17) and Norway (Fig. 15) were of the rounded type. Greenland shells (Fig. 19) were also rounded, some to a lesser degree but the auricle although long was weakly elevated. Shells from the Faeroes (Fig. 18) were almost as pyriform as some of the Loch Eil material.

Conclusions

On shell characters the experienced eye can separate *T. gouldi* from *T. flexuosa* by the shallow sulci, longer auricle and generally more rounded form of the former. However, the variations in adult form and the marked growth changes are confusing and it is strongly suggested that all samples of putative *T. flexuosa* from Scotland be checked for prodissoconch size.

REVISED DISTRIBUTION OF *T. GOULDI*

Following this re-examination of Scottish and North Sea material the following samples of *T. gouldi* were isolated.

Loch Etive Dunstaffnage Marine Laboratory – c. 200 specimens believed to be the residue from Blacknell & Ansell's work (56°32.5′N 05°03.5′W).

Loch Etive Sailean Ruadh 56°27.3′N 05°16.3′W. 27.iv.1992. Mud and organic detritus dredged from 16-25m. *c.* 100 specimens, in Killeen, Light & Smith collections.

Loch Eil no precise data. *c.* 100 specimens ex Dunstaffnage Marine Laboratory (1980) in SMS collection.

Loch na Cille (outer Loch Sween) 55°57.4′N 05°42.0′W. 04.ix.1985, 8 specimens, SMS collection, mixed with *T. flexuosa*.

Shetland Around Calbeck Ness, Sullom Voe, 60°29.6′N 01°17′W iv.1975, 32 lots NMS1977.100.337. iv.1983, NMW.Z1997.092, mixed with *T. flexuosa*.

'Cape Wrath' 4 juveniles, mixed with *T. flexuosa*. This sample was part of a sea loch survey which included Lochs Laxford, Inchard and Eriboll but only carries the "Cape Wrath" survey title.

Jura/Islay Dredge II, 1 specimen, RSMNH 1983009.337.03.

Firth of Forth Forth Spatial Survey, station 5, 56.04050°N 03.26967°W, 9m. NMS, mixed with *T. flexuosa*.

The locations of these samples considerably extend the range of *T. gouldi* in British waters and confirm its existence in Shetland. The presence of *T. gouldi* in Scottish sea lochs may be even more extensive and all samples should be reviewed.

There are relatively little data on the habitat preferences of *T. gouldi* and in most samples examined here there was a mixture of *T. gouldi* and *T. flexuosa*. Blacknell (1973) reports that in Loch Etive the two species are not mixed and that *T. gouldi* inhabits lower salinity conditions. This preference cannot be regarded as indicative as a whole as the sites in Sullom Voe and Loch Sween are in full salinity. Sediment particle size cannot be cited other than stating that both species prefer substrates with a relatively high mud content. The apparent restriction of *T. gouldi* to sea lochs and inlets may indicate a need for high concentrations of organic material and it may be more reliant on symbiotic bacterial chemoautotrophy than *T. flexuosa*. The data available on the gill structures and symbiotic bacteria do not indicate widely different adaptations, and the ecological preferences of *T. gouldi* and *T. flexuosa* remain unclear (Southward, 1986; Dando & Southward, 1986). *T. gouldi* does not appear to utilise the anthropogenic sulphide sources around well heads as does *T. sarsi* and this may be primarily due to the short lived and small ranging dispersal stage reported by Blacknell & Ansell (1974, 1975).

CONSERVATION STATUS OF *T. GOULDI*

The results of this review pose a number of issues relevant to the conservation status of *T. gouldi* and which could challenge it's priority position.

The current status is based upon the only previously confirmed population from Loch Etive where it was believed to be a glacial relic and where it had adapted to life in the reduced salinity environment (23-27‰). Furthermore, on the basis of Southward & Southward's (1991) work, and its believed disappearance from Loch Eil, *T. gouldi* was considered to be in serious decline.

Thus, the Objectives and Targets in the Action Plan (section 4) (English Nature 1999) were designed on those premises:

4.1 Maintain and where possible enhance the distribution of the northern hatchet shell within the UK.

4.2 Maintain and where possible, enhance the status of the population in Loch Etive, Scotland.

4.3 Ensure no further declines in the population(s) of the species due to anthropogenic factors.

4.4 Provide adequate legal status for the species to facilitate effective protection.

Proposed actions with lead agencies in Section 5 of the Action Plan include:

5.2.3 Confirm the importance of Loch Etive, Scotland as the site of a relic population of *T. gouldi*, by determining the distribution and status of this population.

5.2.4 Seek to identify any other key sites for this species within the UK, concentrating initial efforts on Loch Eil and Loch Sunart, Scotland.

5.5.1 Within key sites, ensure that the ecological requirements of the species are maintained.

The results of the present study bring into question the above conservation plans and could suggest an alteration in the current conservation status of *T. gouldi*.

The assumed restriction to a single sea loch is now shown to be untrue and instead it is scattered around the Scottish coast. Although it appears to be confined to inlets and sea lochs it can no longer be regarded as specific to a glacial relict type of environment. Similarly it can no longer be particularly associated with low salinity waters and thus the conditions in Loch Etive cannot be used as a general guide to the preferred habitat. Data have also been presented which question the presumed decline in Loch Etive in that numbers were taken as recently as 1992 albeit from a different site within the loch. Our data suggest that *T. gouldi* remains a rare species in British waters and is found at a few scattered localities. In Loch Eil and Loch Etive it appears to occur or have occurred in greater densities, reach a larger size and be ecologically separated from *T. flexuosa*. At all other sites *T. gouldi* and *T. flexuosa* have been found in mixed samples. Current data are insufficient to categorise the preferred habitat of *T. gouldi* and it is not possible to understand why the shell morphology of the Loch Eil and Loch Etive specimens is rather different or why they are larger.

We can surmise that the inlet/sea loch preference relates to the concentration of organic detritus that produces the sulphide required by the symbiotic bacteria. From the studies of Southward (1986) and Dando & Southward (1986) it has been shown that different species of *Thyasira* have different levels of dependence on the symbiotic bacteria and that the bacteria themselves differ between species. Such variation may, therefore, lie at the basis of ecological preferences. Consequently in locations where both *T. gouldi* and *T. flexuosa* occur together these may not be ideal habitats for *T. gouldi*. This may be the reason why the Loch Etive and Loch Eil specimens are larger and the populations apparently more dense. Consequently before altering the conservation status we should understand what it is that constitutes the preferred habitat and assess how many of the sites fulfil the criteria. We should also attempt to make more full analyses of the population sizes and their age structures, again in an attempt to recognise which sites support the fittest populations.

Thyasira gouldi does not have a widely dispersing planktonic larva but rather there is direct development within the large demersal egg. (Blacknell & Ansell, 1974). This may reduce colonisation potential and thus should preferred conditions move geographically, or new habitats appear, *T. gouldi* may not be able to respond. *Thyasira gouldi* may be more subject to localised extinction than species with planktotrophic development such as *T. flexuosa* and *T. sarsi*. The demersal lecithotrophic development may also lessen genetic mixing between populations. At this time we have no knowledge of the origins of the different populations or the relationships of the populations in this pan-arctic species. We need to ask whether the different shell morphologies are ecophenotypic or have a genetic basis. Could some populations such as that in Loch Etive be relict, but those say, in Sullom Voe and Firth of Forth, be due to a post-glacial colonisation with the poor dispersal explaining the few and scattered sites invaded? The anthropogenic introduction to these sites has been considered but we know that *T. gouldi* was present in Sullom Voe before any of the current North Sea oil industry had developed and thus bilge water dispersal between Norway and Scotland seems unlikely.

Although *T. gouldi* has now been shown to be more widespread this can be interpreted as fulfilling item 4.1 of the objectives of the species action plan. We cannot, however, at this time describe the preferred habitat requirements and cannot categorise the status of any of the known populations. Consequently before any changes to the conservation status can be made, survey, ecological and population genetic studies should be undertaken. A revised set of objectives, targets and actions is listed below.

Objectives and Targets

- Maintain the distribution of the northern hatchet shell within the UK.
- Maintain and where possible, enhance the status of chosen populations from Scotland.
- Ensure no further declines in the population(s) of the species due to anthropogenic factors.
- Provide adequate legal status for the species to facilitate effective protection.

Proposed actions

- Confirm the relative importance of the known populations of *T. gouldi*, by determining the distribution within sites, their densities and age structures.
- Assess the phyletic relationships of the Scottish populations and confirm the supposed relict origin of the Loch Etive population
- Seek to identify any other key sites for this species within the UK, concentrating initial efforts on Scottish sea lochs, Shetland voes and possibly Scapa Flow in the Orkneys.
- Research and define the ecological requirements of the species.

ACKNOWLEDGEMENTS

The authors wish to thank all those who kindly lent material for this study; Sankurie Pye (NMS), Tom Schiøtte (ZMC), Shelagh Smith, Environmental Resource and Technology Edinburgh, Cordah Ltd Aberdeen, Robin Harvey (Dunstaffinage Marine Laboratory, Oban) and the Scottish Environmental Protection Agency. To BP/Amoco

(UK) for initial sponsorship and particularly to John Hartley of Hartley Anderson Consultants for his continuing support and enthusiasm.

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THE BRACKISH WATER MUSSEL *MYTILOPSIS LEUCOPHAETA* (CONRAD, 1831) (BIVALVIA: DREISSENIDAE) IN THE RIVER THAMES

The brackish water mussel *Mytilopsis leucophaeta* (Conrad, 1831) is a species native to eastern America from the Hudson River to Tampico, Mexico (Marelli & Gray, 1983[1]), where it occurs in a range of brackish salinities but not in full strength sea-water (Siddall, 1980[2]). It was introduced into Belgium in the early 19th century (Marelli & Gray, 1983), and is presently known from brackish water bodies along the North Sea coasts from Germany through the Netherlands and Belgium into France. It was first recorded in the United Kingdom at Cardiff Docks in 1998 (Oliver *et al.*, 1998[3]).

During a survey of the flooded claypits at Cliffe, on the Hoo Peninsula in Kent, in November 1998 (Bamber *et al.*, 1998[4]), a high density of dead valves of *Mytilopsis leucophaeta* was found in the sediments of Cliffe Fort Lagoon (OS Grid reference TQ713760), being the first record of this species in England (BMNH Reg. No. 20001347). Accordingly, a subsequent visit (February 1999) examined emergent hard substrata, and live specimens were found on wooden posts and piling. The shells of live specimens measured up to 13.2 mm long, while dead valves were up to 15.2 mm. Live specimens showed conspicuous growth halts at around 5–7mm. In the Netherlands *M. leucophaeta* grows to about 13–14 mm in the first year reaching 24–27mm in three years (Gittenberger *et al.* 1998[5]). This suggests that the Kent specimens were probably around a year old with the growth halt possibly representing overwintering.

Cliffe Fort Lagoon is a 44 ha basin up to 4.3 m deep, with water retained around the tidal cycle by a weir and sluice system. The deeper waters overlay a substratum of cohesive mud with some gravel and shell breccia. This stable substratum supported a diverse ENLag.IMS.Ann biotope (Bamber, 1997[6]), with ragworm *(Nereis succinea), Polydora cornuta, Corophium insidiosum, Melita palmata* and a very dense population of the lagoon cockle *Cerastoderma glaucum.* The margins were bedded with gravel, supporting sparse *Ruppia* and emergent *Phragmites,* with some patches of *Scirpus* on the south-western side. Salinity in November 1998 was at 14‰. A previous survey of these lagoons in 1988 reported levels of 6‰ (Sheader & Sheader, 1990[7]), while in 1993 the same authors (Sheader & Sheader, 1993[8]) recorded salinities of 15‰ at a time of a breach in the seawall, since when the new weir and sluice system has been constructed. Neither survey recorded *Mytilopsis leucophaeta,* and it may be concluded that the species arrived no earlier than 1993.

Although *Mytilopsis leucophaeta* is potentially mature at 2.4 mm length, the mean size of sexually mature individuals is >7 mm length, at about 2 months old (Siddal, 1980). This species produces a veliger larva for planktonic dispersion; settled stages attach by a byssus onto hard substrata. With rapid growth to maturity and a dispersive larval phase, *Mytilopsis leucophaeta* has the potential to become a commercially significant fouling pest in potable and service-water pipes and culverts.

It has led to fouling problems in the Netherlands in the Velsen and Hemweg Power Stations which draw their cooling water from the Noordzeekanal (Jenner & Janssen-Mommen, 1993[9]; Rajagopal *et al.*, 1994[10]). Densities in the canal have been recorded at some 15,000 m^{-2}, while spat densities on PVC settlement plates in the Velsen Power Station intake have been recorded up to 6.5×10^6 m^{-2}, an order of magnitude higher than spat densities on similar panels deployed in the Noordzeekanal (Rajagopal *et al.*, 1994). Spawning in the Noordzeekanal occurred between June and September when water temperatures were ≥ 20°C. Settlement densities were highest at 2 m depth in the canal.

Specimens grew to 3 mm length within one month of settlement, and some reached 14 mm after one year.

The introduction of *Mytilopsis leucophaeta* to both Cardiff Docks and Cliffe Fort Lagoon is presumed to be from shipping. Although *M. leucophaeta* was not found in any other lagoons at Cliffe, it seems unlikely that Cliffe Fort Lagoon houses its only population in the Thames Estuary. With its potential for causing serious fouling (and significant economic cost), for example within the cooling-water systems of the Thames-side and adjacent Medway Estuary power stations, it is recommended that further surveys are undertaken to determine the spread of this xenobiont species in the region. Equally, consideration should be given to effective means of fouling control at those sites at risk, although current systems for control of the native mussel *Mytilus edulis* L. should be sufficient where those exist.

[1] MARELLI D.C. & GRAY S. 1983 *Veliger* **25**: 185–193.

[2] SIDDALL S.E. 1980 *Veliger 22*: 378–379.

[3] OLIVER P.G. *ET AL.* 1998 *J. Conch.* **36**: 13–18.

[4] BAMBER R.N. *ET AL.* 1998 *Natural History Museum Consultancy Report to English Nature* No. ECM 635/98.

[5] GITTENBERGER E. *ET AL.* 1998 *Nederlanddse Fauna* 2. Nationaal Natuurhistorisch Museum Naturalis, KNNV Uitgeverij & EISNederand, Leiden.

[6] BAMBER R.N. 1997 *English Nature Research Reports* No. 235.

[7] SHEADER M & SHEADER A. 1990 CSD Report No. 1115; Nature Conservancy Council, Peterborough.

[8] SHEADER M & SHEADER A. 1993 Lagoon Survey of Southern Cliffe pools. Unpublished Report to English Nature.

[9] JENNER H.A. & JANSSEN-MOMMEN J.P.M. 1993 In: *Zebra Mussels. Biology, Impacts and Control.* pp 537–555. Lewis Publishers, London.

[10] RAJAGOPAL S. *ET AL.* 1994 Report No. 163871-KES/WBR 94-3128. KEMA Environmental Research.

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NEW LAND-SNAIL RECORDS FROM TANZANIA

It is clear from fieldwork in forests across East Africa over the period 1995-2001 that there are still many new taxa requiring formal description. The purpose of this short communication is to report new records and range extensions for 3 taxa that are of particular biogeographical interest.

Oreohomorus sp. Nou and Hassama Hill Forest Reserves, Mbulu District, Arusha Region, Tanzania (approximately 140km SW of Arusha town). In forest-floor leaf litter at an altitude of 2000-2300m collected June 1998 (CM/MBS/PT). Shells (largest 35x10mm) have the characteristic pointed apex and patterned shell of Pilsbry's genus *Oreohomorus*[1]. This is apparently the first record of *Oreohomorus* from Tanzania. The genus *Oreohomorus* is represented by up to 21 species and has a geographical range concentrated in the Albertine (western branch) Rift Valley, west Uganda and east Congo. It extends across Uganda eastwards into west and central Kenya (including Mt. Kenya and Nairobi).

Hydrocena sp. Nou Forest Reserve, Mbulu District, Arusha Region, Tanzania collected 24.vi.1998 (CM/MBS/PT) at c. 2300m, and Kimboza Forest Reserve, Morogoro District, Morogoro Region, Tanzania (approx. 26km SE of Morogoro town) collected 19.i.1996 (PT) at 350m. Sieved from forest-floor leaf litter. The only previous report of this genus in East Africa is *Hydrocena kenyana* Connolly, which is considered to be endemic to forests on Mount Kenya[2]. Another species, *H. noticola* (Benson), occurs in South Africa and Malawi. Further study is required to establish the relationships among the Tanzanian, southern African and Kenyan species.

Truncatellina arboricola Tattersfield. Single shell from forest on the Shira Route (west slopes), Mount Kilimanjaro Forest Reserve, Moshi District, Kilimanjaro Region, Tanzania on 2.vii.1998 (CM/PT/MBS) at 2600m. This sinistral species has previously only been reported from afromontane forest at c. 2400-2700m on the west slopes of Mount Kenya[2].

[1] PILSBRY H. 1919 *Bull. Am. Mus. Nat. Hist.* **40:** 1-335
[2] WARUI C.M. *ET AL.* 2001 *J. Conch.* **37***(3):* 271–300.

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REVIEWS

The Liguus *Tree Snails of South Florida* by Henry T. Close 2000, University Press of Florida. 162 pp. ISBN 0-8130-1814-5. Cost US$49.95. Hardback.

Few molluscs have shells exhibiting a greater degree of colour polymorphism than the genus *Liguus.* Although there are only 5 or 6 species no less than 180 colour forms have been named. This book looks at the single species found in Florida, *Liguus fasciatus* (Müller, 1774), which occurs there in some 59 named colour forms. Although the species is also found in Cuba, where at least 32 additional named colour forms occur, these are not discussed here.

The author has brought together a mass of information covering amongst other things; the animal's life cycle, feeding, habitat preference, predators, *Liguus* as the inspiration for Seminole Indian costume, sinistral specimens, etymology, and especially distribution. Many of the colour forms originally existed as isolated populations living on the different Florida Keys or on 'hammocks' - slightly elevated wooded areas within swamps or grassland. Over the years this pattern has been obscured as hurricanes or fires or more recently human land development obliterated colonies or through human intervention with the accidental or deliberate transplantation of colour forms to different areas. Today there are many threats to these animals, which are protected under Florida law, and colonies of the different colour forms have been established on hammocks within the Everglades National Park to try to ensure their continued survival.

The core of this book, some 66 pages looks at the identification of Florida *Liguus.* Each form is discussed commencing with "As much of the original description as you will need to identify the form" together with detailed comments and comparisons with similar forms. Although the quoted original descriptions are indicated by indented paragraphs it would perhaps have been clearer had they been given in quotation marks, many readers will use the identification section without reading the explanatory preamble. To further facilitate identification 8 full colour plates, several of which are double page spreads providing 14 pages of colour in all, illustrate some 266 specimens. Each form is illustrated by several examples showing variation within the form. It is perhaps unfortunate that all bar one specimen is shown in dorsal view, especially since "There are differences in the columellae of certain white shells that make them a little easier to tell apart". The book also contains some 44 black and white photographs and 11 maps. There is a good bibliography, and a useful chronology although it is surprising that several publications mentioned in the chronology are not detailed in the bibliography. The index, however, is totally inadequate, many subjects covered in the text are not indexed or only partially indexed.

This book is best where the author is reporting factual information, however, when it comes to the interpretation of this information the author shows both a lack of understanding of biological principles and of taxonomic practice. As an example of the former the author spends much space discussing hybrids between different colour forms of *Liguus,* whereas the glossary incorporated in the International Code of Zoological Nomenclature specifies that a hybrid is "The progeny of two individuals belonging to different species. The progeny of two individuals belonging to different subspecies of the same species are not hybrids". Therefore, by clear implication, the progeny of two different colour forms should not be considered as hybrids. When it comes to taxonomic practice, throughout the book the author refers to the colour forms simply as *marmoratus* and *castaneozonatus* etc. rather than *Liguus fasciatus* form *marmoratus* or even L.f. form *marmoratus.* This frequently leads to the situation where these names are confusingly capitalised as in the picture caption "*Roseatus* and *castaneozonatus* mating". This is particularly annoying in the principal headings in the identification section, when the genus and specific names are used to show how the original authors treated each form. *Osmenti*, L.f. (Clench 1942) would be clearer as L.f. form *osmenti* Clench, 1942.

These beautiful shells have aroused a passionate interest among some collectors, and the author's own enthusiasm clearly comes over through the text. It is this enthusiasm, together with the extreme polymorphism of these shells, which has led to this group being a 'splitters' delight since "As far as *Liguus* collectors are concerned, once a name has appeared, it will probably never be relinquished, especially by those collectors who happen to have shells exhibiting the subtle distinguishing characteristics involved". Enthusiastic collectors will, no doubt, find this book useful in order to be able to put numerous names to their shells, however the scientific validity of many of these names is somewhat dubious. Henry Pilsbry wrote of *Liguus* colour forms that "Many of them intergrade freely, being selective stages of clines, and most of them are of a taxonomic grade which would not be worth naming in other genera".

Kevin Brown

Molluscos Magallánicos: Guía de Moluscos de Patagonia y del Sur de Chile by Daniel Oscar Forcelli 2000. Vázquez Mazzini Editores (Concepción Arenal 4864 (1427), Buenos Aires, Argentina) 200pp. ISBN 987-9132-01-7 Cost Approx £31. Paperback.

The Molluscan faunas of tropical South America have been well documented in popular literature, A.M. Keen's *Seashells of tropical Western America* and E.C. Rios's *Seashells of Brazil* are key works in any Molluscan library. However there has long been a need for a book covering those species from the colder more southerly part of the continent, this book now fills that need.

Covering, an area roughly between Concepción in Chile and the Valdez Peninsula in Argentina, and including the Falkland Islands (here referred to as Islas Malvinas) this book gives detailed coverage of 627 species of mollusc. Along with the gastropods and bivalves which you would expect the book includes species of scaphopod, chiton, cephalopod and even 9 species of Aplacophora, while the gastropods include the often ignored nudibranchs making the coverage truly comprehensive.

For each species the author gives full scientific names followed by details of synonyms, shell size, the broad distribution within the Magellanic region and an indication of whether the species is endemic, a brief description, and in many cases details of habitat and rarity. Each species is individually illustrated immediately after the description. The majority of species are shown in full colour photographs, although some black and white photographs, microphotographs and line drawings, the latter often taken from original descriptions, have been used especially for the smaller species. The careful use of different methods of illustration has ensured maximum clarity and ease of identification. A number of the shells illustrated are type specimens and a few supplementary pictures illustrating living molluscs have also been included. As well as the 627 species covered in detail the text also refers to a number of additional species cited from the Magellanic region in literature but which have not been covered here in depth. Often helpful comments are given relating to these additional species for example we are informed that *Lissarca notocardensis* Melville and Standon, 1914 cited from the region is an Antarctic species, while *Pareuthria scalaris* (Watson, 1882) and *P. venustula* Powell, 1951 cited from the region may ultimately prove to be synonyms of *P. ringei* (Strebel, 1905). Altogether some 170 extra species are treated in these notes.

Introductory sections of the book include discussions on the region's geography, Molluscan Biology, Systematics and Ecology, Molluscs and Men and Molluscs of Economic Importance. There is also a helpful glossary.

Inevitably there are a few errors, however these are relatively minor and few in, number. The genus *Balcis* is referred to as *Balsis*, and on p 74 *Crepidula* aff. *onix* should surely be *onyx*. A more serious criticism refers to the index. This is generally good, but fails to include any of the synonyms referred to in the text. Thus while *Buccinulum meridionalis* (E.A. Smith, 1881) is fully indexed under both genus and specific name, *Chauvetia euthrioides* (Melville & Standon, 1898) which the author quotes as a synonym of *B. meridionalis* is not indexed either by genus or specific name. Anyone with a specimen labelled *C. euthrioides* will fail to find the appropriate reference using this index.

I also feel that the failure to provide any bibliographical references is a serious omission. One of the problems with studying this region's mollusca is that so much information is scattered, often in obscure journals which are difficult to trace. Even a list of principal references would have been helpful. This omission also means that where illustrations have been reproduced from earlier works it may be unnecessarily difficult to trace the original work. For example the photograph of *Anatoma euglyptus* (Pelseener, 1903) is quoted as reproduced from Dell 1990. I assume that this is taken from R.K. Dell's *Antarctic Mollusca* but have no easy way of checking. If there is any future reprint of this book the publishers should seriously consider both amending the index to include synonyms and adding a bibliography. Neither would involve expensive alteration to the layout of the existing text but would greatly improve the usefulness of the book.

This book is a very welcome addition to the growing number of regional monographs, all the more so since there has been no previous comprehensive work devoted to the Magellanic Region's Molluscs. Moreover many of the species included especially the numerous microshells, are not illustrated in other more general identification guides. That the text is in Spanish should not deter anyone from buying this book which is extremely reasonably priced. It can be highly recommended.

Kevin Brown

CONCHOLOGICAL SOCIETY OF GREAT BRITAIN & IRELAND

REPORT OF THE COUNCIL 2000-2001

The Society announced with regret the deaths of four members, Mr Francis de Bartolomé, member since 1949, past President, Dr Alex Comfort, member since 1939, Mr Geoff Cox, member since 1973 and Mr Dominic Rawlingson-Plant member since 1997.

Council Positions

Dr Rundle began his first year as President of the Society. Mr Gillard was elected as Hon. General Secretary, Mr Buckle as Hon. Treasurer and Mr Boyce as Hon. Programme Secretary. New Ordinary members of Council were Dr Alexander, Ms McIvor and Mr Carr.

Mr Palmer and Dr Honnor began their second year with Mr Wimbleton co-opted, while Mr Brown began his third year with Ms Nelson and Mr Smith co-opted.

Publications

Two issues of the *Journal of Conchology* (Volume **37**: 1–2) and four issues of the *Conchologists' Newsletter* (Volume **9**, Part 3, Numbers 153-156) were published, together with Dr Kerney's *Atlas of the Land and Freshwater Molluscs of Great Britain & Ireland*. The Society also published the Annual Programme Card and a new Members' Guide, giving information about the Society and its activities and incorporating Society Rules, Membership list and mail order form.

Dr Honnor assumed responsibility for Past Publications.

Other Council Matters

Five Council meetings were held and in addition there were three meetings of the Publications Committee.

While regretting the unfortunate loss of Mr Francis de Bartolomé, Council is very grateful for the bequest of £1000 and his collection of Conchological books to the Society. The library was recently auctioned to Members yielding over £18000.

Amongst the issues raised by Council were further discussions on a Members' Guide now published, treatment of non-marine records, future technical editorship of the *Journal*, further joint meetings with the Malacological Society of London, disposal of an ever-growing stock of back copies and adoption of a Reserves Policy document.

I would like to thank all members of Council for their contributions during the year, especially to Ms Reynolds whose efficiency and dedication has made it so much easier to take on the role of Secretary.

Colin Gillard
Hon. Secretary

PROGRAMME SECRETARY'S REPORT - MARCH 2001

The programme for 2000 consisted of six indoor meetings held at the Natural History Museum in London, a joint meeting with the Malacological Society of London held at the Linnean Society at Burlington House in London, seven field meetings and two workshops.

Indoor meetings: Lectures were given by Michael Jackson (Freshwater molluscs of the River Waveney grazing marshes), Janet Ridout Sharpe; (Shells from the ancient Aegean), Brian Eversham (Presidential address: Small scale distributions of non-marine species); Anna McIvor and Stephan Müller (The depressed River Mussel in trouble?), Michael Hughes and David Bolton (Can scale paint a true picture: the Devon recording experience), and Amanda Millar (Woodland snails and coppicing: some results from a woodland in Sussex).

The joint meeting with the Malacological Society of London was on the subject of Molluscs in the new Millennium: the future of molluscan studies and societies in the British Isles.

Field meetings: Were held at the following venues: Isle of Wight (Leaders: Bill Pocock and Malcolm Symonds), Ingleton area, West Yorkshire (Leader: David Lindley), Steep Holm in the Bristol Channel (marine meeting, Leader: Colin Gillard), Kington area, Herefordshire (Leader: Keith Alexander), Shalford, Surrey (Leader: Martin Willing), Grand Union Canal, Hertfordshire (Leader: Pryce Buckle), Quidenham Mere, Norfolk (Leader: Richard Preece), and North Somerset and North Devon (marine meeting, Leader: Colin Gillard).

Most of the field meetings were reasonably well attended, but the meetings in the Isle of Wight and Herefordshire managed to muster only four attendees a piece, which was a pity since both locations were productive.

The following workshops were held: A beginner's guide to naming shells, tutored by Adrian Rundle at his home in Richmond, Surrey; and the Society's fourteenth Molluscan workshop, this time on the subjects of Love Darts and Isle of Wight Fossil Molluscs, held at Judith Nelson's home in Woking, Surrey, and tutored by Adrian Rundle and Bill Pocock.

The Society is grateful to all those people who contributed to the above programme, as speakers, field meeting leaders, and meeting and workshop organisers and tutors.

Ron Boyce
Hon. Programme Secretary

TREASURER'S REPORT 2000

Income
Income from subscriptions was at much the same level as in 1999. Investment income during the year increased by approximately 16%.

Sales
Sales were at a reduced level due to the fact that the 1999 figure includes sales of the *Atlas of the Land and Freshwater Molluscs of Britain and Ireland,* the majority of which have now been sold. 1999 also included the sum realised on the sale of the books bequeathed to the Society by Mr Terry Crowley.

Donations and Legacies
We thank Mr John Wrightson and Mrs. A. Adele-Reynolds for their donations. The Society gratefully acknowledges the bequest of £1,000 from Francis de Bartolomé and the legacy of his library of conchological books which will be auctioned to members during the year 2001.

Publications
The cost of producing the *Journal* and the *Newsletter* has risen by approximately 6%.

Indoor Meetings
The cost of meetings includes £299.25 towards the cost of the very successful joint meeting with the Malacological Society on 8 April 2000, "Molluscs in the New Millennium". The cost of hiring the Palaeontology Demonstration Room at the Natural History Museum increased by nearly 17% as from October 2000.

Investments
The market value of the Society's investments increased by almost £14,220.

Fixed Assets
The computer equipment has been depreciated by £600, as it is the intention to write it off over five years on a straight line basis.

Movement in Reserves
The profit for the year was £2,693, from which has been deducted the grant of £800 made to the University of Cambridge Aquatic Ecology Group towards the purchase of a boat. This is used in connection with research into the invasive Asiatic Clam, *Corbicula fluminea.* £1893 was carried to the reserves, together with the increase in market value of the investments of £14,220.

Summary
The Society continues to be in a good financial position and it is recommended that the subscription rates remain unchanged. Cash at the bank includes approximately £20,000 on deposit, and we should take steps to invest this more profitably in the short term, until such time as Council decides how best to utilise the funds for research and grants.

Pryce Buckle
Hon. Treasurer

CONCHOLOGICAL SOCIETY OF GREAT BRITAIN & IRELAND. ACCOUNTS FOR THE YEAR ENDED 31 DECEMBER 2000

INCOME AND EXPENDITURE ACCOUNT

	31 Dec. 2000 £	31 Dec. 1999 £
Income		
Fees and Subscriptions	11,202	11,013
Investment Income	3,311	2,843
Sales	668	3009
Donations and Legacies	1,025	520
Sundry Income	99	0
	16,305	17,385
Expenditure		
Publication Costs	9,460	8,930
Stationery and Sundry Postage	1,457	1,804
Meetings	1,808	890
Sundry Expenses	269	222
Purchased for resale	18	1,284
Depreciation of computer equipment	600	600
	13,612	13,730
Profit for the year before Grants	2,693	3,655
Grants made	800	0
Profit carried to Reserves	1,893	3,655
Movement in Reserves		
Society Reserve Brought Forward	88,289	79,432
Profit for the year	1,893	3,655
Transfer from Life Membership Fund	0	0
Increase in Market Value of Investments	14,220	4,202
Release of provision for computer	0	1,000
	104,402	88,289

BALANCE SHEET

	31 Dec. 2000 £	31 Dec. 1999 £
Current Assets		
Cash at Bank	21,879	19,723
Debtors	36	128
	21,915	19,851
Current Liabilities		
Creditors and Accrued Charges	3,600	4,000
Subscriptions in Advance	1,412	1,441
Life Membership Fund	2,760	2,760
Other Provisions and Reserves	281	281
	8,053	8.482
Net Current Assets	13,862	11,369
Investments - at Market Value	88,740	74,520
Fixed Assets - Computer Equipment	1,800	2,400
Net Assets	104,402	88,289
Represented by:		
Society Reserves	104,402	88,289

Pryce Buckle	N. Light
Hon. Treasurer	Hon. Examiner

REPORT OF THE TRUSTEES FOR 2000

1 The official name of the charity is:
The Conchological Society of Great Britain and Ireland.

2 Working names for the charity are:
The Conchological Society or "Conch Soc".

3 The charity's Registered Number is:
208205.

4 The official address is:
(Honorary Secretary) Mr C.L. Gillard, 1 Court Farm, Hillfarrance, Taunton, Somerset, TA4 1AN.

5 The objects of the Charity's constitution are:
To promote for the benefit of the public the study of Mollusca in its widest aspects.

6 The Trustees' names are:
B. Colville and D. Long.

7 The body entitled to appoint trustees is:
Council of the Conchological Society of Great Britain and Ireland.

8 Brief review of the main activities and achievements of the society in relation to its objects:

The Society promoted knowledge of Mollusca through indoor meetings with lectures (7 in 2000) 5 workshops (2 in 2000), and field recording meetings (7 in 2000) either in furtherance of its marine and non-marine mollusc distribution recording schemes for Britain, Ireland and surrounding seas or, in one case, to study fossil molluscs. In 1999 the Society published a quarterly Newsletter, and one part of the *Journal of Conchology.* The Hon Conservation Officer has again co-ordinated the provision of molluscan conservation advice to organisations and individuals and has provided molluscan conservation-related news items to the British Wildlife magazine.

9 Signature of the trustee authorised to sign the report:

(B Colville) Date: 16.1.2001

2000 Tax & dividends from Conchological Society Investments

	Tax £	Net Dividend £	Tax £	Net Dividend £
M & G Dividend Fund 50280 Units (£29565)[1]	70.78	(4.1.2000) 637.05	47.48	(3.7.2000) 427.38
Save and Prosper Smaller Companies Income Fund 7040.4 Units (£9236)	1.02	(31.3.2000) 9.15		
Mersey Docks & Harbour Co OS 436 OS (£2317)	5.81	(27.4.2000) 52.32	2.91	(26.10.2000) 26.16
Treasury Stock 2006 $7^{3}/_{4}\%$ £8270 (£9300)	gross	(8.3.2000) 320.46	gross	(8.9.2000) 320.46
Royal Bank of Scotland Group plc 1700 Ordinary Shares and 1700 additional value shares (£28322)	38.34	(18.2.2000) 345.10	17.94	(13.10.2000) 161.50
National Savings Income Bond monthly (£10000)				(gross total for 2000) 581.83

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[1] Valuations in brackets are rounded to the nearest £ and as at close of business 29.12.2000, from the Financial Times 30.12.2000.

RECORDER'S REPORT: NON-MARINE MOLLUSCA

The last year of the twentieth century was one of exceptional activity in mollusc recording, stimulated at least in part by our new *Atlas.* An excellent tetrad atlas for Oxfordshire has appeared, a welcome addition to the small number of such published surveys (S.J. Gregory & J.M. Campbell, *An Atlas of Oxfordshire terrestrial Mollusca.* Oxfordshire Museums Service. Occasional Paper No. 20). The following vice-comital novelties—a larger number than for many years past—have been filed since the last Report *(Journal of Conchology* **37** (2001), p. 239). Unless stated otherwise, all were verified from material collected during the year 2000. Among the many who submitted mapping records I should particularly like to thank Geraldine Holyoak for her intensive work in Cornwall and in Ireland (a country from which the gathering of information has never been easy), and Adrian Sumner for much comparable work in Scotland, including such difficult terrain as the Isles of Lewis and Harris.

Cornwall West (1): *Vertigo moulinsiana, Vallonia pulchella,* Penhale Camp, Cubert (10/7857), Geraldine Holyoak.

Cornwall East (2): *Planorbis carinatus,* R Tamar, Polson Bridge (20/3584; fresh shell). *Spermodea lamellata,* Peter's Wood, Boscastle (20/1190); both Geraldine Holyoak.

Devon South (3): *Limax nyctelius,* Crediton (21/8300; garden), D.E. Bolton.

Wilts North (7): *Hygromia cinctella,* Leigh Delamere (31/8879), J.M.C. Hutchinson, 1999.

Wilts South (8): *Boettgerilla pallens,* Wilton (41/1031; churchyard), J.M.C. Hutchinson, 1999.

Dorset (9): *Pisidium tenuilineatum,* R. Frome, West Holme (3018886), M.J. Willing.

Hants South (11): *Menetus dilatatus,* Hatchet Pond, Beaulieu (41/3601), J. Biggs and Mericia Whitfield; *Arion flagellus,* Titchfield (41/5205), M.J. Willing.

Sussex West (13): *Hygromia cinctella,* Midhurst (41/8820; garden), M.J. Willing.

Essex South (18): *Zonitoides excavatus,* Heather Hills, Little Baddow (52/7807), S.H. Hudgell.

Middlesex (21): *Hygromia cinctella,* Fulham (51/2477; garden), Ann Kuter.

Berks (22): *Perforatella subrufescens,* Badbury Forest (41/2595), K.N.A. Alexander, 1995.

Oxford (23): *Hygromia cinctella,* Oxford (42/5307), J. Webb (*per* S.J. Gregory).

Suffolk East (25): *Hygromia cinctella,* Felixstowe (62/2935; garden), I.J. Killeen.

Norfolk East (27): *Hygromia cinctella,* Acle (63/4010), G.M. Coupland.

Gloucester East (33): *Gyraulus laevis,* Whelford Pools (41/1799), D.C. Long; *Pisidium tenuilineatum,* R. Coln, Coln St Aldwyn (42/1405), I.J. Killeen.

Gloucester West (34): *Lehmannia valentiana,* Westbury-on-Trym (31/5677; allotment gardens), J.M.C. Hutchinson, 1999.

Monmouth (35): *Boettgerilla pallens,* Abergavenny Castle (32/2913), J.M.C. Hutchinson.

Radnor (43): *Boettgerilla pallens,* Llandrindod Wells (32/0561), J.M.C. Hutchinson.

Montgomery (47): *Arion owenii, Boettgerilla pallens,* Newtown (32/1091), J.M.C. Hutchinson.

Caernarvon (49): *Planorbarius corneus,* Cors Geirch (23/3335), I.J. Killeen, 1999; *Menetus dilatatus,* Glanllynnan, Llanystumdwy (23/4537), J.H. Bratton; *Cochlicella barbara,* Bardsey Island (23/1121), I. Bonner (*per* R.W. Marriott).

Anglesey (52): *Anodonta cygnea,* Llyn Maelog (23/3273), J.H. Bratton.

Lincoln South (53): *Boettgerilla pallens, Lehmannia valentiana,* Spalding (53/2824; garden centre), C. du Feu.

Lincoln North (54): *Arion flagellus,* Walesby (53/19), C. du Feu.

York South-east (61): *Arion flagellus,* Brough (44/9525), A. Norris.

York South-west (63): *Limax maculatus,* Rotherham (43/4392; pavement), W.A. Ely.

York North-west (65): *Vertigo genesii,* Cronkley Fell (35/8428), B. Colville and I.J. Killeen.

Cumberland (70): *Arion flagellus, Lehmannia valentiana,* Carlisle (35/4255; garden), S.P. Dance.

Haddington (82): *Limax cinereoniger,* Pressmennan Wood (36/6273); *Candidula gigaxii,* North Berwick (36/5885; confirmation of old Census record); both A.T. Sumner.

Edinburgh (83): *Lehmannia valentiana,* Edinburgh University Ecology Greenhouses (36/2673; garden), Adèle du Feu.

Linlithgow (84): *Lymnaea glabra, Zonitoides nitidus,* Lochcote Marsh (26/9774), A.T. Sumner.

Perth East (89): *Limax flavus,* Pitlochry (27/9458; gardens), C. du Feu.

Kincardine (91): *Vertigo angustior,* Red Man Bay, Stonehaven (37/8988), R.W. Marriott.

Easterness (96): *Boettgerilla pallens,* Cawdor Castle (28/8449; garden), C. du Feu.

Ross East (106): *Aplexa hypnorum,* Ferryton, Black Isle (28/5766), T. Huxley.

Hebrides (I 10): *Arion flagellus,* Portnan Giuran, Lewis (19/5537); *Arion owenii,* Gress, Lewis (19/4941); *Tandonia budapestensis,* Stornaway, Lewis (19/4132); all A T. Sumner.

Roscommon (H25): *Viviparus viviparus, Bithynia leachii, Dreissena polymorpha,* R. Shannon (south bank), Carrick-on-Shannon (M9399), Geraldine Holyoak.

Leitrim (H29): *Viviparus viviparus, Bithynia leachii, Dreissena polymorpha,* R. Shannon (north bank), Carrick-on-Shannon (M9399; *Vertigo geyeri,* Cloontypruhlish (G7848); *Boettgerilla pallens,* Rossinver (G9147); *Pisidium amnicum,* R. Shannon, Jamestown (M9897); *Pisidium lilljeborgii,* Lough Macnean (H0239); all Geraldine Holyoak.

Fermanagh (H33): *Vertigo lilljeborgi,* Meenameen Lough (H0255); *Vertigo geyeri* Glencreawan Lough (H0256); *Boettgerilla pallens,* Hanging Rock (H1136); *Limax cinereoniger,* Glencreawan Lough (H0357); *Musculium lacustre, Dreissena polymorpha,* Lady Craigavon Bridge, Upper Lough Erne (H3327); all Geraldine Holyoak.

Our knowledge of the genus *Vertigo* in the British Isles continues to grow and there have been several discoveries of importance. The rare Arctic-Alpine species *Vertigo genesii* has been found at a second site in Teesdale, this time in north Yorkshire (v.c. 65), a mile or two south of the original discovery at Widdybank Fell in Co. Durham in 1979. The new site at Cronkley Fell is a base-rich hillside flush of similar character to that at Widdybank Fell. *Vertigo geyeri* has been found in calcareous flushes in two additional Irish vice-counties, Leitrim and Fermanagh, and *Vertigo lilljeborgi* was detected in a *Carex* mire by a lough in Co. Fermanagh. *Vertigo angustior* was found on the coast of Kincardineshire in short *Festuca ovina* turf just above high-water mark, in two small colonies about three-quarters of a mile apart – the most northerly yet detected in Britain. Lastly, the mainly lowland snail *Vertigo moulinsiana* was unexpectedly discovered in a *Phragmites* swamp in Cornwall, about 130 miles from its nearest recorded sites in Dorset.

Some other finds of native terrestrial snails are worthy of note. *Spermodea lamellata* has been found in an oak wood in Cornwall, a very isolated locality for this declining north western species (see *Conchologists' Newsletter* No. 155 (2000) p. 429). *Zonitoides excavatus,* a calcifuge barely known from eastern England, has turned up at several spots in ancient acidic woodland near Chelmsford in Essex, a county from which only Postglacial fossils were previously known. It is pleasing to record also *Perforatella subrufescens* in ancient coppice woodland in Berkshire, an outlier from its more continuous area of distribution in Gloucestershire and the Welsh borders.

Among introduced species, the outstanding success story is of *Hygromia cinctella,* a snail which is evidently still spreading rapidly. It has been found in gardens and waste ground in six new vice-counties across southern England, northwards to Norfolk. The mediterranean helicellid *Cochlicella barbara,* previously known only from Devon and Glamorgan, has appeared in north Wales, living among *Carex arenaria* in sandy ground on Bardsey Island. A much older introduction, *Candidula gigaxii,* has been rediscovered in coastal grassland not far from its sole recorded Scottish occurrence near North Berwick (Haddington) where it was last seen in 1930. Among the slugs, *Boettgerilla pallens* continues its seemingly unstoppable advance, colonies being reported from both wild and disturbed habitats in eight additional vice-counties, north as far as Inverness-shire (gardens at Cawdor Castle). The so-called 'greenhouse slug' *Lehmannia valentiana* is also spreading and has been found in Scotland for the first time, in glasshouses and in adjacent gardens belonging to Edinburgh University. Most interesting of all, the north African species *Limax nyctelius* has been confirmed living in the open in the British Isles. This slug was first noted in Britain in 1934 by A.R. Waterston in greenhouses at the Edinburgh Botanic Gardens, and a little later on also at the Glasgow Botanic Gardens. In 1988 a possible juvenile specimen was found by David Long under a churchyard wall at Pakefield in Suffolk (62/5390), but a dissection proved inconclusive. David Bolton has now found undoubted specimens (confirmed by Stella Davies) in a garden at Crediton and at two other sites in South Devon, and the species is evidently firmly established in the area.

Arion flagellus is a slug of more doubtful status in the British Isles. Clearly it is still badly under-recorded. It has been confirmed from four further English vice-counties, and Dr Sumner's work in the Outer Hebrides has shown it to be by far the commonest large arionid there (and not *Arion ater,* as might have been expected).

Among freshwater molluscs the most important discovery is perhaps that of *Pisidium tenuilineatum* in rivers in Dorset and Gloucestershire. This minute and probably declining species was found in several places in the course of a distributional and ecological study undertaken by Martin Willing and Ian Killeen. Finds of *Lymnaea glabra* (Linlithgow) and *Aplexa hypnorum* (Ross East) are also worthy of remark; both species are very rare in Scotland. *Anodonta cygnea,* mainly a lowland species in the British Isles, has been verified from a eutrophic lake on Anglesey. The north American planorbid *Menetus dilatatus* appears to be spreading, and has been noted in Hampshire and Caernarvon, in both cases in ponds. Though not new to the county, Dr Bratton has also discovered a further locality for *Menetus* in Merionethshire (v.c. 48), in a ditch behind the sea wall at Draenogan-bach (23/6035). In Ireland, a surprise has been the discovery of *Viviparus viviparus* living freely in a stretch of the River Shannon south of Carrick-on-Shannon. Can this be a recent introduction? Despite scattered old reports of *V. viviparus* in Ireland, including possible Postglacial fossils in Co. Waterford and Co. Carlow, its history in that country remains obscure. A population was reported a few years ago from a lake on the Shannon floodplain about seven miles away at Drumshanbo, Co. Leitrim (G 9609), though the species was seemingly absent from the river itself *(Irish Naturalists' Journal* **25** (1996), p. 278). *Dreissena polymorpha* is a more certain introduction to Ireland, and a very recent arrival. This unwelcome pest is spreading rapidly, having invaded further sites along the River Shannon in Roscommon and Leitrim, and, abundantly, Upper Lough Erne in Co. Fermanagh.

This is my last annual Recorder's Report. I took over from Mr A.E. Ellis on 18 February 1961. Looking back forty years one is naturally struck by the great increase in knowledge that has take place over that period. Grid mapping schemes were then only just beginning, and ours was the first for any invertebrate group, set up at the friendly prompting of Dr Frank Perring, then running the highly successful mapping project pioneered by the Botanical Society of the British Isles and based at the Cambridge Botanic Garden. It is curious to reflect how attitudes to biological recording have changed since then: our activities were, for the most part, regarded with amused tolerance by professional biologists, and considered as little superior to stamp collecting or train spotting. The terms 'environment', 'conservation' and 'heritage' scarcely existed in their modern senses. Today, by contrast, the authority of our Society is widely respected. Our advice is sought by government agencies, and funds are provided by the taxpayer to protect invertebrates, including molluscs.

It is pleasant to acknowledge the help I have received over the years. First come the many members of the Conchological Society, past and present, for without their energy and dedication nothing could have been achieved. I owe a great debt also to my predecessors as honorary Recorders: the high standards that they set for the verification of data remain central to any scheme, however sophisticated. Outside the Society, people of the most diverse backgrounds supplied me with specimens or information; many I never met, but often they became regular correspondents and firm friends. The Society's association with the Biological Records Centre (Monks Wood) since its inception in the early 1960s has been mutually enriching, and I would like to single out for thanks Frank Perring (first director of BRC); his successor Paul Harding; Diana Scott, who did most of the work in preparing our 1976 *Atlas*, and Mark Telfer, without whose calm expertise the 1999 *Atlas* would not have been possible. Monks Wood continues to play an important role in facilitating the free interchange of information between local record centres, statutory bodies, and societies like our own. Lastly, I am most grateful to the authorities of the Natural History Museum—in particular Dr John Peake and Dr Peter Mordan—for providing me with postal and other facilities within the Department of Zoology, an arrangement that has been of much benefit to the Society. I am very pleased to report that the Museum has agreed to give a permanent home to the paper database of the national scheme, i.e., the 350,000 or so gridded records submitted between 1961 and 2000, together with all my correspondence and related files. This archive will continue to be freely accessible to future Non-marine Recorders and all *bona fide* enquirers, and will join other important material in the Department of Zoology associated with our history, such as the Taylor and Roebuck 'Monograph notebooks', the early vice-comital Census ledgers, and the papers and collections of several of my predecessors, notably L.E. Adams, Charles Oldham, A.E. Boycott and A.E. Ellis.

M.P. Kerney

RECORDER'S REPORT: MARINE MOLLUSCA

Computerisation of marine records has continued and at the end of the year the long-awaited revised version of Recorder 2000 was introduced. Michael Weideli (who has played an important part in progressing the Society's computerisation of marine mollusc data) is a JNCC approved supplier of Recorder 2000. He will continue to give voluntary support to the Society's marine data input including managing the transfer of our data from RECORDIT to Recorder 2000. This move will achieve two important aims. The first means we will be using the same system as other organisations involved in compiling and maintaining biological record databases. The second means that our database will eventually mesh in with others linked to MarLIN and the National Biodiversity Network. The mechanics of this latter objective are still in early stages of formulation and in the first instance the Society's presence on the MarLIN web site is likely to be represented by some pages giving information about our recording activities and sample data and maps. It is the hope of those who are managing the MarLIN project that all marine records, whether collated and managed by individual specialist societies such as the Conchological Society, or local Recording Centres for example, will be accessible on the Web. I believe this ideal is some years in the future and there are some important issues of data management including authentication of records and protocols related to availability which will have to be resolved.

The Society's field recording activities continue to be an important source of marine molluscan records. In September a field trip to the Somerset coast, under the leadership of Colin Gillard, took place. During the week various coastal sites between Kilve, Somerset and Bucks Mill, Devon were examined. Much of this area was new territory for Society field recording. Whilst that trip was under way, English Nature-funded survey work was carried out in southern Cornwall and the Isles of Scilly. The objective was to search more widely for sites of *Paludinella littorina* and during a total of two and a half weeks, a further 24 sites were identified. A significant number of these sites were on the Isles of Scilly where the snail was living in interstitial microhabitats on exposed and rugged granite boulder upper shores. Earlier in the year (July) John Llewellyn Jones found *P. littorina* living in caves at Holywell Bay, which is the first record for the north Cornwall coast. This is a satisfactory find as it provides a linking population between sites in southern Cornwall and north Devon. During May and June 2000 much of the Cornish coast from Land's End north to the Camel Estuary experienced mass strandings of cuttlebones. In the past most bones have been attributed to *Sepia officinalis* with a minority of small specimens with a pink flush on the dorsal surface identified as *S. elegans.* Closer inspection of the pink bones (*c.* 5% of the total) has revealed the presence of a third species, *Sepia orbigniana* for which there are only 2 former 19th century and 2 early 20th century records for mainland Britain. Re-examination of Cornish material in the collections of some current members has shown that this species has been collected in the very recent past so it has clearly been overlooked and may turn up in collections from elsewhere in the British Isles.

At the time of compiling my 1999 report I was able to affirm a prediction of further records for 2 of 3 species reported in my 1998 report. No new records for the third species, *Truncatella subcylindrica,* were then forthcoming. However, during fieldwork for the Irish marine mollusc atlas, Shelagh Smith and Julia Nunn located 2 sites for this species on the west coast of Ireland. *T. subcylindrica* was known only from the south coast of England in the British Isles and these records represent a significant extension in the species' distribution being the northernmost records for the species reported in the Northeast Atlantic. In addition to those exciting finds, Julia Nunn reports several important updates of records to post-1990 status from 5 Irish Sea Areas, 2 new sea area records, namely *Retusa umbilicata* (S37) and *Rissoella opalina* (S29A), and also *Pseudopythina macandrewi* (S37) as new to Ireland. In Essex, Pam and Peter Wilson have found yet more sites for *Tenellia adspersa.* One Blackwater site also yielded 2 further aeolid species: *Tergipes tergipes* and *Eubranchus exiguus,* the first record for the latter species in S 13. These nudibranchs were also found to be living on the hydroid *Laomedea flexuosa.*

Recording for the DOMMIC project has been less intense than for earlier years, however, several species have been recorded for the first time in S15: *Doto tuberculata, Cuthona foliata, Limatula subauriculata* (shell) and *Neolepton sulcatulum.* All of these have resulted from detailed examination of a piece of an old shipwreck hooked by an angler 31 miles off Brighton. Additionally I have received several batches of valuable sublittoral records from an amateur diver, Jane Lilley, who is a member of Porcupine but not of the Conchological Society. Whilst these include sites in the Channel, there are also lists from North Wales, Isle of Man and Outer Hebrides. Further interesting records, submitted by Shelagh Smith, result from a Porcupine meeting to the Trink, off the Northumberland coast. This is a famous area and indeed a new and updated *Marine Fauna and Flora of the Cullercoats District* has just been published. However, despite regular and focused sampling of this special site over many years, the Porcupine work was able to update records still further and even provide new records of the rarely recorded species, *Melanella frielei* and *Jordaniella truncatula.*

Appropriately, an auspicious year has yielded rather more noteworthy items than for some years previously. I would like to thank all those whose communications have enabled this report to be compiled.

Jan Light

REPORT OF THE HON. CONSERVATION OFFICER 2000–2001

Selected key items from the 2000–21 year are summarised below.

Biodiversity Matters

- Four Molluscan Conservation Group members continue involvement on UK BAP Steering Groups for a number of the Biodiversity Steering Group's Priority Species. Mollusca include (1) the terrestrial species: *Vertigo geyeri, V. genesii, V. angustior, V. moulinsiana* and *Catinella arenaria* and (2) the freshwater species *Pseudanodonta complanata, Pisidium tenuilineatum, Segmentina nitida, Anisus vorticulus* and *Myxas glutinosa.*
- Several Molluscan Conservation Group members have continued to assist Alisa Watson, a PhD student who is working upon a NERC/Environment Agency Research Studentship/Fellowship aimed at determining the key habitat requirements of the Biodiversity Steering Group Priority Species *Segmentina nitida* and *Anisus vorticulus.*
- Several Society members have been involved on a professional basis with survey and monitoring work on Biodiversity Steering Group Priority Species including *Anisus vorticulus, Segmentina nitida, Pisidium tenuilineatum, Vertigo moulinsiana, V. geyeri, V. genesii, Myxas glutinosa, Catinella arenaria* and *Margaritifera margaritifera.* Work has also involved Biodiversity Steering Group Species of Conservation Concern such as *Helicodonta obvoluta* and *Valvata macrostoma.*

Advice and help

Has been given to a wide range of individuals and organisations including:

- Help given to a number of undergraduate and postgraduate students undertaking molluscan based projects and research by identifying specimens, providing background information and assisting with report writing.
- Information given to the Environment Agency concerning the management of sites for *Pisidium tenuilineatum* and *Anisus vorticulus.*
- To English Nature on a wide variety of issues including; the identification of shells collected during surveys; help on the identification and habitat management options for the slug *Tandonia rustica* in Kent; advice on the extension and management of several SSSIs of particular molluscan importance (e.g. hanger woodlands on the South Downs).
- To The London Wildlife Trust on a range of rare and local molluscan species living inthe London area.
- Advice and help has been given to many other organisations and individuals on a range of small-scale molluscan conservation issues.

British Wildlife

The production of a biannual molluscan wildlife report for this journal has continued. The Conservation Officer has sought to use this column to publicise a variety of conservation initiatives undertaken by Society members including many published in *The Journal* or *Newsletter.*

Joint Committee for the Conservation for British Invertebrates (JCCBI) & links with other organisations

Membership of the Committee continues providing valuable contacts with other organisations. The Conservation Officer has attended all meetings and he is also a member of the Executive. An updated version of the consultative 'Green Paper', exploring the possibility of forming a staffed, national invertebrate co-ordinating body, 'The Invertebrate Conservation Trust' was finally circulated in March 2001. The JCCBI has members on the Steering Groups for two newly created invertebrate posts. These were first described in last year's report as being focussed specifically toward invertebrate species covered by the UK BAP. The first 'Action for Invertebrates' post is run as a partnership project with Biodiversity Challenge, Butterfly Conservation and the JCCBI and is chiefly concerned with a group of BAP beetles. The second post of 'Invertebrate Biodiversity Co-ordinator', is run by English Nature and the Natural History Museum. This latter post is more wide ranging and is intended to address the need for development of working links between UK BAP, SAPs (species action plans) and UK HAPs (habitat action plans); local action plans the National Biodiversity Network.

Shortly after the delivery of this report a conference will take place arranged by Invertebate Link (formerly JCCBI) and English Nature. This conference titled, 'Unity of Purpose for Invertebrate Conservation - Launch of the Invertebrate Conservation Trust', will be held in Peterborough on 31 March 2001. A number of Conchological Society members will be attending and one of the speakers will be Dr David Aldridge talking on 'Rivers and freshwater mussels'. This conference is very much the start of what may become a more co-ordinated and integrated movement to advance the conservation value and interest of all invertebrates including Mollusca.

Links with other organisations

The Conservation Officer continues to attend conservation committee meetings of The Sussex Wildlife Trust. He wrote an article for the Sussex Biodiversity Partnership on 'Molluscan candidates for Sussex Species Action Plans. A Sussex Species Action Plan for *Mercuria confusa* was prepared and another for *Helicella itala* is being completed. Additionally a Species Action Plan for *Valvata macrostoma* was prepared for Hampshire Biodiversity Partnership. Two field meetings were held to assess the molluscan importance of National Trust properties on the River Wey Navigation at Shalford in Surrey and in Herefordshire *Lymnaea glabra* was searched for on property in the Kington area East Sussex and at Wicken Fen, Cambridgeshire. Further survey meetings on National Trust properties are planned for the 2001 season.

An integrated local biodiversity action plan conservation initiative

The Hampshire Wildlife Trust and East Hampshire District Council enlisted the help of the Conchological Society in planning and running a project to interest and involve local people in a molluscan survey of the chalk hanger woodlands of East Hampshire. This involved surveys for four species, including *Ena montana* and *Helicodonta obvoluta,* two rare species with local populations. Dr June Chatfield and the Conservation Officer planned information sheets, delivered a talk to local people and led a field trip training day in July 2000. Assistance with the project continues.

Conservation work undertaken throughout the Society

Many other conservation activities have been undertaken throughout the year by Society members, often in a professional capacity. These are too numerous to mention individually, but range from continued work with the DOMMIC (English Channel) marine molluscan mapping project, to molluscan surveys of freshwaters and wetlands throughout the country.

M.J. Willing
Hon. Conservation Officer

REPORT ON THE CONCHOLOGICAL SOCIETY DISPLAY MATERIAL/BOARDS

(SUBMITTED BY MR P.T. WIMBLETON, EXHIBITS COORDINATOR)

Since the last AGM, the Conchological Society's display material/boards have been used on many occasions. In April/May 2000 they were at the Havant Museum for four weeks, in conjunction with a shell exhibition by local member Terry Wimbleton, together with smaller additional displays from the late Major Earl Collection and shell art and artefacts from the Hants C.C. Museums Service Collections. A reduced display of shells remained throughout the summer for a further fourteen weeks, until the end of August 2000.

During the summer of 2000, the display material/boards went north to Cumbria, Dumfries and Galloway. Their use at local events was co-ordinated by local member Norman Hammond. They have a large marine conchological show, plus a wide range of other marine biological items including a mobile running rock pool. Conchological Society members, cooperating with a number of local groups, were involved in many public events with wildlife and conservation interests when the display material/boards were employed. These varied from a week to half a day in duration, and included indoor and outdoor events. In particular they included events in connection with World Ocean Day for a week, the Maryport "Songs of the Sea" Festival for two days and a display concerning the Whitehaven Conservation Coastal Park; proposals. Some twenty or so venues throughout Cumbria, Dumfries and Galloway were visited, as well as a number of schools. The conchological and marine biological displays drew crowds and much constructive comment. Although locally there is very great interesi in marine conchology, the display material/boards themselves were not considered an important positive influence.

Mr Hammond has submitted a full and comprehensive report. This contains a number of points concerning the use of the display material/boards in his area, and this has been sent to the Hon President for his consideration. Our thanks and appreciation are extended to Mr Hammond for his enthusiasm and commitment.

Back in the South again in February 2001, the display material/boards were again in use at a Shell Exhibition being held at Cumberland House Natural History Museum, Southsea, Hants, by local member Terry Wimbleton. The shell exhibition included a number of special displays, as well as shells of exotic foreign marine, foreign land snails and British marine, land and freshwater shells.

Both the Havant and Southsea exhibitions included a day at which the public were invited to bring in their own shells for identification.

For the future, Terry Wimbleton and Dr June Chatfield are currently planning a shell exhibition to be held at Hazlemere Museum in September 2001 where, once again, the display material/boards will be used.

Colin Gillard
Hon. General Secretary

MEMBERSHIP SECRETARY'S REPORT FOR 2000

Membership of the Society at the end of 2000 was 331. This includes Life Members, Honorary Members, Ordinary Members, Family Members, Student Members and Institutions. There have been 8 new members in the year, but 25 members have resigned or lapsed through non-payment giving a net loss of 17 members for the year.

During the year there were 78 subscribers to the *Journal of Conchology.* This compares with 89 in 1999.

Mike Weideli
Hon. Membership Secretary

JOURNAL OF CONCHOLOGY, VOLUME 35: INDEX

This index is in three parts: a taxonomic index, a general and geographic index and an author index. It is designed to signpost users to the article they want rather than to be a comprehensive index of every reference in the *Journal of Conchology*.

Page references are to the first page of the article concerned, except for new taxa where the page reference gives the start of the formal description.

TAXONOMIC INDEX

Note: Species names are in alphabetical order according to genus. Taxa newly described in volume 35 are printed in bold.

GENERAL AND GEOGRAPHICAL INDEX

AUTHOR INDEX

JOURNAL OF CONCHOLOGY, VOLUME 36: INDEX

Notes

General This index is in three parts: a taxonomic index, a general and geographic index and an author index. It is designed to signpost users to the article they want rather than to be a comprehensive index of every reference in the *Journal of Conchology.*

Page References These are in the form of a single digit (1 to 6) to denote the Part number of Volume 36, followed by the page number in that part. Page references are to the first page of the article concerned, except for new taxa where the page reference gives the start of the formal description.

TAXONOMIC INDEX

(New Taxa introduced in Volume 36 are in **bold**)

General and Geographical Index

AUTHOR INDEX

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PAPERS Two copies of text and illustrations should be submitted; one set of illustrations must be good quality originals. Authors should refer to *Instructions to Authors* in Volume 37, Part 1 as a guide to format. Authors are reminded of the high cost of printing and therefore are expected to write concisely and to make maximum use of page size when designing artwork and tables.

COMMUNICATIONS These are intended to be short notes of an original nature which do not merit the treatment of a full paper. *Communications* do not normally contain any figures, tables or plates and should conform in style to that of recent issues of the *Journal.*

Journal of Conchology

Vol. 37, Part 4, January 2002

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ISSN 0022-0019

ournal of Conchology

(Established 1874)

Vol. 37, Part 5, May 2002

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MEETINGS are held at the Natural History Museum at 2.30pm usually six times per year between October to May. Field meetings are held in the summer throughout the country.

Printed in the United Kingdom by Henry Ling Limited, at the Dorset Press,
Dorchester, DT1 1HD

FUSINUS NICKI, A NEW FASCIOLARIID GASTROPOD FROM MOZAMBIQUE

MARTIN AVERY SNYDER[1]

Abstract *A new species of fasciolariid gastropod (Mollusca),* Fusinus nicki, *is described. This species, known only from 75–150 m off southern Mozambique, east Africa, is a large carinate species characterized by an inflated body whorl, a detached parietal shield and by determinate (modified) growth.*

Key words *Mollusca, gastropod, Fasciolariidae,* Fusinus, *new species, Mozambique.*

INTRODUCTION

This paper describes a new taxon of *Fusinus* recovered from fish and lobster traps set in fairly deep water off southern Mozambique, east Africa. The fasciolariid genus *Fusinus* is spread worldwide in shallow to deep warm waters. Shells of this genus are elongate with a tall spire and long siphonal canal; the columella is without folds. In nearly all species the lip displays unmodified growth.

This new species has a modified (determined) lip. Comparisons are made with other members of the genus. *F. nicki* is known only from dead collected specimens and, to date, no soft parts are available for study.

Abbreviations for museums and collections are as follows:

ANSP	Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania, USA
HC	Hadorn collection, Roethenbach, Switzerland
MNHN	Muséum national d'Histoire naturelle Paris, France
NM	Natal Museum, Pietermaritzburg, South Africa
SC	Snyder collection, Villanova, Pennsylvania, USA

SYSTEMATIC DESCRIPTION

FASCIOLARIIDAE
FUSININAE

Genus ***Fusinus*** Rafinesque, 1815
Fusinus nicki n. sp.
Figs 1–6

Holotype Collected off Zavora (north of Quissico), Mozambique, at 95–125 m in lobster cages, 1999. ANSP 407934.

Paratypes Paratype 1, in lobster cages at 95–125 m, MNHN; paratype 2, in lobster cages, NM L5610/T1776; paratype 3, in fish trap at 75–90 m, HC 209B2; paratype 4, 120–150 m in lobster cages, and paratype 5, 115–145 m in lobster cages, both SC. All paratypes from type locality.

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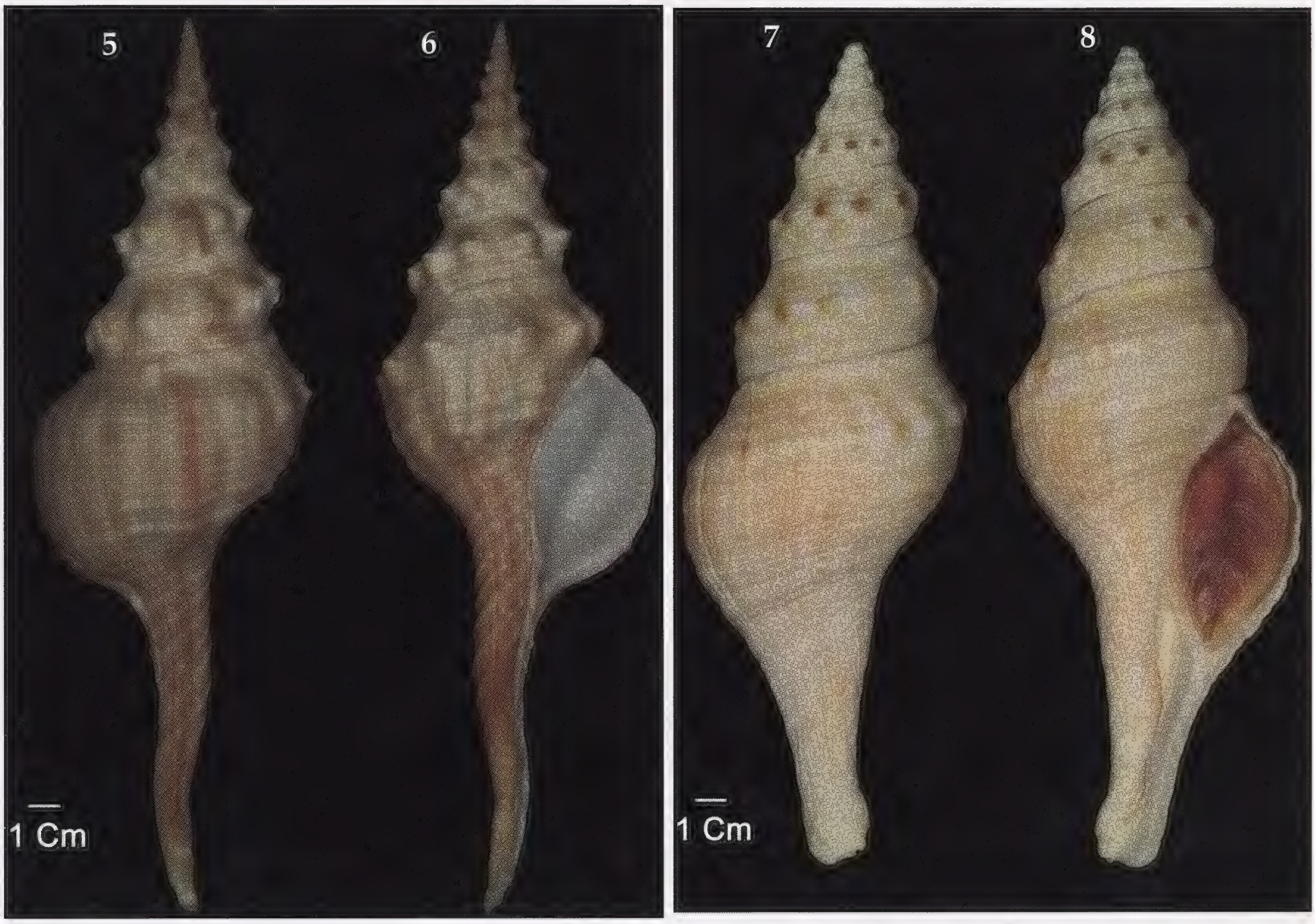
Figs 1 & 2 Holotype shell of *Fusinus nicki* n. sp. **Figs 3 & 4** Paratype 1 of *Fusinus nicki* n. sp., 158 mm

Shell measurements Holotype: length 163 mm, width 47 mm, aperture length 40 mm, aperture width 22 mm, siphonal canal length 60 mm. Paratype 1: length 158 mm, paratype 2: length 152 mm, paratype 3: length 146 mm, paratype 4: length 164 mm, paratype 5: length 168 mm.

Other material examined 18 specimens, SC, from 139.3 mm–170 mm, all from type locality.

Type locality Off Zavora, north of Quissico, Mozambique.

Description Shell large (up to 170 mm), 9–11 whorls, moderately elongate, somewhat high-spired (last whorl length: shell length, 0.60–0.64), heavy and solid. Color white with sparse pale brown markings on early whorls, pronounced in one brownish specimen (paratype 3, figs. 5, 6). Protoconch $1^{1}/_{2} - 1^{3}/_{4}$ shiny white bulbous whorls; spire carinate, subtending about 30° angle, with angulate ribs; body whorl inflated with spiral cords. Prominent yellow to caramel brown axial knobs on early whorls, becoming evanescent on body whorl, 7–8 on early whorls, 10–11 on penultimate whorl. Brown patch often between knobs on mid whorls, becoming in some specimens one or two colored segments between knobs, toward body whorl. 7–13 spiral cords, extending length of siphonal canal; 1–2 more prominent cords cross axial knobs, forming a concave-bottomed groove between them, when there are two. Cords on canal more widely spaced toward distal end, alternating strong and weak; area between cords on canal brownish on some specimens. Cords coalesce below suture to form thickened band. Some specimens have apical portion of body whorl near aperture unattached, creating open crease at suture up to 10 mm along suture and up to 4 mm deep. Aperture



Figs 5 & 6 Paratype 3 of *Fusinus nicki* n.sp., 146 mm. **Figs 7 & 8** *Fusinus ocellifer* (Lamarck, 1816), trawled at 50 m on muddy bottom, False Bay, South Africa, collected 1964, SC, 135 mm.

ovate, large, with distinct well-developed posterior canal. Outer lip with weak denticles, corresponding to spiral cord sculpture. Interior of outer lip shiny white with margin overlaid 0.5–1.0 mm with pearl-colored layer with wavy periphery, wider over denticles. Outer lip shows determinate (modified) growth, being thickened at the apertural margin (see, for example, Hughes, 1986: 111). Parietal shield polished, white, unattached, and flaring on some specimens. Siphonal canal straight, open, roughly one third of shell length; slit twisted about 10° clockwise from plane of aperture (viewed from distal end). Periostracum pale brown.

Derivation of name This species is named for my youngest son Nicholas.

Comparisons The presence of a modified or determined lip is quite unusual in the genus *Fusinus* and serves to differentiate this species from other similar-size *Fusinus* species from east Africa. *F. nicki* has been confused with the South African species *F. ocellifer* (Lamarck, 1816) (figures 7, 8). This latter species has a shorter siphonal canal and attached parietal shield. Although its coloration is similar to *F. nicki,* the sculpture is much weaker and the species lacks the axial knobs present on the early whorls of *F. nicki.* The large protoconch of *F. nicki* suggests a localized habitat.

There are four other large *Fusinus* species found off Mozambique, *F. colus* (Linnaeus, 1758), the type species of *Fusinus, F. cratis* Kilburn, 1973, *F. nicobaricus* (Röding, 1798) and *F. tuberculatus* (Lamarck, 1822). None of these species closely resembles *F. nicki* and hence a few observations will serve to differentiate them from *F. nicki*. The Mozambique form of *F. colus* is very narrow and elongate, and smaller then *F. nicki*. The brownish color on some specimens is accented by dark brown irregularly-shaped patches of color which always fall between the ribs. *F. cratis* was described from deep-water South African material. Specimens from Mozambique tend to be larger (up to 176 mm) than those from South Africa and mostly white with possible light brown axial color stripes (especially on the early whorls) between the very numerous (13) low, gently-rounded, axial ribs which extend from one suture to the next. The shell is narrow (height:width about 3.7 compared to 3.3 for *F. nicki*). The parietal shield is unattached and the open canal turns slightly clockwise, as in *F. nicki*. *F. nicobaricus* is also found in Mozambique, where specimens tend to be smoother than those from the central Pacific. These specimens do, however, display the characteristic strong diagonal cords over the length of the siphonal canal. This sculptural feature, together with the irregular chocolate brown markings, serve to distinguish *F. nicobaricus* from *F. nicki*. *F. tuberculatus* (erroneously synonymized with *F. colus* by Cernohorsky, 1972:162) lacks the strong spiral cords of *F. nicki*. *F. tuberculatus* is irregularly marked by brown longitudinal color striations and the spire is narrower then in *F. nicki*.

Although not known from this area, *Fusinus akitai* Kuroda and Habe in Habe, 1961, collected in southern Japan, superficially resembles *F. nicki*. Both species have inflated body whorls and wide apertures. *F. akitai* lacks the strong axial ribs of *F. nicki* and has more numerous closely spaced spiral cords that are more pronounced on the body whorl than in *F. nicki*. The shell of *F. akitai* is not as solid and heavy as in *F. nicki*. None of these species mentioned for comparison displays determinate growth.

ACKNOWLEDGEMENTS

I am grateful to Richard Kilburn, NM, for helpful suggestions regarding comparable species. Gary Rosenberg, ANSP, also made helpful suggestions which improved this paper. Useful ideas were also contributed by an anonymous referee.

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THE LAND MOLLUSCS OF NORTH RONALDSAY, ORKNEY: HUMAN INTERVENTION AND ISLAND FAUNAL DIVERSITY.

R.A.D. CAMERON[1]

Abstract *A survey in July 2001 found 23 species of land mollusc on the island of North Ronaldsay, Orkney. A total of 26 species have been recorded since 1965. While this species richness is roughly as predicted from the island's area and latitude, the species composition of the fauna differs markedly from those of the Hebridean islands of Colonsay and Ulva. The fauna contains many anthropochorous species, and lacks several species typical of wetland and woodlands which are present on the Hebridean islands. These results are discussed in relation to the islands' histories and their agricultural status.*

Key words *Land mollusc diversity, island faunas, human impact.*

INTRODUCTION

In a recent paper, I gave evidence that a number of islands around the British coast had land mollusc faunas as rich as those of equivalent areas of mainland at the same latitude (Cameron, 2002). This finding runs counter to theoretical expectations (MacArthur and Wilson, 1967), and to the generality of observations on island fauna and flora (Rosenzweig, 1995), except where endemic species have evolved *in situ*.

One explanation of this apparent anomaly is that these island mollusc faunas are enriched by accidental human introductions. Many species are anthropochorous, associated with human-modified habitats. Human activity promotes transport and the creation of appropriate habitats (Mylonas, 1984). Such introductions are well documented, even on remote oceanic islands (Preece, 2001), but can be hard to demonstrate for islands within the natural ranges of the species concerned.

In the context of Britain, another explanation is possible. Many offshore islands will have been connected to the mainland at a time when the molluscs now found on them would be present. Given the small sizes of habitat patches which can sustain minimum viable populations (Soulé, 1987) of molluscs, the richness of some islands may be relictual. In terms of theory, they are not in equilibrium: extinction rates are very slow.

In this context, the Orkney Islands have a particular interest. The evidence suggests that they were isolated from the mainland before habitats suitable for most of the modern mollusc fauna had developed (Berry, 2000). In contrast to most islands off the Scottish coast, their topography, geology and climate make them suitable for intensive agricultural use, which started in Neolithic times, some time prior to 5000BP (Bunting, 1994).

This paper reports on a survey of North Ronaldsay, the most northerly island of the Orkney group. On the evidence available beforehand (Kerney, 1999), the recorded fauna of 16 species was, as expected from theory, depauperate. It differed in this respect from the small Hebridean islands of Colonsay (with Oronsay) and Ulva, surveyed in detail by Paul (1976 and 1992). These Hebridean islands retain rich wetland and woodland faunas unlikely to be the product of human introduction. Results obtained here are compared with those of Paul.

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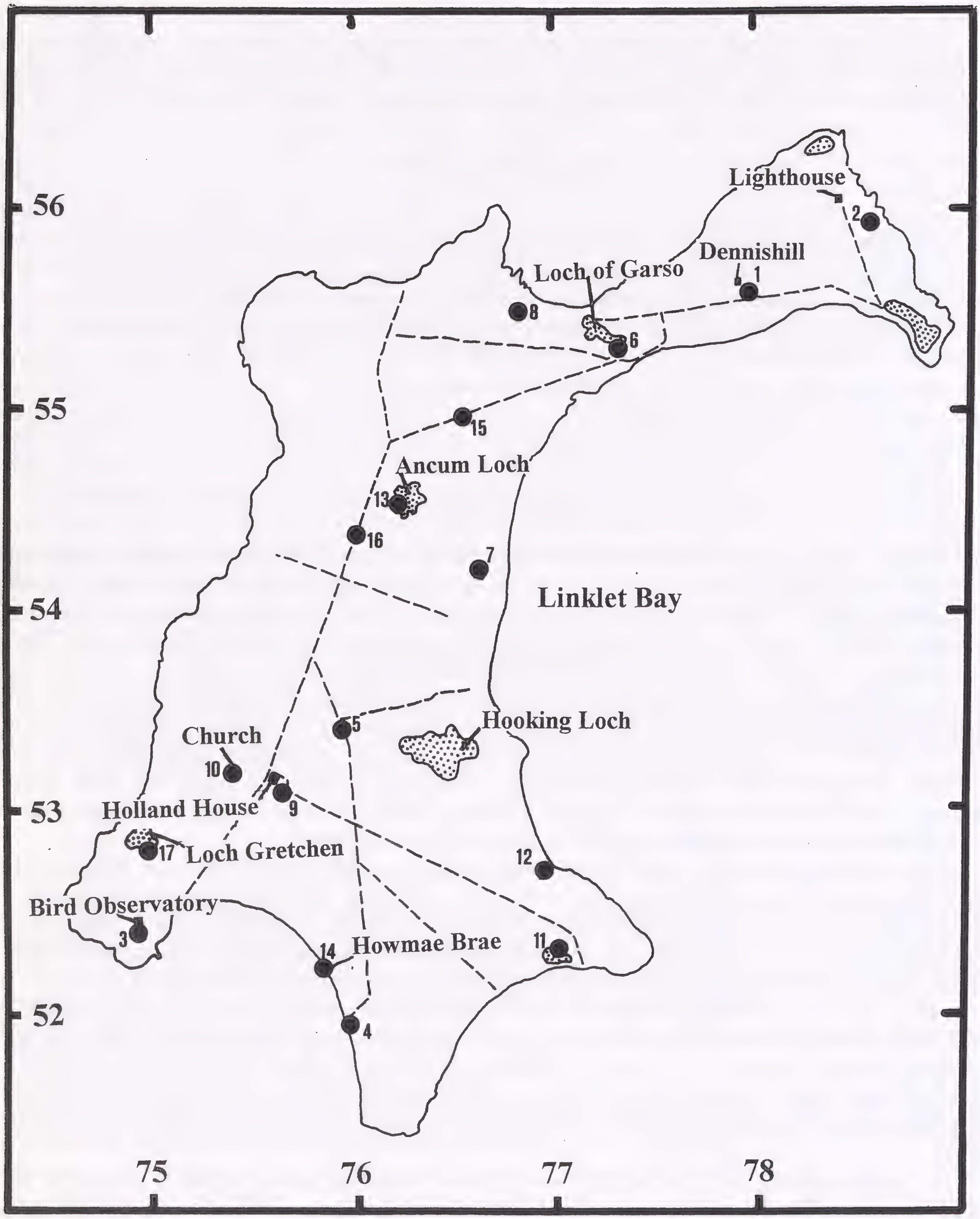

Figure 1 A map of North Ronaldsay, showing the location of sample sites and major features of the island. Roads are indicated by dashed lines, and freshwater lochs by stippling. The Ordnance Survey 1km grid is indicated in the margins. North Ronaldsay is in O.S. 100 km square HY.

THE ISLAND

North Ronaldsay (Figure 1) is the most northern of the Orkney Islands at about 59°23′ north. It is separated from its nearest neighbour, Sanday, by 4 km of sea. It has an area of 7.3 km^2, and it is flat, with the highest point only 23m above sea level. It is composed of Devonian sandstone, overlain in places by blown sand. It shares with the Orkneys as a whole an extreme oceanic climate, with mild winters and cool summers. Its rainfall is probably similar to that of Kirkwall (Orkney Mainland), which is 970mm per year (Berry, 2000).

The interior of the island is mainly pasture and meadows, surrounded by drystone walls and fences. Some pastures have been abandoned, especially in the central region, where the rocks are overlain by blown sand. There are many small roads and tracks, usually with ditches alongside, and with verges of tall herbaceous vegetation. There is no natural woodland, and trees are very scarce. Appreciable cover is found only in the grounds of Holland House, where sycamores *Acer pseudoplatanus* grow over dense scrub sheltered by walls. There are several small freshwater lochs surrounded by eutrophic wetlands. These are sometimes rich fens, but in many cases a grazed and churned sward reaches to the water's edge. Water levels fluctuate, and there may be extensive flooding in winter.

The coastal fringe is separated from the interior by a continuous drystone wall, the Sheep Dyke. Outside the Dyke a large number of the North Ronaldsay breed of sheep graze on seaweed, and on the patches of grassland and machair excluded from the interior. The two largest patches are of machair along the shore of Linklet Bay, and of grassland on rock near the lighthouse in the northeast. All areas available to the sheep are intensively grazed, and the sward is less than 2cm high. Fragments of dune vegetation occur inland of the Dyke in places around Linklet Bay, and on the southern and southeastern coasts.

Humans have occupied the island since prehistoric times (probably since the early Neolithic, *c.*5000BP) (Berry, 2000), and there are many relics of Pictish and Viking settlement. Howmae Brae, and other settlements in the south were partly covered by blown sand, but are now being exposed by coastal erosion.

SAMPLING & SITES

During one week in July 2001, 17 sites, ranging in size from 400m^2 to 1 ha., were searched thoroughly for at least one hour, and samples of litter and soil removed for examination indoors. Casual searches were made elsewhere and are referred to below. Amongst the species found, dissections were made to confirm identification for *Oxyloma pfeifferi, Arion distinctus, Milax gagates, Deroceras panormitanum* and pale specimens of *D. reticulatum*. The single, fresh *Vallonia* shell was juvenile, and could be either *V. pulchella* or *V. excentrica* .

The locations of the sites are shown in Figure 1. For analysis, they have been allocated amongst five habitat categories (Table 1), but there is some heterogeneity within each category. Amongst the Garden sites, sites 1 and 3 included abandoned outhouses, builder's rubble, rubbish, and much tall vegetation, mostly nettles. Sites 9 and 10 were better maintained, with mowing, and had appreciable tree cover. The Roadside sites each included a drystone wall and a ditch with tall herbage. Amongst the Machair sites, 4 and 7 were outside the Sheep Dyke, but had some shelter provided by stones or old timber; the remainder had elements of dune vegetation including marram grass *Ammophila arenaria*. In the Wetlands, sites 6 and 13 were in rich fens with stands of *Iris pseudacorus*, but 11 was in a dense stand of *Phragmites communis*, and 17 came from a loch shore heavily trampled by cattle, with much shorter and sparser vegetation. Site 2 was a wet patch, with a spring and a few piles of rocks within very intensely grazed turf outside the Sheep Dyke.

Comparative data for Colonsay (plus Oronsay) and Ulva has been taken from Paul

TABLE 1
The occurrence of land mollusc species by site and habitat on North Ronaldsay. Asterisks indicate presence in the habitat indicated, GR indicates the non-machair grassland of site 2 (see text).

SPECIES	**GARDENS**					**ROADSIDES**				**MACHAIR/DUNE**						**WETLAND**					**GR**	**TOT**
SITES	1	3	9	10		5	15	16		4	7	8	12	14		6	11	13	17		2	
Carychium minimum																X		X		*		2
Oxyloma pfeifferi																X		X	X	*		3
Cochlicopa lubrica																X		X		*		2
Cochlicopa lubricella		X		X	*	X			*	X	X	X	X	X	*							8
Lauria cylindracea	X	X	X	X	*	X	X	X	*	X	X	X	X	X	*	X	X	X	X	*	X	17
Vallonia sp.																X				*		1
Punctum pygmaeum																X		X		*		2
Arion ater agg.	X				*			X	*	X					*							3
Arion subfuscus		X			*																	1
Arion silvaticus	X				*																	1
Arion fasciatus	X	X	X	X	*																	4
Arion distinctus	X	X	X	X	*																	4
Arion intermedius	X	X	X	X	*		X	X	*		X	X	X	X	*	X		X	X	*	X	14

(1976 and 1992) and for larger areas from Kerney (1999). Nomenclature follows Kerney (1999).

RESULTS

GENERAL

Table 1 lists the species found by site and habitat. 23 species were found live. Kerney (1999) records 16 species, one of which is *Arion circumscriptus* agg. Three species recorded as live post 1965 in Kerney (1999) were not found live in 2001: *Limax flavus*, *Limax maximus*, and *Cepaea hortensis*, though the last was found sub-fossil in exposed soil horizons and a midden at Howmae Brae. Local information suggests that these three species have declined since the recent introduction of hedgehogs onto the island, but *C. hortensis* has certainly been seen alive in the last few years. Eleven species not recorded in Kerney (1999) were found this time, including two segregates of *A. circumscriptus* agg. Thus there are 26 species recorded post 1965, of which one, *Vallonia* sp., cannot be assigned to species.

Of the 23 species recorded in 2001, six were found only in gardens, and five only in wetland. The gardens contain the richest fauna overall, including all species not confined to wetland. All slug species found on the island were present in this habitat. Site 3, the grounds of the Bird Observatory, has the richest fauna of all; it has heavy traffic in goods and people, and a very heterogeneous set of environments. Faunas from roadsides and machair are all much alike in both diversity and species composition. In wetlands, the rich fens have far more diverse faunas than the remainder. Four species, *L. cylindracea, A. intermedius, O. alliarius* and *D. reticulatum*, are nearly universal. They were found in casual searches in many other places.

Although no attempt was made to sample quantitatively, it was apparent that *L. cylindracea* occurred at very high densities in many roadside, machair and wetland sites (several hundreds/m^2). *A. nitidula* also achieved very high density in the Churchyard (site 10), but nowhere else. *L. marginata* was much more widespread than its representation in Table 1 suggests; it was found active on many walls, rock piles and ruined buildings in damp, twilight conditions.

BIOGEOGRAPHICAL AND ECOLOGICAL COMPARISONS.

Cameron (2002) provides data from which it is possible to estimate the number of species to be expected on the island if it is equivalent to the same area of mainland. Table 2 shows five such estimates as follows:

(a) Applying the species/area relationship based on Suffolk, uncorrected for latitude: Log species number = 1.535 + 0.107x Log area (km^2).

(b) Correcting the estimate in (a) for latitude, using the mainland correction in Cameron (2002): Log corrected number = Log uncorrected number - 0.018 x number of 100km bands north from Suffolk.

(c) As for (b) above, but using the overall correction (-0.021), using data from the Orkney, Shetland and Channel Islands as well as mainland.

(d) Using the Suffolk slope (0.107) to estimate the N. Ronaldsay fauna from that of the northernmost mainland latitudinal 100km band (band 3 in Cameron, 2002), corrected for latitude.

(e) As for (d) above, but basing the estimate on the fauna of Shetland (band 1 in Cameron, 2002), corrected for latitude.

The last two estimates allow for a possible steepening of the richness/latitude relationship in the far north (Cameron, 2002). All estimates, corrected for latitude, involving

TABLE 2
Estimates of expected species richness on North Ronaldsay, allowing for area and latitude. For details, see text, page 449.

ESTIMATION METHOD	ESTIMATED NO OF SPECIES
(a) Suffolk regression uncorrected	42
(b) Suffolk regression corrected for latitude (mainland)	30
(c) Suffolk regression corrected for latitude (all)	29
(d) Northernmost mainland corrected	28
(e) Shetland corrected	25

TABLE 3
The species richness of land molluscs on Colonsay (including Oronsay), and on Ulva, compared with estimates based on a latitudinal correction of the Suffolk species/area regression, and on the fauna of the mainland in the same 100km latitudinal band, using the slope of the Suffolk regression. Island data from Paul (1976 and 1992).

	COLONSAY	ULVA
Area	44km^2	18km^2
Species recorded	45	37
Suffolk regression (corrected)	44	38
Same latitude of mainland	44	40

mainland are in the range 28–30 species. The estimate based on Shetland is lower, but involves inter-island comparisons. The fauna of North Ronaldsay appears to be very slightly impoverished relative to the same notional area of mainland at the same latitude.

Direct biogeographical and ecological comparisons can be made with the faunas of Colonsay and Oronsay combined (Paul, 1976) and of Ulva (Paul, 1992). Colonsay lies *c.*8km from the nearest land (Islay), but Ulva is separated from the much larger island of Mull by less than 150m. Table 3 shows the species richness of these islands, together with estimates based on the Suffolk regression corrected for latitude, and on direct comparison with the mainland in the same latitudinal band, scaled for area using the slope of the Suffolk regression (Cameron, 2002). Colonsay appears to have a faunal richness appropriate to the same area of mainland; Ulva, like North Ronaldsay, appears marginally impoverished.

Examination of species composition, however, reveals significant differences between the faunas of the islands studied by Paul and that of North Ronaldsay. Table 4 lists the species found on all these islands combined, separated by occurrence and by habitat preference. Of 54 species considered, 28 are absent from North Ronaldsay, but present on one or both of the other islands. They include many woodland and wetland specialists, and some open country species from Colonsay. Only two species can be considered anthropochorous. A minority of these species may be excluded from N. Ronaldsay by climate, since they are absent from Orkney and Shetland altogether, but the majority have been recorded from these archipelagos. Species common to all three islands are overwhelmingly species of wide habitat tolerance. Species found on N. Ronaldsay, but not on the others are either catholic or, at this latitude, definitely anthropochorous. Eight out of the eleven species in this group are slugs, compared to only 2 out of 28 found only in the other islands, and four out of 15 common to all three.

TABLE 4

Species recorded on N. Ronaldsay, Colonsay and Ulva, by distribution and habitat preference. In A, species highlighted in bold type are recorded from Orkney or Shetland. C=present on Colonsay, U= present on Ulva. In B, all species without comment have wide habitat distributions. In C, -C= absent from Colonsay,-U= absent from Ulva. The indeterminate *Vallonia* from N. Ronaldsay has been assigned here to *V. pulchella* on the basis of habitat.

A. Species missing from N. Ronaldsay

Wetland species
Vertigo antivertigo C
***Vertigo substriata* CU**
***Vertigo pygmaea* CU**
***Leiostyla anglica* CU**
***Deroceras laeve* CU**
***Euconulus alderi* C**
Ashfordia granulata C

Open country species
***Vallonia excentrica* C**
Cepaea nemoralis CU
***Helicella itala* C**
Cochlicella acuta C

Anthropochorous species
***Tandonia sowerbyi* C**
Helix aspersa C

Woodland species
***Carychium tridentatum* U**
Acanthinula aculeata CU
Spermodea lamellata CU
***Aegopinella pura* CU**
Zonitoides excavatus CU
Perforatella subrufescens U

Catholic and other species
***Columella aspera* CU**
***Discus rotundatus* CU**
***Arion circumscriptus* CU**
***Vitrea crystallina* CU**
***Nesovitrea hammonis* CU**
***Euconulus fulvus* CU**
***Clausilia bidentata* CU**
***Balea perversa* CU**
***Trichia hispida* C**

B. Species present on all islands

Carychium minimum Wetland
Cochlicopa lubrica
Cochlicopa lubricella
Lauria cylindracea
Punctum pygmaeum
Arion ater agg.
Arion intermedius
Vitrina pellucida
Vitrea contracta
Aegopinella nitidula
Oxychilus cellarius
Oxychilus alliarius
Deroceras reticulatum
Lehmannia marginata Trees and rocks
Cepaea hortensis

C. Present on N. Ronaldsay, but missing from one or both other islands

Wetland species
Oxyloma pfeifferi -U
Vallonia pulchella? -CU

Anthropochorous species
Oxychilus draparnaudi -CU
Milax gagates -CU
Limax flavus -CU
Deroceras panormitanum -U

Catholic species
Arion subfuscus -C
Arion silvaticus -C
Arion fasciatus -U
Arion distinctus -C
Limax maximus -U

DISCUSSION

The land mollusc fauna of North Ronaldsay is only marginally poorer than that expected in the same area of mainland at that latitude. It thus resembles the faunas of other islands off Britain discussed in Cameron (2002). The faunas of Colonsay (Paul, 1976) and Ulva (Paul, 1992) show the same phenomenon. If the three species of North Ronaldsay not found in 2001 have died out, the impoverishment is greater.

Detailed comparisons with the faunas of Colonsay and Ulva, however, show striking differences in species composition, which suggest that the levels of species richness found have different causes. North Ronaldsay lacks many wetland, woodland and even generalist species found on the other islands, even though most of these species can be found elsewhere on Orkney or Shetland. Roadsides on Orkney Mainland, for example, frequently hold *D. rotundatus, T. striolata, T. hispida, A. arbustorum* and *C. hortensis* (personal observation).

No remnant woodland survives on North Ronaldsay, nor are there patches of scrub or inland cliffs and screes to provide refuges. Remnant woods are very scarce throughout Orkney, although parts of the archipelago were covered in birch and hazel forest in pre-Neolithic times, and alder and even oak were also present (Bunting, 1994 and 1996). There are, however, no pollen records for N. Ronaldsay itself. Wetland is present, and often calcareous, but most of it is heavily disturbed; water levels show big seasonal fluctuations, and may be influenced by irregular drainage operations. Substantial areas of the island are covered in blown sand. Where this lies outside the Sheep Dyke, it is subject to exceptionally heavy grazing and trampling; there are few refuges. Inside the Dyke, fragments of dune and machair vegetation are also affected by agriculture, including heavy cattle grazing. Snail species usually restricted to short calcareous grassland or dunes, such as *H. itala, P. muscorum* or *V. excentrica*, are absent, although they are present on dunes on Orkney Mainland, for example at Skaill Bay (GR: HY2319)(personal observations). Only members of the grassland fauna with a wider range of habitat tolerance are present like *C. lubricella, L. cylindracea* and *V. pellucida*.

Thus, in contrast to the Hebridean islands, the fauna of North Ronaldsay is deficient in native species. Amongst possible causes are the following:

(a) Some woodland and wetland species failed to reach Orkney at all, despite the existence of potentially suitable habitats. *A. aculeata, S. lamellata and V. antivertigo*, for example, occur in SW Scandinavia, but not on Orkney or Shetland.
(b) Some species reach their environmental limits to the south or west of Orkney. *C. nemoralis, A. granulata, Z. excavatus* and *P. subrufescens* are all present in western Scotland, but not (as natives) in SW Scandinavia (Kerney, Cameron and Jungbluth, 1983).
(c) Some species have been extinguished by intensive human modification of the habitats, in circumstances where there are few non-exploitable refuges.
(d) Some species reaching Orkney have failed to reach North Ronaldsay.

Without a good subfossil record, we cannot tell whether the absence of such catholic species as *D. rotundatus, C. bidentata*, or *V. crystallina* is a consequence of (c) or (d).

Conversely, North Ronaldsay has a rich fauna of anthropochorous species, and especially of slugs. Around half of the British slug fauna (excluding Testacellidae) lives there. The richest faunas are found in gardens, where more than half the species are slugs, including the relatively recent arrival for Britain, *D. panormitanum*. Colonsay and Ulva, subject to less intensive agriculture, have fewer anthropochorous species.

In this case, therefore, a set of island faunas approximately match predictions derived from a general model for different reasons; the match may be fortuitous. Further detailed studies of extreme northern islands with varying environmental histories would clarify this. From Kerney (1999), it is possible to extract records for the very remote islands of the St. Kilda group, Fair Isle and Foula. Many records are old, but they have, respectively, 21, 10 and 10 species records. Of the three, the environment of Fair Isle will be the most modified by humans; eight of the 10 records are slugs, including *D. panormitanum.* 14 of the St Kildan records, however, are of snails, including many species absent from North Ronaldsay. This suggests that the absences of many catholic species on North Ronaldsay are a product of local, human induced extinction, rather than of failures to colonise.

ACKNOWLEDGEMENTS

I should like to thank Mr Alastair Pout and Dr Kevin Woodbridge for local information, and Dr. Jane Bunting for information about Holocene Orkney.

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REDESCRIPTION OF TWO WEST EUROPEAN *OXYCHILUS* SPECIES: *O. ALLIARIUS* (MILLER, 1822) AND *O. HELVETICUS* (BLUM, 1881), AND NOTES ON THE SYSTEMATICS OF *OXYCHILUS* FITZINGER, 1833 (GASTROPODA: PULMONATA: ZONITIDAE)

F. GIUSTI[1] & G. MANGANELLI[1]

Abstract Oxychilus alliarius *(Miller, 1822) and* O. helveticus *(Blum, 1881), two west European species sometimes confused with each other, are redescribed. Their identification is easy, but requires both conchological and anatomical characters. The two species are readily distinguished by shell shape and size and internal ornamentation of the penial complex.* O. alliarius *has a smaller shell (shell diameter: 4.5 – 7.0 mm) with a proportionately larger umbilicus (about* $^1/_6$ *of shell diameter), usually lacks blackish mantle edge and has internal ornamentation of proximal penis consisting of not more than four longitudinal pleats, usually straight, sometimes slightly wavy, but never laterally branched or papillate.* O. helveticus *has a larger shell (shell diameter: 7.3–12.2 mm) with proportionately smaller umbilicus (about* $^1/_8$ *of shell diameter), a blackish mantle edge and internal ornamentation of proximal penis consisting of more than seven longitudinal pleats, sometimes straight and distinct, sometimes wavy, slender and connected by lateral projections giving a reticulate appearance.*

Key words Oxychilus alliarius, Oxychilus helveticus, *taxonomy, systematics, distribution, western Europe.*

INTRODUCTION

In the last few years we have redescribed various Italian *Oxychilus* species (Giusti & Manganelli, 1997, 1999; Manganelli *et al.*, 1999; Manganelli & Giusti, 2000, 2001). In this context, we have also looked at species not reported from Italy but living close to the northern border, such as *O. cellarius* (Müller, 1774). The present paper, in which *O. alliarius* (Miller, 1822) and *O. helveticus* (Blum, 1881) are redescribed, is another such case. These species are known from the western Swiss Alps not far from the Italian border (Turner *et al.*, 1998) and one of them has sometimes been erroneously reported from Italy (Giusti, 1969; Alzona, 1971; Cossignani & Cossignani, 1995).

MATERIALS AND METHODS

Whole shells were photographed under the light microscope (Wild M5A). All dimensions (NW number of whorls, SD shell diameter, SH shell height, UD umbilicus diameter) were measured using a micrometer.

Live specimens were drowned in water, then fixed and preserved in 75% ethanol buffered with $NaHCO_3$. The bodies were isolated after crushing the shells and dissected under the light microscope (Wild M5A) using thin pointed watchmaker's tweezers. Anatomical details were drawn using a Wild camera lucida. Some parts of the genital organs (e.g. duct of bursa copulatrix, distal vagina, epiphallus, flagellum, penis, and penial sheath) were measured by micrometer.

Radulae were manually extracted from the buccal bulbs, washed in pure 75% ethanol, mounted on copper stubs with electronconductive glue, sputter-coated with gold and

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photographed using a Philips 505 SEM.

The material examined is listed as follows: locality, UTM reference, collector(s), date, number of specimens in parentheses (ps spirit preserved specimen/s, ss shell/s). Unless otherwise indicated, all the material examined is kept in the Giusti collection (Dipartimento di Scienze Ambientali, Via Mattioli 4, I-53100 Siena, Italy).

Key to the acronyms used in Figs 3–15, 18–30: BC bursa copulatrix, BW body wall, DBC duct of bursa copulatrix, DL dorsal lobe, DP distal portion of penis, E epiphallus, EO epiphallus opening, F flagellum, FO free oviduct, LLL left lateral lobe, P penis, POS prostatic portion of ovispermiduct, MB mantle border, PP proximal portion of penis, PR penial retractor, PS penial sheath, RLL right lateral lobe, UOS uterine portion of ovispermiduct, V vagina VD vas deferens, VG vaginal gland.

Oxychilus alliarius (Miller, 1822)

Helix alliaria Miller, 1822: 377.

Type series Unknown.

Type locality No precise locality is indicated, other than "Environs of Bristol" in the title of Miller's paper.

Identification *O. alliarius* is one of the smallest species of *Oxychilus (s.str.) sensu* Giusti & Manganelli (1999), a "subgenus" of *Oxychilus* characterized by: penis with flagellum (1); penial retractor inserted at apex of flagellum (2); epiphallus usually longer than proximal penis, its internal wall with slender longitudinal pleats (3); mucous gland mainly vaginal (4); long mesocone of central tooth (5). It is readily distinguished by a small (shell diameter: 4.5–7.0 mm) yellowish shell consisting of 4–4$^1/_2$ whorls, with an umbilicus representing $^1/_6$ of shell diameter and internal ornamentation of proximal penis consisting of not more than four longitudinal pleats, usually straight, sometimes slightly wavy, but never laterally branched or papillate.

Description Shell (Figs 1–2; Taylor, 1907: Pl. 2, 1909: Pl. 6; Adam, 1960: Fig. 92; Wütrich, 1963, Fig. 4; Kerney & Cameron, 1979: Pl. 10, fig. 3a–c; Gittenberger *et al.*, 1984: Fig. 101; Falkner, 1990: Fig. 2 at p. 181; Turner *et al.*, 1998, Fig. at p. 276; Barker, 1999: Fig. C28) dextral, small in size, discoidal, depressed, slightly convex above, compressed below, thin, subtransparent, variably glossy, yellowish to yellowish-brown or reddish or greenish in colour, opalescent below; surface rather smooth, with faint growth lines most pronounced at sutures and microsculpture consisting of very fine wavy spiral lines; spire of 4–4$^1/_2$ whorls, rather slowly and regularly increasing in size, last whorl not dilated near aperture, its last quarter descending to some extent; sutures distinct, but shallow; umbilicus rather broad, wide about $^1/_6$ of maximum shell diameter, sometimes eccentric; aperture oval, oblique; peristome interrupted, simple, not thickened nor reflected, its superior vertex starting above periphery of last whorl. Shell dimensions: diameter: 4.5–7.0 mm; height: 2.5–3.5 mm; (Taylor, 1907; Kerney & Cameron, 1979; Gittenberger *et al.*, 1984).

Body (Figs 3–4; Taylor, 1907: Pl. 2; Kerney & Cameron, 1979: Pl. 10, fig. 3d; Falkner, 1990: Fig. 2 at p. 181; Barker, 1999: Fig. C28) dark slate blue in colour; neck and upper part of sides with wide areas with pits (with phylacites) and glandular crypts; mantle border grey; upper wall of mantle (near border) with or, more frequently, without dark black-brown edging; faintly darker zebra–like transverse stripes perceptible on body sides; foot slender, of aulacopod type, slate-gray, with sole longitudinally tripartite; kidney sigmurethrous; jaw oxygnathous (Taylor, 1907: Fig. 98). This species may emit a

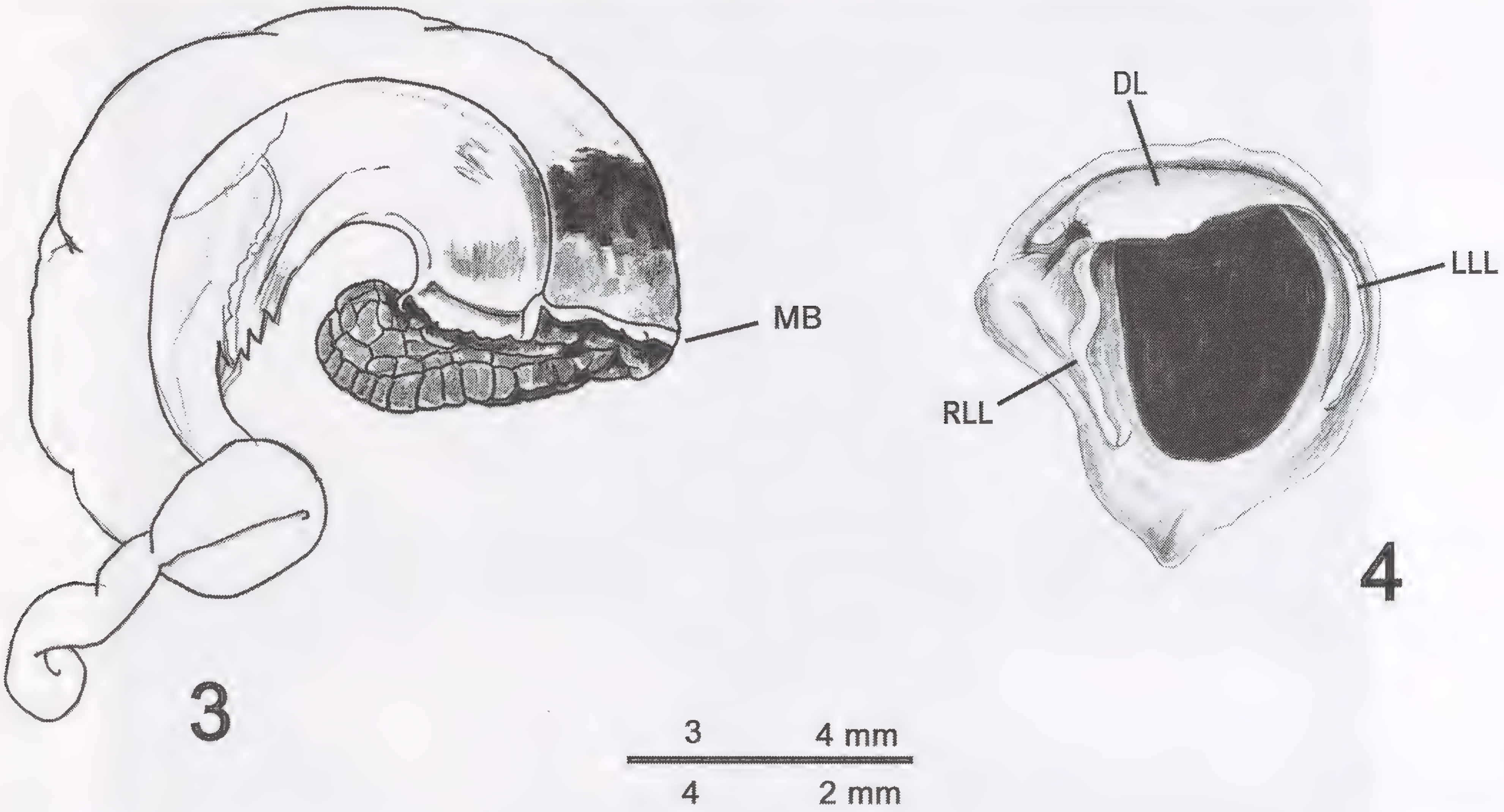
Figs 1–2 Two shells of *Oxychilus alliarius* (Miller, 1822) from Cambe Meat, Kingsbarus, F. Giusti & G. Manganelli leg. 3.9.1986 (Fig. 1) and Box Hill near Dorking, J.F. Peake leg. 9.1961 (Fig. 2).

garlic-like scent, particularly when disturbed.

Genitalia (Figs 5–15; Taylor, 1907: Figs 95–96; Riedel, 1957: Fig. 26–27; Wütrich, 1963: 132, Fig. 2; Gittenberger *et al.*, 1984: Fig. 95; Castillejo, 1985: Fig.9A). General scheme of genitalia as in *Oxychilus (s.str.) sensu* Giusti & Manganelli (1999). Only distal genitalia described here (7 specimens examined).

Female distal genitalia include free oviduct, bursa copulatrix and its duct and vagina. Initial portion of duct of bursa copulatrix, distal portion of free oviduct and $^1/_3$–$^1/_2$ of proximal vagina enveloped by variably large and long muff of spongy glandular tissue forming vaginal gland; duct of bursa copulatrix variably long (0.8–1.6 mm; n: 7), initially moderately flared, narrowing before entering oval or pyriform bursa copulatrix; distal vagina (that without glandular muff) variably long (0.7–1.3 mm; n: 7) and wide, not or slightly reducing in calibre near genital atrium.

Male distal genitalia include vas deferens, epiphallus, and penial complex (flagellum and penis). Epiphallus variably long (1.3–2.5 mm; n: 7) and slender. Flagellum variably

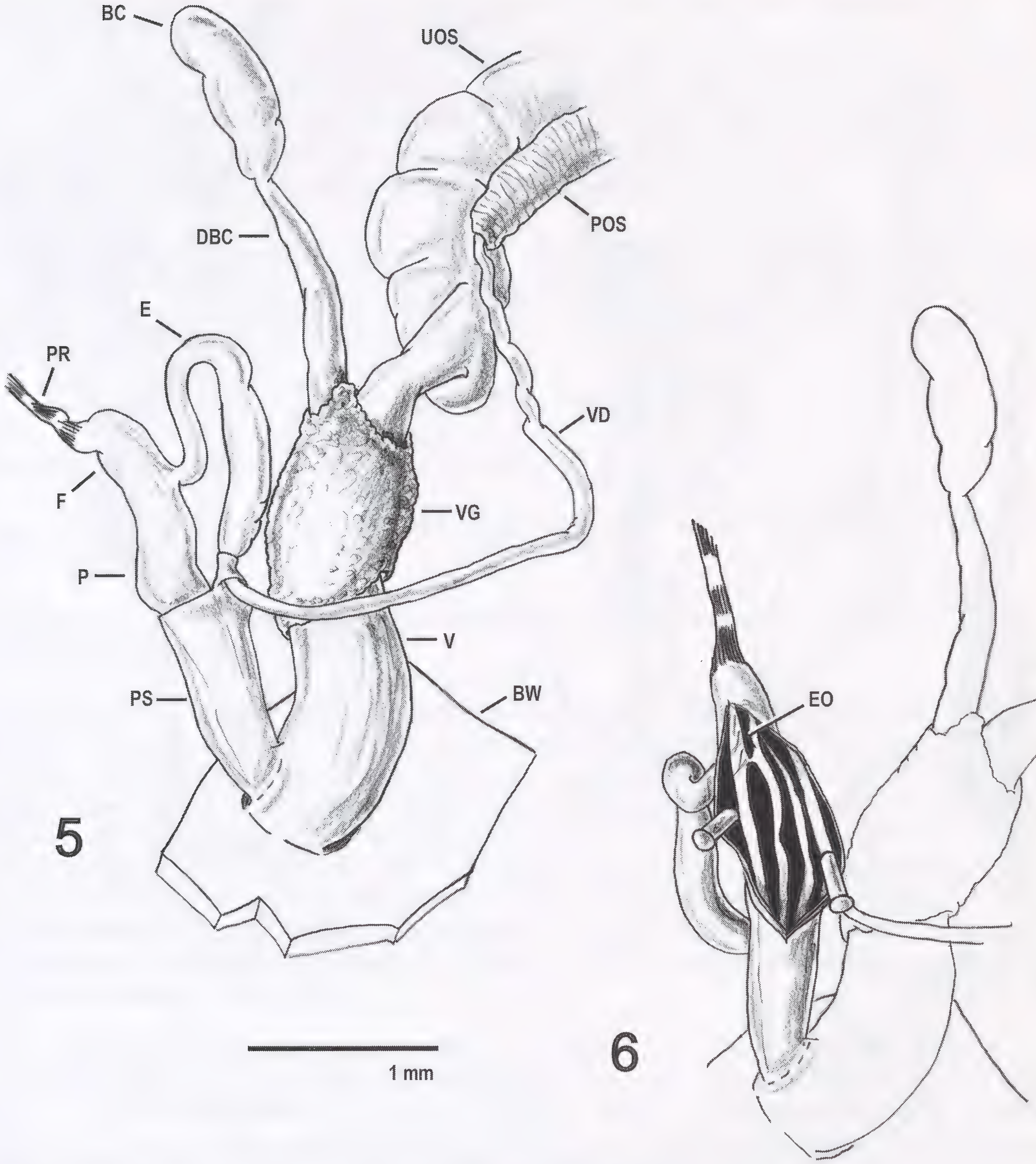


Figs 3–4 Body (Fig. 3) and mantle edge (Fig. 4) in a specimen of *Oxychilus alliarius* (Miller, 1822) from South of Endsleigh, G.A. Holyoak leg. 20.1.2001 (Fig. 3) and Box Hill near Dorking, J.F. Peake leg. 9.1961 (Fig.4).

long (0.5–1.1 mm; n: 7), with penial retractor muscle ending at apex. Penis variably long (1.8–2.5 mm; n: 7) without clear distinction into proximal and distal parts from both outside and inside (internal pleats of proximal penis continue with those of distal penis without interruption). Only in few cases the border line between proximal and distal penis is externally indicated by a slightly evident constriction (minimum diameter recorded: 0.07 mm). Proximal penis wider at its beginning, then slightly reduced in calibre. Internal surface of flagellum and proximal penis surrounding epiphallus opening into penis with 3–4 longitudinal pleats, the two bordering the opening of epiphallus into penis wider and sometimes fragmented into small, transversally elongated, droplike papillae. Internal walls of proximal penis with 4 pleats, variably wide, tapering in distal part before continuing, usually without interruption, inside distal penis, where they become wider and often have jagged sides. Distal penis enveloped by variably long (0.3–1.5 mm; n: 7) penial sheath, initially very thin, traversed on one side by vas deferens, then slightly thickened for rest of length. A very short, thin walled duct connects the distal penis (level with where the penial sheath originates) to the genital atrium in which the vagina also ends.

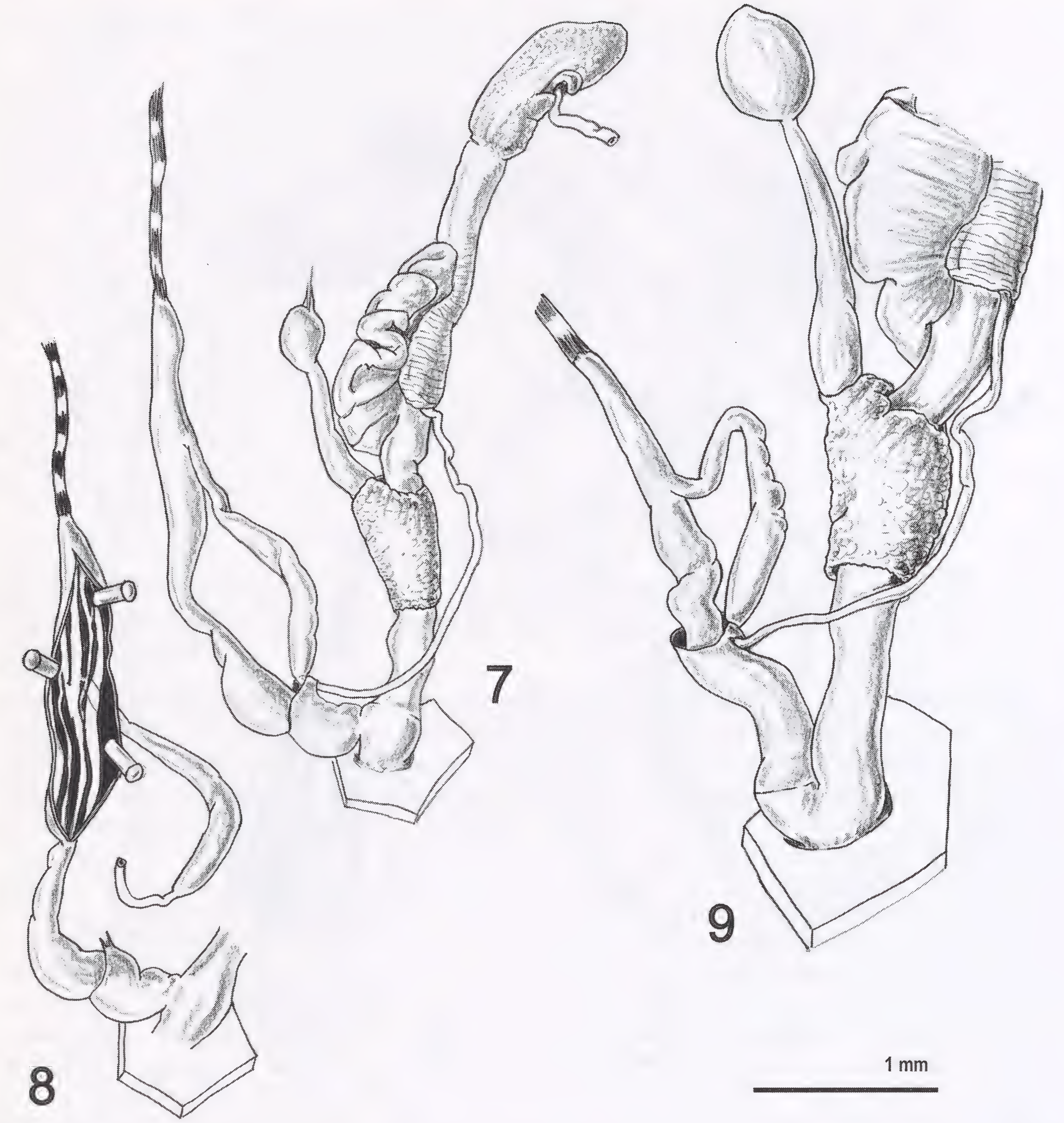
Radula (Fig. 16; Taylor, 1907: Fig. 99; Riedel, 1957, Pl. 46, fig. 9; Wütrich, 1963: 132; Castillejo, 1985: Fig.9B) consisting of many rows of about 27–31 teeth, according to the formula: 9-14 M/1 + 0-1 LM/2 + 2-3 L/3 + C/3 + 2-3 L/3 + 0-1 LM/2 + 9-14 M/1. Central tooth with well developed basal plate, the apical portion of which is V-like, with pointed vertices; body of tooth wide, providing base for long, slender, pointed mesocone flanked by two very short ectocones. On both sides of each central tooth are two–three lateral tricuspid teeth, sometimes one latero-marginal bicuspid tooth and series of monocuspid marginal teeth in decreasing order of size.

Material examined GREAT BRITAIN – Box Hill near Dorking, J.F. Peake leg. 9.1961 (3 sp). Cambe Meat, Kingsbarus, Fife (Scotland), F. Giusti & G. Manganelli leg. 3.9.1986 (9 sp). West of Chiverton House, underneath fallen branch of beech, VCI SW 793511, G.A. Holyoak leg. 13.1.2001 (1 sp). South of Endsleigh, under fallen beech/oak branches in



Figs 5–6 Distal genitalia (Fig. 5) and internal ornamentation of flagellum and proximal penis (Fig. 6) in a specimen of *Oxychilus alliarius* (Miller, 1822) from Box Hill near Dorking, J.F. Peake leg. 9.1961.

woodland, VC2 SX 389784, G.A. Holyoak leg. 20.1.2001 (8 sp). South of Four Lanes, collected from sieved leaf litter from Sallow Carr., VCI SW 685365, G.A. Holyoak leg. 14.1.2001 (2 sp). Dollar Glen (Scotland), F. Giusti & G. Manganelli leg. 3.9.1986 (1 sp). HOLLAND – Landvoort, 1961 (14 sp.; Nationaal Natuurhistorisch Museum, Leiden, The Netherlands, no. 8584). POLAND – Łódź, rezerwat Polesie Konstantynowskie, A. Piechocki leg. 17.5.1962 (2 sp). Orłowo near Gdynia Polesie Konstantynowskie, S. Kazubski leg. 7.1959 (1 sp). SPAIN – Navarredonda de la Sierra (Avila), 30TUK17, K. Altonaga leg. 24.9.1987 (1sp). Piedrahita (Avila), 30TUK0284, K. Altonaga leg. 22.9.1987 (2 sp), Vidau (Santiago de Compostela, Coruna), 29TNH34, K. Altonaga leg. 15.12.1976 (1 sp).



Figs 7–9 Distal genitalia (Fig. 7, 9) and internal ornamentation of flagellum and proximal penis (Fig. 8) in specimens of *Oxychilus alliarius* (Miller, 1822) from Cambe Meat, Kingsbarus, F. Giusti & G. Manganelli leg. 3.9.1986 (Figs 7-8) and Piedrahita, K. Altonaga leg. 22.09.1987 (Fig. 9).

Derivation of name The specific epithet is based on the Latin adjective "*alliari-us -a, -um* referring the garlic scent of this (and some other) *Oxychilus* species.

Geographical distribution *Oyxchilus alliarius* has a central western European distribution. It is recorded from Iceland, Ireland, Great Britain, the Scandinavian Peninsula (western and southern Norway, southern Sweden and Finland), Denmark, Poland, Germany, Switzerland, Holland, Belgium, France, northern Spain and the Azores (Adam, 1960; Kerney *et al.*, 1983; Gittenberger *et al.*, 1984; Wiese, 1991; Altonaga *et al.*, 1994; Vogt *et al.*, 1994; Riedel 1980, 1988, 1998; Turner *et al.*, 1998; Kerney, 1999). It has been reported from northern Dalmatia and western Macedonia (Greece) (Riedel, 1983, 1998). Giusti (1969) reported it from Tuscany (Italy), but his record was based on misidentification of *O. meridionalis* (Manganelli & Giusti, 2001).

It has been introduced into Greenland, North America, St. Helen I., Juan Fernandez I., South Africa and Australia (Pilsbry, 1946; Zilch & Jeackel, 1962). It is also recorded from New Zealand (Barker, 1999), but since the internal proximal penis of the New Zealand specimens has been described as papillate (Barker, 1999: Pl. 5, fig. 50), there are doubts as to whether this material actually belongs to *O. alliarius*.

Remarks The identification of *Oxychilus alliarius* from *O. helveticus* on the basis of mantle border colour (grey without deep-black edging) is unreliable, because certain specimens have a mantle border with brownish-black edging of different darkness (Fig. 3), very similar to that in *O. helveticus*.

Oxychilus helveticus (Blum, 1881)

Hyalina (Polita) helvetica Blum, 1881: 139, 141.

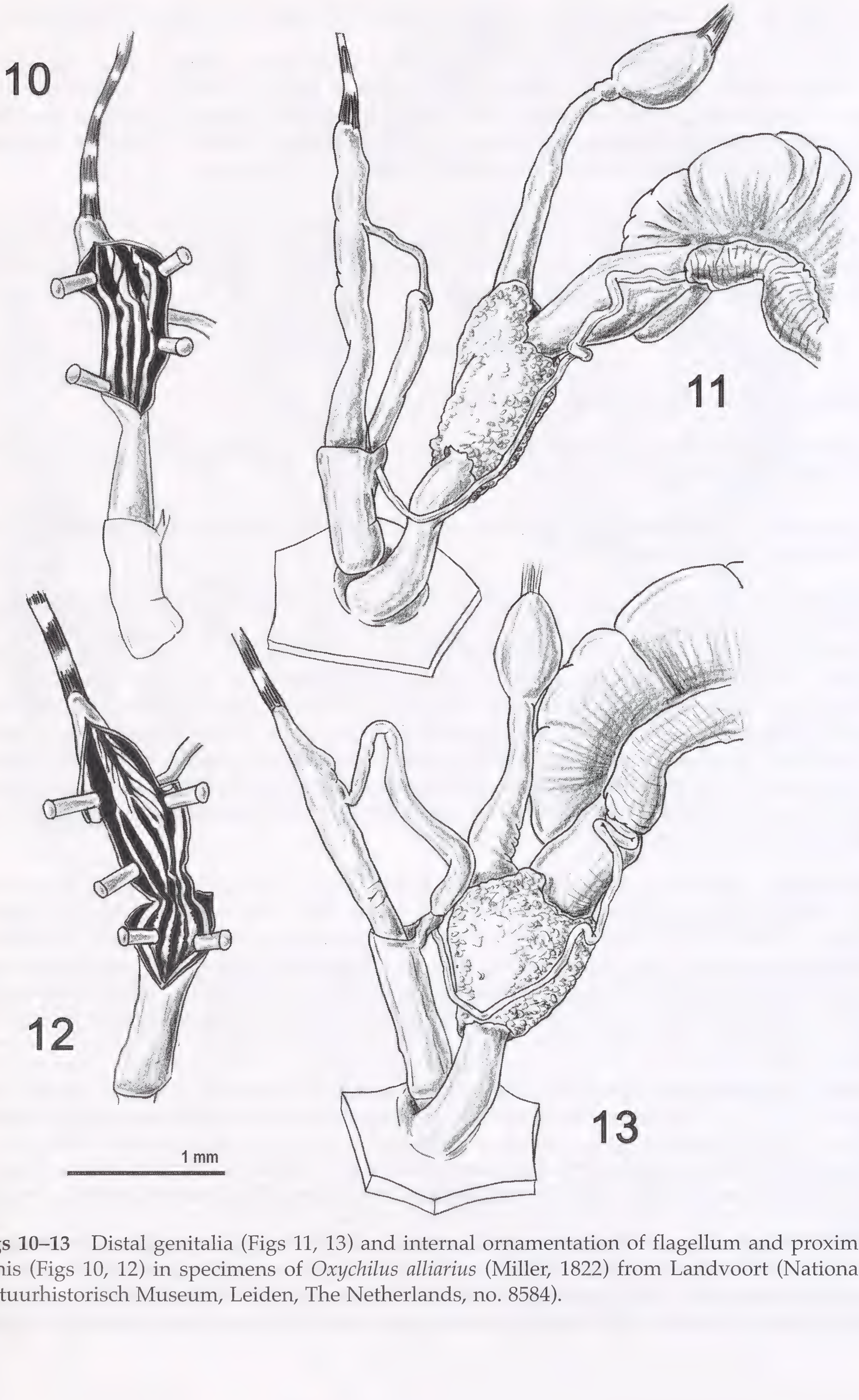
Type series The holotype (SMF 4287, shell) is at the Senckenberg-Museum (Frankfurt am Main, Germany).

Type locality "Sub foliis putrescentibus in silvis humidis fagorum ad Wessenstein, Cant. Solothurn", Switzerland.

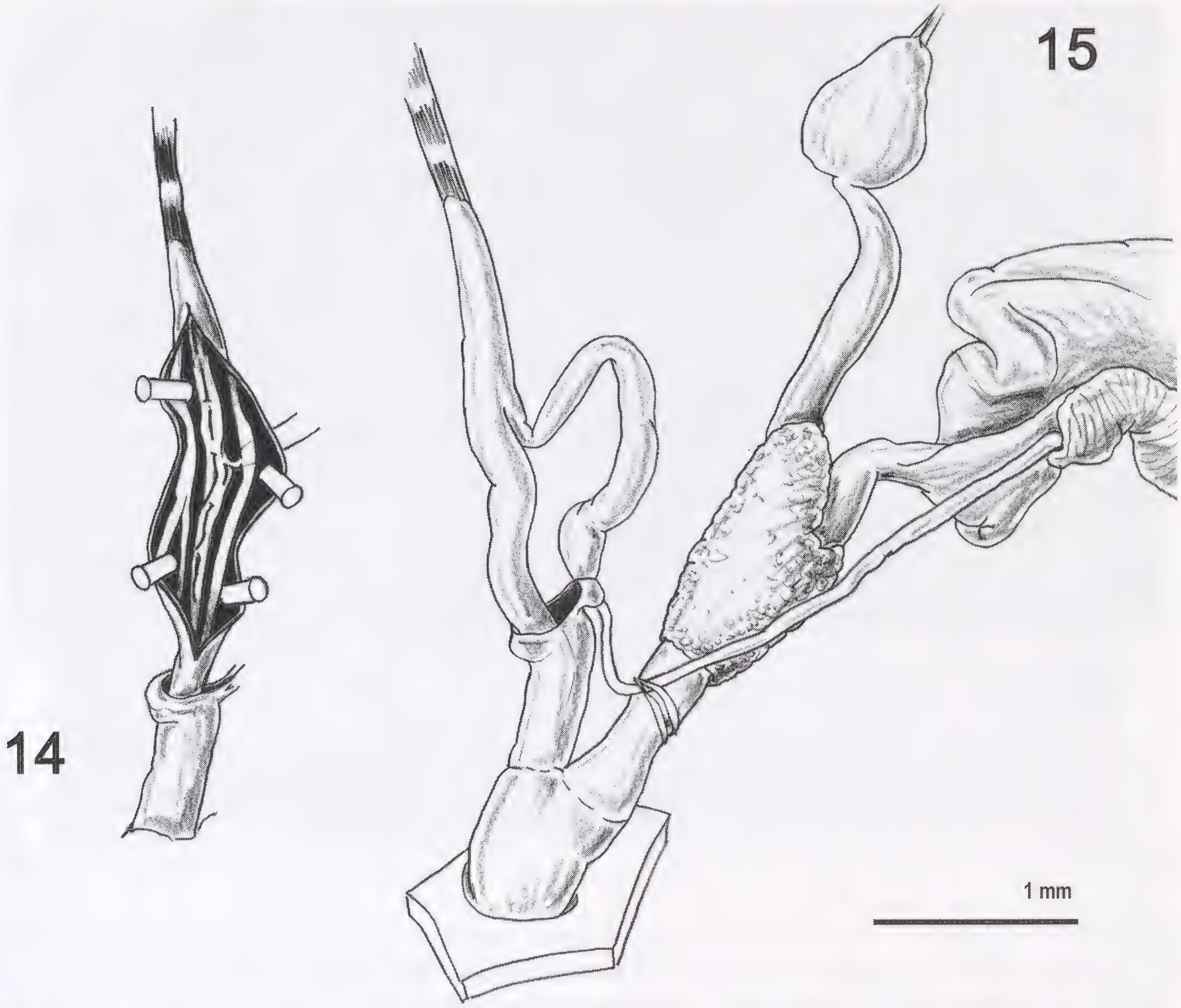
Identification *Oxychilus helveticus* belongs to *Oxychilus (s.str.) sensu* Giusti & Manganelli (1999), a "subgenus" of *Oxychilus* characterized by: penis with flagellum (1); penial retractor inserted at apex of flagellum (2); epiphallus usually longer than proximal penis, its internal wall with slender longitudinal pleats (3); mucous gland mainly vaginal (4); long mesocone of central tooth (5). It is readily distinguished by the shell (shell diameter: 7.3–12.2 mm) with a proportionally small umbilicus measuring about $^{1}/_{8}$ of shell diameter (resembling *Morlina* shells), the blackish mantle edge and internal ornamentation of proximal penis consisting of more than seven longitudinal pleats, which may be straight and distinct, or wavy, slender and connected by lateral projections to resemble a network.

Description Shell (Fig. 17; Taylor, 1907: Pl. 2, 1909: Pl. 6; Adam, 1960: Fig. 93; Kerney et al., 1983: Pl. 10, fig. 5a–c; Falkner, 1990: Figs 3–4 at p. 181; Altonaga, 1991: Figs 1–6, 19–24, 37–42, 55–60, 73–77, 96–99, 107–110) dextral, small to medium in size, discoidal, depressed, more or less convex above, slightly compressed below, thin, subtransparent, variably glossy, yellowish to yellowish-brown, reddish or greenish in colour, opalescent below; surface rather smooth with faint growth lines and microsculpture consisting of very fine wavy spiral lines; spire of 4 $^{1}/_{8}$– 5 $^{3}/_{8}$ whorls (Altonaga, 1991), rather slowly and regularly increasing in size, last whorl slightly dilated near aperture, its last quarter descending to some extent; sutures distinct, but shallow; umbilicus rather small, wide about $^{1}/_{8}$–$^{1}/_{10}$ of maximum shell diameter; aperture oval to roundish, oblique, sometimes slightly descending; peristome interrupted, simple, not thickened or reflected, its superior vertex starting at or above periphery of last whorl. Shell dimensions: diameter: 7.3–12.2 mm; height: 3.4–5.9 mm (Taylor, 1907; Kerney & Cameron, 1979; Altonaga, 1991).

Body (Fig. 18; Taylor, 1907: Pl. 2; Kerney *et al.*, 1983: Pl. 10, fig. 5d; Falkner, 1990: Figs 3–4 at p. 181; Turner *et al.*, 1998, Fig. at p. 277) pale slate blue in colour, sometimes brown or cream (Wütrich, 1963; Altonaga, 1991); mantle border with deep-black edging; neck and upper part of sides with wide areas with pits (with phylacites) and glandular crypts;



Figs 10–13 Distal genitalia (Figs 11, 13) and internal ornamentation of flagellum and proximal penis (Figs 10, 12) in specimens of *Oxychilus alliarius* (Miller, 1822) from Landvoort (Nationaal Natuurhistorisch Museum, Leiden, The Netherlands, no. 8584).



Figs 14–15 Distal genitalia (Fig. 15) and internal ornamentation of flagellum and proximal penis (Fig. 14) in a specimen of *Oxychilus alliarius* (Miller, 1822) from Łódź, rezerwat Polesie Konstantynowskie, A. Piechocki leg. 17.05.1962.

faintly darker zebra-like transverse stripes distinctly perceptible on the body sides; foot slender, of aulacopod type, with sole longitudinally tripartite, paler in colour than body; kidney sigmurethrous; jaw oxygnathous (Taylor, 1907: Fig. 81).

Genitalia (Figs 19–30; Taylor, 1907: Fig. 80; Wütrich, 1963: Fig. 1; Riedel, 1970: Fig. 9; Riedel, 1972: Figs 4–5 [*O. helveticus cantabricus*], Fig. 15 [*O. altimirai*]; Altonaga, 1991: Figs 7–18, 25–36, 43–54, 61–72, 78–87, 88–95, 100–106). General scheme of genitalia as in *Oxychilus (s.str.) sensu* Giusti & Manganelli (1999). Only distal genitalia described here (7 specimens examined).

Female distal genitalia include free oviduct, bursa copulatrix and its duct and vagina. Initial portion of duct of bursa copulatrix, distal portion of free oviduct and $^1/_3$–$^2/_3$ of proximal vagina enveloped by variably large and long muff of spongy glandular tissue forming a vaginal gland; duct of bursa copulatrix variably long (2.7–5.4 mm; n: 2), initially flared, narrowing before entering oval or pyriform bursa copulatrix; distal vagina (that without glandular muff) variably long (1.1–1.7 mm; n: 2) and wide, not or slightly reducing in calibre near genital atrium.

Male distal genitalia include vas deferens, epiphallus, and penial complex (flagellum and penis). Epiphallus variably long (2.6–4.4 mm; n: 2; P/EP 4/10–9/10 acc. to Altonaga, 1991) and slender. Flagellum variably long, but usually rather short (0.7–2.1

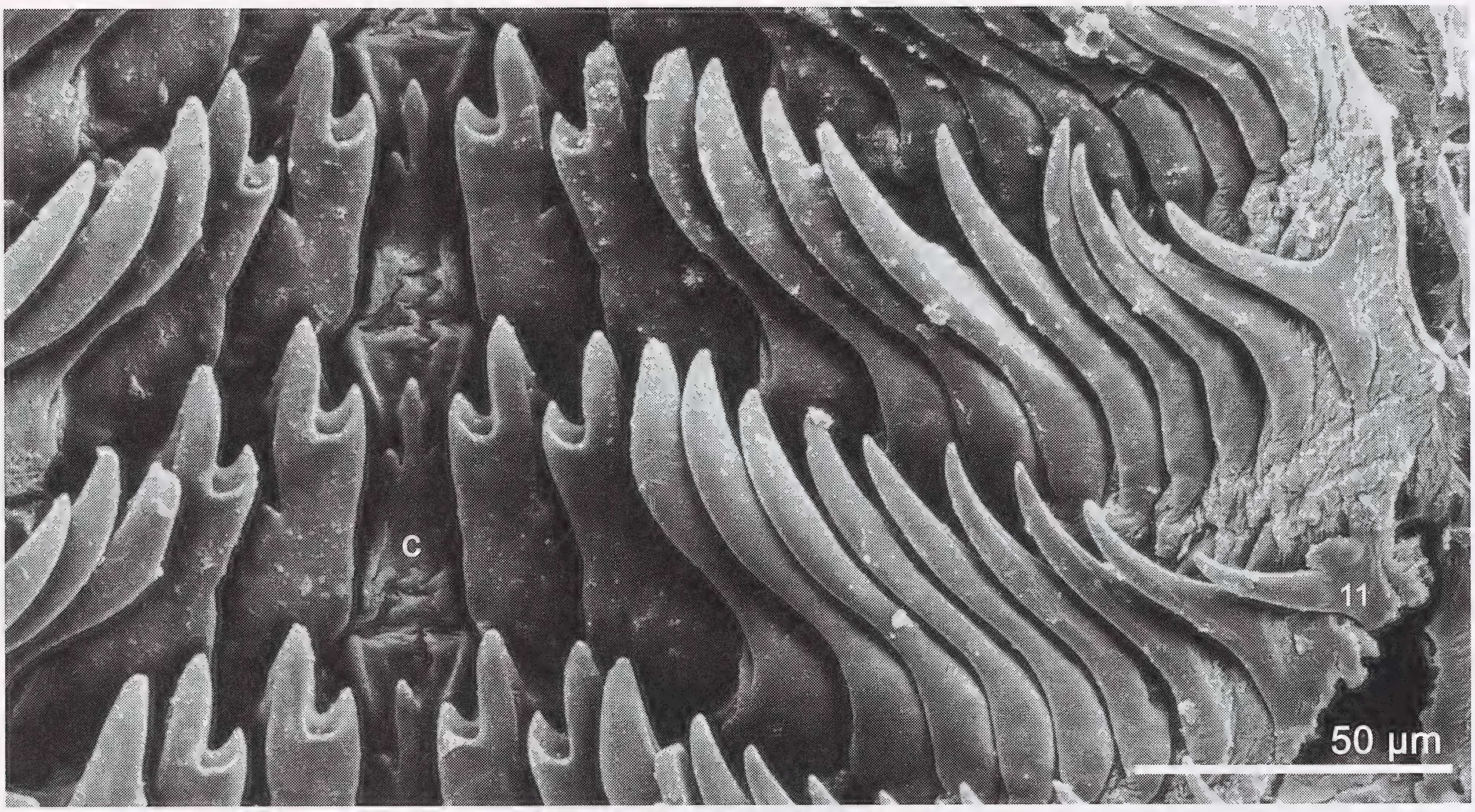


Fig. 16 The radula of a specimen of *Oxychilus alliarius* (Miller, 1822) from Cambe Meat, Kingsbarus, Fife, F. Giusti & G. Manganelli leg. 3.9.1986.

mm; n: 2; F/P 1/20–1/2 acc. to Altonaga, 1991), with penial retractor muscle ending at apex. Penis variably long (6.9–7.2 mm; n: 2; 3.4–9.7 mm; acc. to Altonaga, 1991) without clear distinction into proximal and distal parts from outside or inside. Proximal penis frequently wider at its beginning, then slightly reduced in calibre. Internal surface of flagellum and proximal penis surrounding the opening of the epiphallus into penis with numerous (more than four) longitudinal pleats, the two bordering the opening of epiphallus into penis straight, with jagged sides, or fragmented into small, transversely elongated, drop-like papillae. Proximal penis usually longer than distal, with numerous (7–12) pleats, variably wide, sometimes straight and distinct, sometimes wavy, slender and connected by lateral projections (to resemble a network), tapering in the distal part before continuing, usually without interruption, inside the distal penis, where they maintain the same calibre or become wider; pleats inside the distal penis straight or undulating, connected to one another by lateral branches. Distal penis almost entirely enveloped by penial sheath (1.6–2.8 mm; n: 2) initially very thin, traversed on one side by vas deferens, then slightly thickened for rest of length. A very short, thin walled duct connects the distal penis (level with where penial sheath originates) to the genital atrium in which vagina also ends.

Radula (Fig. 31; Taylor, 1907: Figs 74–77, 82–83; Wütrich, 1963: 132) consisting of many rows of about 31–41 teeth (25 to 35, according to Taylor, 1907), according to the formula: 12-17 M/1 + 1 LM/2 + 2 L/3 + C/3 + 2 L/3 + 1 LM/2 + 12-17 M/1. Central tooth with well developed basal plate, apical portion of which V-like, with pointed vertices; body of tooth wide, providing base for long, slender, pointed mesocone flanked by two very short ectocones. On both sides of each central tooth are two lateral tricuspid teeth, one latero-marginal bicuspid tooth and series of monocuspid marginal teeth in decreasing order of size.

Material examined SWITZERLAND – "Weissenstein bei Solotthurn", J. Blum leg. (1 sh; holotype of *Hyalina helvetica*, SMF no. 4287/1). Weissenstein (Solothurn), 32TLT83M, Bodon & G. Manganelli leg. 12.06.1996 (4 sh, 2 sp). GREAT BRITAIN – Pringle Wood, M.J. Bishop leg. 1.1.1972 (9 sp; University Museum of Zoology, Cambridge UK).

Fig. 17 Holotype (SMF no. 4287/1) of *Oxychilus helveticus* (Blum, 1881) from "Weissenstein bei Solotthurn".

FRANCE – "Nivetal bei Errobisala und Pas du Roland (bei Cambo les Bains)", L. Forcart leg. 20.04.1953 (Naturhistorisches Museum Basel, Switzerland, no. 756q). SPAIN – Pradoluengo (Burgos), 30TVM8386, K. Altonaga, C.E. Prieto & R. Martin leg. 20.10.1984 (10 sp). Murieta (Navarra), 30TWN6923, K. Altonaga & C.E. Prieto leg. 26.09.1983 (10 sp). Kampezu - Santa Cruz de Campezo (Alava), 30WN5324, K. Altonaga & C.E. Prieto leg. 24.09.1983 (10 sp).

Derivation of name The specific epithet is based on the Latin adjective "*helvetic-us, -a, -um*" meaning Swiss.

Geographical distribution *Oyxchilus helveticus* has a western European distribution. It is reported from Great Britain, Germany, Belgium, France, Switzerland and northern Spain (Adam, 1960; Riedel 1980, 1998; Kerney *et al.*, 1983; Van Goethem *et al.*, 1987; Altonaga, 1991; Altonaga *et al.*, 1994; Vogh *et al.*, 1994; Turner *et al.*, 1998; Kerney, 1999). It is also recorded from Poland but was a misidentification of *O. translucidus* (Mortillet, 1854) (Riedel, 1988).

It has been introduced into Ireland and North America (Pilsbry, 1946; Kerney, 1999).

Remarks The penial complex of *Oxychilus helveticus* is usually long and slender (Figs ; Wütrich, 1963: Fig. 1; Riedel, 1970: Fig. 9; Riedel, 1972: Fig. 5 [*O. helveticus cantabricus*], Fig. 15 [*O. altimirai*]; Altonaga, 1991: Figs 9, 15, etc.), but sometimes short or very short (Fig. 19; Altonaga, 1991: Figs 7, 11, 13, 17, etc.). Flagellum length is quite variable: 0.7 to 2.1 mm in the specimens examined by us; $^1/_{20}$ to $^1/_2$ the total penis length in the specimens examined by Altonaga (1991). In a few cases, the border between proximal and

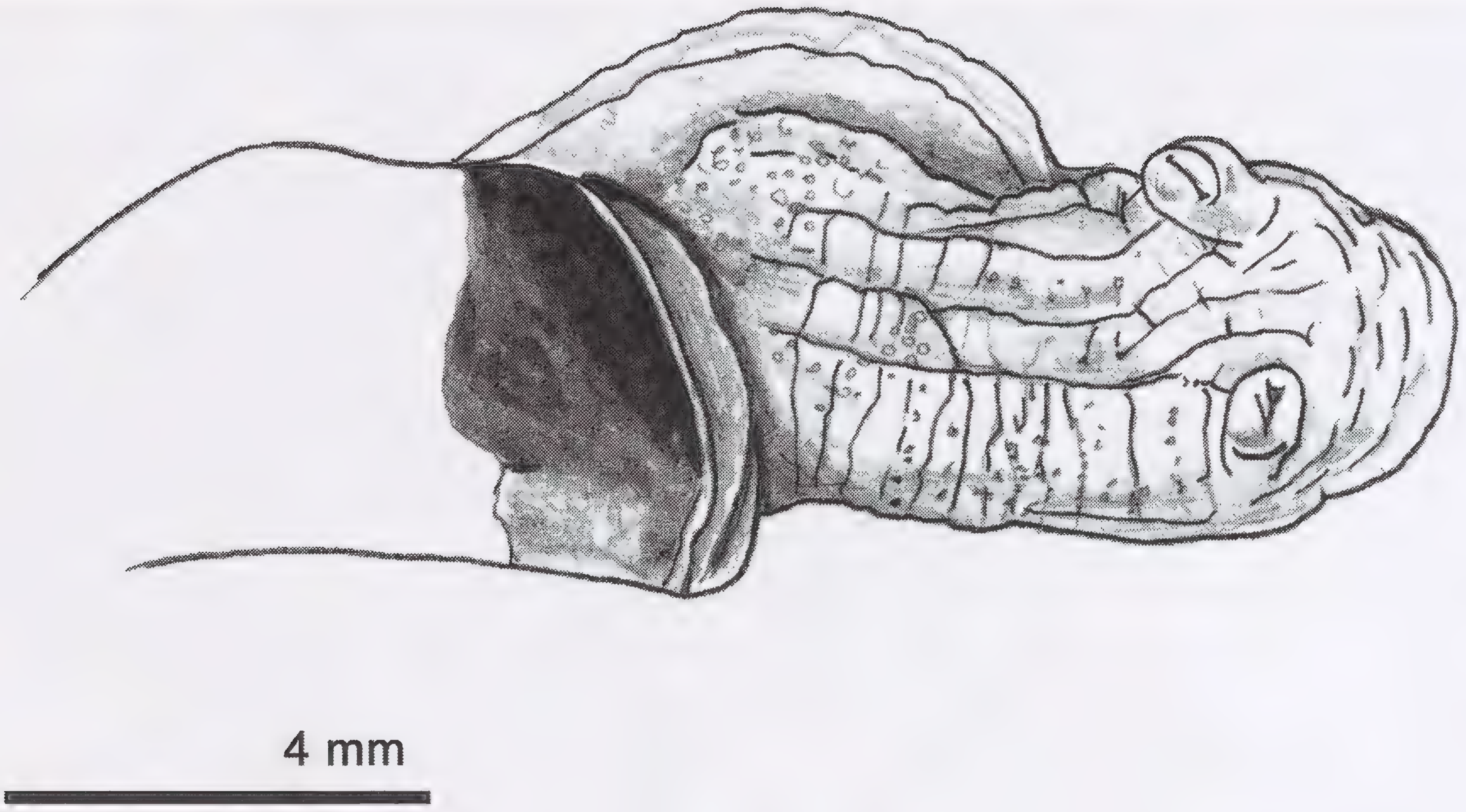


Fig. 18 Mantle edge in a specimen of *Oxychilus helveticus* (Blum, 1881) from Kampezu - Santa Cruz de Campezo, K. Altonaga & C.E. Prieto leg. 24.09.1983.

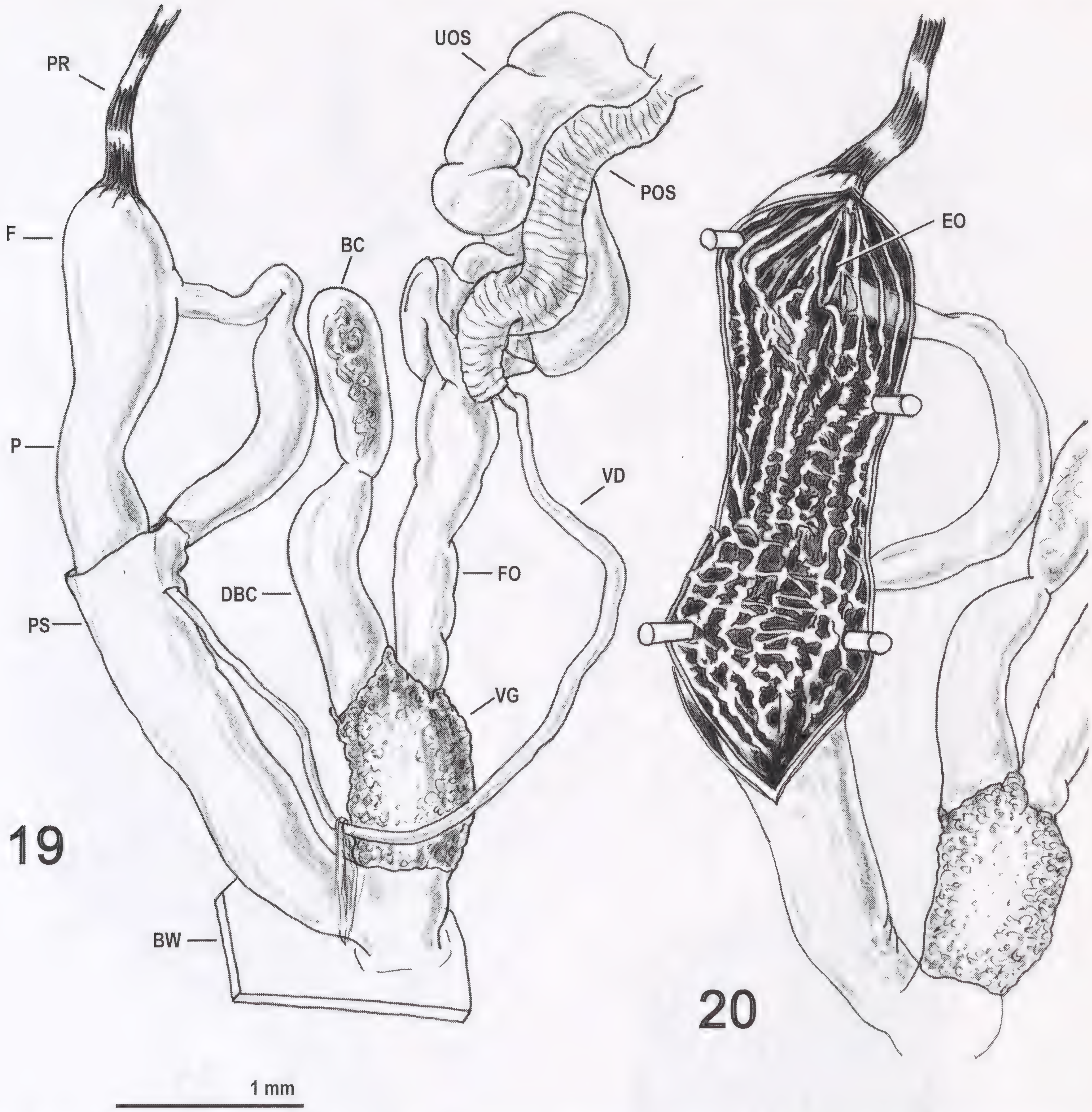
distal penis seems externally marked by a constriction (Altonaga, 1991, Figs 9, 63).

Discussion

Hyalina (Polita) helvetica Blum, 1881, is the type species of *Ortizius* Forcart, 1957, a subgenus of *Oxychilus* Fitzinger, 1833, the validity of which was initially disputed by us due to the intermediate position of some species (Manganelli & Giusti, 1985; Manganelli *et. al.*, 1991; Giusti & Manganelli, 1997). It was subsequently proposed by us as junior synonym of *Oxychilus (s.str.)*, because of the impossibility of distinguishing it from *Oxychilus (s.str.)* and many other subgenera (Giusti & Manganelli, 1999).

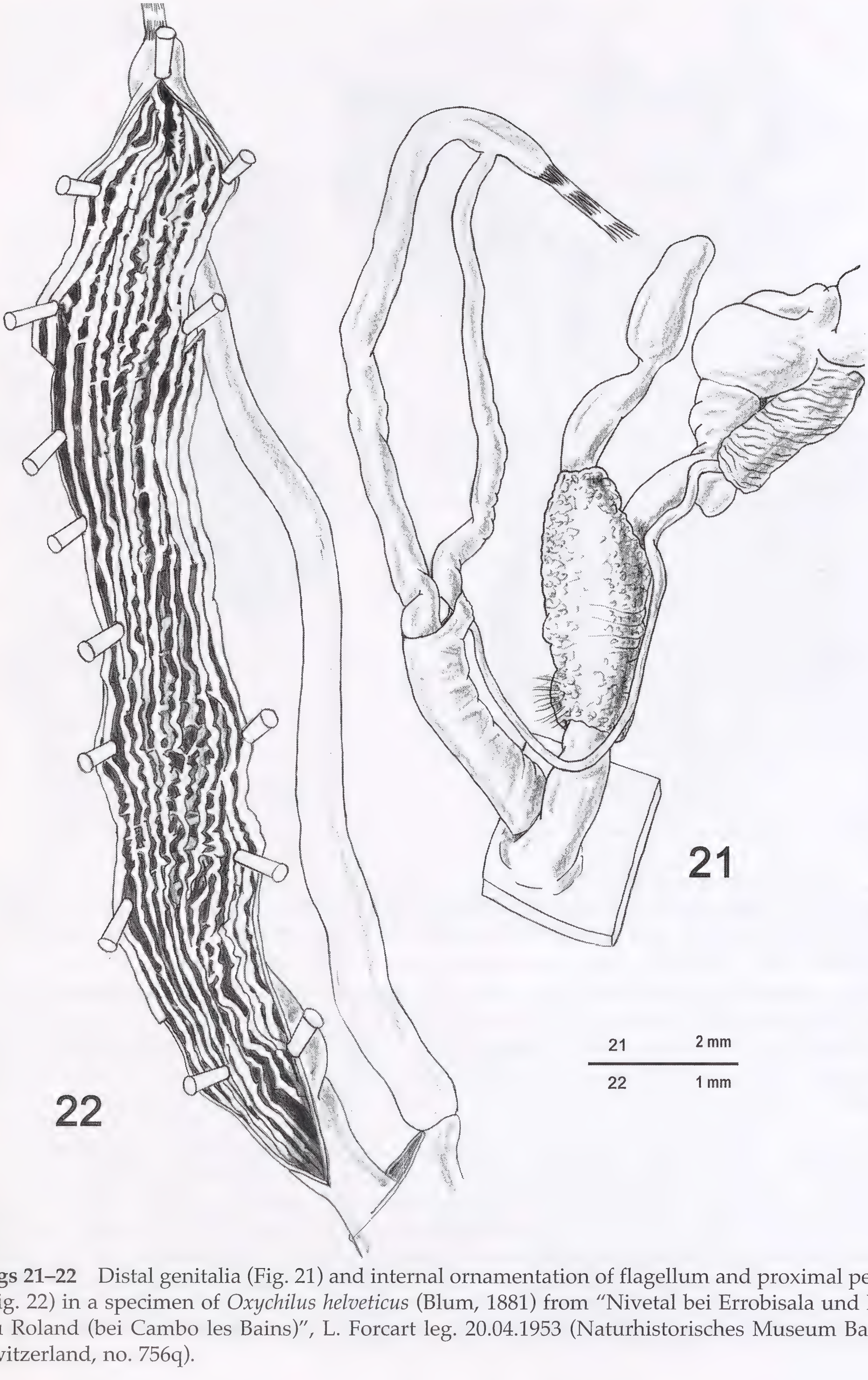
Oxychilus is a large, speciose genus of the zonitids, currently split into 23 subgenera (Riedel, 1998). Many of these subgenera, introduced following the praxis of evolutionary taxonomy, do not represent natural groups and are in need of revision (Giusti & Manganelli, 1999). One of the few natural groups identified by sets of anatomical characters, some of which may be synapomorphies, is "*Oxychilus*" (including *Alzonula* Giusti, 1968, *Atlantoxychilus* Riedel, 1964, *Calloretinella* Haas, 1934, *Drouetia* Gude, 1911, *Helicophana* Westerlund, 1886, *Hyalocornea* Monterosato, 1892, *Hyalofusca* Monterosato, 1892, *Longiphallus* Riedel, 1958, *Ortizius, Oxychilus s.s.* and *Radiolus* Wollaston, 1878). *Oxychilus (s.str.)* is in fact rather well characterized by: flagellum present; penial retractor inserted at apex of flagellum; internal ornamentation of penis consisting of pleats or pleats and rows of papillae; epiphallus long, usually as long as proximal penis, its internal wall with slender longitudinal pleats; mucous gland mainly vaginal; long mesocone of central tooth except in *Helicophana*).

Like some of the other subgenera in use, which are also characterized and presumably natural groups (*Mediterranea* Clessin, 1880, *Cellariopsis* Wagner, 1914, *Conulopolita* Boettger, 1879, *Morlina* Wagner, 1914, *Schistophallus* Wagner, 1914, etc.), we prudently continue to consider them as subgenera of *Oxychilus*. However they could be treated as distinct genera, because there is no evidence that *Oxychilus*, as currently conceived, is a natural taxon. In fact, we failed to find even one synapomorphy supporting the monophyly of the genus. We examined various characters but none are peculiar to *Oxychilus* or to oxychiline zonitids. All *Oxychilus* species have a penial sheath (except for

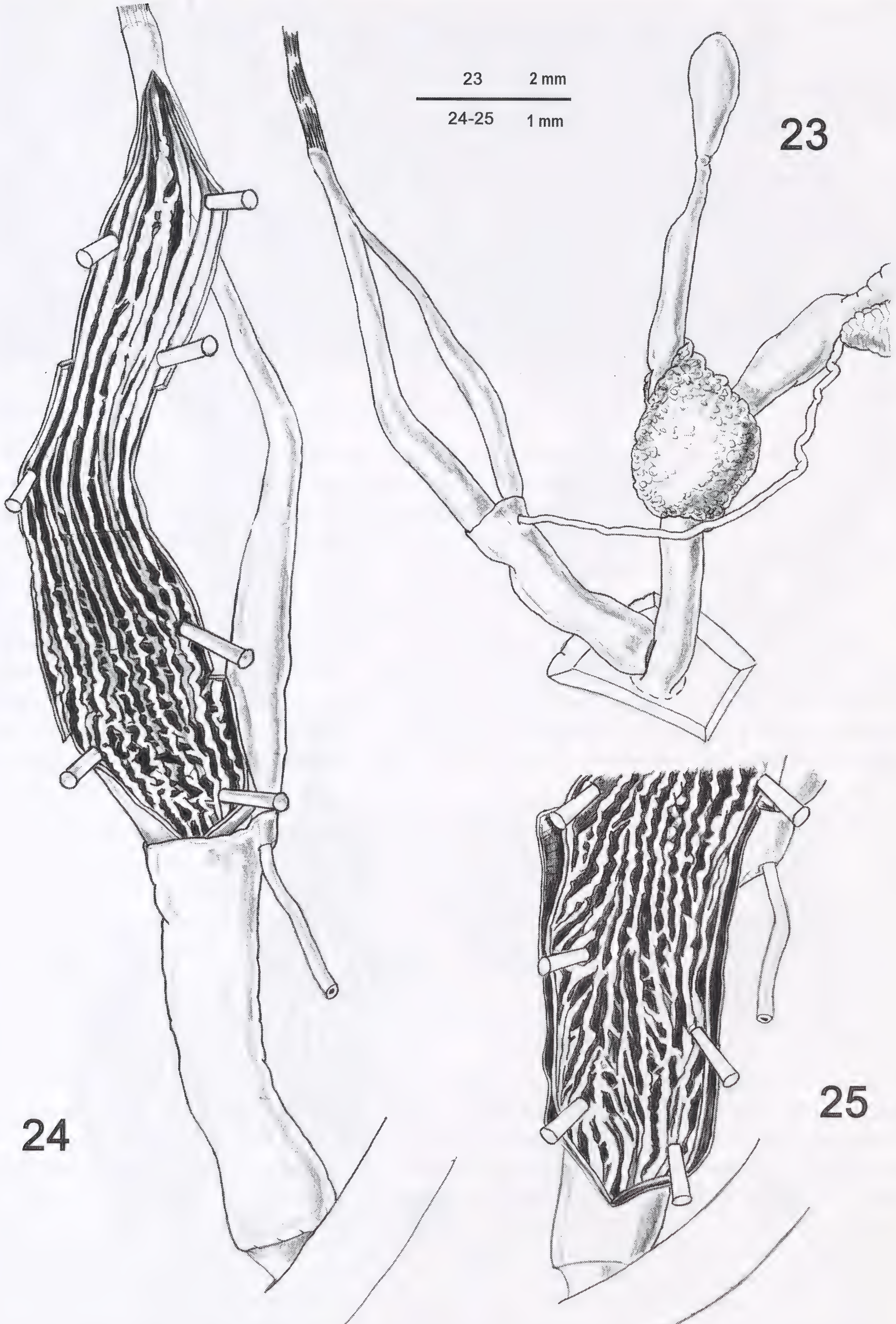


Figs 19–20 Distal genitalia (Fig. 19) and internal ornamentation of flagellum and proximal penis (Fig. 20) in a specimen of *Oxychilus helveticus* (Blum, 1881) from Weissenstein, M. Bodon & G. Manganelli leg. 12.06.1996.

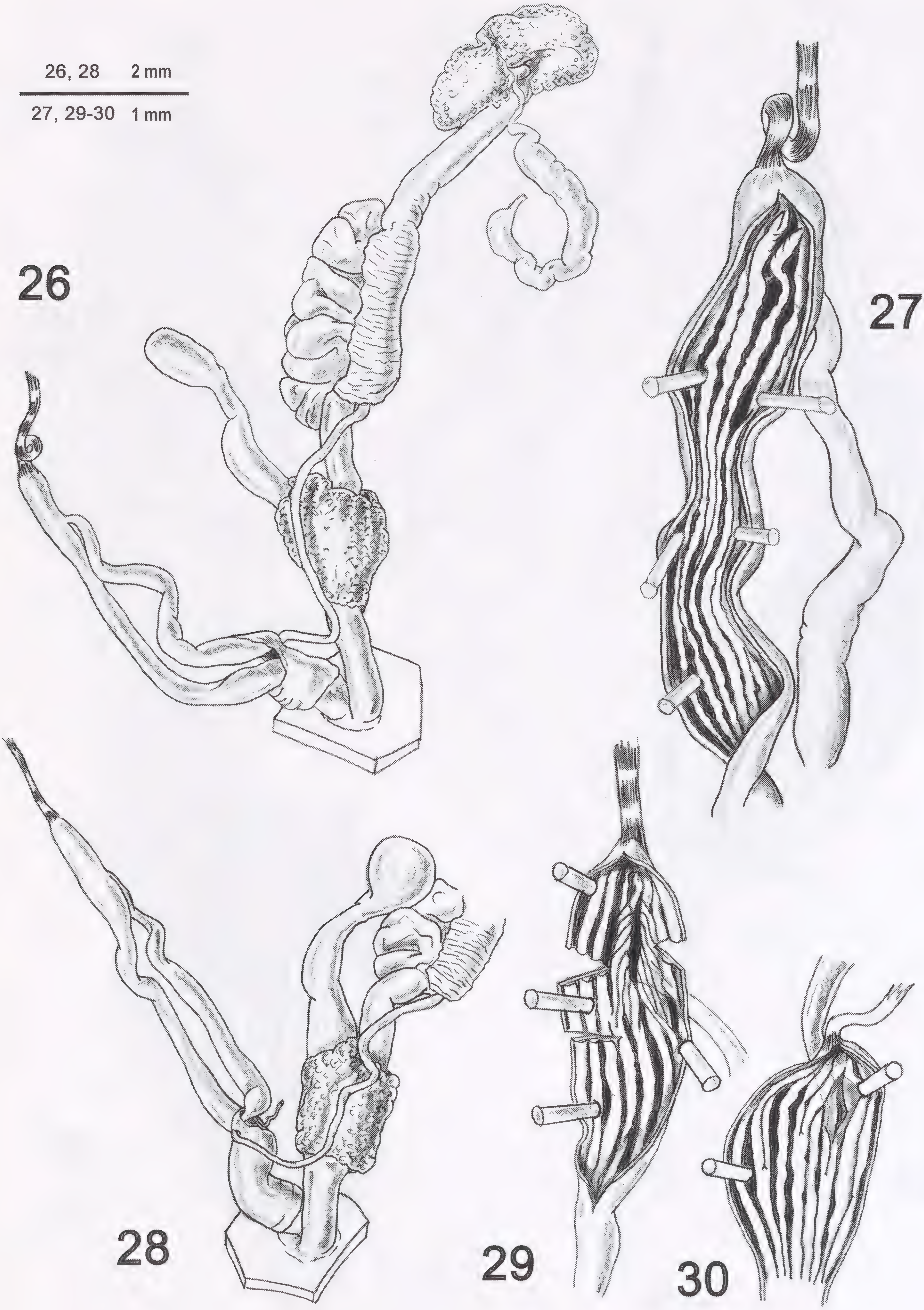
Conulopolita), an epiphallus (i.e. the widened muscular distal portion of the vas deferens), the penial retractor muscle inserted on the flagellum, or in the absence of the latter, in the area between the distal epiphallus and proximal penis, an oxychiloid shell (except for some species which have *Vitrea*-like shells), and a mucous gland forming a muff around the proximal vagina, this muff frequently extending to cover the distal portion of the free oviduct and/or of the duct of the bursa copulatrix (except for *Conulopolita* and *Retowskiella*, which have this muff on the free oviduct). Many other genera of non-oxychiline zonitids have one or more of these characters, whereas some oxychiline zonitids lack one or more of them. For example, *Zonites algirus* (Linnaeus, 1758) (Zonitini), has a scheme of the distal genitalia identical to that of most *Oxychilus* species, the only difference being that the penial retractor is inserted laterally on the flagellum. This may be due to the fact that at least some of these characters (penial sheath, vaginal gland, long epiphallus) are symplesiomorphies in *Oxychilus s.l.* and therefore support the monophyly of a larger group of taxa (Giusti & Manganelli, 1999).



Figs 21–22 Distal genitalia (Fig. 21) and internal ornamentation of flagellum and proximal penis (Fig. 22) in a specimen of *Oxychilus helveticus* (Blum, 1881) from "Nivetal bei Errobisala und Pas du Roland (bei Cambo les Bains)", L. Forcart leg. 20.04.1953 (Naturhistorisches Museum Basel, Switzerland, no. 756q).



Figs 23–25 Distal genitalia (Fig. 23) and internal ornamentation of flagellum and proximal penis (Fig. 24) and distal penis (Fig. 25) in a specimen of *Oxychilus helveticus* (Blum, 1881) from Kampezu - Santa Cruz de Campezo, K. Altonaga & C.E. Prieto leg. 24.09.1983.



Figs 26–30 Distal genitalia (Figs 26, 28) and internal ornamentation of flagellum and proximal penis (Figs 27, 29) and distal penis (Fig. 30) in specimens of *Oxychilus helveticus* (Blum, 1881) from Pringle Wood, M.J. Bishop leg. 1.1.1972 (University Museum of Zoology, Cambridge UK).

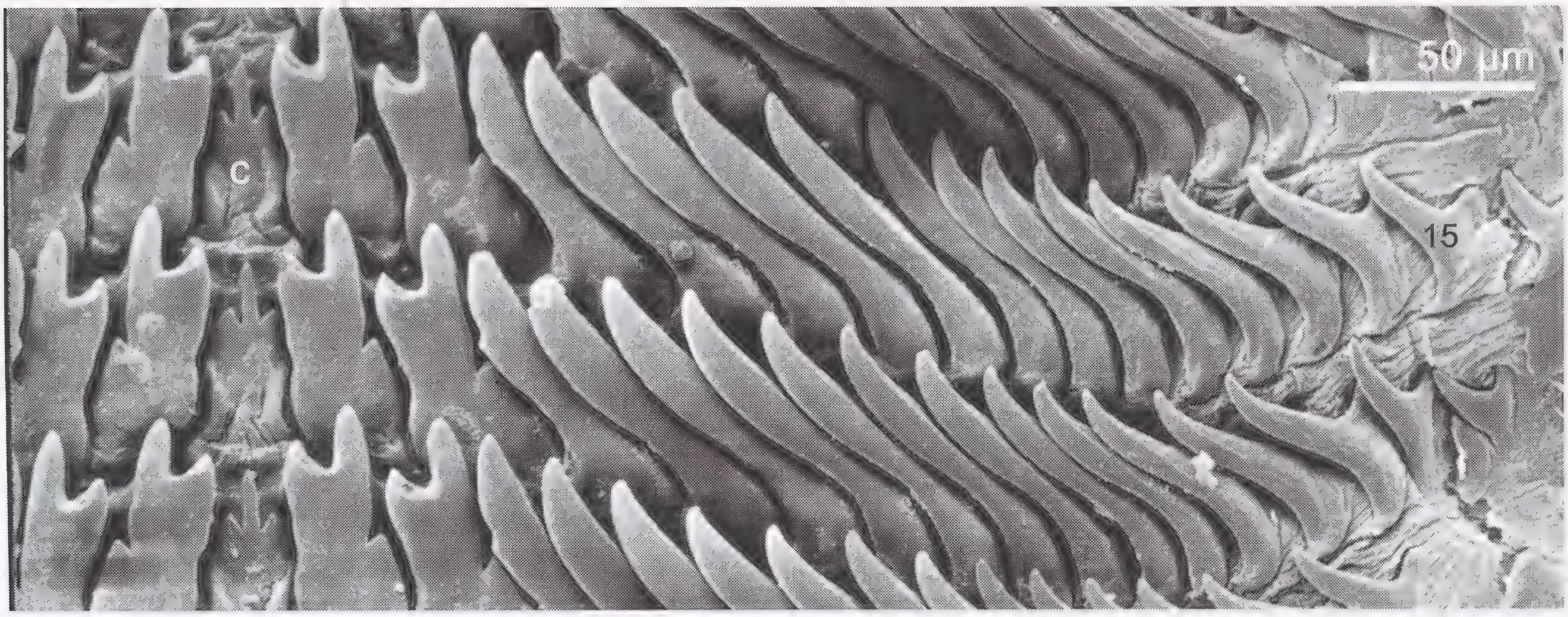


Fig. 31 The radula of a specimen of *Oxychilus helveticus* (Blum, 1881) from Weissenstein (Solothurn), 32TLT83 M. Bodon & G. Manganelli leg. 12.06.1996.

Oxychilus alliarius and *O. helveticus* are two very similar species, sometimes confused (Taylor, 1907; Wütrich, 1963; Altonaga, 1991). Their identification is easy, but requires both conchological and anatomical characters. In fact, they are readily distinguished by different shell shape and size and internal ornamentation of penial complex. *O. alliarius* has a smaller shell (shell diameter: 4.5–7.0 mm) with proportionally larger umbilicus (about $^1/_6$ of shell diameter), usually lacks blackish mantle edge and has internal ornamentation of proximal penis consisting of not more than four longitudinal pleats, usually straight, sometimes slightly wavy, but never laterally branched or papillate. *O. helveticus* has a larger shell (shell diameter: 7.3–12.2 mm) with proportionally smaller umbilicus (about $^1/_8$ of shell diameter), a blackish mantle edge and internal ornamentation of proximal penis consisting of more than seven longitudinal pleats, sometimes straight and distinct, sometimes wavy, slender and connected by lateral projections giving a reticulate aspect.

O. alliarius and *O. helveticus* belong to *Oxychilus (s.str.) sensu* Giusti & Manganelli (1999). In fact they share the following characters with the *Oxychilus (s.str.)* species: penis with flagellum; penial retractor inserted at apex of flagellum; internal ornamentation of penis consisting of pleats (and/or rows of papillae); epiphallus long, usually longer than proximal penis; internal wall of epiphallus with slender longitudinal pleats; mucous gland mainly vaginal; long mesocone of central tooth. Among the *Oxychilus (s.str.),* they share a sac-like penis, without the evident mid-penial constriction (bottleneck) with *O. cellarius* (Müller, 1774), *O. meridionalis* (Paulucci, 1881) and *O. pilula* (Paulucci, 1886) and most species assigned to *Ortizius* and the pleats inside the proximal penis with the *Ortizius* – species.

Conchologically, *O. alliarius* is readily distinguished from *O. cellarius, O. meridionalis* and *O. pilula* by its small size (shell diameter: 4.5–7.0 mm vs. 9–12 mm of *O. cellarius;* 13.1 ± 2.0 mm [range: 8.9–16.6 mm] of *O. meridionalis;* 10.8 ± 0.6 mm [range: 9.5–12.4 mm] of *O. pilula*) and *O. helveticus* by its small umbilicus which makes the shell resemble those of *Morlina* (*O. cellarius, O. meridionalis* and *O. pilula* have shells with larger umbilicus) (for *O. cellarius,* see Kernery & Cameron, 1979: Pl. 9, fig. 5; Giusti & Manganelli, 1997, Fig. 2; for *O. meridionalis,* see Manganelli & Giusti, 2001: Figs 1–8; for *O. pilula,* see Manganelli *et al.*, 1999: Figs 16–18). Anatomically, both are distinct from *O. cellarius, O. meridionalis* and *O. pilula* by the internal ornamentation of the penis (6–8 rows of large sparse papillae in *O. cellarius;* 5–6 to 13–15 longitudinal pleats, usually straight, sometimes wavy or lobate in *O. meridionalis;* 8–10 rows of numerous, polygonal or pyramidal papillae in *O. pilula;* for *O. cellarius,* see Giusti & Manganelli, 1997: Figs 3–14; for *O. meridionalis,* see Manganelli & Giusti, 2001: 10–31; for *O. pilula,* see

TABLE 1
Species assigned (an asterisk indicates tentative assignment) to *Oxychilus (Ortizius)* by Riedel (1980, 1998).

Species	**Size range**	**Geographical distribution**	**Main references**
O. alliarius (Miller, 1822)	5.5–7.0 mm (Kerney *et al.*, 1983)	Central western Europe	Taylor (1907), Wütrich (1963), Riedel (1957, 1980), Gittenberger *et al.* (1984), Castillejo (1985)
O. anjana Altonaga, 1986*	7.3–10.1 mm (Altonaga, 1986)	Northern Spain	Altonaga (1986, 1989)
O. basajauna Altonaga, 1990	10,1–13.0 mm (Altonaga, 1990)	Northern Spain	Altonaga (1990)
O. caspius (Boettger, 1880)	7.0–9.0 mm (Riedel, 1996)	Northern Iran	Riedel (1959, 1966, 1980, 1981)
O. clarus (Held, 1838)	4.0–4.2 mm (Kerney *et al.*, 1983)	Western Europe	Forcart (1957), Riedel (1980), Giusti *et al.* (1985), Manganelli & Giusti (1993)
O. concinnus (Westerlund, 1896)	not more than 8.0 mm (Riedel, 1966)	Northwestern Iran	Riedel (1966, 1980, 1981)
O. courquini (Bourguignat, 1870)	5.0–5.6 mm (Riedel, 1972)	Northwestern Spain (Catalonia)	Riedel (1972, 1980)
O. decipiens (Boettger, 1886)	6.5–10.5 mm (Riedel, 1966)	Northeastern Turkey and Caucasus	Riedel (1966, 1980)
O. emmae (Akramowski, 1955)	not more than 5.8 mm (Riedel, 1966)	Lesser Caucaus	Riedel (1966, 1980, 1995)
O. gardinii Manganelli, Bodon & Giusti, 1991*	13.0–16.5 mm (Manganelli *et al.*, 1991)	Northern Italy (Liguria)	Manganelli *et al.* (1991)
O. helveticus (Blum, 1881)	8.0–10.0 mm (Kerney *et al.*, 1983)	Western Europe	Riedel (1957, 1964a, 1970, 1980), Wütrich (1963), Altonaga (1991)
O. juvenostriatus Riedel, 1964	5.5–7.8 mm (Riedel, 1964b)	Azores (Faial I.)	Riedel (1964b, 1980)
O. lentiformis (Kobelt, 1882)	up to 13.0 mm (Riedel, 1969)	Balearis Is. (Mallorca and Menorca)	Riedel (1969, 1980)
O. lineolatus Frias Martins & Ripken, 1991	7.5–10.6 mm (Frias Martins & Ripken, 1991)	Azores (Santa Maria I.)	Frias Martins & Ripken (1991)
O. mercadali Gasull, 1969	7.0–10.5 mm (Riedel, 1972)	Western Spain (Valencia)	Riedel (1972, 1980)
O. miguelinus Pfeiffer, 1856	up to 15.0 mm (Riedel, 1964b)	Azores	Riedel (1964b, 1980)
O. ornatus Riedel, 1964	4.7–5.6 mm (Riedel, 1964b)	Azores (Faial I.)	Riedel (1964b, 1980)
O. patulaeformis (Boettger, 1889)*	7.0 mm (Riedel, 1966)	Northwestern Iran	Riedel (1980, 1998)
O. paulucciae (De Stefani, 1883)	17.9–18.7 mm (Forcart, 1967, as *O. lanzai*)	Central Italy (Tuscany)	Forcart (1967), Riedel (1980), Manganelli *et al.* (1995)
O. perspectivus (Kobelt, 1881)	6.0–8.5 mm (Giusti, 1973)	Southern Italy	Giusti (1973), Riedel (1980), Giusti *et al.* (1985)
O. pityusanus Riedel, 1969	up to 9.3 mm (Riedel, 1969)	Balearic Is. (Pityuses Is.)	Riedel (1969, 1980)
O. rateranus (Servain, 1880)	10.0–13.0 mm (Riedel, 1972)	Southern Spain	Riedel (1972, 1980)
O. scoliura Frias Martins, 1989	13.7 mm (Frias Martins, 1989)	Azores	Frias Martins (1989)
O. subeffusus (Boettger, 1879)	up to 4.7 (Riedel, 1966)	Northeastern Turkey and northern Iran	Riedel (1966, 1980), Akramowski (1976)
O. tomlini (Smith, 1905)	up to 16 mm (Riedel, 1966)	Southern Greece	Riedel (1980, 1990)
O. translucidus (Mortillet, 1854)	7.0–7.5 mm (Riedel, 1966, as *O. komarowi*)	Northern Iran? Introduced to western Caucasus, Turkey, Bulgaria and Poland	Riedel (1966, 1980, 1989)
O. tropidophorus (Mabille, 1869)	19.0–20.0 mm (Germain, 1930)	Corsica	Germain (1930)
O. uziellii (Issel, 1872)*	9.8–12.5 mm (Giusti & Manganelli, 2000)	Central Italy (Tuscany and Emilia)	Manganelli & Giusti (1985, 1993, 2000)

Manganelli *et al.*, 1999: Figs 19–21).

The distinction of *O. alliarius* and especially of *O. helveticus* from many "*Ortizius*" species is more problematical, due to the fact that this alleged subgenus is a large assemblage of species, many of which are relatively unknown. Among the 28 species assigned to this subgenus by Riedel (1980, 1998), *O. patulaeformis* (Boettger, 1889) is anatomically unknown and *O. subeffusus* (Boettger, 1879) is possibly related to another subgenus, i.e. *Mediterranea* Clessin, 1880 (type species: *Helix hydatina* Rossmässler, 1838) (see Giusti & Manganelli, 1999). All remaining species are known anatomically, but the internal structure of the penial complex (flagellum, proximal and distal penis) is only known in sufficient detail in six of them: *O. anjana* Altonaga, 1986, *O. basajauna* Altonaga, 1990, *O. clarus* (Held, 1838), *O. gardinii* Manganelli, Bodon & Giusti, 1991, *O. lineolatus* Frias Martins & Ripken, 1991, and *O. uziellii* (Issel, 1872). The internal structure of the penis is known in three other species, but the details of the ornamentation around the epiphallus opening are missing or unclear: *O. miguelinus* (Pfeiffer, 1856), *O. perspectivus* (Kobelt, 1881) and *O. translucidus* (Mortillet, 1854). The internal anatomy of the other species is relatively or completely unknown.

Two of the "*Ortizius*" species (Table 1) have a size range falling within that of *O. alliarius*: *O. courquini* (Bourguignat, 1870) and *O. ornatus* Riedel, 1964. They have very similar shell and anatomy (no information is available on internal ornamentation of penial complex) to *O. alliarius*. The former seems to be distinct from *O. alliarius* by a more depressed shell and larger umbilicus and the latter by a smaller umbilicus (for *O. ornatus*, see Riedel, 1964b, pp. 22–25, Figs 16–20; for *O. courquini*, see Riedel, 1972, pp. 123–126, Figs 6–7, 10–11, Pl. 1, Figs 4–6). Three other "*Ortizius*" species have a size range which overlaps with that of largest *O. alliarius: O. decipiens* (Boettger, 1886), *O. juvenostriatus* Riedel, 1964, and *O. perspectivus* Kobelt, 1881. Again, two of them (*O. decipiens* and *O. juvenostriatus*) have very similar shell and anatomy (no information is available on internal ornamentation of penial complex) to *O. alliarius*. They seem to be distinct from *O. alliarius* mainly by their larger size and *O. juvenostriatus* also by the microsculpture of the first whorls. On the contrary, *O. perspectivus* is easily distinguished by its whitish shell (for *O. decipiens*, see Riedel, 1966: 82–91, Figs 58–62; for *O. juvenostriatus*, see Riedel, 1964b: 15–19, Figs 8–13; for *O. perspectivus*, see Giusti, 1973: 159–161, Figs 11A–C; Giusti et al., 1985: Pl. 1, fig. C, Pl. 2, fig. B).

Major problems exist in differentiating *O. helveticus* because most of the "*Ortizius*" species, have a shell size range overlapping that of this species (see Table 1). It can be distinguished by shell shape (which resembles *Morlina*) and internal ornamentation of flagellum and penis (with more than seven longitudinal pleats, sometimes straight and distinct, sometimes wavy, slender and connected by lateral projections to create a reticulate appearence). *O. anjana, O. basajauna* and *O. translucidus* have a very similar shell, but they are readily distinguished by their anatomy (very short, pear-like inflated penial complex in *O. anjana*; internal surface of penis with many (30–35) small longitudinal pleats in *O. basajauna*; very long flagellum, evident constriction between proximal and distal penis, few large pleats on internal walls of flagellum and proximal penis in *O. translucidus*; for *O. anjana*, see Altonaga, 1986: Figs 1–19; for *O. basajauna*, see Altonaga, 1990: Figs 2–4; for *O. translucidus*, see Riedel, 1966; Figs 50–56 [as *O. komarowi*], 1989: Fig. 7). *O. lineolatus* is distinguished by its anatomy (very short penial complex with large flagellum; Frias Martins & Ripken, 1991: Fig. 5). *O. caspius, O. concinnus, O. decipiens, O. mercadali, O. rateranus* and *O. pityusanus* seem to differ in shell shape (with a larger umbilicus; *O. caspius disciformis* is also angled at periphery; for *O. caspius*, see Riedel, 1966: Figs 73–75, 78–84; for *O. concinnus*, see Riedel, 1966: Figs 87–89; for *O. decipiens*, see Riedel, 1966: Figs 58–64, 68–70; for *O. mercadali*, see Riedel, 1972: Pl. 2, Figs 14–16; for *O. rateranus*, see Riedel, 1972: Pl. 2, Figs 20–22; for *O. pityusanus*, see Riedel, 1969: Pl. 1, Figs 1–3). Finally, *O. perspectivus* is readily distinguished by shell characters (whitish shell and larger umbilicus; Giusti *et al.*, 1985: Pl. 1, fig. C, Pl. 2, fig. B).

ACKNOWLEDGMENTS

We thank Antonella Daviddi, Leonardo Gamberucci and Eugenio Paccagnini for technical assistance, Helen Ampt for revising the English, Kepa Altonaga (Bilbao, Spain), Martin J. Bishop (Cambridge, UK), Marco Bodon (Genoa, Italy), Antonio Frias Martins (Sao Miguel, Azores, Portugal), Edmund Gittenberger (Leiden, Holland), Ambros Hänggi (Basel, Switzerland), Geraldine A. Holyoak (Tuckingmill, Camborne, UK), Jolanda Ineichen-Riedi (Basel, Switzerland), Ronald Janssen (Frankfurt, Germany), Peter Mordan (London, UK) and Adolf Riedel (Warsaw, Poland), for information about or loan of material from their respective museums.

Research financed by MURST (grant no. 9905317452 "Aspetti descrittivi e metodologici della biodiversità animale in Italia").

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ARGONAUTA NODOSA SOLANDER, 1786 (CEPHALOPODA: ARGONAUTIDAE) IN ARGENTINE WATERS

GUIDO PASTORINO[1] & LEANDRO TAMINI[2]

Abstract Argonauta nodosa *Solander, 1786 is formally recorded off Puerto Quequén, in the south of Buenos Aires province, Argentina. Despite some scanty dubious citations in early local malacological literature this is the first record from Argentine temperate waters. Two females were collected from the stomach contents of the blue shark* Prionace glauca *and one empty egg case was recovered by fishermen nets. Two other lots were found in museum collections. Morphological data on the animal, shell and beaks are provided. Some remarks are pointed out about the presence of this worldwide tropical species.*

Key words *Cephalopoda,* Argonauta, *south-western Atlantic,*

INTRODUCTION

Stomach contents provide information about feeding behaviour and preferences of individual predators. However, the possibility exists of using the predators as samplers of the ecosystem to reveal aspects of the distribution and biology of uncommon groups such as Argonautids.

Argonautids are a curious group of octopuses which develop a distinctive thin shell. This shell is produced only by females, basically to protect the eggs. In addition, flotation and protection of the adult is also provided. Voss & Toll (1998) cited seven valid living species grouped in the genus *Argonauta,* the only one existing in the family Argonautidae.

The probable presence of *A. nodosa* in Argentine waters (Brunetti, 1995; sometimes as *A. tuberculata* Lamarck, i.e. Carcelles, 1944) is a recurring issue in malacological literature from South America. However, most of the records are based on old citations without sampling or collection support.

In this paper we formally record for the first time the presence of *Argonauta nodosa* Solander, 1786 in Argentine waters, from direct and indirect documental sources. In addition several morphological measurements, including those of the beaks, are provided to facilitate comparison with material from other localities.

MATERIALS AND METHODS

Two complete females of *Argonauta nodosa,* including parts of broken shells and eggs, were recovered from the stomach of a female Blue Shark, *Prionace glauca* (Linnaeus, 1758) caught by fishermen off Puerto Quequén (38°37′S–58°50′W) in Buenos Aires province. The stomach was immediately dissected and frozen. Together with *A. nodosa,* one specimen of *Engraulis anchoita* Hubbs & Marini, 1935 and one of *Galeorhinus galeus* Linnaeus, 1758 were recognized in the stomach contents of this shark, a fact suggesting non specific or opportunistic feeding habits. The total length and weight of the predator were 2200 mm and 52 kg respectively.

Additional material available for examination included one shell collected by the boat "*Eusonia*" at its fishing area also off Puerto Quequén, and two lots of empty shells from the invertebrate collection of the Museo Argentino de Ciencias Naturales (MACN).

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TABLE 1

Measurements for *Argonauta nodosa* female specimens. The symbols denote: *=the material was not in good condition to be measured, +=distal arm tip suckers severely damaged and #= shortened by predator action. Acronyms follow Roper & Voss (1983) and O'Shea (1999).

MACN #34812		**Specimen 1**	**Specimen 2**
ML		83	88
TL		304	300
MW		52	45
HW		26	24
HdL		26	22
AL1	R/L	211 / 174	170 / 110
AL2	R/L	98 / 128	167 / 178
AL3	R/L	211 / 212	121 / 132
AL4	R/L	180 / 200	170 / 146
WDA		37.1	20.7
WDB	R/L	20.3/16.3	15.3/ 14.6
WDC	R/L	15/13.9	17.2/19.3
WDD	R/L	17.8/ 14.3	21/19.4
WDE		16.7	19
ASC1	R/L	23+/18+	25+/17+
ASC2	R/L	32#/33#	48+/26+
ASC3	R/L	73/112	28+/23+
ASC4	R/L	86/83	17+/18#
ASn1	R	3.4	*
ASn2	R	3.6	2.7
ASn3	R	3.7	*
ASn4	R	3.9	L 2.7
GiLC	inner	12	11
GiLC	outer	12	12
Fful		49	58
FFL		28	44*
ED		14	13.4

RESULTS

Argonauta nodosa Solander in Lightfoot, 1786

Figs 1a–b; 2a–f.

Argonauta nodosa Solander in Lightfoot, 1786:96.

Material examined MACN 17825, East of English Bank, Mar del Plata, in 18.3–36.6 m; MACN 9877, Mar del Plata, Buenos Aires; MACN 34781, Puerto Quequén, Buenos Aires province; all empty shells; MACN 34812, 2 complete females.

Remarks The first mention of the name was attributed to Solander; however the author of the Catalogue where it was published was Lightfoot (according to Rehder, 1967). Most of the classical measurements were taken following the general description tips published by Roper & Voss, 1983. Since both complete females came from stomach contents, it was impossible to take measurements on some of the parts, although the general morphometrics agree with those pointed out by O'Shea (1999). In addition the

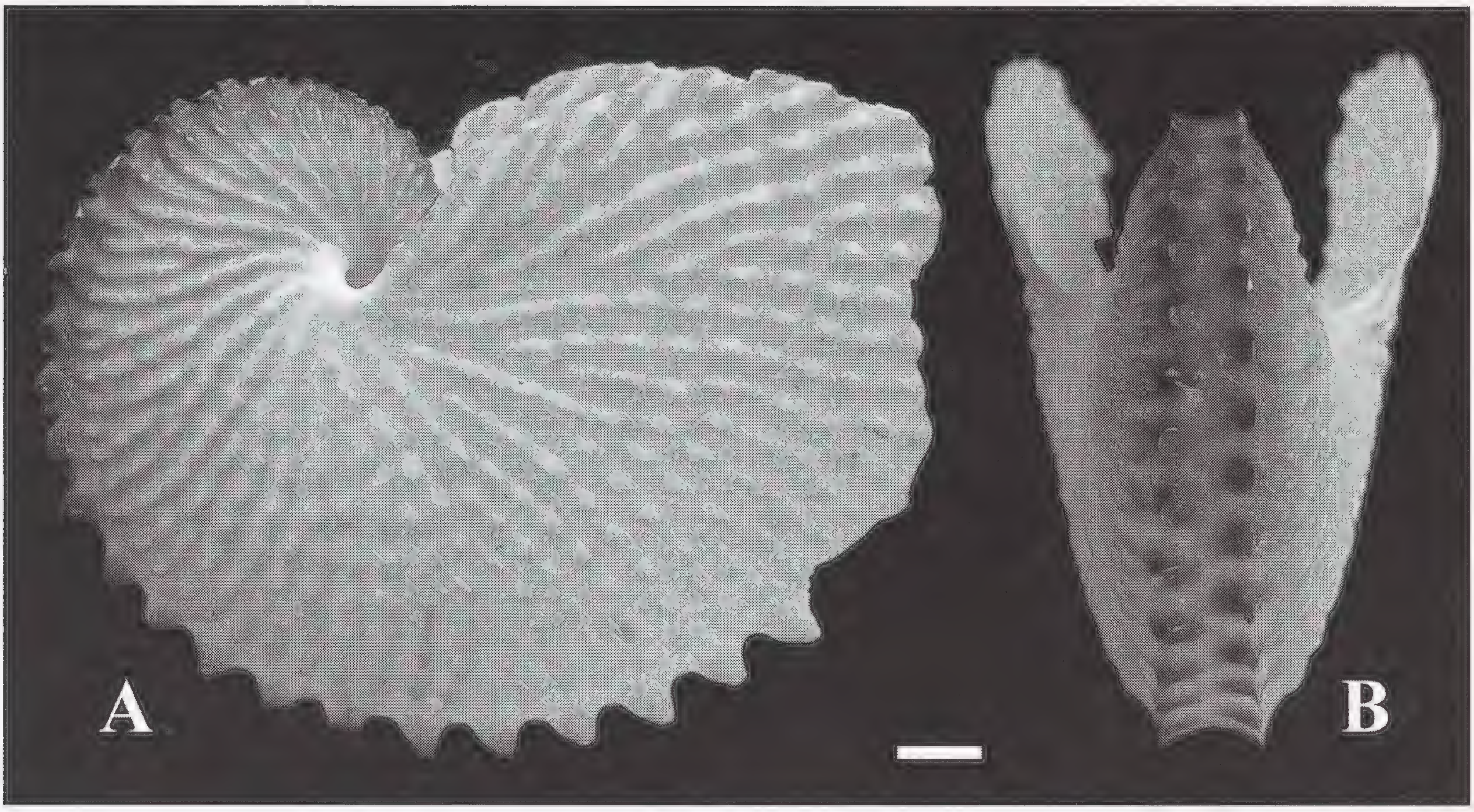

Fig. 1 *Argonauta nodosa* Solander, 1786 **A** MACN 34781, egg case lateral view **B** posterior view of the same shell. Scale bar = 1 cm.

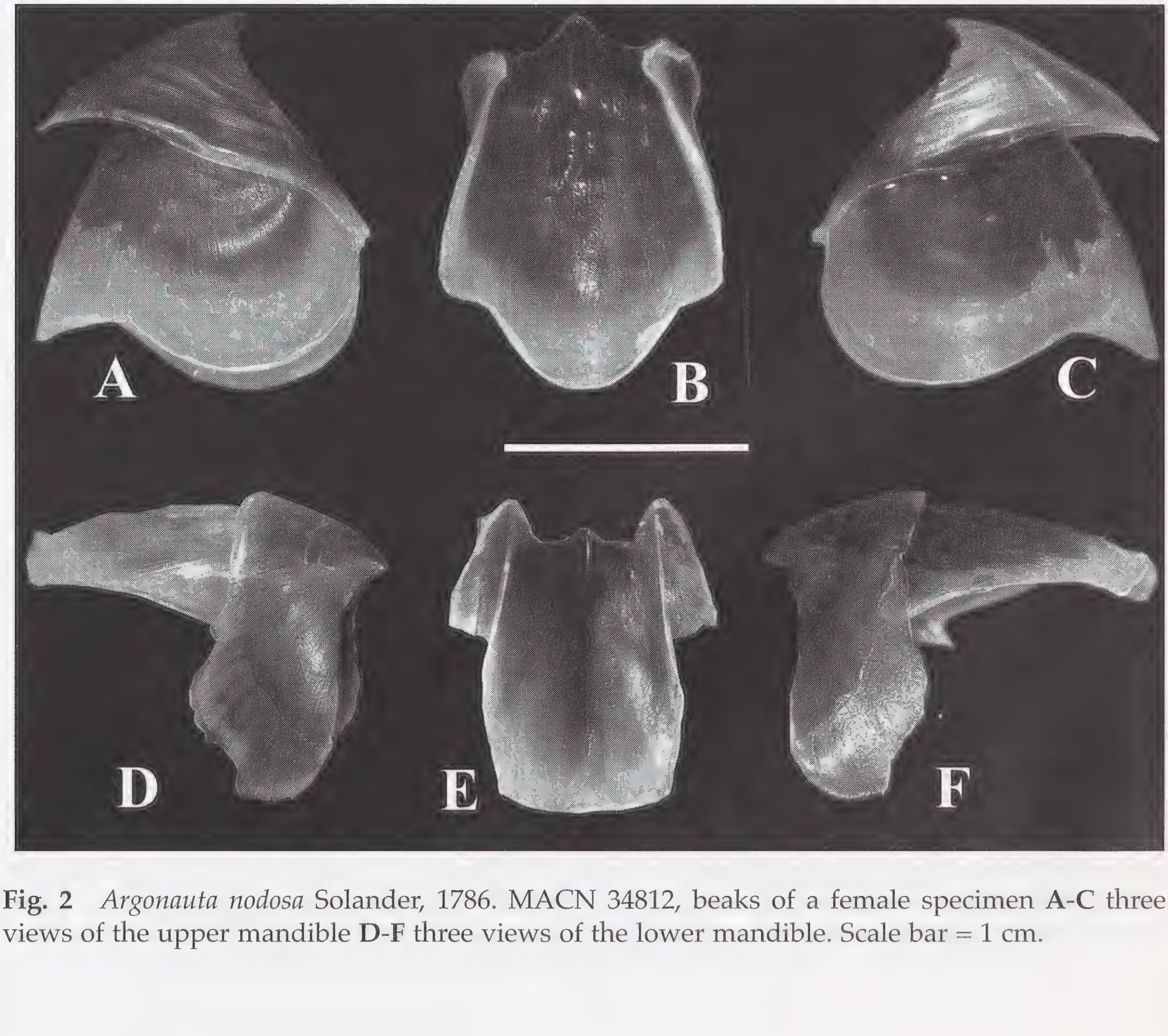

Fig. 2 *Argonauta nodosa* Solander, 1786. MACN 34812, beaks of a female specimen **A-C** three views of the upper mandible **D-F** three views of the lower mandible. Scale bar = 1 cm.

TABLE 2
Measurements of the beaks. Terminology follows O'Shea (1999). [1]Refers to the complete specimen in g.

Beak measures	**MACN 34812**	
	Specimen 1	**Specimen 2**
Lower Beak		
Width	15.6	16.0
Length	15.05	15.4
Height	10.7	10.3
Hood length	7	6.2
Wing length	12	11.9
Upper beak		
Width	11.3	11.7
Length	15.2	14.4
Height	13.5	14.2
Hood length	9.7	8.9
Total Weight[1]	89.6	45.8

morphology of both beaks is illustrated (Fig. 2a–f) and quantified (Table 2). They match perfectly well with previous illustrations (Change, 1999; O'Shea, 1999, among others). Data on total weight of both specimens are provided with the aim of exploring its relationship with the size of the beak, a ratio that could possibly be used for future inferences of stomach contents (Clarke, 1962).

DISCUSSION

Argonauta species seem to be predated by several different animals all around the world. Ortiz-Corps *et al.* (1995) confirmed the presence of *A. argo* and *A. hians* in the gut contents of the dolphin fish, *Coryphaena hippurus* from Puerto Rico, in the Caribbean. Many sharks are known to include these cephalopods as part of their diet. Smale (1991) and Dunning *et al.* (1993) recorded *Sphyrna zygaena* (Linnaeus, 1758), *Galeocerdo cuvieri* (Peron & Le Sueur, 1822) and *Prionace glauca* as predators. Also, Dunning (1993) and Clarke *et al.* (1996) recorded *P. glauca* as a common predator of Argonautids. However, the authors did not identify the species.

The blue shark *P. glauca* is one of the most abundant pelagic species with a virtually circumglobal distribution in tropical and temperate seas (Stevens, 1973). In the northern hemisphere, during the warmer season, the geographic range is extended northwards in the Pacific and the Atlantic oceans (Le Brasseur, 1964; Templeman, 1963). The southwestern Atlantic populations that usually live in Brazilian warmer waters could easily go farther south along the Argentine coast. In fact, they are captured in oceanic waters off Buenos Aires province in Argentina and the marine coast of Uruguay (Marín *et al.*, 1998).

Stevens (1990) mentioned speeds of 2.1 to 7.5 km day^{-1} for an adult specimen of *Prionace glauca* based on tagging calculations. Therefore one adult shark probably will need around two months to travel the distance of 500 km from the southernmost marine point of Uruguay (~35°S–55°W) to Puerto Quequén area. Even if we take into account the telemetry experiment demonstrated by Casey (1985, in Stevens, 1990) that showed a speed of 37 km day^{-1}, it would be necessary around two weeks to cover the same distance. Due to the fine preservation of the octopuses in the stomach we have no doubt about the real presence of *Argonauta nodosa* in Argentine waters.

Most of the records of *A. nodosa* are from warm waters, and the samples here studied suggest that Puerto Quequén, mostly a temperate locality, is the southernmost record of its real range. O'Shea (1999) mentioned records from the Indo-West Pacific, southern Japan to southern Africa, Australia and Polynesia. Chile was mentioned by Nesis (1987: 327) as a doubtful record. Rios (1994) and Haimovici & Andriguetto (1986) collected specimens from Rio Grande do Sul state (Brazil) and Uruguay, albeit only in summer. Despite the latter citations Cheng (1998) ranges this species only from the Indian and Pacific Oceans in the Southern Hemisphere.

Together with *Tamoya haplonema* (Cnidaria: Cubozoa) (Pastorino, 2001) and several other fishes (Tamini, in prep.) collected in the same area and during the same seasonal period, *A. nodosa* confirms the existence of climatic phenomena that allow the presence of warm water species in temperate regions.

Acknowledgements

We appreciate the information and papers hard to obtain in Argentine libraries provided by B. Marshall (Museum of New Zealand Te Papa Tongarewa) and M. Dunning (Fisheries Division, Queensland, Australia). Also M. Braccini (MACN), L. Nogueira (EHPQ), R. Bruno (St. C.) and the crew and the skipper of the boat "*Eusonia*" from Puerto Quequén helped during the field work. M. Griffin's help improved the English version of the manuscript. An anonymous reviewer made interesting suggestions. This study was supported in part by a research grant from Fundación Antorchas, Argentina (A-13672/1-3 1999-2002) and the project PICT 98 No. 01-04321 from the National Agency for Scientific and Technical Promotion, Argentina.

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THE RELATIONSHIP BETWEEN SNAILS, SOIL FACTORS AND CALCITIC EARTHWORM GRANULES IN A COPPICE WOODLAND IN SUSSEX

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Abstract *A variety of environmental parameters including soil aggregate size and earthworm granules were examined in relationship to snail abundance and diversity in different aged coppice compartments in a deciduous woodland in Sussex, England. The results indicate, in general, a positive relationship between snail abundance and intermediate sized aggregates (5mm and 2.36mm) and a negative relationship with <0.6mm and 20mm. Several individual species also followed this trend. The reason for this correlation is not clear.*

Ordination of snails, sites, soil fractions and other environmental variables achieves a clear geographical site separation. Soil aggregate sizes are the principal components along with pH and earthworm calcitic granules. It is clear that the soil aggregate size proportions vary substantially between coppice compartments and this may be an important factor in explaining variation in snail distribution in the study area. Earthworm granules correlate strongly with certain factors such as pH and chalk, and also with certain snail species. This link is likely to be caused by similar environmental preferences such as with pH and litter depth. Earthworms may facilitate favourable conditions for certain snails by aggregate production and litter breakdown.

INTRODUCTION

The abundance and distribution of snails is believed to be affected by a variety of environmental variables such as pH (Bishop 1976, 1977, 1980; Cameron 1973, 1978; Cameron & Redfern 1972; Gardenfors 1992; Hermida, Ondina & Outeiro 1995a, 1995b; Outeiro 1993; Tattersfield 1990; Walden 1981; Wareborn 1969, 1970, Valovirta 1968), litter (Berry 1973; Bishop 1977; Mason 1970; Outeiro 1993; Wareborn 1969, 1970), moisture (Hermida *et al.* 1995a, 1995b, Paul 1978, Wardhaugh 1995; Wareborn 1969) and vegetation (Bishop 1976, 1977, 1980; Fog 1979; Mordan 1977). Very little is known of the exact requirements of small woodland snails, many of which can be found in the leaf litter and surface layers of soil. Snails may penetrate the soil not only for food, but also for protection, egg laying and aestivation. An investigation was carried out in a coppiced woodland recording various environmental parameters (pH, chalk, litter depth, vegetation cover and time since coppicing) in relation to snail abundance and richness (Millar & Waite 1999) and initial analysis suggested that fractions of different aggregate sizes of combined surface soil and litter may have some links with snail abundance. Soil texture has been suggested to be a factor in the abundance and distribution of gastropods by several people (Boycott 1934, Dickinson 1974, Hermida *et al.* 1995a, 1995b, Lozek 1962, Outeiro 1993 and Tattersfield 1990).

Calcareous granules have been found with snail shells in many Quaternary and contemporary investigations and frequently show correlations with snail abundance (Bal 1977, Canti 1998, Kerney 1971, Meijer 1985, Preece, Kemp & Hutchinson 1995, Preece, Bridgland & Sharp 1998, Preece & Bridgland 1999). The granules are now known to be produced by certain species of earthworm (Canti 1998, Darwin 1881, Morgan 1981, 1982, Piearce 1972) Although the presence, and sometimes the quantity, of granules has been noted in the past, their presence in relation to several soil parameters and snail species has not been examined before. In this paper we examine the relationships between various soil and environmental factors with snail presence and abundance and

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possible relationships between snails and earthworms through the calcareous granules they produce. In this paper the term granule *sensu* Canti (1998), Preece *et al.* (1995, 1998, 1999) and Kerney (1971) has been used. The alternative term 'concretions' used by Darwin (1881) Morgan (1981, 1982) and Piearce (1972) normally refers to an aggregate of small particles and implies a means of formation, which has not been examined in this paper. The earthworm granules found in the present study did not appear to be composed of subunits, although the granules obtained from *Arion ater* slugs for comparison were. For simplicity the term granules has been used throughout.

SITE DESCRIPTION

West Dean Woods Nature Reserve, West Sussex (Grid Reference SU845155) is a small (16.6 hectare) semi-natural, deciduous woodland owned by The Edward James Foundation and leased and managed by the Sussex Wildlife Trust (SWT) since 1975. This SSSI woodland is on a gentle south-facing slope of the South Downs. The predominantly oak and hazel woodland, with bluebells (National Vegetation Classification W10, Rodwell, 1991), has been divided into a number of compartments which are coppiced in a 11 to 15 year cycle. Although on the Chalk of the Upper Cretaceous the site is overlain by Head deposits which vary in thickness over the site and the soil pH is generally less than 7.0. Further details on the site and geology are given in Millar & Waite (1999).

SAMPLING

One compartment of each period from 1 to 12 years since coppicing was selected and also two compartments which had not been coppiced for over 40 years. In each compartment four quadrats from computer generated random coordinates of 0.5m by 0.5m were examined and measurements taken of litter depth and litter percentage cover, vegetation cover, bare soil cover and moss cover. All loose topsoil and litter was removed for examination. Each sample was dried, sieved and the fractions were weighed. The snails, shell fragments and earthworm granules were extracted, the chalk content was visually assessed and the pH was tested (details are given in Millar & Waite, 1999). Sieve sizes used were 20mm, 10mm, 5mm, 2.36mm and 0.6mm. The soil fractions represent aggregate size and not absolute particle size as the aggregate size was expected to have the greater influence, if any, on soil dwelling molluscs and earthworms.

Earthworm granules were collected from the samples, in the sieve sizes 0.6mm to 2.36mm. No granules were found in the 5mm or larger sieves. They were counted for each quadrat. They were also examined under a Scanning Electron Microscope (SEM) and Electron Probe Microanalysis (EPMA) for composition was carried out at the same time. Specimens were gold-coated, photographs taken at accelerating voltage of between 5 and 12 kV. EPMA was based on a lithium-drifted silicon detector.

ANALYSIS

Relationships between physical factors and snail species abundance were investigated using both univariate and multivariate statistical procedures. Multivariate methods of analysis were used to provide an objective description of the relationship between measured variables. Spearman's rank correlation was used to describe the relationship between snail species abundance and the physical factors recorded at each quadrat. The results of Spearman's rank correlation, like other correlation coefficients, are sensitive to large numbers of zeros. Where species were absent from less than 6 out of the 56 quadrats sampled the analysis was performed on the complete data set. If a species was absent from more than 6 quadrats but occurred in more than 50% of samples, quadrats not containing the species were excluded from the analysis and a Spearman's rank correlation performed. Following Grieg-Smith (1983), where species were absent from more than 50% of the quadrats or where species density was uniformly low, the data set was divided into two groups; those quadrats containing the species and those in which the species did not occur. Group medians for the physical factors were then compared using the Mann-Whitney U test. The analysis was performed using the computer program MINITAB version 12.

The relationships between site physical characteristics were also investigated using Principal Component Analysis (PCA) which was applied to the matrix of site correlation values. This procedure performs a standardised and centred PCA. The PCA ordination diagram, which depicts the relationship between quadrats based on their physical characteristics, was produced by plotting the quadrats' scores for the first two components (Kent & Coker 1992, Waite 2000). While PCA generally performs well when used to analyse physical factor data it is rarely appropriate to use the PCA for the analysis of community data sets. Detrended Correspondence Analysis (DCA) is a more appropriate technique and has the advantages of producing both a site (sample) and species ordination (Hill & Gauch 1980, Waite 2000). The snail community data set was subjected to a DCA with rare species down-weighted. Both sets of ordinations were performed using the computer package PC-ORD version 3.0 (1997). To aid the interpretation of the DCA community ordination use was made of the PC-ORD program facility to plot species abundance against each axis and to correlate physical factors used in the PCA ordination against each DCA ordination axis. Thus the physical and snail community data matrices were initially analysed separately, subsequently the physical factors were used to interpret the analysis of the community data set. The frequently advocated alternative strategy of analysing both sets of data simultaneously using Canonical Correspondence Analysis (CCA) (ter Braak 1986, Jongman *et al.* 1995, Waite 2000) was initially used but performed poorly and did not aid the interpretation of the data collected. The results of this analysis are not presented here.

RESULTS

SOIL FRACTIONS, SNAILS AND ENVIRONMENTAL FACTORS

Initial examination of the mean proportions of the various soil and litter aggregate sizes compared with total number live snails per compartment suggested a positive relationship with the 5.0mm and 2.36mm fractions and a negative relationship with fractions less than 0.6mm. This is confirmed by Spearman's rank correlation analysis (using data from 56 quadrats). Complete data correlation of snails, environmental factors and soil particle sizes is given in Table 1. There is a strong negative correlation ($p<0.001$) between the weights of 20mm fractions and weights of smaller fractions (5mm to 0.6mm). The smaller fractions have a negative correlation with the finest fraction of <0.6mm. The link between chalk content and pH is also strong ($p<0.001$).

There is a correlation between percentage vegetation cover and the pH of the quadrat. Vegetation cover also shows a link with the presence of earthworm granules and soil fraction size of less than 0.6mm, but has a strong negative correlation with 10mm size ($p<0.001$). Snail shells whether alive, dead or total shells all correlate with pH and dead

TABLE 1

Spearman's rank correlation analysis of environmental data using 56 quadrats. (Probability levels given underneath. Bold indicates where p<0.01)

	pH	Free Chalk	Worm granules	Soil aggregate sizes						Litter Depth	%Bare Soil	%Litter Cover	%Moss Cover	%Veg Cover	Total Snails	Live Snails
				20mm	10mm	5mm	2.36mm	6mm	<0.6mm							
Free Chalk	0.574 <0.001															
Worm granules	0.813 <0.001	0.643 <0.001														
20mm																
10mm																
5mm				-0.58 <0.001												
2.36mm	0.513 <0.001		0.38 0.004	-0.56 <0.001		0.728 <0.001										
0.6mm				-0.51 <0.001	-0.59 <0.001											
<0.6mm					-0.48 <0.001	-0.61 <0.001	-0.383 0.004	0.571 <0.001								
Litter Depth			-0.366 0.006					-0.32 0.015								
%Bare Soil				-0.49 <0.001						-0.4 0.003						
%Litter cover																
%Moss cover												-0.82 <0.001				
%Veg cover	0.344 0.009		0.303 0.023		-0.57 <0.001				0.296 0.027							
Total snails	0.674 <0.001	0.323 0.015	0.428 0.001			0.439 0.001	0.477 <0.001		-0.428 0.001							
Live snails	0.586 <0.001	0.262 0.051	0.31 0.020			0.558 <0.001	0.486 <0.001		-0.655 <0.001						0.92 <0.001	
Dead snails	0.647 <0.001	0.324 0.015	0.442 0.001	-0.32 0.018		0.347 0.009	0.454 <0.001								0.945 <0.001	0.772 <0.001

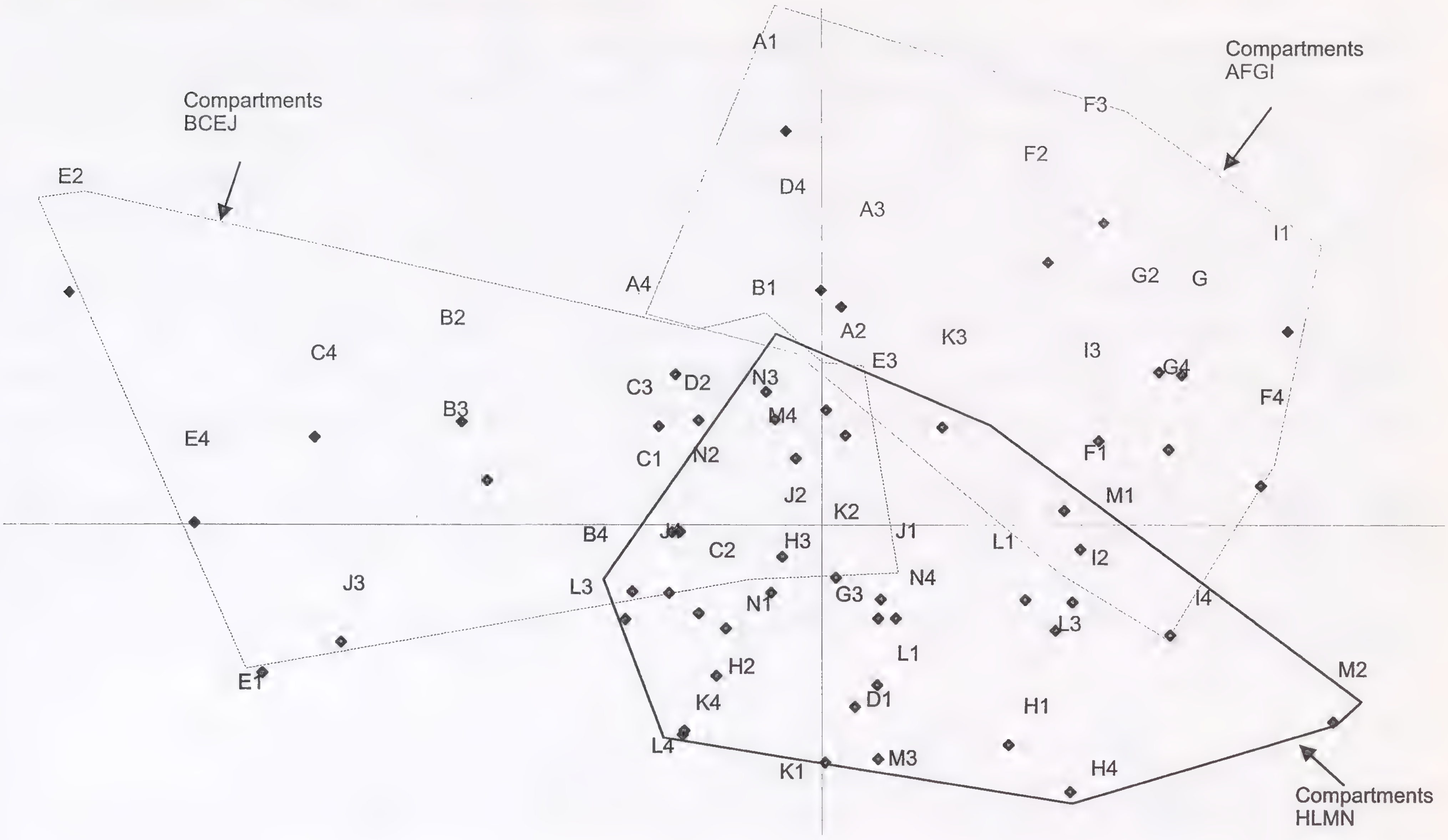

Figure 1 Principal Component Analysis: Ordination of compartments (quadrats) based on soil fractions.

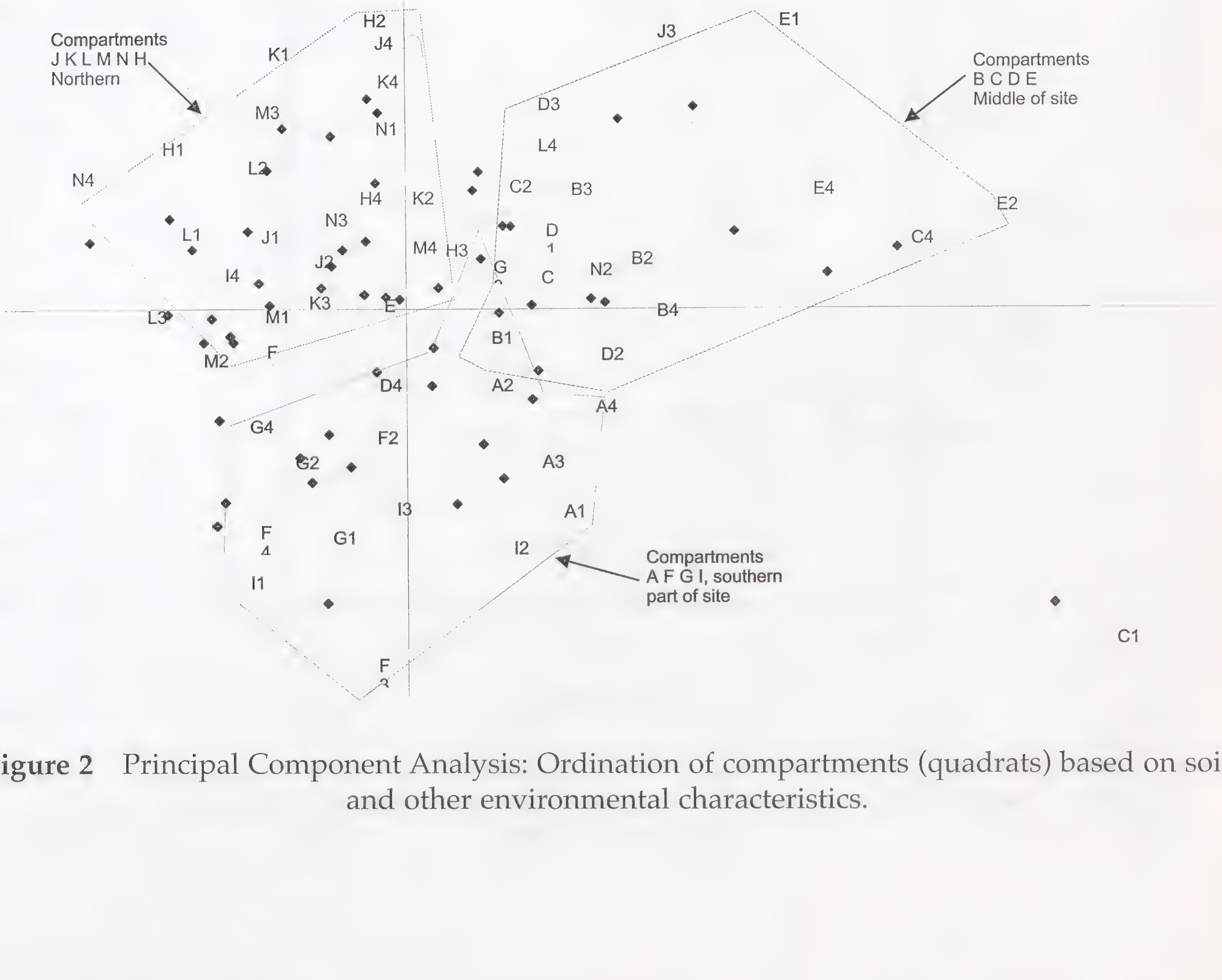

Figure 2 Principal Component Analysis: Ordination of compartments (quadrats) based on soil and other environmental characteristics.

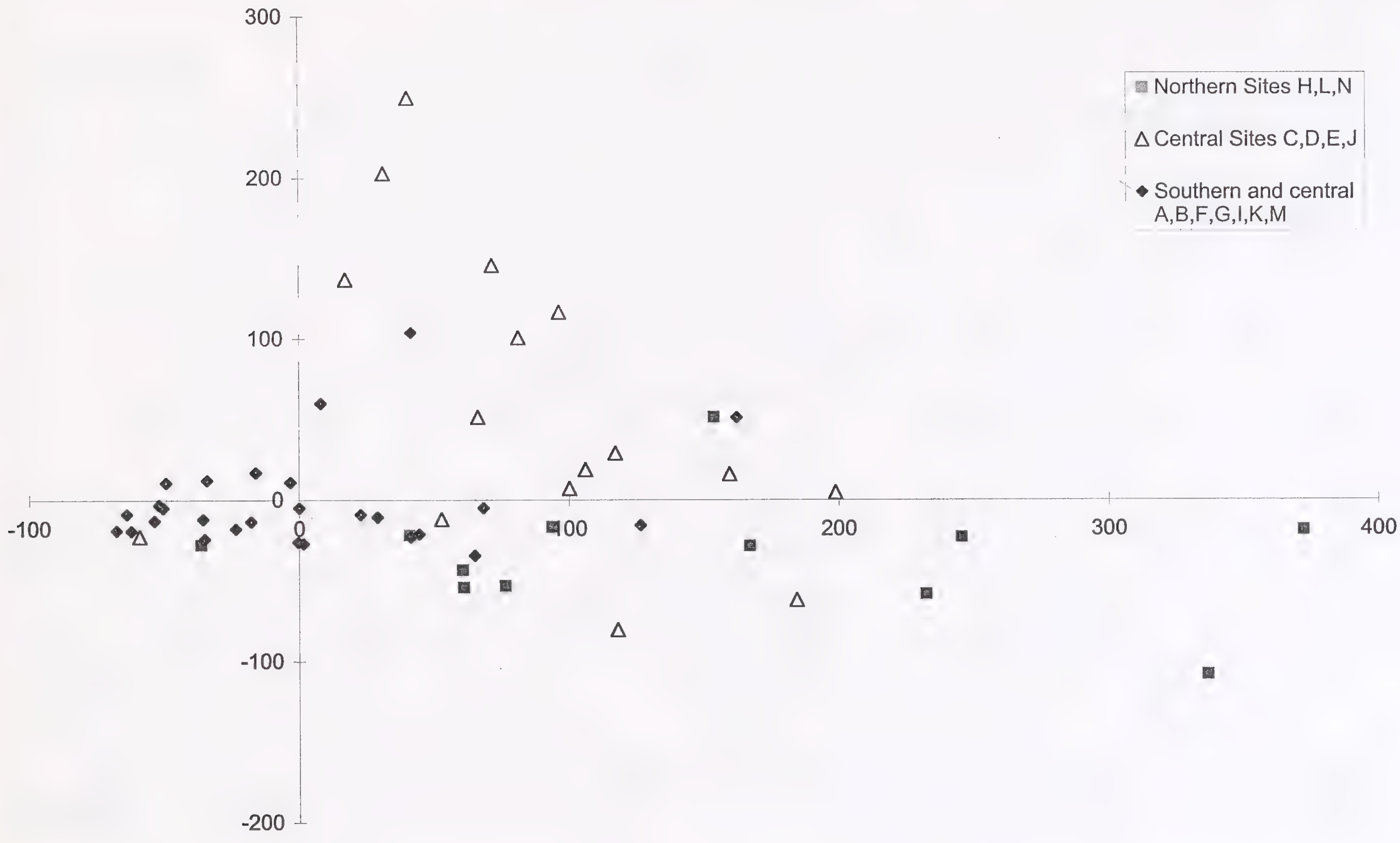

Figure 3 Detrended Correspondence Analysis. Differences between sites based on snail species composition. (Axes are SD x 100)

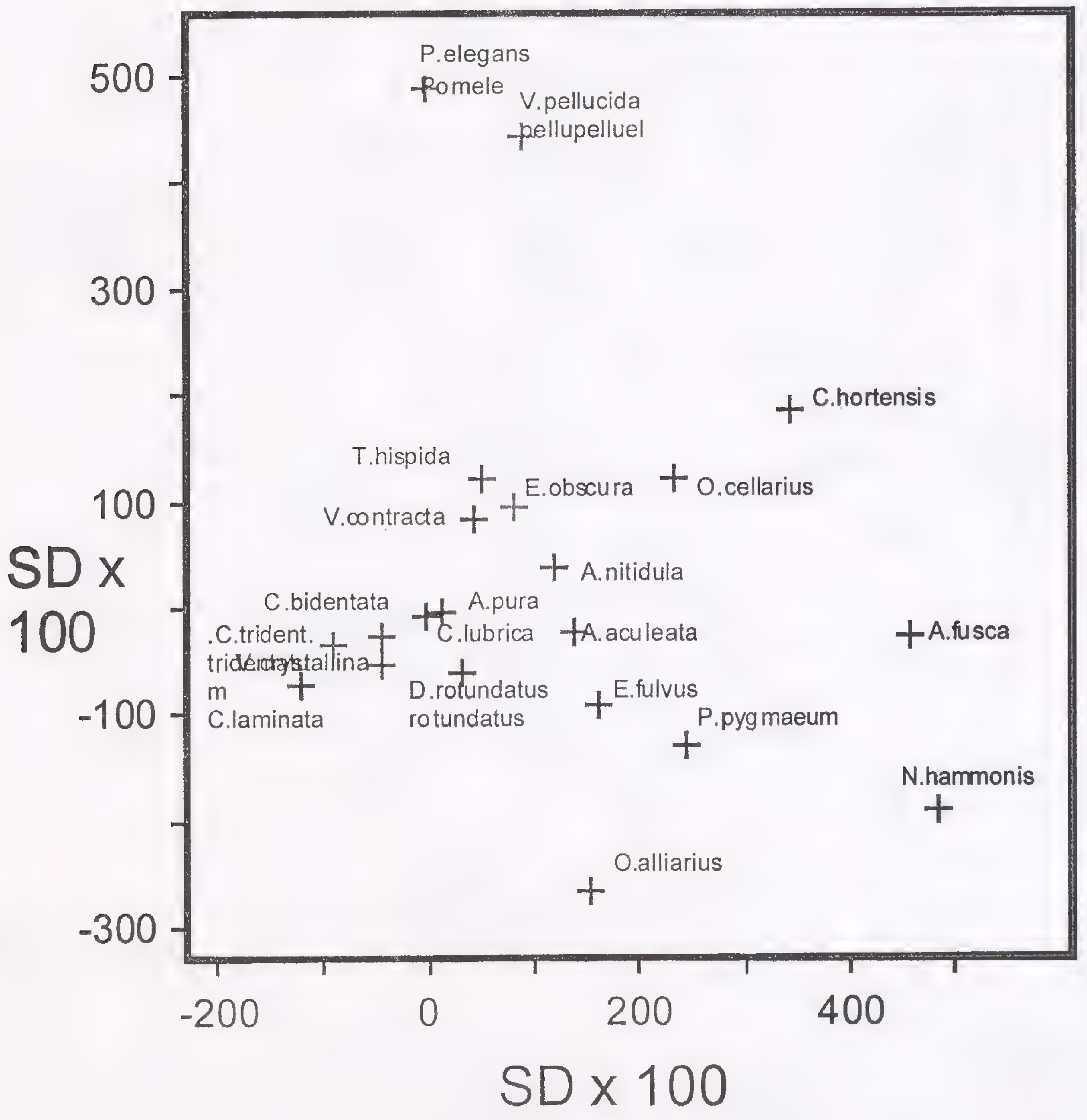

Figure 4 Detrended Correspondence Analysis. Species ordination. (Axes are Standard Deviation x 100)

and total shells correlate with free chalk.

The results for Spearman's rank correlations for the most abundant species; *Carychium tridentatum, Discus rotundatus, Vitrea contracta, Aegopinella nitidula* and *A. pura* are given in Table 2. The Mann Whitney U test results for the remaining, less abundant species, are presented in Table 3. In general, where there are relationships between snails and soil aggregate sizes, there would appear to be positive relationships between snail abundance and occurrence with the intermediate soil aggregate sizes and negative with over 20mm and below 0.6mm. Two species show a negative correlation with the 20mm fraction *(Acicula fusca* and *Acanthinula aculeata),* and three with the 10mm fraction *(Pomatias elegans, A. fusca, Vitrina pellucida).* Several species show positive correlations with the 5mm and 2.36mm fractions and three show negative correlations with 0.6mm and below *(C. tridentatum, D. rotundatus* and *Cochlicopa lubrica).*

Of the five most abundant species, all but *A. nitidula* correlate with soil pH (and chalk in the case of *V. contracta). V. contracta* and *A. nitidula* have a positive relationship with litter depth.

All these snails show correlations with total and live snails and *A. nitidula* is the only

TABLE 2

Spearman's rank correlation analysis of snail species data.
Probability levels given underneath, bold indicates where $p <0.01$
(Aegopinella pura absent from more than 6 quadrats but present in more than 50%)

	Carychium tridentatum (all quadrats)	*Discus rotundatus* (all quadrats)	*Vitrea contracta* (all quadrats)	*Aegopinella nitidula* (all quadrats)	*Aegopinella pura* (quads present)
pH	**0.529** <0.001	0.300 0.025	**0.438** 0.001		**0.612** <0.001
Chalk			**0.358** 0.007		
Worm granules	0.326 0.014		**0.355** 0.007		**0.500** 0.001
20 mm					
10 mm	0.294 0.028				
5 mm	**0.635** <0.001	0.336 0.011	0.288 0.032		
2.36 mm	**0.516** <0.001		0.264 0.049		
0.6 mm	**-0.365** 0.006				
<0.6 mm	**-0.730** <0.001	**-0.462** <0.001			
Litter depth			0.287 0.032	0.308 0.021	
%Bare soil					
%Litter cover					
%Moss cover					
%Veg cover					
Total snails	**0.676** <0.001	**0.508** <0.001	**0.644** <0.001	0.312 0.019	**0.573** <0.001
Live snails	**0.795** <0.001	**0.605** <0.001	**0.583** <0.001	0.333 0.012	**0.482** 0.005
Dead snails	**0.560** <0.001	**0.405** 0.002	**0.598** <0.001		**0.601** <0.001

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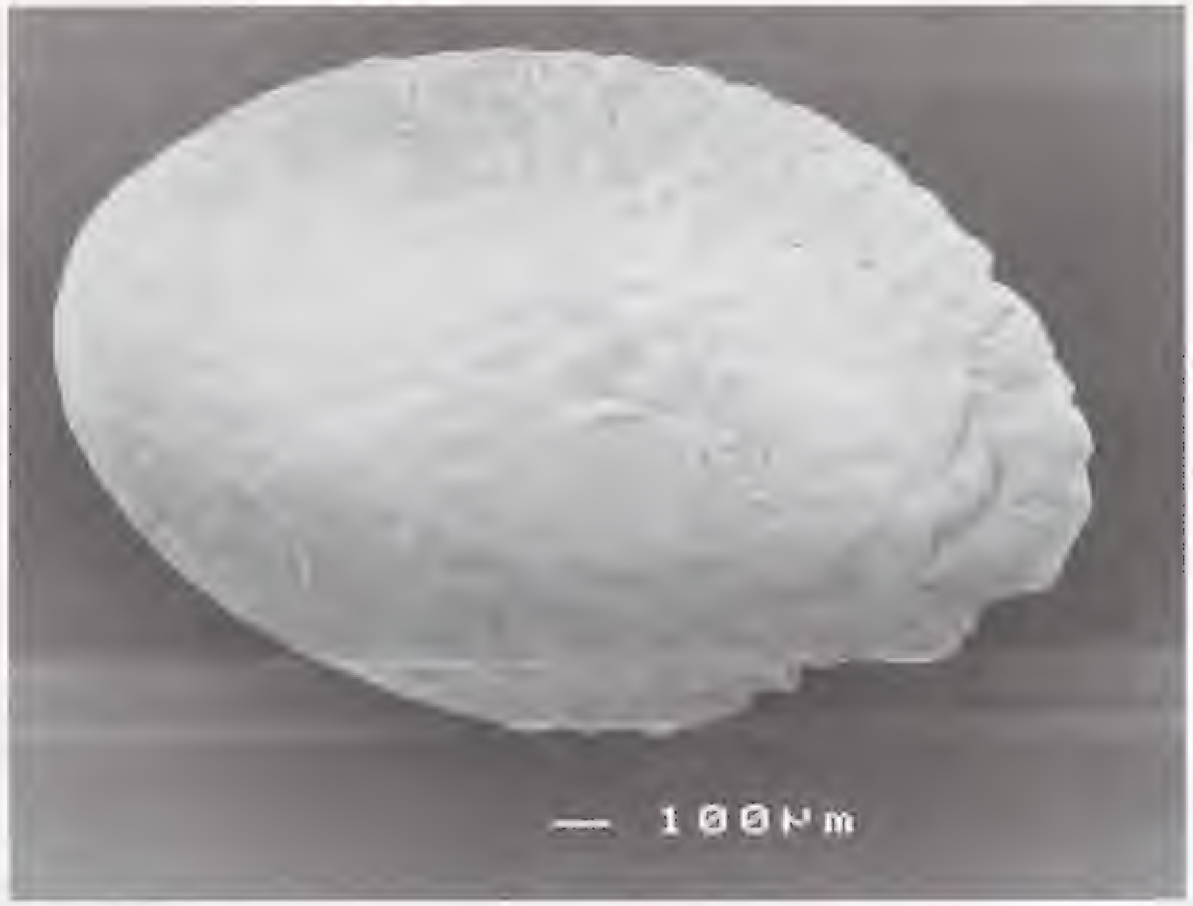

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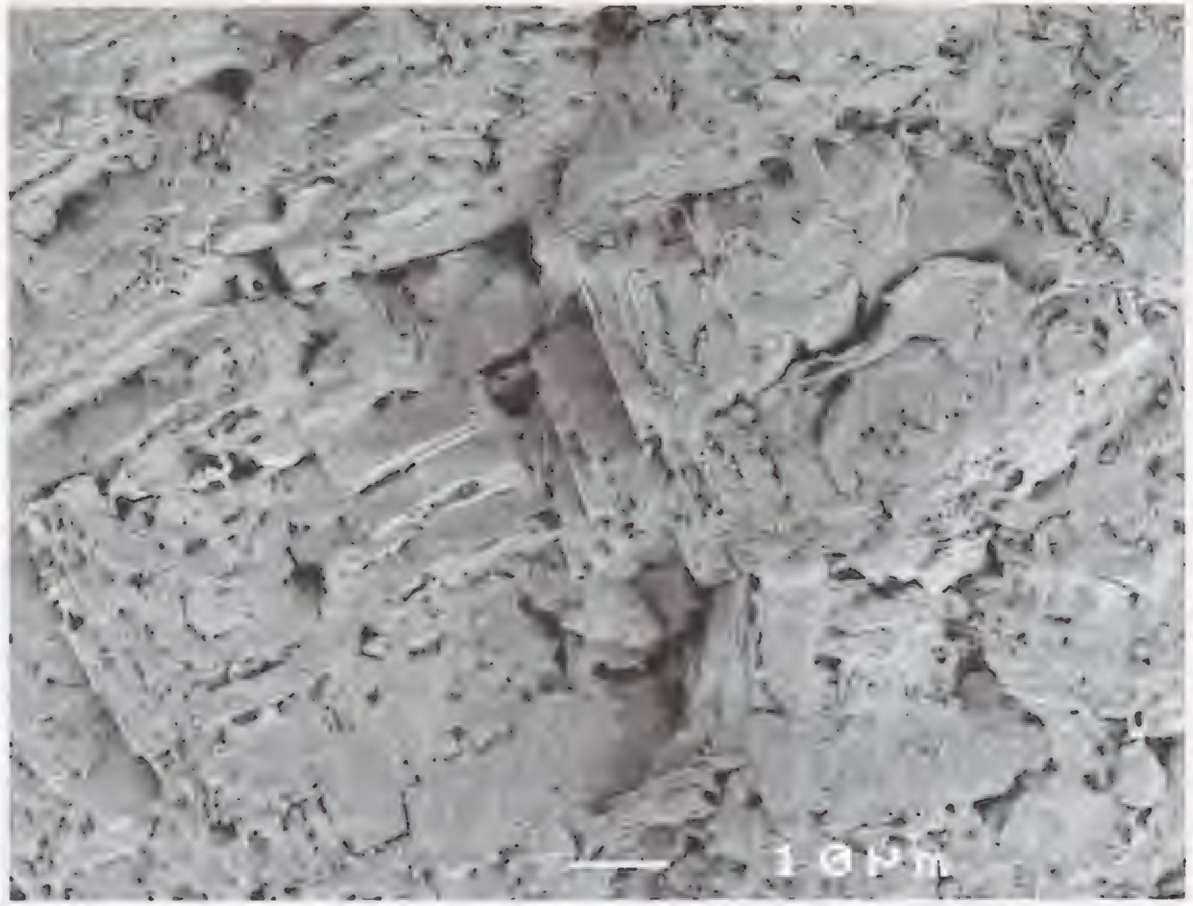

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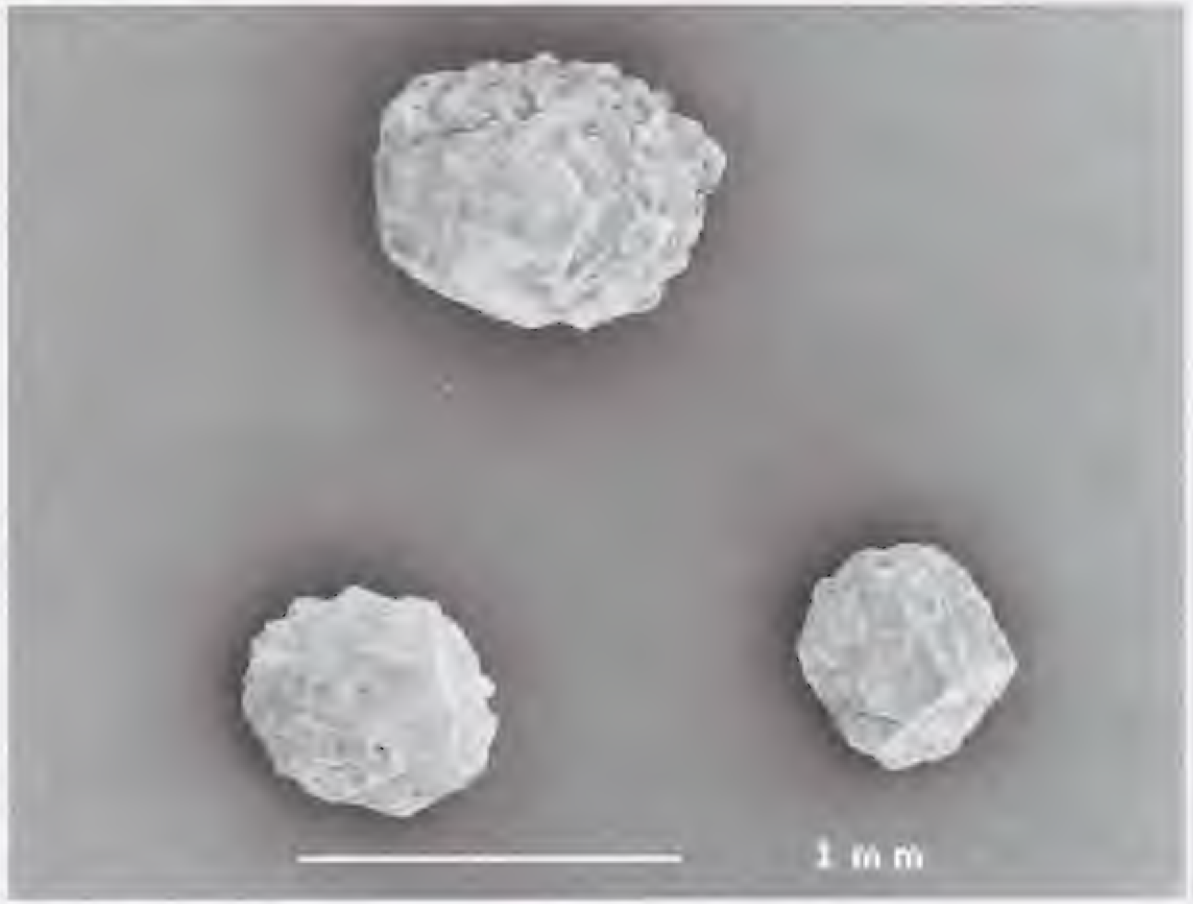

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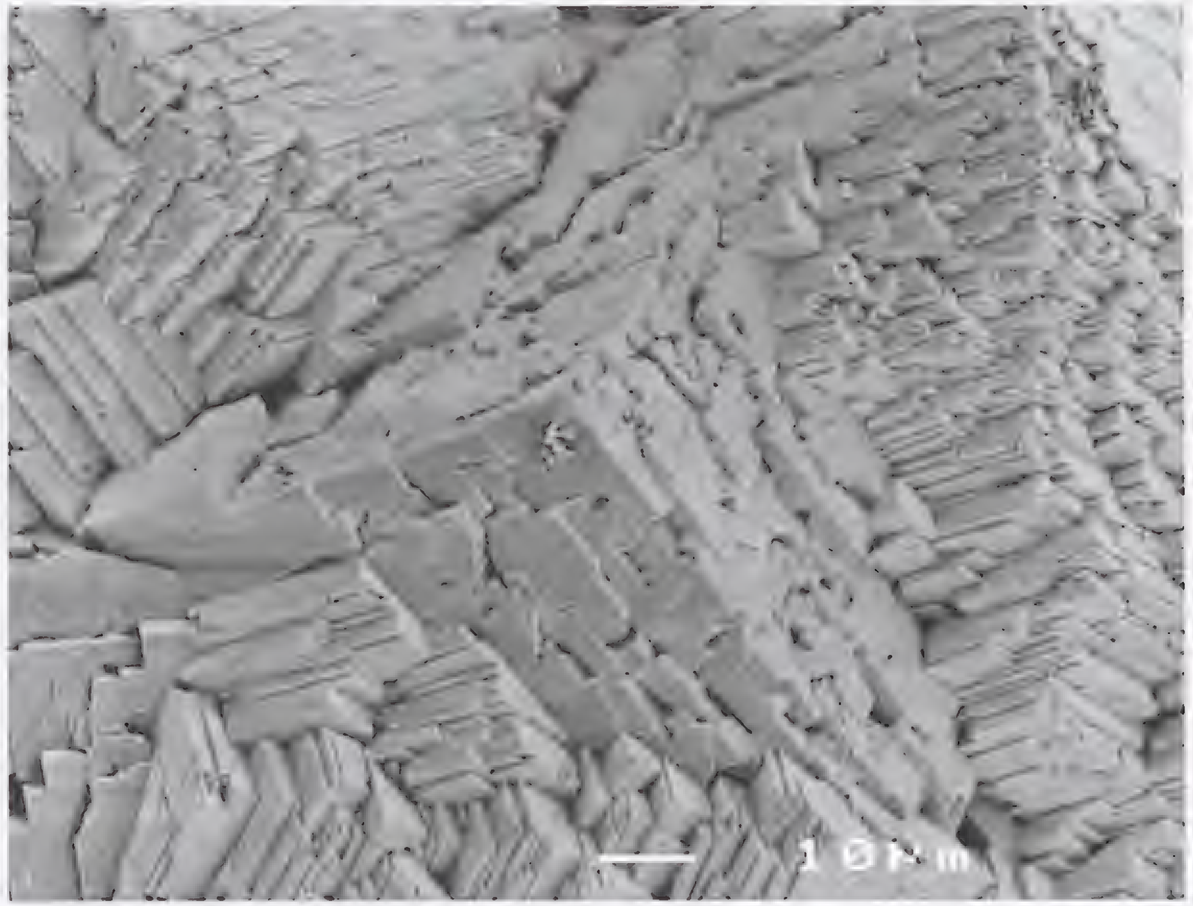

Figure 5 Single large calcitic granule from the soil at West Dean Woods Nature Reserve. Scale bar = 100μm. **Figure 6** Detail of granule from soil in figure 5. Note crystalline appearance in spite of some abrasion of edges. Scale bar = 10μm. **Figure 7** Three small fresh granules from *Lumbricus terrestris* earthworm. Scale bar = 1mm. **Figure 8** Detail of fresh *Lumbricus terrestris* granule. Note similar crystalline appearance to Figure 6. Scale bar = 10μm.

species not to have a similar relationship with dead shells. Several species show strong positive relationships ($p<0.01$) with earthworm granules: *V. contracta, A. pura, P. elegans, C. lubrica, V. pellucida, N. hammonis* and two others also correlate ($p<0.05$): *C. tridentatum* and *A. fusca* .

PCA

The PCA ordination of sites based on soil fraction characteristics reveals a clear separation of compartments along both the first and second components (Figure 1). The first component accounts for 44.5% of the variation in the data. Large site scores on this axis are associated with soils that have large amounts of the 5mm and 2.36mm soil particle fractions and low amounts of both the largest (20mm) and the smallest (<0.6mm) soil fractions. The second principal component, which accounts for 35.3% of the variation in the data set, may be interpreted as a contrast between the amount of large and small sized soil fractions. High sample scores along this axis are associated with soil dominated by fine, small sized fractions.

Although there is some overlap, compartments B, C, E and J are at one end of the first axis and separated from F, G and I at the other end. On the second axis H, K and L are one end and separated from A. D is evenly spaced along the second axis and M and N overlap in the middle of the ordination diagram.

For explanation of the compartment numbering and age please see appendix 1.

The explanatory power of the site PCA ordination is decreased when additional soil characteristics (pH, free chalk, earthworm granules and shell fragments) and site characteristics (percentage cover of moss, litter, live vegetation and depth of surface litter) are included (Figure 2). The first component only accounts for 20.9% of the variation and is associated with high pH, chalk, earthworm granules, vegetation cover, large quantities of fine soil fractions (0.6mm and below) and small quantities of the larger sized frac-

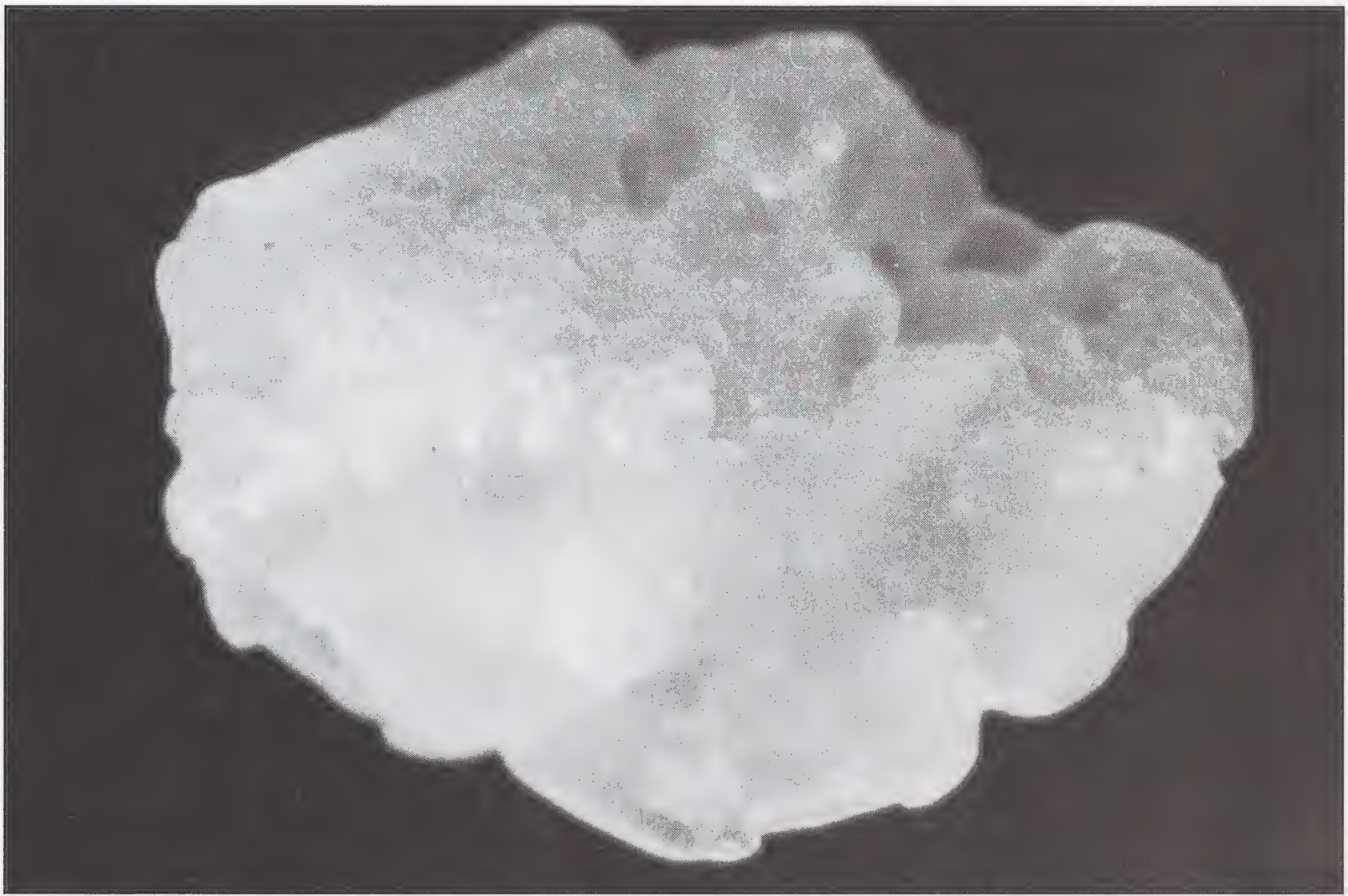

Figure 9 Photomicrograph of granule from the mantle of slug *Arion ater.* Note smoother, less crystalline surface than earthworm granule, concave surface and cluster of small spherical particles adhering to the granule. Length 1.8mm.

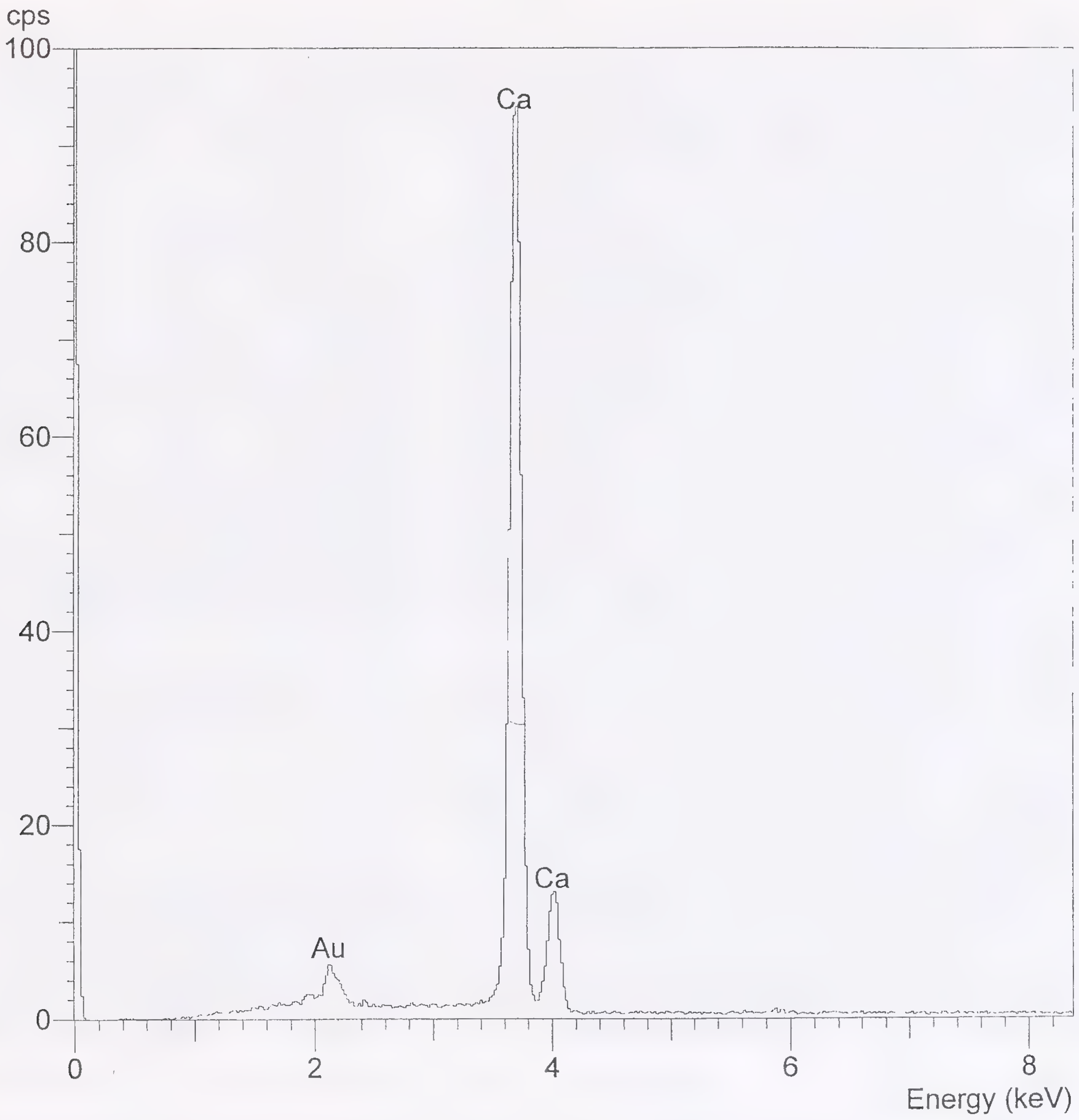

Figure 10 Electron probe microanalysis of fresh granule from *Lumbricus terrestris*. The gold peak (Au) is from the preparation coating.

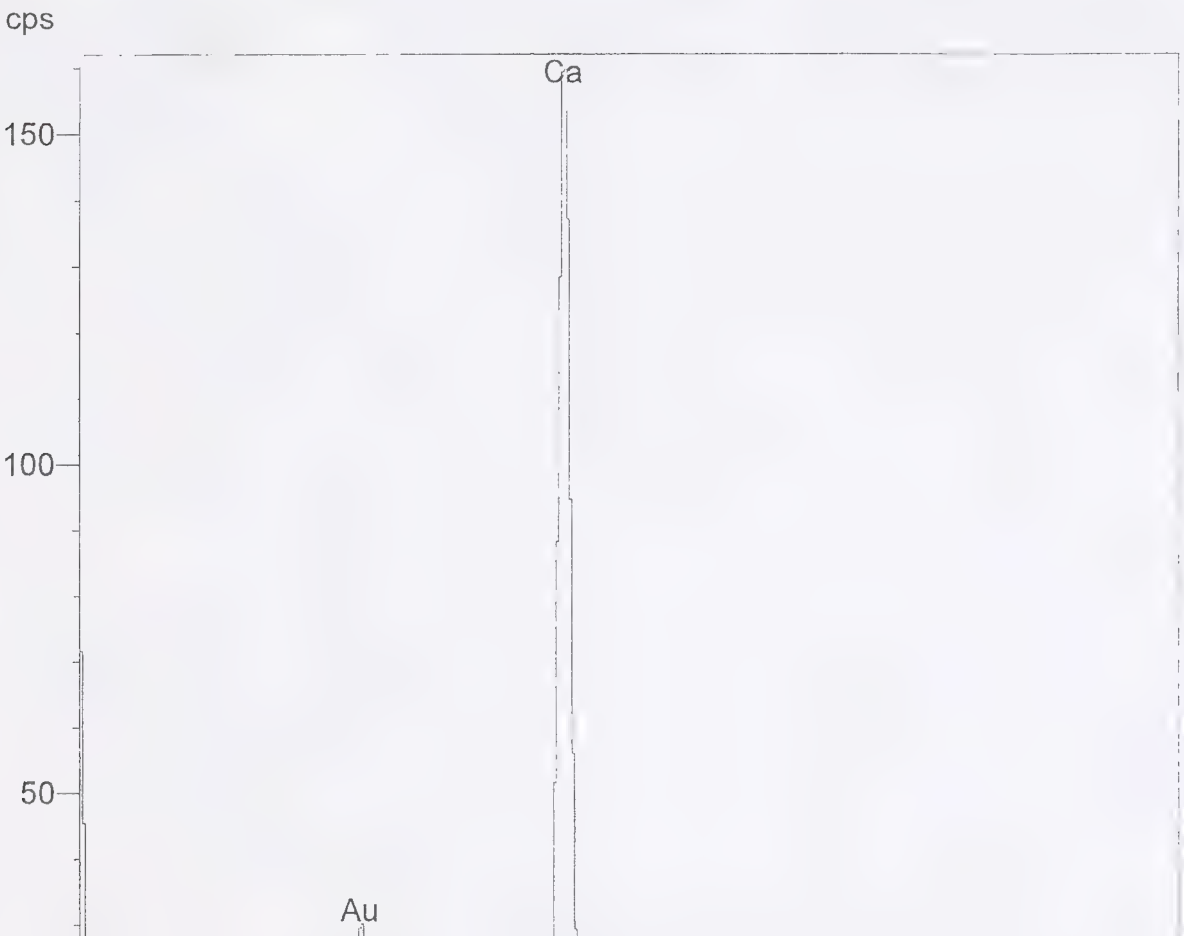

Figure 11 Electron probe microanalysis of granule from soil at West Dean Woods Nature Reserve. The gold peak (Au) is from the coating, and the Al, Si and Fe peaks are probably due to soil adhering to unwashed granule. Note similarity of Ca peak to fresh earthworm granule in Figure 10.

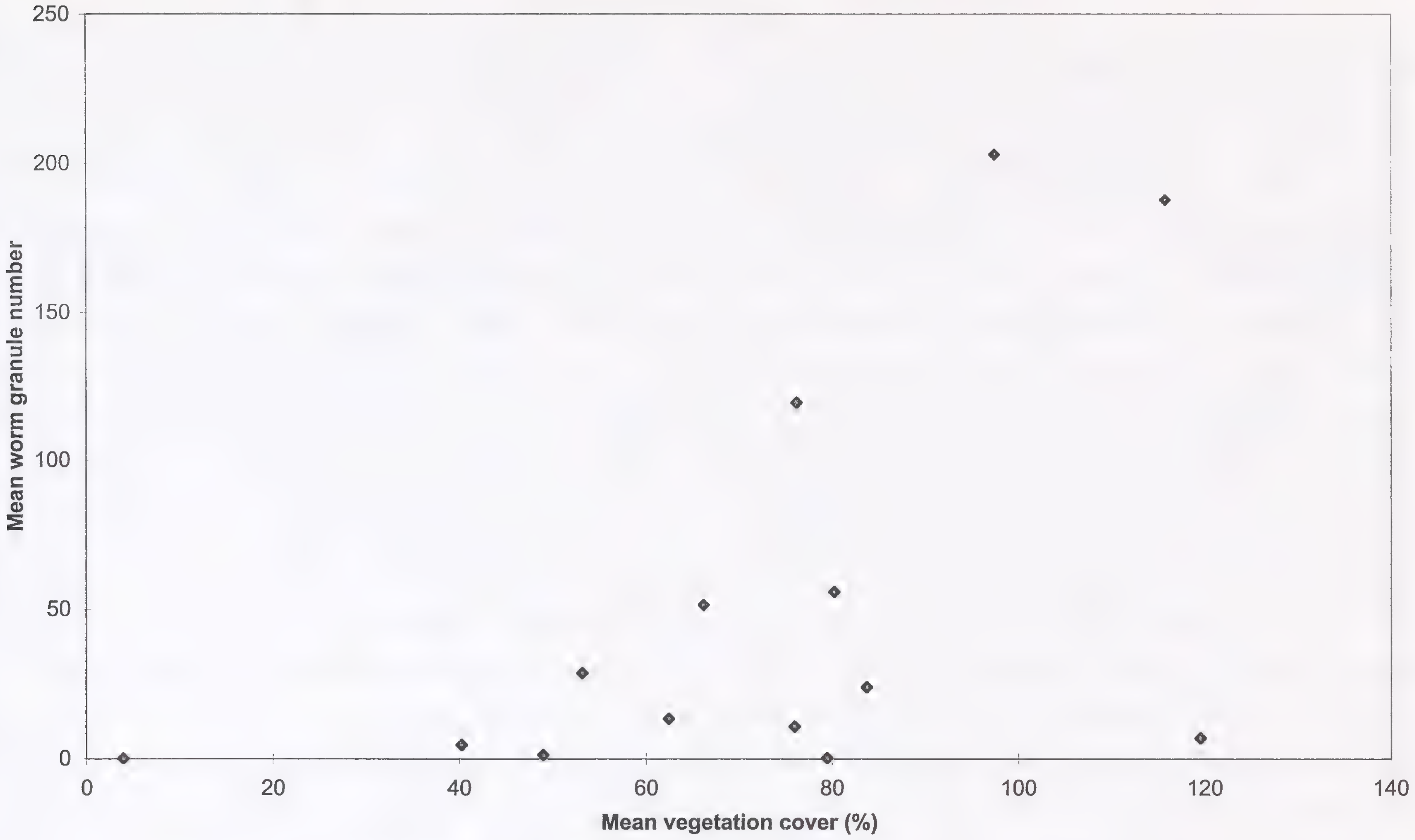

Figure 12 Relationship between earthworm granules and vegetation cover.

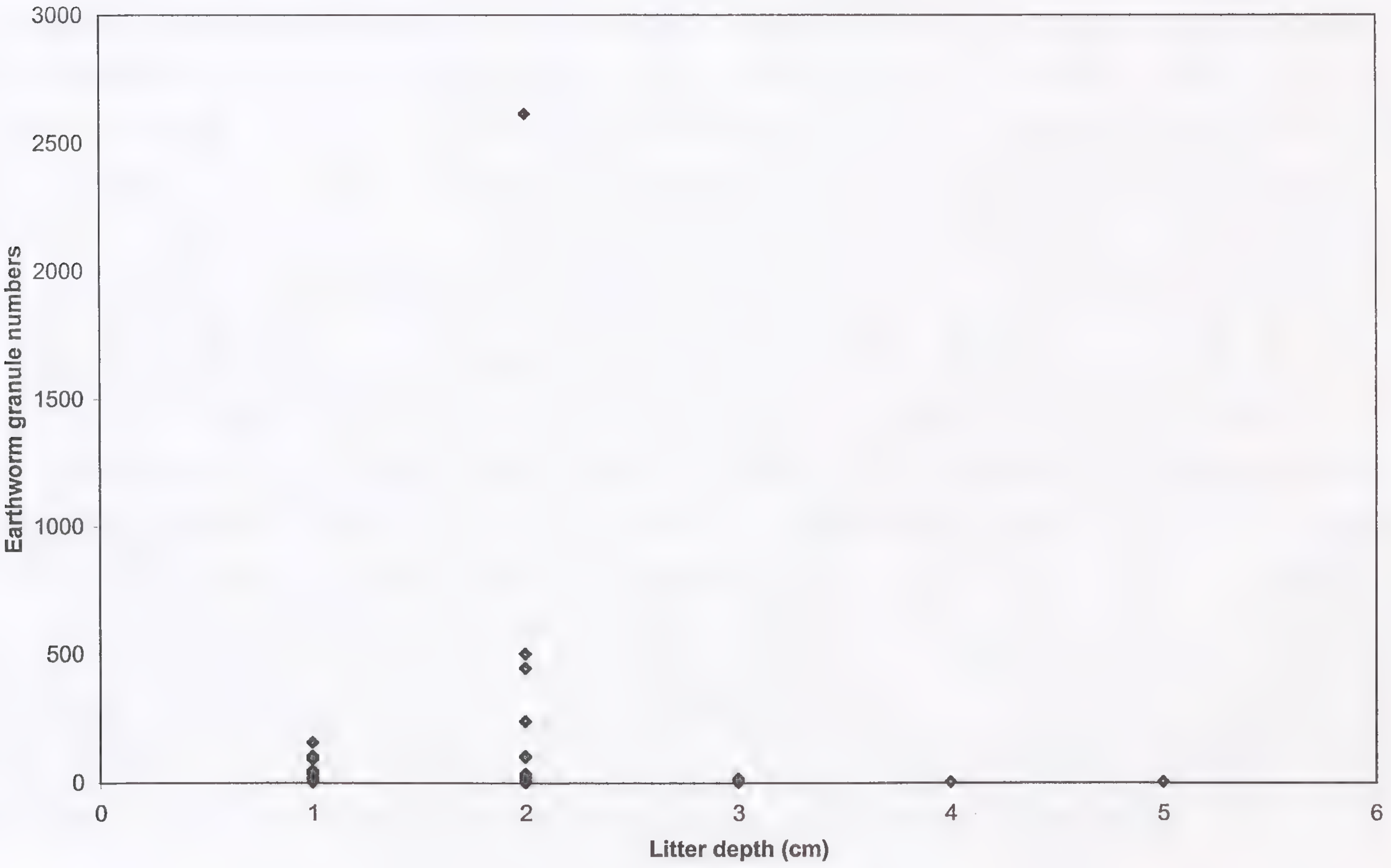

Figure 13 Relationship between earthworm granules and litter depth per quadrat.

tions (2.36mm and 5mm). The second component accounts for 16.4% and is associated with larger quantities of coarse soil (20mm) and small quantities of 5mm to 0.6mm. The third component accounts for 15.7% with large scores for earthworm granules, shell fragments, coarse fractions and small quantities of fine sized particles. However a greater degree of geographical grouping and separation of compartments is apparent in Figure 2. Sites associated with the northern and southern woodland compartments are spread along the second principal component, while along the first principal component sites associated with the northern end and middle compartments of the wood are clearly separated.

TABLE 3

Mann-Whitney test on snail species present in low numbers of quadrats. (Probability levels given underneath, bold indicates where $p < 0.01$)

	P. elegans	*A. fusca*	*C. lubrica*	*A. aculeata*	*P.pygmaeum*	*V.pellucida*	*N. hammonis*	*O. cellarius*	*O. alliarius*	*E. fulvus*	*C. laminata*	*T. hispida*	*C. hortensis*
pH	2.48		**4.44**			**2.69**	**-3.46**					2.45	
	0.013		<0.001			0.007	-0.001					0.014	
Freechalk	2.2		**2.63**								2.09	2.00	
	0.028		0.008								0.036	0.028	
Worm granules	**3.56**	2.19	**2.70**			**2.66**	**-3.94**						
	<0.001	0.028	0.007			0.008	<0.001						
Fragments			**3.4**				2.46			-2.29			
			0.001				0.014			0.022			
20 mm		-1.96		-2.47									
		-0.05		-0.014									
10 mm	-2.04	-2.02			2.33	-2.34							
	-0.042	-0.044			0.020	-0.019							
5 mm			2.12	2.42									
			0.034	0.016									
2.36 mm			**3.19**										
			0.001										
0.6 mm													
<0.6 mm			-2.09							-2.04	-2.27		
			-0.037							0.042	-0.023		
Litter depth	**-3.41**	-2.23											
	-0.001	-0.026											
%Bare soil	2.33												
	0.020												
%Litter cover								2.55					
								0.011					
%Moss cover								-2.46					
								-0.012					
%Veg cover	**2.80**					**2.71**	-2.47						
	0.005					0.007	-0.013						
Total snails			**4.62**	**2.62**	**2.57**						2.20	2.19	
			<.001	0.009	0.010						0.028	0.029	
Live snails			**4.37**	**3.14**	**2.96**						2.37	2.14	
			<.001	0.002	0.003						0.018	0.025	
Dead snails			**4.12**			2.00					2.06	2.08	
			<.001			0.046					0.04	0.037	

DCA

DCA ordination scores were plotted in units of average standard deviation of species turnover (SD) along the constructed environmental gradient represented by the axis. The greater the number of SD units separating the plotted samples the larger the difference in their species composition, typically points separated by one SD unit have approximately 50% of their species in common. From Figure 3 it is apparent that snail species composition differs substantially between sites, which are spread along the axes, both of which are longer than 3 SD units, indicating a substantial turnover in snail species composition along both axes. The first axis scores are negatively correlated with the soil fractions 2.36mm and 5mm, the amount of free chalk and pH, but positively with soil fraction <0.6mm. The first axis may thus be interpreted as modelling a gradient in soil fraction size and pH. The second axis is positively correlated with the numbers of earthworm granules and shell fragments recovered in each quadrat and pH. Soil fraction sizes 5mm, 2.36mm and 0.6mm are strongly associated with the middle of the second axis with proportions decreasing towards either end of the axis.

The general pattern has similarities to the PCA distribution pattern of sites but is not so clear cut. The bulk of the sites are in the bottom left hand corner. Sites L, M, N and H (part) are separated along the positive first axis. These sites are all in the north of the woodland where coppicing has not recently been carried out (8 to 40+ years previous to sampling). Sites C, D and E , at the top of the second axis and spreading right, along the first axis, are separated from the rest of the sites along the second axis. They are all found in the middle of the woodland, their time since coppicing is 3, 4 and 5 years respectively.

When snail species abundance is plotted along the DCA axes some patterns are apparent. The abundance of *C. tridentatum, D. rotundatus, C. lubrica* and *A. pura* decreases along the first axis and *N. hammonis* increases. The abundance of *N. hammonis* and *P. pygmaeum* tends to decrease along the second axis while that of *A. fusca* tends to increase. Six species *(C. tridentatum, D. rotundatus, C. lubrica, A. nitidula, A. pura* and *V. contracta)* are most abundant among quadrats associated with the middle of the second axis, their abundance decreasing towards either end of the axis.

The species ordination is shown in Figure 4. The majority of species are clustered around the left-hand end of the first axis and middle of the second axis. Reflecting different patterns of species abundance among the samples, some species are clearly separated by the ordination. *A. fusca* and *N. hammonis* occur at the extreme right hand end of the first axis, suggesting preference for very fine sized particles in the soil (<0.6mm) and low pH. They are separated from the majority of species, which are clustered towards the left-hand end of the axis. *P. elegans* and *V. pellucida* occur close together at one end of the second axis, while *Oxychilus alliarius* occur at the opposite end of the axis. This may reflect a preference by *P. elegans* for high pH soils where earthworm granules are also abundant, and a tolerance by *O. alliarius* of lower pH.

EARTHWORM GRANULES

The earthworm granules were extracted from sieve sizes 0.6mm and 2.36mm. Collection of granules of less than 0.6mm was not attempted as total extraction would have been unlikely. The largest granule found was 2mm. Scanning electron micrography (SEM) of the calcareous granules revealed that they consist of spherical to ovate highly crystalline white opaque to translucent granules (Figures 5–8). The larger ones have a fairly even crystalline structure and the smaller ones are relatively more coarse grained and angular. The external and internal appearance seems identical to earthworm granules examined and illustrated by Canti (1998) and Preece *et al.* (1995, 1998, 1999) and bear no resemblance to granules obtained from slugs (illustrated and discussed by Canti 1998) Figure 9. The membrane enclosed mass of calcareous material, (diameter 10mm by 1mm thick) extracted from several large *Arion ater* consists predominantly of small spherical or oval calcitic particles with rounded edges (size range of most are between 0.025mm and 0.15mm), with about a dozen larger particles, the largest being 1.8mm (Figure 9). The larger slug granules are of irregular shapes with rounded, microscopically granular surfaces and frequently with a concave surface not seen on any earthworm granule which tend to be oval with flat crystal faces (Figures 5, 7). The small spherical particles seen adhering to fresh slug granules would probably soon erode away in the soil, but no such particles were seen adhering to fresh earthworm granules, all these differences suggest a different mechanism of formation, function and possibly composition.

Electron probe microanalysis, in the SEM, of earthworm granules indicated that they were calcium rich but of very low-magnesium content. Most earlier studies consider the granules to be calcium carbonate (Bal 1977, Canti 1998, Darwin 1881, Kerney 1971, Morgan 1981, 1982, Piearce 1972, Preece *et al.* 1995, 1998, 1999). Figure 10 is the microanalysis of a fresh granule extracted from the earthworm *Lumbricus terrestris* and Figure 11 from a granule from the West Dean site. The peaks representing aluminium, silicon, iron and manganese in Figure 11 are likely to be from residual soil adhering to the surface of the granule, the gold peak is from the coating it was given.

There is no correlation between granules and age of compartment; however earthworm granule numbers are clearly related to the abundance of free chalk in the soil, with low numbers or none when no free chalk is present. They are most abundant in compartments C, D and I (ages 3, 4 and 9 years), which have the highest mean pH and the highest free chalk. These coincide with the peaks for dead snails in the quadrats.

The relationship between the earthworm granules and quadrat pH are given on Table 4. Of the 4757 granules extracted only 0.19% were from quadrats with pH below 5. Quadrats of pH between 5 and 5.9 accounted for 11%, and quadrats over pH6 accounted for 88.5% of granules.

Rank Spearman correlation analysis confirms this correlation between earthworm granules and pH and chalk (Table 1). There is also a strong correlation between earthworm granules and the 2.36mm fraction (p=0.004) and a negative correlation with litter depth (p=0.006) (Table 1) and a positive correlation with percentage vegetation cover (p=0.023) (Figure 12). However, when granule numbers per quadrat are compared with litter depth there is a distinct preference shown for 2cm litter (Figure 13). Earthworm granules also correlate strongly with several snail species including *A. pura* (p=0.001), *V. contracta* (p=0.007) and *C. tridentatum* (p=0.014) (Table 2).

DISCUSSION

SOIL FRACTIONS, SNAILS AND ENVIRONMENTAL FACTORS

The numbers of live, dead and total snails correlate with pH and chalk as expected and is consistent with previous results (Bishop 1976, Cameron 1973, 1978, Millar & Waite 1999, Valovirta 1968, Wareborn 1970).

The five most abundant snail species correlate with total shells and live snails (Table 2). It is interesting that of these *A. nitidula* is the only one to show no correlation at all with dead shells. This suggests that there may be selective removal from the quadrats, for example the empty shells may be less durable in some way. However, evidence from predation damage suggests it is a favoured prey item and may be removed that way (unpublished data).

The link between certain snails and litter depth has already been observed and discussed (Millar and Waite 1999). In summary seven species showed greater abundance when the litter depth was 2cm, *V. pellucida* numbers declined with increasing litter depth and *P. pygmaeum* and *N. hammonis* increased with litter depth.

TABLE 4

Relationship between earthworm granules and pH of quadrats

Quadrat pH	No. of quadrats	Mean no. of granules	Range (nos of granules)
4	3	0	0
4.1 - 4.4	3	0.66	0 - 2
4.5 - 4.9	11	0.64	0 - 3
5.0 - 5.4	20	9.1	0 - 43
5.5 - 5.9	7	50.6	0 - 156
>6.0	13	324	6 - 2614

The various links between certain species of snail and soil/litter aggregate sizes are more difficult to explain. Several show negative correlations with the largest fractions and the smallest. The negative correlation between *C. tridentatum* and the smallest fraction sizes may be a reflection of the small size of the snail (up to 2mm long). Where abundant fine material exists, it may fill in between aggregates and prevent movement by the snail or reduce surface area available for grazing, or reduce spaces to lay eggs or retreat to (Outeiro 1993, Boycott 1934). However, *P. pygmaeum,* also a very small snail (up to 1.5mm), does not show similar preferences, but this may be related to different microhabitat preferences. Outeiro (1993) and Hermida (1995) suggest that there may be a link between size of snail and particle size, however there is little evidence of this from the present study. Outeiro (1993) found similar lack of support for this theory from their data.

A large proportion of fine material, possibly loess derived, could lead to firmer more compact soil with reduced air voids, less favourable to vegetation, soil fungi and bacteria which the snails feed on, thus affecting them indirectly. Those snails which are confined solely to the surface litter or vegetation and never burrow into the soil are unlikely to be affected by the soil texture. However, such differential activity is unlikely to be satisfactorily tested here as the soil and litter were combined and the litter being less dense has less apparent significance in the measured weights.

Four species show a negative relationship with the larger sized particles (10mm, 20mm and over). Much of the large fraction consisted of pieces of flint and chalk as well as leaves and twigs (which although a small proportion of the weight may be a large proportion in terms of volume). It is possible that when there is a high proportion of large particles in the soil the snails are indirectly affected via other environmental variables, such as increased drainage leading to drier soil, reduced vegetation cover and lower humidity. More research is required as to the exact positioning of snails in relation to soil, litter and vegetation, and measurements of weight/volume of each component before this can be satisfactorily explained.

PCA

The PCA ordination demonstrates a separation is obtained between compartments on the basis of soil particle size. This seems to be best explained by the geographical location and aspect of the site; for example the soils are known to be thicker at the northern, higher end of the south facing site. The present composition and thickness of the soil at this site has it origins in the solifluction or 'head' deposits laid down during periglacial conditions during the last ice age (Reserve Management Plan 1994 (unpublished); Avery, 1980; Catt & Hodgson, 1976). The fine fractions of <0.6mm may be linked to the quantity of wind-blown loess deposited at that time. However, it is also going to be linked to the strength and degree of soil aggregation which is affected by earthworms (casts and burrows bound by mucus), soil-eating invertebrates (mucus bound faecal pellets), gum-producing soil bacteria, soil fungus (binding particles), soil organic matter and clay content (Russell 1988) The stability of aggregates is also related to the number of cycles of wetting, drying and exposure to direct raindrop activity, which would be higher in the exposed recently-coppiced compartments.

Although there is an apparent relationship with age as well as geographical location, this is more likely to be because of the sequence of coppicing, which is carried out in adjacent plots. Previous analysis (Millar & Waite 1999) showed little direct relationship between snail abundance or diversity and the age of compartment (time since last coppiced). It is more likely, in this study, to be linked with the geographical location.

Other studies have suggested that snail distribution may have a relationship with soil particle size (Boycott, 1934; Dickinson, 1974; Hermida *et al.* 1995a, 1995b; Lozek 1962; Outeiro *et al.*, 1993; Stephenson 1968; Tattersfield 1990). For example Hermida *et al.* (1995b) found a negative correlation with the largest (>2mm) and smallest particle size measured, but no correlation with intermediate sizes. Hermida *et al.* (1995a) found, in line with this study, that neither *N. hammonis* nor *A. nitidula* showed any significant correlation with soil particle sizes. Tattersfield (1990) thought that soil characters including physical structure of the soil might be important for some species. Stephenson (1968) found that slugs were more numerous on heavy soils and believed that its open texture provided a favourable habitat for slugs. Outeiro *et al.* (1993) found that soil texture, in terms of clay, gravel and sand, best explained the distribution of snail species. It should be noted that all the above studies used absolute soil particle size. The present study used oven dried aggregate size.

From this analysis it is clear that the soil (including litter) aggregate size proportions vary substantially between compartments and this may, therefore, be an important factor in explaining the variation in snail distribution within the study area.

Some studies of Quaternary sediments may show an apparent correlation between shells and sediment texture. However, this is more likely to be due to the rate of accumulation of sediment. Slow accumulation of fine sediments allows more time for shells to accumulate, conversely, coarser sediments may accumulate rapidly and produce fewer shells (Preece & Bridgland 1998).

DCA

The DCA analysis (Figure 3) separation of sites reflects the difference in particle size, with pH and earthworm granules also of some importance. The grouping and separation of the sites is also geographical and reinforces the groupings and interpretations of the PCA analysis. The DCA figure demonstrates greater proximity of the sites to the individual axes than PCA (Figure 2).

The strong link that certain species have with the middle of the second axis may be explained by their correlation with the mid-range aggregate sizes. Apart from a strong correlation with earthworm granules and pH by *A. pura,* it is difficult to interpret the link *A. nitidula* and *A. pura* have with the middle of this axis as neither of these species correlates with any of the soil sizes.

The separation of the species by the DCA species ordination in Figure 4 is a little clearer. The separation of *P. elegans* and *V. pellucida* suggests preferences to similar conditions favouring the production of earthworm granules. These snails are also known to prefer high pH (Rank Spearman results above; weighted averages for pH, Table 5, Millar & Waite 1999). *P. elegans* is only found on calcareous soil (Kerney & Cameron, 1979), and is a snail which is known to burrow often in quite coarse chalk rubble, so the negative Rank Spearman correlation to the 10mm aggregate size is difficult to explain, but it would not be expected to be restricted to the mid-range aggregate size as the bulk of the other species are. *N. hammonis* and *A. fusca* are separated along axis 1 and from the weighted averages published earlier (Millar & Waite 1999) these species had the lowest weighted average pH preference. This is likely to have the greatest influence in their separation. In the general search in the woodland compartments, *O. alliarius* was often found under loose bark of rotting branches and is probably not greatly influenced by the soil texture, hence its separation from the rest of the species, at the lower end of axis 2. It is also tolerant of acid conditions.

The suggestion that soil aggregate size is an important determinate of snail community composition is supported by the significant correlation between the first axis sample scores for the soil fraction PCA ordination and the snail community DCA ordination (Pearson's moment correlation coefficient $r = -0.5476$, $p < 0.001$).

EARTHWORM GRANULES

Calcitic granules have been found in soil deposits and reported by several authors (Bal 1977; Canti 1998 (and references therein), Kerney 1971; Preece *et al.* 1995, 1998, 1999).

These granules were, until relatively recently, thought to be internal granules produced by arionid slugs (Kerney 1971). They are now known to be produced in the calciferous glands of certain species of earthworm especially those of the genus *Lumbricus,* and are passed out during the life of the earthworm (Bal 1977; Canti 1998; Darwin 1881; Meijer 1985; Morgan 1981, 1982; Piearce 1972). Although it cannot be certain which species produced these granules it is likely to include the common species *Lumbricus terrestris* which have been found to produce granules of 0.5 to 1.5mm (Meijer 1985; Morgan 1981). Fresh slug granules have a much smoother, fine grained appearance (Canti, 1998; Rundle (pers. comm.) Figure 9) and large granules, from species such as *Arion ater* and *Arion subfusca,* are clearly distinguishable from fresh earthworm granules. However, below 0.5mm slug and earthworm granules are probably not easily distinguishable (Rundle pers. comm.). Granules extracted from Quaternary sediments and archaeological sites, even though slightly worn, retain their characteristic crystalline surface sculpture (Preece *et al.* 1995; 1998). If granules have been worn by digestive processes of other animal, as when birds or mammals consume earthworms, then distinguishing larger granules may become more difficult, however, further work would be required to test this idea.

Several species of earthworm are now known to produce granules (Bal 1977; Darwin 1881; Morgan 1982; Piearce 1972) A. Rundle (pers. comm.) found that out of 9 species of earthworm examined, 7 possessed granules. *L. terrestris* and *L. rubellus* produced granules up to 1.5mm and 1.35mm respectively. *Allolobophora virescens, Aporrectodea caliginosa, Aporrectodea longa, Dendrodrilus rubidus* and *Lumbricus castaneus* yielded granules up to between 0.3mm and 0.7mm long. None were found in *Eisenia fetida* or *Octolasion cyaneum.*

The granules can vary in size, shape and number from even a single species of earthworm. Such variations are likely to depend upon environmental conditions and the age of earthworm so it is unlikely that they could be used to identify species or give more than a very rough indication of earthworm population size. This is supported by the difference in maximum size of granule found from different soils. Bal (1977) found *L. rubellus* produced granules only up to 160μm from soil with 10% Calcium carbonate. A. Rundle (pers. comm.) extracted granules up to 1.35mm long from *L. rubellus* (soil unknown), whereas one author (Millar) did not find any granules in one specimen of *L. rubellus* from Weald Clay based garden soil but extracted 10 granules up to 0.5mm from a single *L. terrestris* from the same Weald Clay soil.

Kerney (1971) had his Quaternary granules analysed and they were found to be of pure calcite of non-magnesium type. He also found that numbers of these granules fluctuated in proportion to land snail abundance in the deposits he examined. A weak correlation ($p = 0.02$) between live snail numbers and earthworm granule numbers was also found in the present study but a strong correlation ($p = 0.001$) was found with dead shells. Preece *et al.* (1995) also found a close correlation between snail shell numbers and earthworm granules, in a late-Glacial soil sequence.

The strong relationship found in this study between earthworm granules and pH and chalk content of the soil may be for a number of reasons:

1) The earthworms may be more abundant in a calcium rich/high pH soil or vegetation (feeding preferences, metabolism, soil texture, drainage etc. Edwards & Lofty 1972; Edwards, Crawley & Heard 1999)
2) The calcium secreting species of earthworm may be more abundant or secrete more actively in Ca rich/high pH environment (Piearce 1972)
3) Granules may only be excreted in chalky soil as excess Calcium excreted (Piearce 1972),
4) The granules, being of calcium, may be preserved longer in chalk rich soil.
5) In soil low in free chalk, granules may be eaten as a source of calcium by snails and other organisms, and so have a shorter retention time.

Edwards and Lofty (1972) found that *Lumbricus terrestris* preferred a soil pH of 7.0 although this species has been found in pH 5.4. Wareborn (1992) suggested that granule-making earthworms (Lumbricidae) are negatively affected by lowered pH. If numbers of granules are in any way an indicator of earthworm population size then the results of this study are in line with his findings.

There is also a positive link with vegetation cover (Table 1, Figure 11), however, the retention time of earthworm granules in the soils at West Dean is unknown. The granules may represent previous populations, decades or centuries ago, as well as the present one, whereas the vegetation cover represents mainly the present environmental conditions with some influence from the light and nutrient input levels of the previous year. From years one to four the vegetation cover in a coppice woodland might be expected to increase on the previous year, whereas from year five onwards it might be expected to decrease. There may be a lag of one generation time (12–24 months) or more for earthworms to increase in response to improving conditions. It is not known how rapidly they respond, by death or removal, to deteriorating conditions, although Edwards & Lofty (1972) suggest it could be two years for a population to recover from a prolonged drought. Therefore, even though the data on Table 1 indicates a correlation, a direct relationship between vegetation cover and granule numbers cannot be expected (unless the granules numbers reflect only the current population). It should be noted that on Figure 12 it is not a straight line plot but rather that higher vegetation cover allows the potential for greater numbers of granules providing other environmental factors are not limiting. Numbers of living earthworms may correlate with such environmental factors as vegetation cover and type. Meijer (1985) found that *Lumbricus terrestris* preferred soils covered by dense vegetation.

A negative correlation was found between granules and litter depth (Table 1). Replotting as in Figure 13 reveals greater abundance for 2cm litter depth. Earthworms are believed to prefer soil rich in organic matter, and decaying leaves in woodlands favour earthworm multiplication (Edwards and Lofty 1972). Earthworms are known to remove a large part of the annual leaf fall, when a healthy population is present (up to 80% in an apple orchard, Edwards and Lofty 1972), usually by drawing leaves into their burrows. Only certain species of earthworm are active litter-feeders, such as the *Lumbricus* spp. which are also believed to have the most active calciferous glands (Piearce 1972). In the woodland at West Dean, earthworms are believed to play an important part in the litter decomposition as suggested by the numbers of calcareous earthworm granules which were counted. High earthworm populations would remove the litter more quickly. The abundance and species of litter-decomposing micro- and macrofauna is likely to change as litter depth changes.

The connection between earthworm granules and certain snail species is not likely to indicate a direct relationship but rather that both earthworm granules and certain snails both show strong relationships with another environmental factor such as pH. Thompson *et al.* (1993) found that numbers of snails were not affected by the presence or absence of earthworms. However, this was in a very simple laboratory Ecotron community and the present study clearly shows that there are links, albeit indirect, between earthworms and snails. Earthworms produce casts with a diameter of between 1 and 3mm which are coiled into aggregates of between 5mm and 10mm. Larger accumulations readily break down to the 5–10mm size. It is possible that the apparent relationship between snails and mid-sized soil aggregates is a reflection of conditions which favour both earthworms and snails which are strongly correlated via the granules. It is also possible that earthworms *create* conditions favourable for snails by binding fine soil particles into aggregates. Also, depending upon the species and its food, these casts are generally richer in nitrogen, organic matter and micro-organisms, such as bacteria and fungal spores, and are a higher pH than the surrounding soil (Edwards & Lofty 1972). All these factors may benefit snails, either directly as a food source or microhabitat, or indirectly by encouraging favourable vegetation, moisture retention, drainage etc. but further research would be required to support this theory.

ACKNOWLEDGEMENTS

We are grateful to the Conchological Society of Great Britain and Ireland and to English Nature for grants enabling A.J.M. to carry out the fieldwork. We should also like to thank the Sussex Wildlife Trust and The Trustees of the Edward James Foundation for permission to work on the reserve, and the Division of Biology, University of Brighton, for the use of their SEM and pH meter, and the School of Environmental Sciences for the use of oven and sieves. Many thanks go to Adrian Rundle for assistance and data on earthworm identification and granule extraction, to Richard Preece for his references, and to the referees for their comments.

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APPENDIX 1

The explanation of compartment numbers and ages is as follows:

This study	A	B	C	D	E	F	G	H	I	J	K	L	M	N
West Dean site numbers	101	122	121	120	112	103	104	116	102	113	111	109	124	123
Age/years at sample time	1	2	3	4	5	6	7	8	9	10	11	12	40+	40+

ATLANTIC BATHYAL CANCELLARIIDAE (NEOGASTROPODA: CANCELLARIOIDEA): ADDITIONAL DATA, AND DESCRIPTION OF A NEW SPECIES.

A. VERHECKEN[1]

Abstract Study of unpublished deepwater cancellariid material from the Atlantic Ocean resulted in description of a new species of Bonellitia *and range extension for* Brocchinia azorica, B. clenchi, B. nodosa, *and possibly for the genus* Gerdiella. *Intraspecific variability of* Axelella brasiliensis *(described on 1 sh) has now been documented.*

Key words Cancellariidae, Atlantic, bathyal.

INTRODUCTION

Because of their deep-water habitat, bathyal Cancellariidae are rarely collected, and are poorly represented in museum collections. Only a small number of these species occur in the Atlantic Ocean, and some of them were described on very few or even single specimens. Subsequent publications on newly collected material have remained scarce. Consequently, data on the geographic and bathymetric distribution of the Atlantic deep-water cancellariids are often very limited.

The last publication including such species was by Bouchet & Warén (1985), who restricted their study to the Northeast Atlantic. More material has become available for study since: some was collected by British, Dutch and French expeditions during the last decades, other material was taken in 1873 by the *Challenger* expedition. The latter is now in the Melvill-Tomlin collection in NMWZ, but was not mentioned in the published catalogue of the Cancellariidae of that collection (Trew, 1990).

ABBREVIATIONS

BMNH	Natural History Museum, London
MNHN	Muséum national d'Histoire naturelle, Paris, France
NMSZ	National Museums of Scotland, Zoology, Edinburgh
NMWZ	National Museums & Galleries of Wales, Dept. of Zoology, Cardiff
RMNH	Nationaal Natuurhistorisch Museum, Leiden, the Netherlands
USFC	United States Fisheries Commission
USNM	National Museum of Natural History, Washington, USA
SAM	South African Museum, Cape Town, Republic of South Africa
o.d.	original designation
s.d.	subsequent designation

SYSTEMATIC DESCRIPTION

CANCELLARIIDAE Forbes & Hanley, 1851
Genus *Axelella* Petit, 1988

Type species (o.d.) *Cancellaria smithii* Dall, 1888, western Atlantic.

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Replacement name for *Olssonella* Petit, 1970, non Glibert & Van de Poel, 1967.

Axelella brasiliensis Verhecken, 1991a
Figs 1–3

Axelella brasiliensis Verhecken, 1991a: 549, figs 5–6.

Holotype 4.8 x 2.0 mm (only sh known in 1991), MNHN, no reg. number.

Type locality "Marion-Dufresne" MD 55, Stn SY 74, 682 m, 18°58′S37°49′W, off Brazil.

Material examined Holotype; 24 sh *Marion–Dufresne* MD 55, Stn CB 76, 18°59′S37°50′W, off Espirito Santo, Brazil, 637 m, 27 v 1989, MNHN; 2 sh *Marion–Dufresne* MD55, Stn DC 73, 19°00′S37°48′W, off Espirito Santo, Brazil, 607–620 m, 27 v 1989, MNHN; 1 sh, *Challenger* Stn 122, 9°35′S34°50′W, off Pernambuco, Brazil, 637 m, 20 ix 1873, NMWZ 1955.158.02257.

Measurements For 26 sh: shell height: mean 2.65 mm, range 2.3–3.2 mm; shell width: mean 1.53 mm, range 1.3–1.8 mm; shell height/width ratio: mean 1.73, range 1.60–1.86.

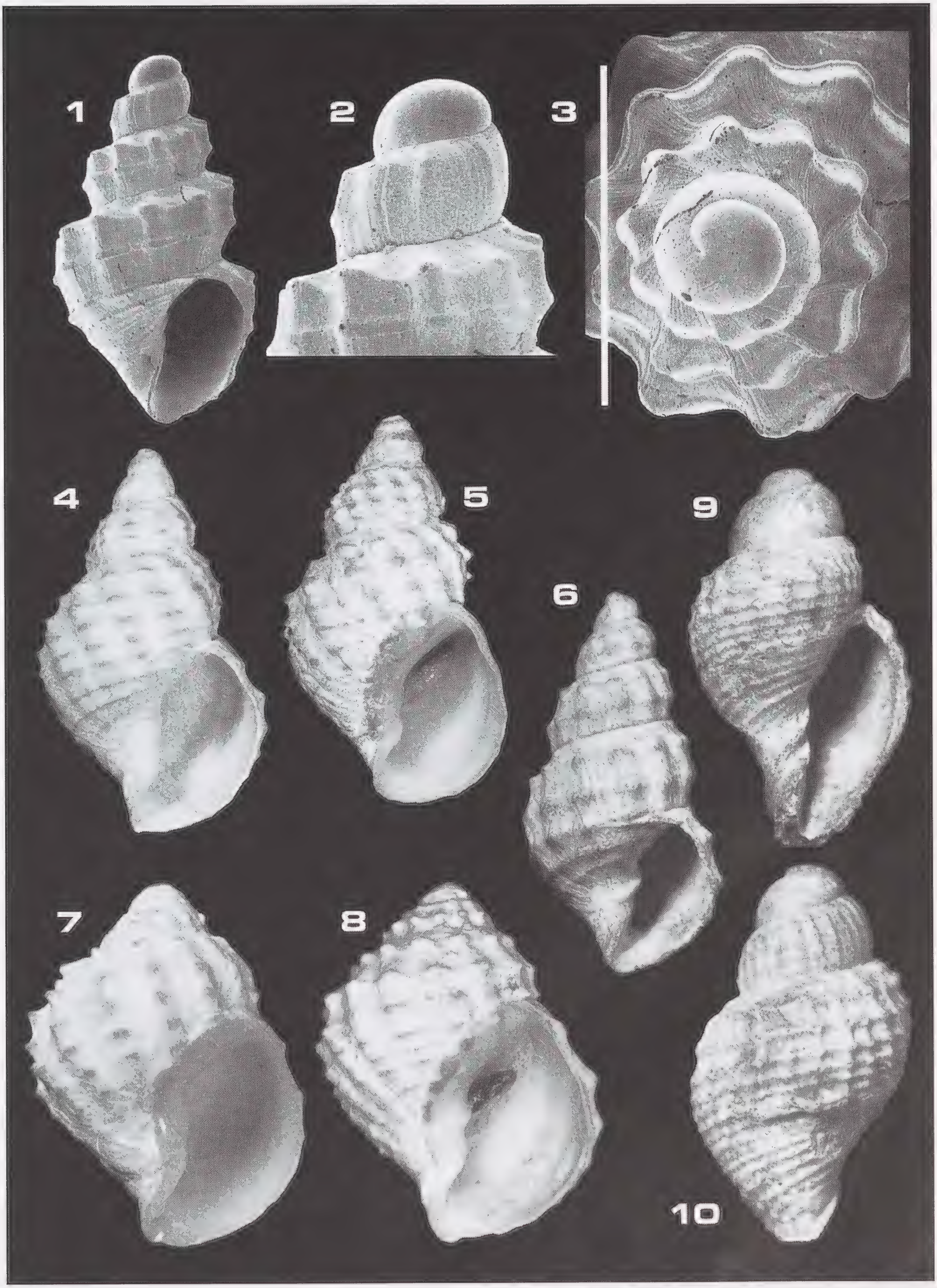
Geographic range Off Brazil, 9°–19° S, 607–637 m.

Remarks The intraspecific variability has been evaluated on the material now at hand. Given for each parameter are: number of shells measured, mean, range. Protoconch: paucispiral, number of whorls: 13, 1.2, 1–1.5; exposed height: 25, 0.49, 0.43–0.63 mm; diameter: 24, 0.48, 0.4–0.6 mm. Teleoconch: number of whorls: 24, 2.8, 2.5–3.25; axials on wh 1: 24, 10.5, 9–13; wh 2: 23, 10.3, 9–11; wh 3: 3, 10.7, 10–11, last wh: 24, 9.8, 8–12; spirals on wh 1: 25, 2.1, 1–3; wh 2: 25, 3.7, 2–6; wh 3: 7, 5.6, 4–9; last whorl: 24, 10.7, 8–14. Last whorl height: 24, 1.74, 1.5–2 mm. Aperture: height: 23, 1, 0.95–1.2 mm; width: 23, 0.67, 0.6–0.8 mm. Columella always straight, vertical; folds: 24, 1.9, 1 (sometimes very weak)-2. No lirae in aperture; umbilicus: very narrow slit (much narrower than in holotype) to completely closed. To illustrate the variability, a shell with few spirals and its protoconch (in better condition than the holotype's) is shown in figs 2–3; remark the resemblance to (slightly larger and less slender) shells of *Cancellaria patricia* Thiele, 1925 (cfr Verhecken, 1991b: fig 8) from off East Africa and South-East Australia.

Genus *Bonellitia* Jousseaume, 1887
Type species (o.d.) *Cancellaria bonellii* Bellardi, 1841, Mio-Pliocene, Italy

Admetula Cossmann, 1889 is a synonym (cfr Verhecken, 1986: 33).

Figs 1–3 *Axelella brasiliensis* Verhecken, 1991. MD55 Stn CB76, off Espirito Santo, Brazil, 18°59′S37°50′W, 637 m, 27 v 1988, MNHN, 2.6 x 1.4 mm. **2**, **3**: protoconch, scale bar = 1 mm **Fig 4–5** *Brocchinia azorica* Bouchet & Warén, 1985, off W. Ireland. **4** *Shackleton* 2A/77 Stn 121, off W. Ireland, 54°37′N12°09′W, 2910 m, 29 i 1977, NMSZ 1979111.13001, 15.4 x 9.4 mm **5** *Challenger-II* 71/90 Stn 401, 54°40′N12°16′W, 2900 m, 10 ix 1990, NMSZ1994128.13002, 19.6 x 11.6 mm **Fig. 6** *Brocchinia clenchi* Petit, 1986. *Challenger* Stn 122, off Pernambuco, Brazil, 9°05′S34°50′W, 637 m, 20 ix 1873, NMWZ 1955.158.02258, 6.3 x 3.4 mm **Fig. 7–8** *Brocchinia nodosa* Verrill & Smith, 1885 **7** *Challenger-II* Stn AT219, off W. Scotland, 57°25′N10°28′W, 1991 m, 3 viii 1982, NMSZ 1994128.13001, 11.1 x 8.6 mm. **8** Stn MAU 105, off Banc d'Arguin, Mauritania, 19°43′N17°44′W, 1600–1900 m, 17 vi 1988, RMNH, 14.8 x 11.9 mm **Fig. 9–10** *?Gerdiella* spec., fragment, *Challenger* Stn 122, off Pernambuco, Brazil, 9°35′S34°50′W, 637 m, 20 ix 1873, NMWZ 1955.158.02259, 5.5 x 3.4 mm.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Bonellitia gittenbergeri spec. nov.
Figs 11–14

Holotype 12.2 x 8.4 mm, RMNH 56456.

Paratypes 3 shs, all from type locality, 13.4 x 8.8mm; 11.6 x 8.3 mm; 11.9 x 8.1 mm, RMNH 56457.

Type locality *TYRO* Mauritania-II Exped. 1988, Stn MAU 040, 18°51'N16°53'W, off Mauritania, 500 m, fossil coral debris, macrourids, 10 vi 1988.

Description Shell solid, with rounded whorls and a relatively large body-whorl. Colour whitish.

Protoconch paucispiral, with $^{7}/_{8}$ whorl. Maximum diameter 1.1 mm, exposed height 0.8 mm. Fine spiral striae remain on otherwise eroded protoconch.

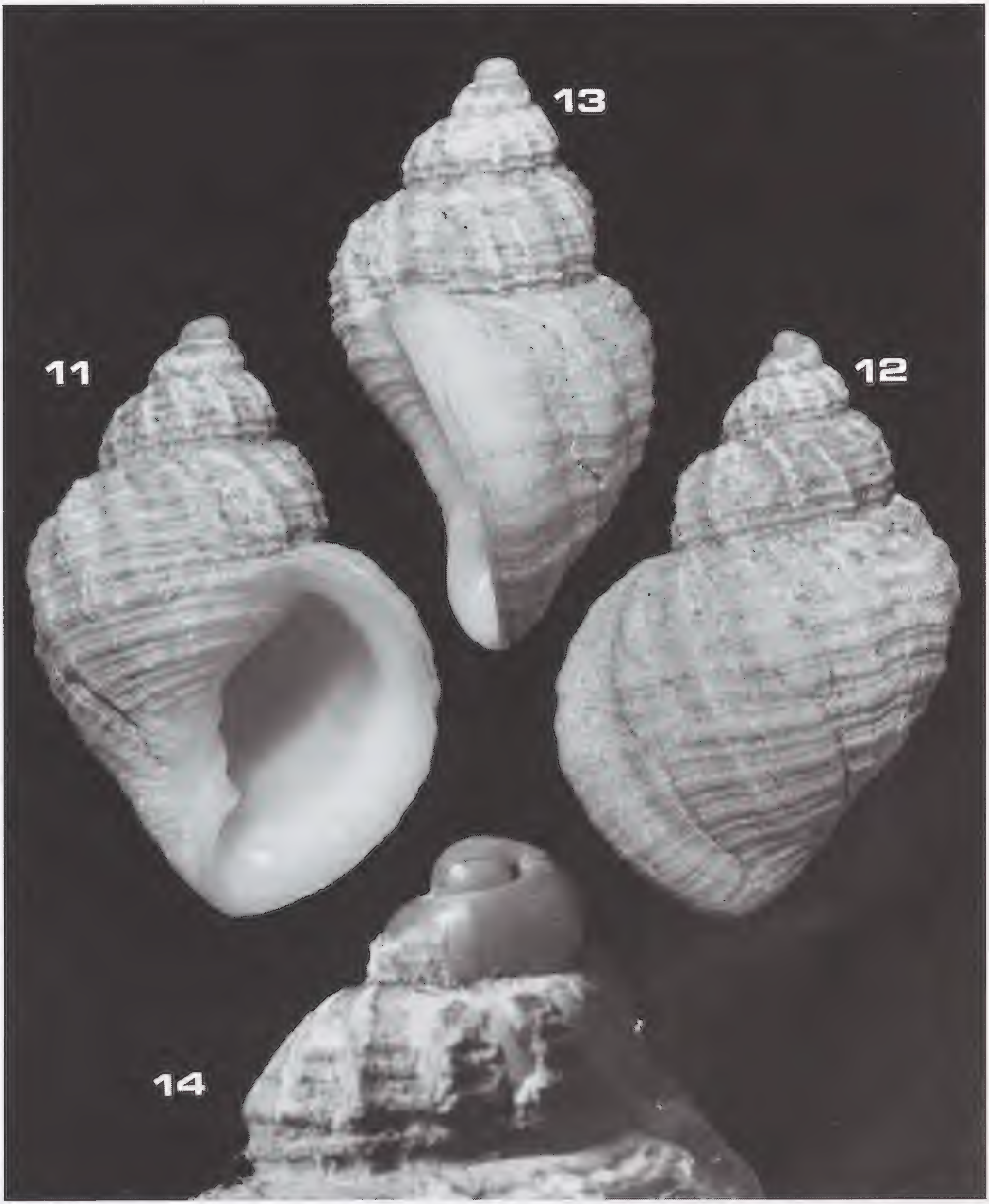
Teleoconch with up to 3.5 whorls. Spiral sculpture starts abruptly. The second and third teleoconch whorl have 5 main spiral bands consisting of two close-set ridges, separated by a very thin line; width of complete spiral bands about 0.1–0.15 mm, on third whorl a single secondary spiral in between main spirals. Body-whorl with 12 main spiral bands, up to 0.3 mm wide; a set of secondary and tertiary spirals is also present. Axial sculpture of 12 and 13 low rounded ribs on second and third teleoconch whorl respectively; 10 axials on the body-whorl. Aperture porcellaneous white, large, semicircular; height 7.0 mm, width 4.6 mm. Outer lip thick, flared out, with no inner lirae in the holotype; but 8 short solid ridges in the paratypes, the posterior one placed somewhat apart. Columella typical for a *Bonellitia* , with two sharp folds and a prominent "tooth" at the rim of the short wide siphonal canal. Columellar glaze white, on the holotype very thin adapically, thicker in the umbilical region; the paratypes have a thicker callus. Umbilicus completely closed by the callus, but a concave region is formed by the weak fasciolar ridge. Periostracum very thin, fawn, with short hairs (up to 0.3 mm length) arranged along the middle line between the close-set spiral cords.

Geographic range Known only from the type locality.

Derivation of name Named in honour of Prof. Dr. E. Gittenberger (RMNH) who kindly made this material available for study.

Comparisons This new species is similar to *Bonellitia cornidei* (Altimira, 1978) living in the same area, which is more slender and has a thinner shell (to be described and illustrated in a forthcoming paper). The new species has wider and more rounded axial ribs; and a spiral sculpture of double bands, versus a single broad band in *B. cornidei. B. gittenbergeri* can have eight lirae inside the outer lip, and shell and periostracum are whitish, against six lirae for the brown *B. cornidei.*

In general outline, shells of *B. gittenbergeri* resemble juvenile shells of *Cancellaria africana* Petit, 1970 (= *Cancellaria imbricata* Watson, 1882, non *C. imbricata* Hoernes, 1854) from the Cape of Good Hope area, which have a larger protoconch, a relatively higher spire and lack the inflection of the columella. *B. bayeri* (Petit, 1976), from off Yucatan Peninsula, Mexico, 585–591 m, is larger, has more axial ribs and a relatively shorter spire than the new species. *B. vossi* (Petit, 1976), from off the Bahamas, 622–695 m, has the same size and about the same sculpture as *B. gittenbergeri,* but it has a more impressed suture, the shoulder of the whorls more pronounced, a relatively smaller and less rounded aperture and the columella more inflected.



Figs 11–14 *Bonellitia gittenbergeri* spec. nov. **11–13** holotype, Stn MAU40, off Mauritania, 18°51'N16°53'W, 500 m, 10 vi 1988, RMNH 56456, 12.2 x 8.4 mm. **14** protoconch of paratype, scale bar = 1 mm

Remarks The first teleoconch whorl of all four sh is strongly eroded, so that its sculpture has disappeared. For the rest, the holotype is in perfect condition, but the outer lip of the aperture is slightly less developed than in the paratypes.

Genus *Brocchinia* Jousseaume, 1887

Type species (s.d. Sacco, 1894): *Voluta mitraeformis* Brocchi, 1814 (non Lamarck, 1811), Pliocene, Italy.

The genus *Brocchinia* is here used according to Verhecken (1991a: 549).

Brocchinia azorica (Bouchet & Warén, 1985)
Figs 4–5

Admete azorica Bouchet & Warén, 1985: 260, fig. 690.
Brocchinia azorica - Verhecken, 1991a: 549.

Holotype 7.6 x 4.6 mm, MNHN, no reg. number.

Type locality *BIACORES* Stn 53, 38°7′N28°18′W, SE of Pico, Azores, 1820 m.

Material known 4 sh mentioned by Bouchet & Warén (1985); 1 sh. 15.4 x 9.4 mm, *Shackleton* 2A/77 Stn 121, 54°37′N12°6′W, 2910 m, 29 i 1977, NMSZ 1979111.13001; 2 sp, 5.0 x 3.6 mm and 5.6 x 4.0 mm, *Challenger-II* Stn 2, 55°04′N 12°33′W, 2857 m, 4 vi 1973, NMSZ 1976004–13005; 1 sp, 19.6 x 11.6 mm, *Challenger-II* Stn 401, 54°40′N12°16′W, 2900 m, 16 ix 1990, NMSZ 1994128.13002.

Geographic range Known only from the Azores in 1985; 4 sp now extend its occurrence to off NW Ireland.

Comparisons In general form and number of spirals, the larger specimens from off NW Ireland are much like *B. decapensis* (Barnard, 1960) from off Cape Point, South-Africa, 2890–2963 m, known only from 2 heavily eroded sh. Better material of the latter species is needed to establish conspecificity of the two names involved.

Remarks The protoconch of most *B. azorica* shells is eroded, but a sh from the Azores (*Talisman* dr. 129, 38°00′N27°03′W, 2220 m, MNHN) has a multispiral protoconch with 2 $^3/_4$ whorls, max. diameter 1.4 mm, exposed height 1.3 mm. A sp and a sh from off NW Ireland (figs 4–5) are much larger than the material of that species known so far: 15.4 and 19.6 mm height versus 7.8 mm for the holotype. The larger shells were identified as this species based on sculptural details; and on their dimension's close fitting to the extrapolated linear regression line (fig 15) for those of the 7 smaller *B. azorica* shells, as evidenced by the correlation factors (r^2=0.929 for the 6 sh, 0.996 for the 8 sh).

Brocchinia clenchi Petit, 1986
Fig. 6

Brocchinia clenchi Petit, 1986: 24, figs 1–4.
Cancellaria mitraeformis (Brocchi, 1814) - Jeffreys, 1885: 49.
Cancellaria pusilla H. Adams, 1869: 274 (non *C. pusilla* Sowerby, 1832).

Holotype 4.5 x 2.3 mm, USNM 849002.

Paratypes 2 shs: 5.2 x 2.6 mm, USNM 189694; 6.0 x 2.5 mm, BMNH 1885.4.4.202.

Type locality Josephine Bank (about 37°N14°W), 610–770 m.

Material examined 1 sh, *Challenger* Stn 122, 9°05′S34°50′W, off Pernambuco, Brazil, 637 m, 20 ix 1873, NMWZ 1955.158.02258 (fig 6): this locality is the first record from the Western and Southern Atlantic. Canary Islands: 2 sh, *CANCAP-II* Stn 2155, S of Hierro, off Punta de la Restinga, 27°35′N17°59′W, 700 m, fine sand with pteropod ooze, 10 ix

1977, RMNH; 4 sh, *CANCAP-II* Stn 2062, SE of Fuerteventura, Punta de Gran Tarajal, 28°7′N13°45′W, 1520 m, plain with pteropod ooze, 29 viii 1977, RMNH; 6 sh, *SEAMOUNT-2* Stn DW130, 28°08.9′N15°53.1′W, Gran Canaria, 660 m, 6 i 1993, MNHN. 2 sh, *SEAMOUNT-1* Stn DE48, Josephine Bank, 36°47.8′N14°31.7′W, 1350–1360 m, 5 x 1987, MNHN; 2 sh , Azores, 1250 m, MOM; 1 sp *CANCAP-III* Stn 3107, 24°17′N16°49′W, off Western Sahara, 1000–1100 m, RMNH.

Geographic range In depths from 15–1520 m off the Azores, Portugal, the Canary Islands and N.W. Africa; now also off Brazil.

Comparisons In general form this species resembles small *Brocchinia mitraeformis* (Brocchi, 1814) from the European Miocene and Pliocene, but the fossil species has a multispiral protoconch, an elaborate spiral sculpture, and the nodules, if present, are much broader. The Brazilian shell differs from *B. pustulosa* Verhecken, 1991a, in lacking the strong sutural ramp of the latter, and in the number of spirals. *B. clenchi* differs from *B. azorica* in its paucispiral protoconch, its more elongated form with a top angle of only 44° versus 60° for *B. azorica,* and its spiral sculpture of only 2 nodule rows on the first 3 teleoconch whorls (3 and 4 resp. on 2nd and 3d teleoconch whorl of *B. azorica*).

Remarks The single sh from off Pernambuco has a paucispiral protoconch, a strong sculpture of nodules formed on the crossing of the 2 spiral lines and the rounded axial ribs, and 2 columellar folds, the adapical one being the strongest. This sculpture is rather atypical for *B. clenchi,* but the existence of other strongly sculptured sh of that species in the eastern Atlantic (to be described and illustrated in a forthcoming publication) pleads against separation of this sh from the typical form, at least for the time being.

Apart from the deepwater material, fairly rich material of this species is known from rather shallow water: Tenerife South, 43 m (Petit, 1986); 10 sh, Azores, 15–38 m, MNHN; 16 sh, off Saõ Miguel Isl., 50 m, MNHN. Moreover, the Recent species *B. clenchi,* as actually understood, seems to comprise two groups of shells: the typical form is small, clear white, and with a very smooth surface; the other form has whitish larger shells with a much stronger sculpture. This, together with the extreme depth-range (15–1520 m) might indicate the existence of two forms or species which however cannot be clearly separated on conchological basis now.

Brocchinia nodosa (Verrill & Smith in Verrill, 1885)
Figs 7–8

Admete nodosa Verrill & Smith, 1885: 419, pl. 44 fig. 9.
Admete nodosa - Dall, 1927: 43. Abbott, 1974: 248. Kaicher, 1978, card 1884. Bouchet & Warén, 1985: 258.
Brocchinia nodosa - Verhecken, 1991a: 549.

Holotype USFC *Albatross* Stn 2234, 39°9′N72°3′W (off New Jersey), 1475 m, USNM 44646, 12 x 8 mm.

Paratype 1 sh, USFC Stn 2217, 39°47′20″N69°34′15″W, 1670 m, whereabouts unknown.

Type locality USFC *Albatross* Stn 2234, 39°9′N72°3′W (off New Jersey), 1475 m. The shell catalogued USNM 44646 measures 11.8 x 8.4 mm, which is reasonably close to the dimensions in the original description, and is clearly the holotype. However, a label with it stated: "off Cape Hatteras, N. C.". "The station number was correctly indicated, and the detailed data had been published both in the cruise report and in the original description of the species." Obviously, that label was not correct. "The locality label accompanying the type has now been clarified" (Harasewych, in litt. 10 v 2000).

Material known Apart from the 2 types, and the 9 sp mentioned by Bouchet & Warén (1985), 15 more are known: 3 young sh, *Albatross* Stn 2668, 30°58′N 79°38′W, off Fernandina, Florida, 678 m (Dall, 1927: 1, 43); 2 sp, RV *Eastward* Cr E-6-78, Stn 43, 38°45.8′N 72°41.6′W, SE of Cape Henlopen, Delaware, 1850–1950 m, 1975, USNM 757000; *Albatross* Stn 2739, Delaware Bay, 1460 m, USNM 76786; 1 sh RV *Gillian* Cr. 75–089, Stn 29, N.E. of Norfolk, 1630–1760 m, 12 ix 1975, USNM 757272; 5 sp, up to 14.3 x 9.6 mm, *Biogas* 1972–80 Stn CP07, 44°10′N04°16′W, Bay of Biscay, 2170 m, MNHN; 1 sp, 11.1 x 8.6 mm, *Challenger-II,* AT219, 57°25′N10°28′W, 1991 m, 3 viii 1982, NMSZ 1994128.13001; 1 sp, 14.8 x 11.9 mm, Stn MAU105, 19°43′N17°44′W, off Banc d'Arguin, Mauritania, 1600–1900 m, RMNH. Dall (1927: 43) also mentions unspecified material from off Nantucket, 1470 m, and south of Long Island, New York, 1765 m.

Measurements Fig. 15 gives the available biometric data of shell height and width, as compared to those of *B. azorica.*

Geographic range Off the Atlantic west coast from about 42°N, off Nantucket, Massachussets, to 31°N, off Fernandina, Florida (Dall, 1927); off the Atlantic East coast from 57°N, off N.W. Ireland, south to the Bay of Biscay and Mauritania 19°N.

Remarks Espinosa & Rams (1988: 3) report this species in "the Antillean area"; if correct, this would constitute its southernmost record in the Western Atlantic. The basis for that statement is not clear, and an inquiry in Cuba remained unanswered. Possibly, this might be based on confusion by the Cuban authors of Fernandina, the old name of the Cuban town Cienfuegos, with the homonym town in Florida.

The occurrence of this species off NW Ireland, based on a very small shell (2.2 x 1.7 mm, Bouchet & Warén, 1985) is now confirmed by a large specimen (NMSZ 1994128–13001).

Genus *Gerdiella* Olsson & Bayer, 1972

Type species (o.d.) *Gerdiella gerda* Olsson & Bayer, 1972, Straits of Florida, 648–864 m

Three species of *Gerdiella* are known from bathyal stations in the Straits of Florida and south of Jamaica, in depths of 516–897 m. Since 1972, only a single sp of *G. cingulata* Olsson & Bayer, 1972 has been reported, from the northern Gulf of Mexico (Petit, 1983: 250).

? *Gerdiella* spec.

Figs 9–10

Material studied 2 very juvenile sh, 3.0 x 2.2 mm and 2.8 x 2.1 mm (mere protoconchs with about 0.5 teleoconch whorl), NMWZ 1955.158.02260, and a fg, 5.5 x 3.4 mm (the top of a broken slender shell), NMWZ 1955.158.02259; all from *Challenger* Stn 122, 9°35′S34°50′W, 637 m, off Pernambuco, 20 ix 1873

As far as can be judged, the three fragments are conspecific. The relatively large size of the protoconchs suggests that the adult shell is rather large for a cancellariid. The protoconchs are bulbous, paucispiral with $1^1/_2$ smooth whorls, maximum diameter 1.5–1.7 mm, exposed height in the fg 1.4 mm; diameter of embryonic shell ("nucleus" according to Verduin, 1982: 129) 0.3 mm. The two very juvenile sh already show two columellar folds. Passage into teleoconch almost invisible, merely marked by the

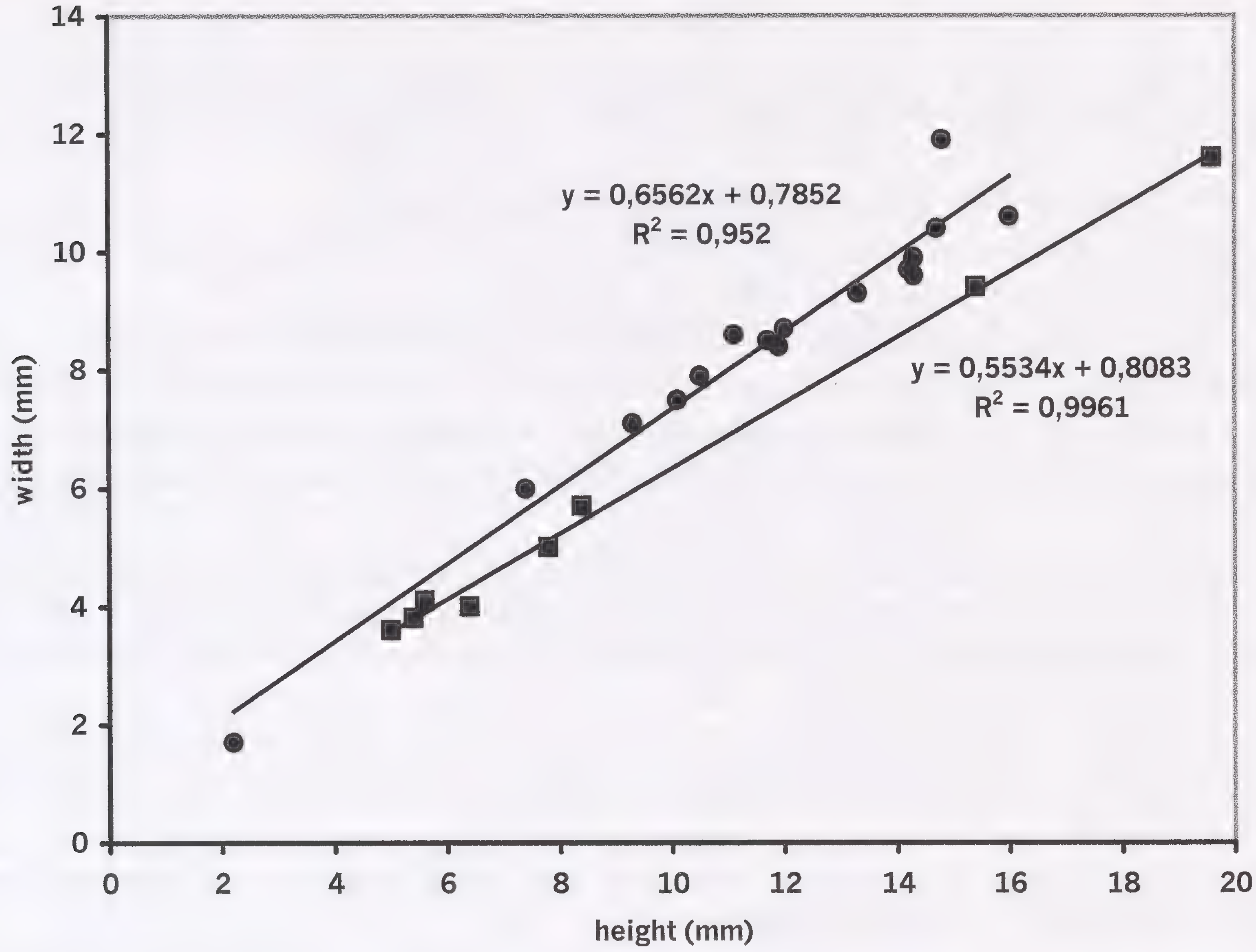


Fig. 15 Biometric data for *Brocchinia nodosa* (circles) and *B. azorica* (squares)

appearance of soft axial riblets of the teleoconch sculpture. Teleoconch: first whorl has 22 axial ribs and 3 very softly indicated spirals; second whorl has 6 spirals, forming a neat reticulation and small nodules when passing over the axials. Columella with 2 very oblique folds.

Remarks The fragment suggests a general shell form like that of *Gerdiella* or *Perplicaria* species. In fact, Dall (1890: 90, pl. 3 fig. 1) described *Perplicaria perplicata* gen. & spec. nov., based on an analogous but much larger fragment. The protoconch and early sculpture of the present sh differ strongly from that of Miocene to Pliocene species of *Perplicaria* from the Caribbean region, and no living *Perplicaria* species is known from the western Atlantic. The protoconch conforms that of the three known *Gerdiella* species. Consequently, placement in *Gerdiella* seems acceptable, although not evident, since protoconch characters are not considered of diagnostic importance at generic level by this writer. The fg cannot be identified with certainty as one of the three Caribbean *Gerdiella* species. It may belong to an undescribed species, but more and better material is needed for further identification at species level.

This tentative generic identification may widen considerably the known distribution area of *Gerdiella* (between 17°–26°N) southwards, to 9°S.

ACKNOWLEDGEMENTS

Thanks are due to D. Heppell (then at NMSZ), A. Trew and H. Wood (NMW), P. Bouchet (MNHN), E. Gittenberger and J. Goud (RMNH) for the loan of material and for information on it, and to M. G. Harasewych (USNM) and R. E. Petit (North Myrtle Beach, S. Carolina, U.S.A.) for information on the labelling of the holotype of *B. nodosa*. J. Cillis (Royal Belgian Institute for Natural Sciences, Brussels) made the SEM photographs.

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MORPHOMETRIC ANALYSIS OF *CARYCHIUM EXILE* AND *CARYCHIUM EXIGUUM* IN THE GREAT LAKES REGION OF NORTH AMERICA

JEFFREY C. NEKOLA[1] & MATTHEW BARTHEL[1]

Abstract *Statistical analyses were conducted on shell heights and widths of 5177* Carychium exile *and 1178* Carychium exiguum *individuals from 141 locations across a 1300 x 1000 km region centered on the North American Great Lakes. Both within co-occurrence sites, and between all sampled populations, the shell dimensions of these taxa were bimodally-distributed and statistically distinct. Thus,* C. exile *and* C. exiguum *are clearly separated and represent different species. Continuous latitudinal variation was observed in the shell size of both species, with largest individuals occurring in the north. In* C. exile, *these larger forms have often been referred to as* C. e. canadense. *Scanning Electron Micrographs of individuals from eight populations ranging from southern Illinois to northern Michigan to southern Ontario demonstrate that internal lamellae shape is too variable both within and between populations to be taxonomically useful. Analysis of the within population proportion of* C. e. exile, C. e. canadense, *and intermediate size classes demonstrate that most support individuals representing all three classes. Thus, the division of* C. exile *into distinct subspecies does not appear warranted.*

Key words Carychium exiguum, Carychium exile, Carychium exile canadense, *morphometrics, North America, systematics.*

INTRODUCTION

The genus *Carychium* Müller, 1774 comprises a group of minute terrestrial snails with highly elongated shells that occur in North America, Eurasia, the Caribbean, Indonesia, and the Philippines (Pilsbry 1948). Currently eight taxa are reported from eastern North America (Burch & Van Devender 1980, Hubricht 1985): *Carychium clappi* Hubricht, 1959; *Carychium exiguum* (Say, 1822); *Carychium exile* H.C. Lea 1842; *Carychium exile canadense* Clapp, 1906; *Carychium mexicanum* Pilsbry, 1891; *Carychium nannodes* Clapp, 1905; *Carychium riparium* Hubricht, 1978; and *Carychium stygium* Call, 1897.

As these species tend to not possess unique soft-body anatomies, conchological features are most often used for classification (Harry 1951, Burch & Van Devender 1980). Eastern North American taxa are generally distinguished by the degree of shell striation and size. Shell striation is lacking or weak in *C. exiguum, C. mexicanum, C. nannodes, C. riparium, C. stygium,* while *C. clappi, C. exile, C. e. canadense* have strongly striate shells. Shell dimensions range from the short, narrow (1.3 x 0.4 mm) *C. nannodes* to the tall, narrow (2.1 x 0.7 mm) *C. e. canadense* and the tall, wide (2.5 x 0.9 mm) *C. stygium*. Other morphological features that have been used to identify these species include the thickness and width of the apertural lip, the shape, size and placement of the internal lamellae, and general shell form (Burch & Van Devender 1980).

Perhaps the most taxonomically contentious entities within this group are *Carychium exiguum, Carychium exile exile,* and *Carychium exile canadense* (Figure 1). *Carychium exiguum* has 1.6–2.0 mm long x 0.7–0.8 mm wide shells that are smooth or only weakly striate and of whitish or clear corneous color (Pilsbry 1894, 1948; Burch & Van Devender 1980). It is a common denizen of open and forested wetlands ranging from Kansas and South Dakota to Newfoundland, Nova Scotia, and the coastal plain of South Carolina (Hubricht 1985). *Carychium exile* has 1.6–2.2 mm long x 0.6–0.7 mm wide shells that are strongly striate and of whitish or clear corneous color (Pilsbry 1894, 1948; Burch & Van Devender 1980). It has been found throughout most of the eastern U.S. and southeastern

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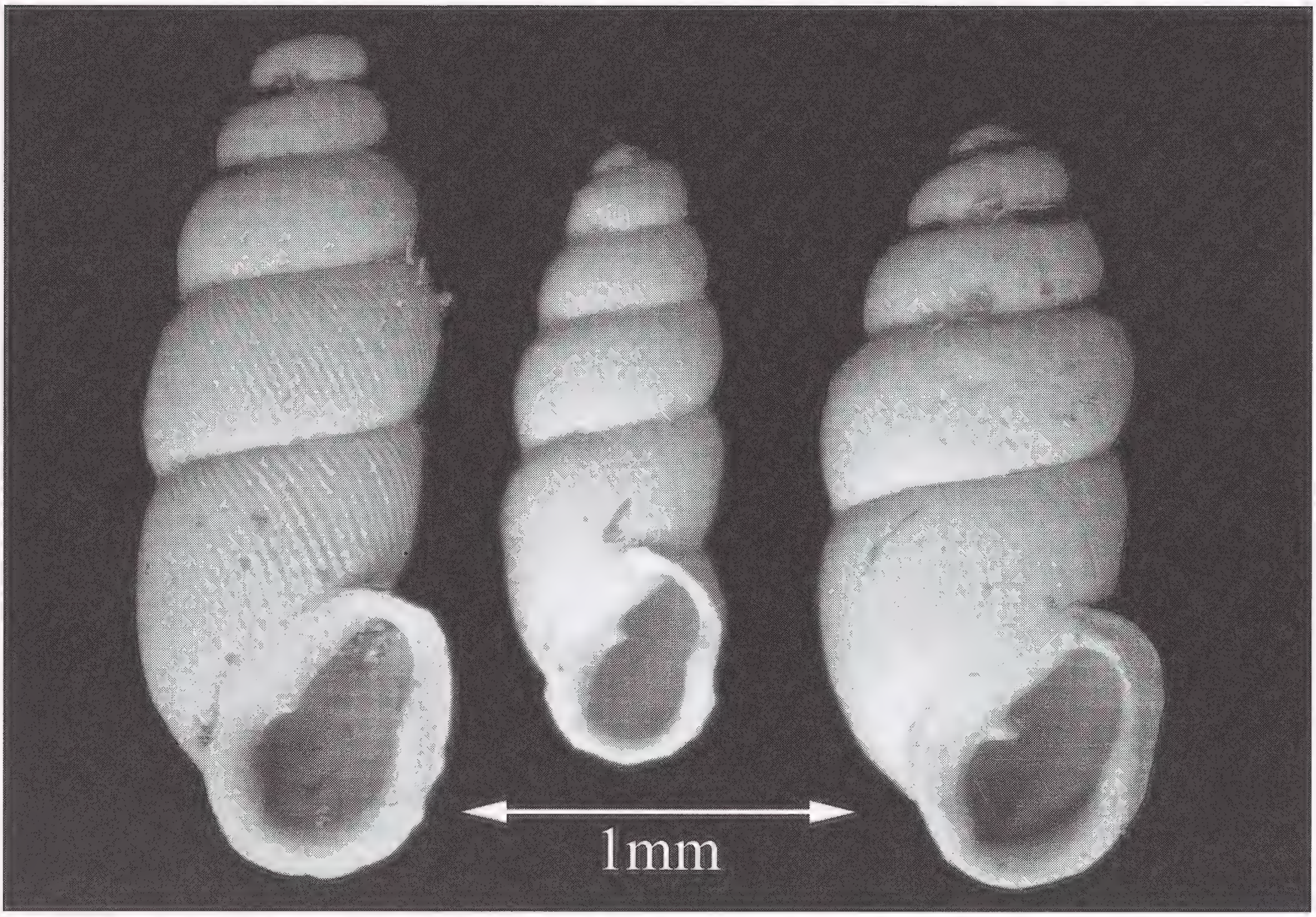


Figure 1 Scanning electron micrograph of *Carychium exile, Carychium nannodes* and *Carychium exiguum* from the western Great Lakes region of North America. From left to right: *C. exile*, UWGB 935, Buck Creek Tributary 1, Clayton County, Iowa, USA (91°10'55"W, 42°51'47"N); *C. nannodes*, UWGB 3866, Crawford Lake, Halton County, Ontario, Canada (79°56'27"W, 43°28'27"N); *C. exiguum*, UWGB 3676, Cedarburg Bog, Ozaukee County, Wisconsin, USA (88°1'4"W, 43°22'59"N).

Canada, and is most frequently encountered in decaying leaf litter of mesic upland woods, bedrock outcrops, and wooded swamps (Oughton 1948, Pilsbry 1948, Hubricht 1985). The nominate subspecies is reported to have shells <1.75 mm tall, a V-shaped internal lamellae, and be more southern in distribution. *Carychium exile canadense* is reported to have shells >1.75 mm tall, a flat internal lamellae, and be more northern in distribution (Clapp 1906, Winslow 1922, Burch & Van Devender 1980, Hubricht 1985).

Oughton (1948) reported considerable overlap in shell characteristics between some Ontario *Carychium exile* and *Carychium exiguum* populations. Harry (1951) stated that sufficient data did not exist to recognize more than one natural species in this group. Both Harry (1951) and Burch & Van Devender (1980) suggest that *C. exiguum* and *C. exile* canadense represent endpoints along a morphological range of continuous variation, with *C. e. exile* representing intermediate individuals. Based on these conclusions, some North American malacologists (Branson 1961, Baerris 1980, Burch & Van Devender 1980, Frest & Dickson 1986) have chosen to lump *C. exile* into *C. exiguum*.

However, Baker (1939), Pilsbry (1948), Oughton (1948), Robertson & Blakeslee (1948), Leonard (1959), Hubricht (1985), and Burch & Jung (1988) have all maintained these as separate taxa. Hubricht (1963) stated that *Carychium exiguum* and *Carychium exile* were always readily separable, even at sites of sympatric occurrence. In spite of such contrasting statements, hypotheses relating to the conchological distinctness of these taxa have never been subjected to potential falsification through objective, statistical tests. For instance, even though Harry (1951) measured the dimensions of over 2000 individuals from 38 sites in the Lower Peninsula of Michigan, he used no inferential statistical tests

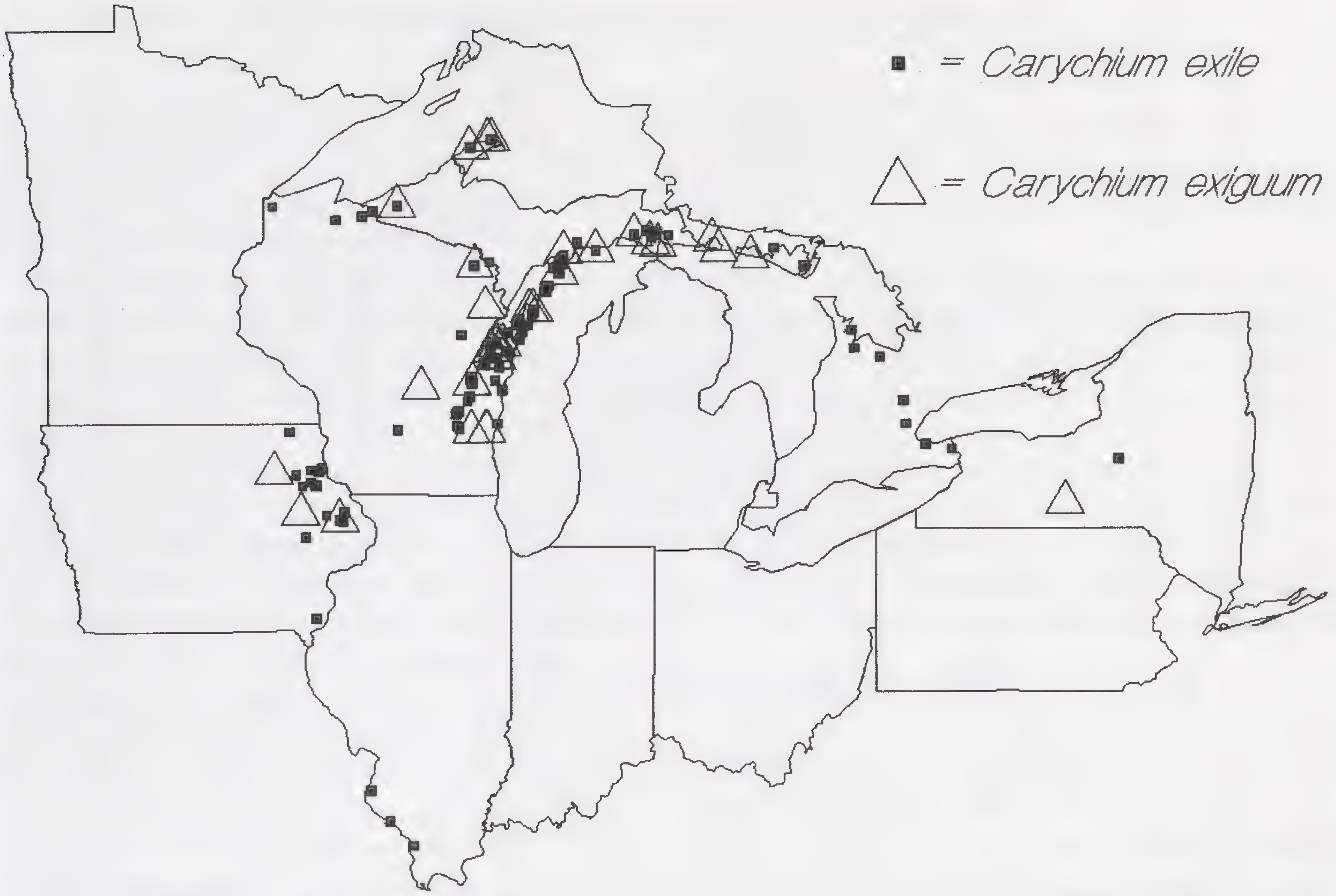


Figure 2 Map of study region, showing location of 116 measured *Carychium exile* and 35 measured *Carychium exiguum* populations.

to analyse these data.

To help resolve questions about appropriate taxonomic divisions within this group, we have conducted such analyses on *Carychium exiguum* and *Carychium exile* shells collected from Illinois, Iowa, Michigan, Minnesota, New York, Ontario, and Wisconsin. These populations span a considerable portion of the geographic range of *C. exiguum*, *C. exile exile* and *C. exile canadense*. Three main questions will be addressed: (1) How distinct are shell dimensions of *C. exiguum* and *C. exile* within the region and within sites of co-occurrence? (2) How strong is clinal variation in shell size for *C. exiguum* and *C. exile* across the region? (3) Do internal lamellae configuration and shell size patterns of *C. exile exile* and *C. exile canadense* confirm the presence of two subspecies?

METHODS

STUDY SITES

Populations of both *Carychium exiguum* and *Carychium exile* were collected during a regional survey of terrestrial gastropod faunas of over two dozen habitat types within a 1300 x 1000 km area centered on the Niagaran Escarpment in the Great Lakes region of North America (Nekola 1999). All *C. exile* populations, and approximately $^2/_3$ of all *C. exiguum* populations encountered by October 1998 were measured for a total of 116 *C. exile* and 35 *C. exiguum* stations (Figure 2). Analysed *C. exile* populations originated from 6 states or provinces, including Illinois (2 sites), Iowa (22), Michigan (20), New York (2), Ontario (9) and Wisconsin (60). Analysed *C. exiguum* populations originated from the states or provinces of Iowa (3 sites), Michigan (12 sites), New York (1 site), Ontario (1 site), and Wisconsin (18 sites). The single encountered population of *C. nannodes* (from

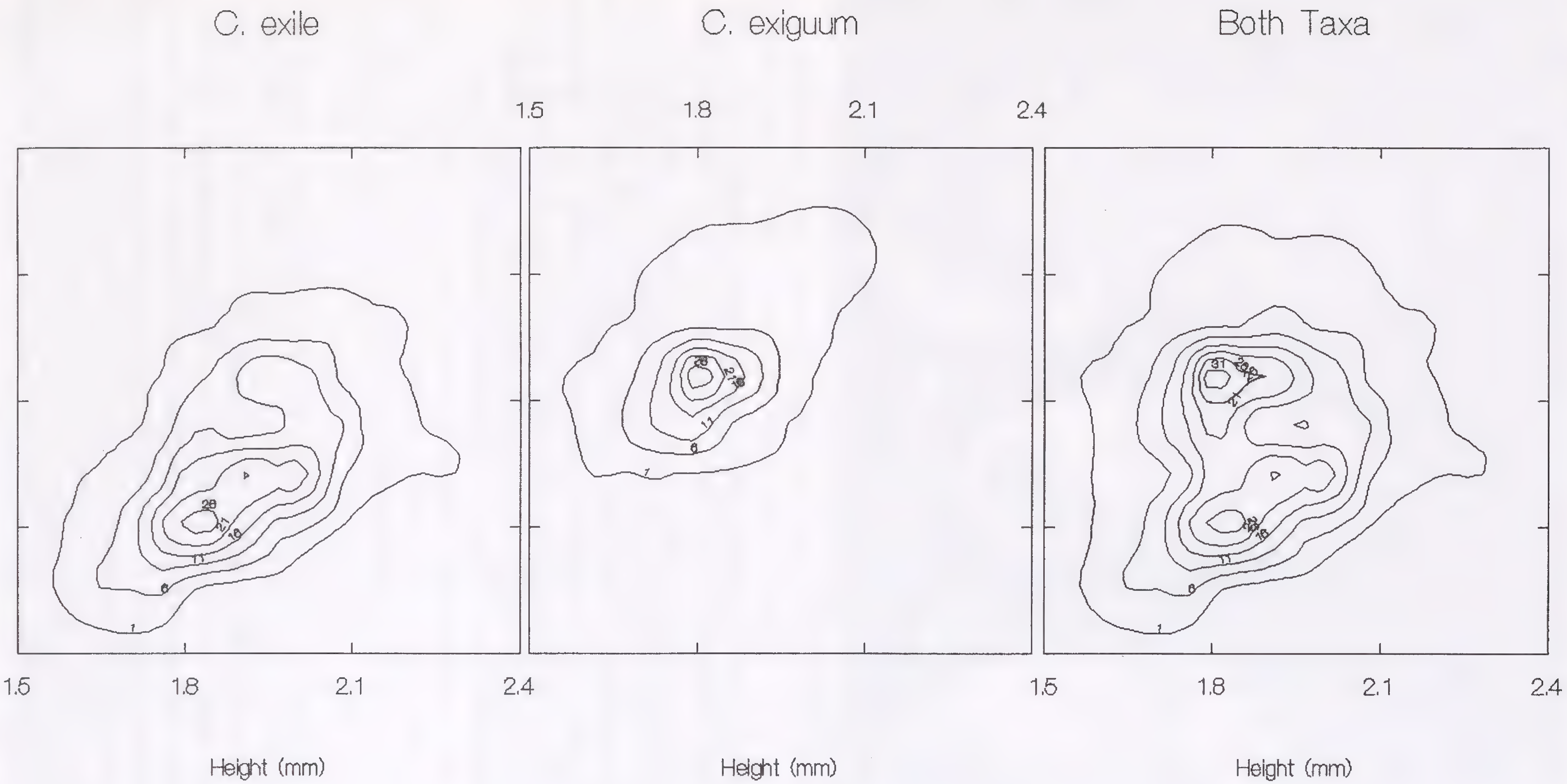


Figure 3 Contour diagram shell size frequency of *Carychium exile, Carychium exiguum* and all *Carychium* individuals from sites of co-occurrence. Contour intervals were drawn using distance weighted least squares smoothing.

Crawford Lake Park in Halton County, Ontario) was also measured.

Field and Laboratory Procedures

The latitude-longitude coordinates for each population was determined through digitization of USGS (or equivalent) 7.5 minute topographic maps. To minimize statistical bias from use of polar coordinates, these locations were converted to Cartesian UTM Zone 16 coordinates using ARCINFO.

Soil litter samples were collected and slowly dried. These samples were then soaked in water and subjected to careful but vigorous water disaggregation through a standard sieve series (ASTME 3/8" (9.5 mm), #10 (2.0 mm), #20 (0.85), and #40 (0.425 mm) mesh screens). Sieved fractions were dried and hand picked against a neutral-brown background. All *Carychium* shells and shell fragments were removed.

Individuals were provisionally assigned to either *Carychium exiguum* or *Carychium exile* based upon the degree of shell striation. Like Hubricht (1963), we found this feature to demarcate two groups (Figure 1), with one being smooth to weakly and irregularly striate (*C. exiguum*) and the other being strongly and regularly striate (*C. exile*). *Carychium nannodes* individuals from Crawford Lake were identified by their smooth shell surface and size (height <1.5 mm).

In order to compare shell shapes of these forms, the height and width of all fully grown, undamaged *Carychium* shells from each site were measured in increments of 0.02 mm using a dissecting microscope with a calibrated ocular micrometer. Shells were measured with the aperture facing down. Height was calculated from the tip of the protoconch to the base of the body whorl, while width was measured at the widest section of the body whorl in back of the apertural lip. The apetural lip was not considered as its width varied with shell maturity and weathering, providing unstable estimates of maximum shell width. A total of 5177 *Carychium exile*, 1178 *Carychium exiguum*, and 25 *Carychium nannodes* individuals were measured. These data are available from the corresponding author upon request.

Lastly, variation in the shape of the internal lamellae within and between selected *Carychium exile* populations were documented using scanning electron micrographs taken with a Hitachi S-2460N Scanning Electron Microscope in N-SEM Mode (10 Pa; 22 kV) with a backscatter detector and #2 Gamma Correction. Eight populations were chosen from across the study region. Within each, a segment of the penultimate whorl was removed from a dozen individuals to expose the internal lamellae. Three individuals were then selected from each population to illustrate the observed range of lamellae shapes.

Statistical Analyses

Histograms of shell height and width were constructed for each population of more than 20 measured shells (52 *Carychium exile*, 20 *Carychium exiguum*), and visually inspected to ensure that none seriously violated assumptions of normality or included bimodal distributions.

1. How distinct are the shell dimensions of *Carychium exiguum* and *Carychium exile* within the region and within sites of co-occurrence?

As *Carychium* typically reproduces through self fertilization (Bulman 1990), it is highly likely that individuals within a population will be genetically uniform and lack statistical independence. To help minimize this form of pseudoreplication (Hurlbert 1984), two different analyses were employed for between vs. within population comparisons.

Canonical discriminant analysis (Kleinbaum *et al.* 1988) was used to determine if significant segregation existed in the height and width of shells between the 584 *Carychium exile* and 255 *Carychium exiguum* shells encountered at all 10 co-occurrence

TABLE 1
Summary statistics for canonical discriminant analysis of *Carychium* shell dimensions for sites of *Carychium exile* and *Carychium exiguum* co-occurrence.

Factor	Value
Canonical Correlation	0.761
Eigenvalue	1.378
Likelihood Ratio	0.421
Approximate F	575.8
Number df	2
Density df	836
p	0.0001

TABLE 2
Classification summary for canonical discriminate analysis of *Carychium exile* vs. *Carychium exiguum* shell dimensions from sites of co-occurrence.

Shell Surface			Size Cluster	
		Wide Group	Narrow Group	Total
Striate				
	Number	487	97	255
	Percent	83.39	16.61	
Smooth				
	Number	7	248	584
	Percent	2.75	97.25	
Total				
	Number	494	345	839
	Percent	58.88	41.12	
Total Error Count Estimate Percent			9.68%	

TABLE 3
Summary statistics for height vs. width regression for *Carychium exile* and *Carychium exiguum,* with width serving as the dependent variable.

Variable	C. exile	C. exiguum
Intercept	0.1950	0.5132
Intercept Std. Error	0.0381	0.0985
Intercept p	<0.0005	<0.0005
Slope	0.2310	0.1247
Slope Std. Error	0.0193	0.0538
Slope p	<0.0005	0.0268
r^2	0.5633	0.1400

p-value for difference between *C. exile* and *C. exiguum* intercepts:	<0.0005
p-value for difference between *C. exile* and *C. exiguum* slopes:	0.0547

sites. Shell height and width were used as dependent variables while species identity (based on level of shell striation) was used as the categorical predictor. A contour diagram showing the frequency of all *Carychium* shell sizes within these sites was drawn using distance weighted least squares smoothing (McLain 1974). Because the null hypothesis in this test assumes only a single taxa to be present, and because only sites of co-existence were considered, the potential lack of genetic independence between individuals within sites was controlled. As such, all individuals were considered independent observations.

Multiple least-squares linear regression was used to compare shell height vs. width relationships between all *Carychium exiguum* and *Carychium exile* populations. Because of the likely genetic uniformity within populations, combined with the fact that most of the sampled sites did not contain both taxa, individual shells could not be considered to represent independent observations. To control for this potential bias, mean height and width was calculated for each population (116 *Carychium exile* and 35 *Carychium exiguum*), and used for further analysis. While this greatly decreases sample size, it represents a more conservative statistical test as a greater degree of independence will exist between observational units. Testing for differences between the best-fit slopes and intercepts was accomplished by adding a binary variable (representing species identity) into the model following methods outlined by Kleinbaum *et al*. (1988). These data were displayed using a scatterplot in which 95% Gaussian confidence ellipses (Sokal & Rohlf 1981) were drawn around each species in graph space.

2. How strong is clinal variation in shell size for *Carychium exiguum* and *Carychium exile* across the region?

Least-squares linear regression was used to analyse the relationship between mean population shell width and height vs. UTM N and UTM E coordinates. Because only four measured *Carychium exile* populations exist south of UTM 4600 km N, and the potential that these sites might bias results, these analyses were also repeated following their exclusion. Mean shell height and width were plotted against UTM N and UTM E coordinates, with central tendencies being indicated through locally weighted scatterplot smoothing (Cleveland 1979).

3. Do internal lamellae configuration and shell size patterns of *C. exile exile* and *C. exile* canadense confirm the presence of two subspecies?

SEM images of internal lamellae from the 24 selected individuals (three each from eight populations) were arranged in a single plate to allow for easy comparison of variation within and between populations. Additionally, the frequency of *Carychium exile* (<1.8 mm tall), *C. e. canadense* (>2.0 mm tall), and intermediate (1.8–2.0 mm tall) individuals was calculated within each population. These frequencies were mapped using bar icons in which the percentage of black represents the frequency of that particular size class within each population. No icon was mapped if a given size class was absent.

RESULTS

Visual inspection of height and width histograms demonstrated that none of the 52 *Carychium exile* and 20 *Carychium exiguum* populations with 20 or more measured shells seriously violated assumptions of normality. The minor violations noted were in the form of skewing. None of the populations showed any tendency for biomodality.

1. How distinct are the shell dimensions of *Carychium exiguum* and *Carychium exile*

within the region and within sites of co-occurrence?

The contour plot of shell dimension frequencies from sites of *Carychium exiguum* and *Carychium exile* co-occurrence demonstrated a highly bimodal distribution, particularly in relation to shell width (Figure 3). The great majority of highly striate individuals *(C. exile)* were limited to the narrower cluster, while essentially all of the smooth individuals *(C. exiguum)* were limited to the wider group. Canonical discriminant analysis documented that these clusters were significantly differentiated ($p=0.0001$; Table 1). Use of shell striation as the sole discriminating factor lead to only a 9.68% error rate (Table 2). These errors were not symmetrically distributed, with 2.75% of non-striate individuals being members of the narrower cluster, and 16.61% of striate individuals being members of the wider cluster.

Similar patterns were found when mean shell height vs. width was compared between all populations. Highly significant ($p<0.0005$) differences were observed in the intercepts of the best-fit regression lines, being 2.5 times larger in *Carychium exiguum* as compared to *Carychium exile* (Table 3). Marginal differences ($p=0.0538$) were also present in the best-fit slopes, with *C. exiguum* populations tending to increase in width as a function of height at almost one-half the rate observed in *C. exile*. Comparison of the 95% Gaussian ellipsoids for both species demonstrates essentially no statistical overlap in height-width space (Figure 4). Within both species, continuous variation in average shell dimensions was noted between populations. Additionally, for both species at shell heights <1.8 mm, the correlation between shell width and height appeared to weaken or vanish.

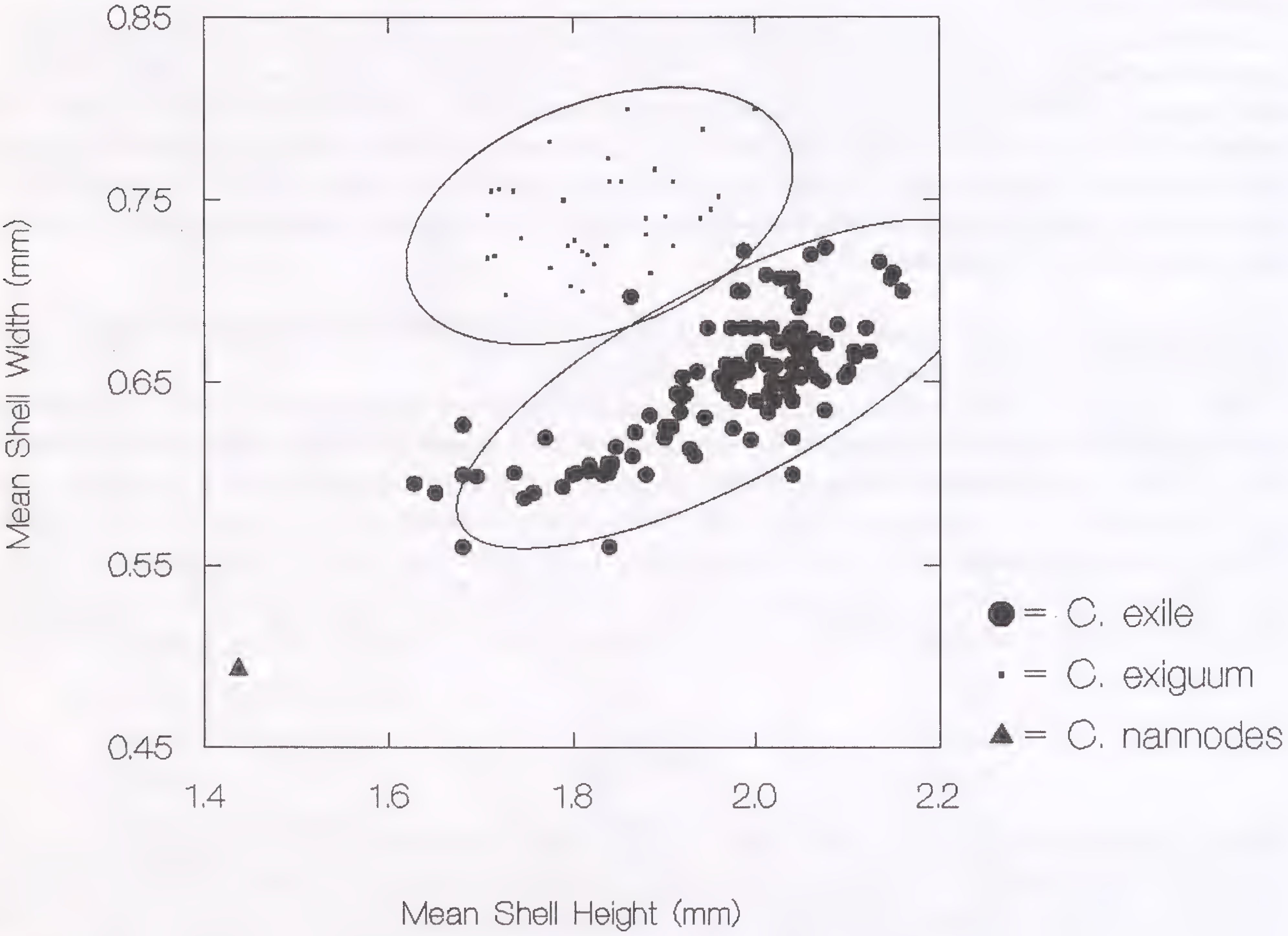


Figure 4 Scatterplot of mean shell width vs. mean shell height for all measured *Carychium* populations. 95% Gaussian ellipsoids have been drawn around the distributions of *Carychium exile* and *Carychium exiguum* in this graph space.

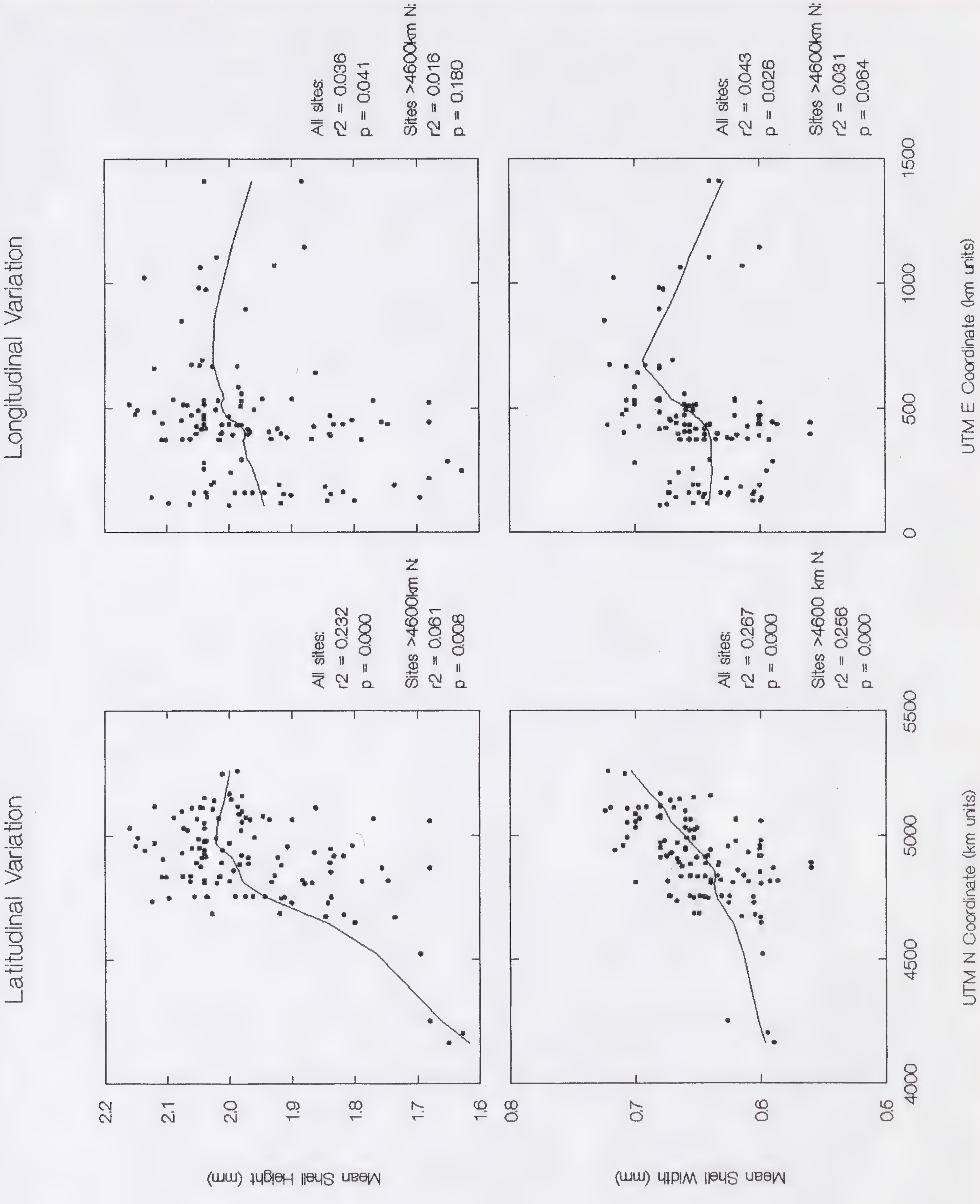


Figure 5 Scatterplots showing mean *Carychium exile* shell height and width vs. longitudinal and latitudinal position. Response lines in these graphs were fit using locally weighted scatterplot smoothing.

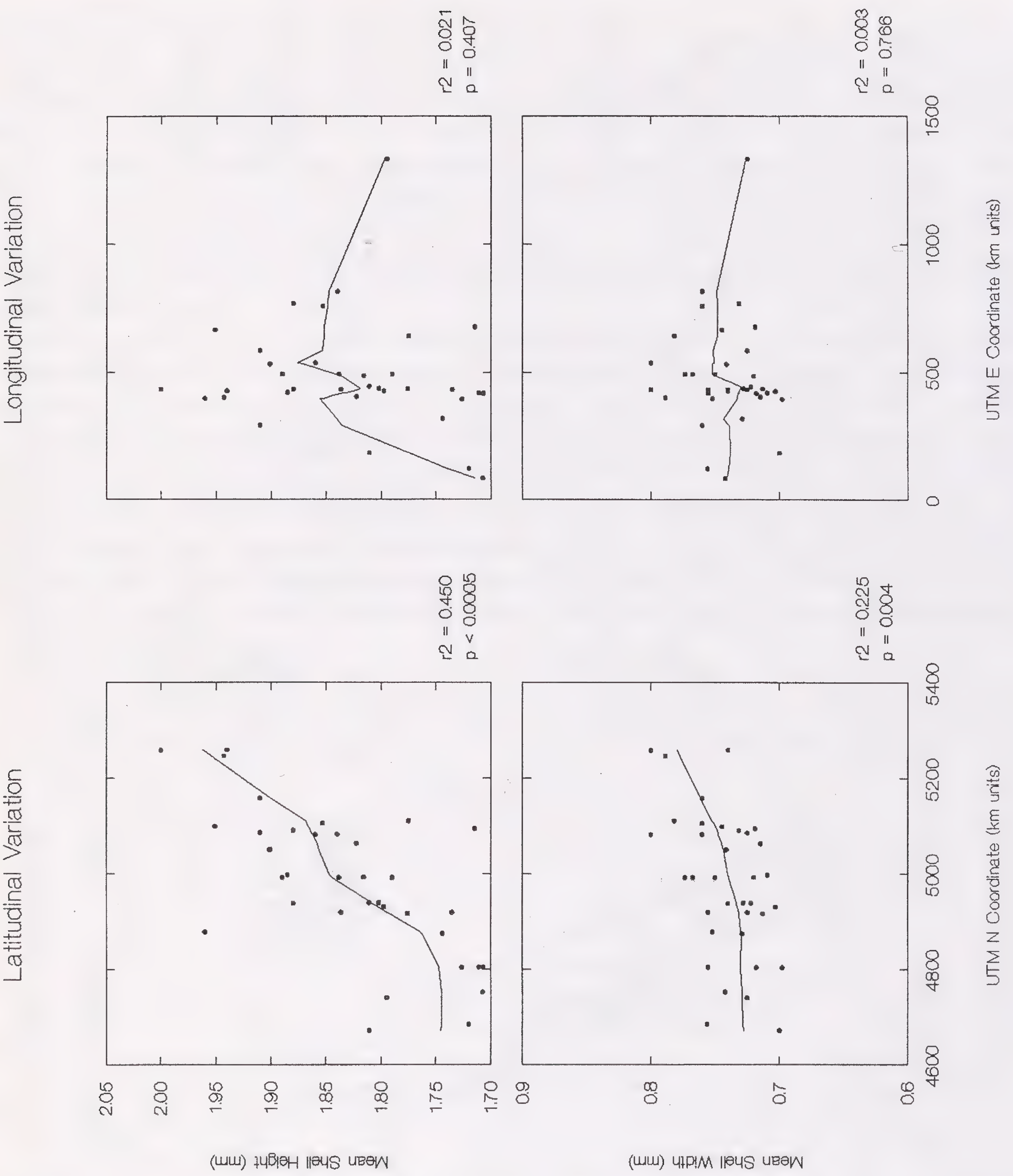
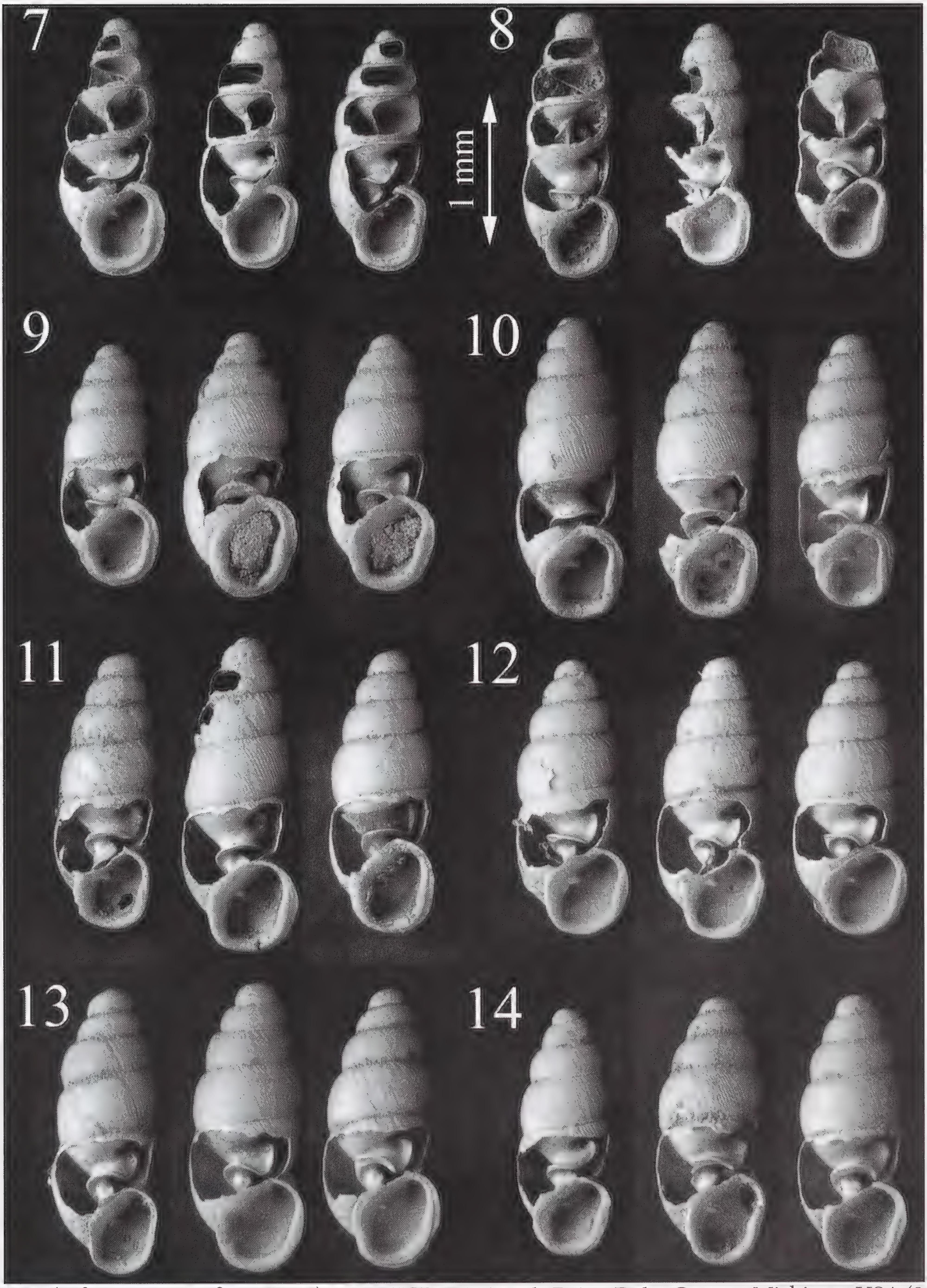


Figure 6 Scatterplots showing mean *Carychium exiguum* shell height and width vs. longitudinal and latitudinal position. Response lines in these graphs were fit using locally weighted scatterplot smoothing.

Figures 7–14 Scanning electron micrographs of internal lamellae shape and size from eight *Carychium exile* populations. Three shells from each are used to illustrate the range of variation. Populations are ordered based on their geographical location from the most southwestern through the most northern to the most southeastern. **7** UWGB 3862, Franklin Hill, Calhoun County, Illinois, USA (90° 36' 38" W, 39° 3' 57" N). **8** UWGB 39, Pine Creek, Jackson County, Iowa, USA (90° 50' 41" W, 42° 8' 27" N). **9** UWGB 5137, Williams Creek, Allamakee County, Iowa, USA (91° 28' 41" W, 43° 8' 14" N). **10** UWGB 1393, Oakfield Brickyard, Fond du Lac County, Wisconsin,



USA (88° 33' 10" W, 43° 40' 27" N). **11** UWGB 521, Ansels Point, Delta County, Michigan, USA (86° 34' 26" W, 45° 48' 12" N). **12** UWGB 3063, Copper Harbor Marina, Keewenaw County, Michigan, USA (87° 54' 14" W, 47° 28' 19" N). **13** UWGB 2249, Maple Hill, Chippewa County, Michigan, USA (84° 46' 55" W, 46° 9' 34" N). **14** UWGB 2472, Skinners Bluff, Grey County, Ontario, Canada (80° 59' 31" W, 44° 47' 36" N).

2. How strong is clinal variation in shell size for *Carychium exiguum* and *Carychium exile* across the region?

Regression of *Carychium exile* shell height (Figure 5) demonstrated a significant ($p<0.0005$) and moderately strong ($r^2=0.232$) positive correlation with latitude over the entire data set. Shell height ranged from less than 1.7 mm in the south to almost 2.2 mm in the north. While this relationship remained highly significant ($p=0.008$) after removal of the southernmost 4 sites, the strength of the relationship fell to almost 1/4 its previous level ($r^2=0.061$). Regression of height vs. longitude demonstrated only a marginally significant ($p=0.041$) trend, which vanished ($p=0.18$) when the southernmost sites were removed. This trend is not monotonic, with shells from central sites being taller than those to the east or west.

Regression of *Carychium exile* shell width (Figure 5) demonstrated a significant ($p<0.0005$) and moderately strong ($r^2=0.267$) positive correlation with latitude for the entire data set. Shell widths ranged from less than 0.56 mm in the south, to almost 0.72 mm in the north. This relationship remained highly significant ($p=0.008$) and moderately strong ($r^2=0.256$) following removal of the southernmost 4 sites. Regression of width vs. longitude demonstrated only a marginally significant ($p=0.026$) trend, which decreased in significance ($p=0.064$) when the southernmost sites were removed. This trend is not monotonic, with shells from central sites being wider than those to the east or west.

Regression of *Carychium exiguum* shell height (Figure 6) demonstrated a significant ($p<0.0005$) and strong ($r^2=0.45$) positive correlation with latitude. Shell heights ranged from less than 1.7 mm in the south to 2.0 mm in the north. Regression of height vs. longitude demonstrated no significant ($p=0.407$) trends.

Regression of *Carychium exiguum* shell width (Figure 6) demonstrated a significant ($p=0.004$) and moderately strong ($r^2=0.225$) positive correlation with latitude. Shell widths ranged from 0.7 mm in the south to 0.8 mm in the north. Regression of height vs. longitude demonstrated no significant ($p=0.766$) trends.

For both species, the rate of increase in shell height and width with latitude was not constant. In *Carychium exile,* little decrease in shell size was apparent south of UTM 4600 km N, and in *Carychium exiguum,* little decrease in shell size was noted south of UTM 4900 km N.

3. Do internal lamellae configuration and shell size patterns of *Carychium exile exile* and *Carychium exile canadense* confirm the presence of two subspecies?

SEM imaging of the internal lamellae of the 24 *Carychium exile* individuals from eight stations (Figures 7–14) demonstrates that considerable variation is present both within and between populations. Lamellae shape did not fall into clearly identifiable classes, with most individuals possessing intermediate shapes. All populations demonstrate at least some variation in this feature, with Franklin Hill (Illinois; Figure 7), Ansels Point (Michigan; Figure 11), and Copper Harbor Marina (Michigan; Figure 12) possessing the least. Populations with the flattest lamellae include Franklin Hill (Illinois; Figure 7) and Pine Creek (Iowa; Figure 8), while those with the most V-shaped include Copper Harbor Marina (Michigan; Figure 12) and Maple Hill (Michigan; Figure 13). No clear relationship between lamellae shape and shell size was noted: flat lamellae were present in both small (Figure 7) and large (Figure 10) shells while V-shaped lamellae were present in both small (Figure 9) and large (Figure 10) shells. However, flatter lamellae may be become somewhat more common as shell size decreases.

Mapping of the three *Carychium exile* size class frequencies within populations (Figure 15), demonstrated that while *C. e. exile* individuals are largely restricted to areas west of Lake Michigan, *C. e. canadense* and intermediate individuals are found in all but the most southern sites. Forty-five stations harbored individuals that fell into all three size

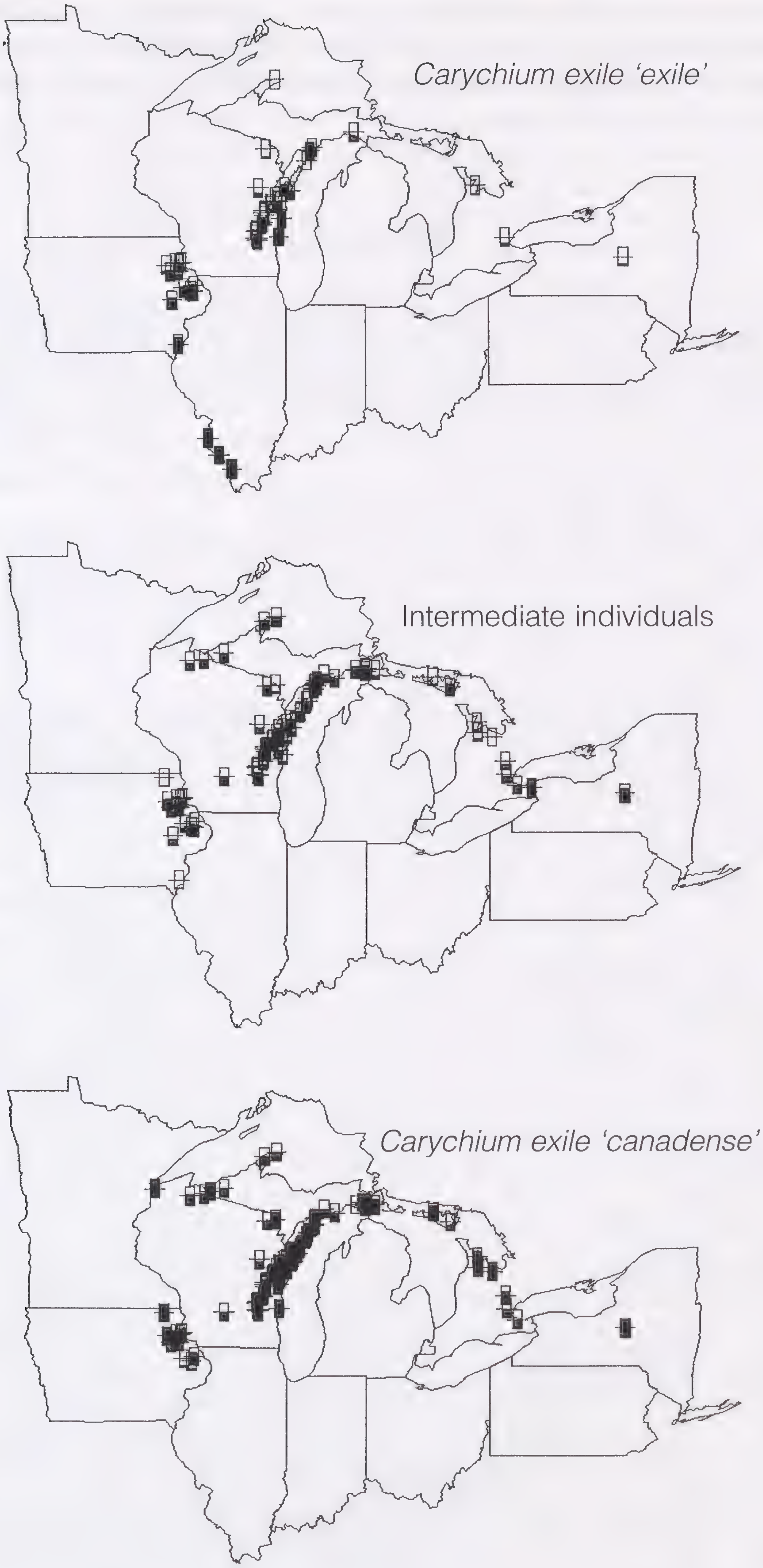


Figure 15 Distribution of *Carychium exile exile* (shell height <1.8 mm), *Carychium exile canadense* (shell height >2.0mm) and intermediate (shell height 1.8-2.0mm) within sampled *C. exile* populations. Box icons are printed if a site possessed individuals within the given size class. The amount of black fill in each box is equal to the proportion of individuals within that population which fall into the size class.

classes. Five sites were represented by *C. e. exile* and 18 by *C. e. canadense* individuals only. Only a single site (Buck Creek 4 in Clayton County, Iowa) was found to have *C. e. exile* and *C. e. canadense* individuals but no intermediates. However, only 5 measurable shells were recovered from this site.

DISCUSSION

DISTINCTNESS OF *CARYCHIUM EXILE* AND *CARYCHIUM EXIGUUM*

These analyses clearly document that *Carychium exile* and *Carychium exiguum* should be maintained as separate species. Within sites of co-occurrence, *Carychium* individuals exhibit a strongly ($p=0.0001$) bimodal distribution in shell height & width, with smooth shells (*C. exiguum*) being approximately 15% wider than striate shells (*C. exile*) of the same height. The degree of shell striation can be used with over 90% accuracy in assigning individuals into either of these two size classes.

The distinctness of these species was maintained when mean shell dimensions were compared for populations across the entire study region. Essentially no overlap was noted between the 95% Gaussian ellipsoids characterizing each species range of shell heights and widths. Accordingly, the best-fit height-width regression lines also had significantly ($p<0.0005$) different intercepts.

Given such obvious distinction between these two taxa at both local and regional scales, it is unclear why some have maintained them as a single, continuously varying species. The main source of this confusion can be traced to inadequacies in the analysis provided by Harry (1951). First, unlike the current study, the populations upon which his analyses were based were limited to only a portion of the Lower Peninsula of Michigan, and were sampled across only a few distinct habitat types. As such, it was not possible for him to document broad-scale morphological patterns.

Second, he only used shell measurement data in a descriptive sense and never subjected them to statistical tests. Because of this, obvious trends were ignored. This can be most clearly seen in his Plate 9, which was used to support the contention that continuous variation exists in the height and width of *Carychium exiguum* and *Carychium exile* shells. In fact, his data actually demonstrate a bimodal distribution of shell dimensions, with one mode occurring at 1.95 x 0.80 mm, and the other at 1.85 x 0.85 mm. These two modes correspond exactly to our analyses, with the first mode likely representing *C. exile* and the second *C. exiguum*. It is interesting to also note that these two groups also differed in their habitat affinities, with mode 1 individuals (*C. exile*) being primarily collected from upland woods, and mode 2 individuals (*C. exiguum*) from wetlands.

Another likely source for confusion between these two taxa is the fact that degree of shell striation is a more variable morphological feature than shell dimension. Even though very useful, shell striation alone is not sufficient to assign individuals unquestionably to one species or the other. This is especially true for *C. exiguum*, where almost 17% of individuals were assigned to *C. exile* even though they possessed shell widths characteristic of *C. exiguum*. Based upon accounts provided in Oughton (1948) and Harry (1951), it seems likely that such moderately-striate *C. exiguum* individuals were considered as intermediates. However, our analyses demonstrate that when the number of distinguishing features is extended to include shell width and height, these species are readily and easily sorted. Intermediate forms do not exist even within sites of co-occurrence.

CLINAL VARIATION IN *CARYCHIUM EXILE* AND *CARYCHIUM EXIGUUM*

Both *Carychium exile* and *Carychium exiguum* demonstrate significant clinal variation with larger individuals occurring in the north. This variation is continuous in both species. The magnitude of this change is 67% greater in *Carychium exile* as compared to *Carychium exiguum*. This may help explain why Clapp (1906) and Pilsbry (1948) chose to designate the northern and southern forms of *C. exile* as different subspecies, while at the same time keeping *C. exiguum* a single entity possessing a latitudinal 'zonal variation' in shell size. However, even though of smaller total magnitude, the strength of clinal variation in *C. exiguum* shell size is actually almost twice as great as that for *C. exile.*

The weak longitudinal relationships noted in *Carychium exile* shell size, however, appear to simply reflect a sampling artifact. As collections were focussed along the Niagaran Escarpment, populations from the center of the study area also tended to be more northern in location. This non-regular sampling pattern, combined with strong latitudinal changes in size, should be enough to explain the observed weak, non-monotonic longitudinal trends.

TAXONOMIC UTILITY OF *CARYCHIUM EXILE EXILE* AND *CARYCHIUM EXILE CANADENSE*

Subspecies are usually defined as taxonomically distinct aggregates of populations that are limited to a specific subdivision of a species range. Mayr (1963) emphasized that simply showing statistical distinctness between populations does not indicate the presence of subspecies: only when such populations are geographically isolated, leading to a minimal amount of introgression between forms, is the use of subspecies taxonomically useful. Sourakov (1995) suggests that subspecies are a valid taxonomic concept only when at least 95% of individuals and populations can be easily segregated.

Our data clearly shows that neither of these criteria is met for *Carychium exile exile* and *Carychium exile canadense*. Even though Winslow (1922), Harry (1951), Burch & Van Devender (1980), and Burch & Jung (1988) all state that *C. e. exile* possesses a V-shaped lamellae, while that of *C. e. canadense* is flat, we could find no evidence of this pattern. All possible intermediate forms were found, with considerable variation occurring within single populations. In particular, continual gradation between flat and V-shaped lamellae was observed in three of the eight selected populations (Figures 8, 9, 14).

We also saw little evidence to support the contention that smaller shells from more southern locations had more V-shaped lamellae, or that larger shells from more northern sites possessed flatter lamellae. The populations with the flattest lamellae actually occurred in the smallest shells originating from the most southern populations, while the populations with the most V-shaped lamellae actually tended to occur in large shells originating from the north and east. The depth of lamellae indentation did not even vary predictably with shell size within sites. As can be clearly seen in Figure 9, 6, and 8, the largest shells actually tend to have the most deep indentations. Our data support the contention of Brooks & Kutchka (1937) and Pilsbry (1948) that within *Carychium exile* this feature is too variable to be taxonomically useful.

The presence of continuous clinal variation in *Carychium exile* shell size also supports the view that there is little taxonomic utility in recognizing *Carychium exile exile* and *Carychium exile canadense*. The introgression zone between these two forms essentially covers the entire study region, with intermediate individuals being absent from only the far south. Fully 40% of all populations possess individuals referable to *C. e. exile, C. e. canadense,* and intermediate size classes. Only 20% of populations contain *C. e. exile* or *C. e. canadense* individuals but lack intermediate forms. None of the measured *C. exile* populations possess bimodal distributions in shell size, further indicating that segregation of small and large shells does not occur within populations.

As the assignment of individuals and populations into *Carychium exile exile* or *Carychium exile canadense* is impossible over much of the Great Lakes region, it would seem appropriate to treat *C. exile* as a single taxonomic entity that possesses a distinct north-south clinal variation in shell size. This seems especially appropriate given that

C. exiguum, which has always been considered a single taxonomic entity, actually possesses a stronger north-south clinal variation in shell dimension.

ACKNOWLEDGMENTS

Robert Cameron, Douglas Larson, Timothy Pearce, and an anonymous reviewer provided valuable comments on earlier drafts. Robert Wise and Todd Kostman of the University of Wisconsin - Oshkosh kindly allowed use of their SEM facilities for snail imaging. Assistance in litter processing was provided by students in the Land Snail Ecology Practicum at the University of Wisconsin — Green Bay. Funding was provided by the Door County Office of the Wisconsin Chapter of The Nature Conservancy, a Cofrin Arboretum grant (administered by the Cofrin Arboretum Committee at the University of Wisconsin — Green Bay), the U.S. Fish and Wildlife Service, and the Small Grants Program of the Michigan Department of Natural Resources.

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PROTOCONCHS, DISPERSAL, AND TECTONIC PLATES BIOGEOGRAPHY: NEW PACIFIC SPECIES OF *MORUM* (GASTROPODA: HARPIDAE)

PHILIPPE BOUCHET[1]

Abstract Morum clatratum *n. sp. and* Morum roseum *n. sp. are described from depths of 100–200 m in the Marquesas Islands. Mode of development inferred from protoconch morphology and comparison with the protoconchs of* Harpa *with teleplanic larvae suggests that the new species have planktotrophic larval development, and that they are expected to range widely outside the Marquesas. In addition,* Morum kurzi, M. macdonaldi, *and* M. teramachii, *with inferred planktotrophic development, and* M. watanabei, *with inferred non-planktotrophic development, are newly recorded from South Pacific localities. The distribution of individual species of* Morum *appears to reflect dispersal during the planktonic phase, rather than movement of the lithospheric plates on the geological scale. The Caribbean* Morum oniscus *and* M. lamarckii, *respectively with inferred non-planktotrophic and planktotrophic development, are treated as separate valid species.*

Key words *Pacific plate, larval development, protoconch, island endemism, dispersal, vicariance, new species.*

INTRODUCTION

The eastern Polynesian fringes of the Indo-West Pacific Province are known for the low species richness of their marine faunas combined with a significant level of local or regional endemism (see, e.g., Rehder 1980). Colonization of isolated islands and maintenance of genetic exchange between islands is generally thought to take place through the dispersal and drifting of planktonic larvae (Scheltema 1971, 1987, Scheltema & Williams 1983), and narrow distribution ranges are positively correlated with the reduced dispersal capacities associated with the loss of planktotrophy (Leal & Bouchet 1991), resulting in speciation and the appearance of endemic species (for examples see Gofas, 1990, Bouchet & Bail, 1991).

The extreme isolation of the Marquesas in the Pacific has been stressed several times, and it suffices to mention that the nearest land mass is ca. 1500 km away (Society Is.) and the nearest continental mass is 5500 km away (Central America). Within the Marquesas, most individual islands are separated from each other by depths in excess of 2500 m and the sea floor around the archipelago is everywhere deeper than 4000 m. The islands have a volcanic origin, with Eiao in the northwest being the oldest (6.3 MY: Brousse & Bellon, 1974) and Fatu Hiva in the southeast being the youngest (1.3 MY: Duncan & McDougall, 1974). Endemism in the terrestrial biota of the Marquesas has been thoroughly documented to be very high, whereas endemism in the marine biota is rather inconspicuous (Trondle & Cosel, in press). The archipelago presents an impoverished Indo-Pacific fauna with a few local endemics. Among documented gastropod endemics, *Cyrtulus serotinus* (family Fasciolariidae) has a protoconch indicating non-planktotrophic larval development (own observations) and thus conforms with the model of island endemism. The discovery in the Marquesas of new taxa with protoconchs indicating long-lived planktotrophic larval development is therefore paradoxical as it runs contrary to these assumptions. In the present paper I describe two new species of *Morum* from the Marquesas, I record additional species from the South Pacific, and I discuss the significance of the *Morum* protoconch in the context of distribution patterns and tectonic events in the South Pacific.

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SYSTEMATIC DESCRIPTIONS

MURICOIDEA Rafinesque, 1815
HARPIDAE Bronn, 1849
MORUMINAE Hughes & Emerson, 1987
Genus ***Morum*** Röding, 1798

Type species *Morum purpureum* Röding, 1798 [= *M. oniscus* (Linnaeus, 1767)], by monotypy. Recent, western Atlantic.

Morum clatratum n. sp.
Figure 1

Morum sp. – Frydman 1991: 13.

Type material Holotype and 2 paratypes, all dd, in MNHN.

Type locality Off Nuku Hiva, Marquesas Is., 08°45.1′ S, 140°14.1′ W, 108–112 m [MUSORSTOM 9: sta. CP1177].

Material examined Off Nuku Hiva, Marquesas Is., 08°45.1′ S, 140°14.1′ W, 108–112 m [MUSORSTOM 9 Expedition: sta. CP1177], 3 dd (incl. holotype), collected by P. Bouchet, B. Dayrat, B. Richer de Forges and A. Warén, 25 August 1997.— Off Fatu Hiva, Marquesas Is., 10°31.4′ S, 138°39.2′ W, 210 m [N.O. '*Marara*', sta. 303], 3 dd (incl. 2 paratypes), collected by J. Poupin, 3 Sept. 1990. All material in MNHN.

Measurements Holotype (largest adult), height 60.5 mm, width 34.3 mm. Smallest adult, height 49.5 mm.

Description (holotype) Shell large, solid, pyriform, consisting of 6.1 teleoconch whorls. Whorls regularly convex, spire conical, apical angle 85°, last whorl occupying 85% of total shell height. Protoconch damaged, worn, remaining two whorls smooth, initial part missing. Protoconch / teleoconch transition sharp. Teleoconch whorls convex, rather indistinctly shouldered, sculptured with intersecting axial ribs and spiral cords. Axial ribs orthocline except for short adapical portion that is prosoclinely appressed to preceding whorl; ribs sharp and stronger than spirals on spire whorls, broader and about equal to spirals on last whorl, number increasing from about 14 on first teleoconch whorl to 29 on penultimate, and 42 on last whorl. In addition to the main axial ribs, there is a finer sculpture of thin, sharp, fragile lamellae, which are crowded on the ribs and more widely spaced between them; 5–7 lamellae between consecutive axial rib crests. Thick raised spiral cords form small nodules where they intersect axial ribs; one well defined cord above shoulder, 4 (spire whorls) to 5 (penultimate whorl) below shoulder, 17 on last whorl, 2 on canal. Aperture high, narrow; siphonal canal open, very slightly recurved; outer lip thick, recurved, with 17 subequal denticles; parietal shield broad, thin everywhere except in columellar region where it is thicker, raised, and covered with wart-like pustules in abapical half, and small elongated ridges in adapical half. Ground colour light brownish beige with irregular brownish speckles; 4 brown spiral bands on last whorl, breadth of each band extending over 3–4 spiral cords, dark brown at base of outer lip; parietal shield and aperture white.

Derivation of name From the Latin *clatratus, -a, -um*, latticed, with reference to the shell sculpture.

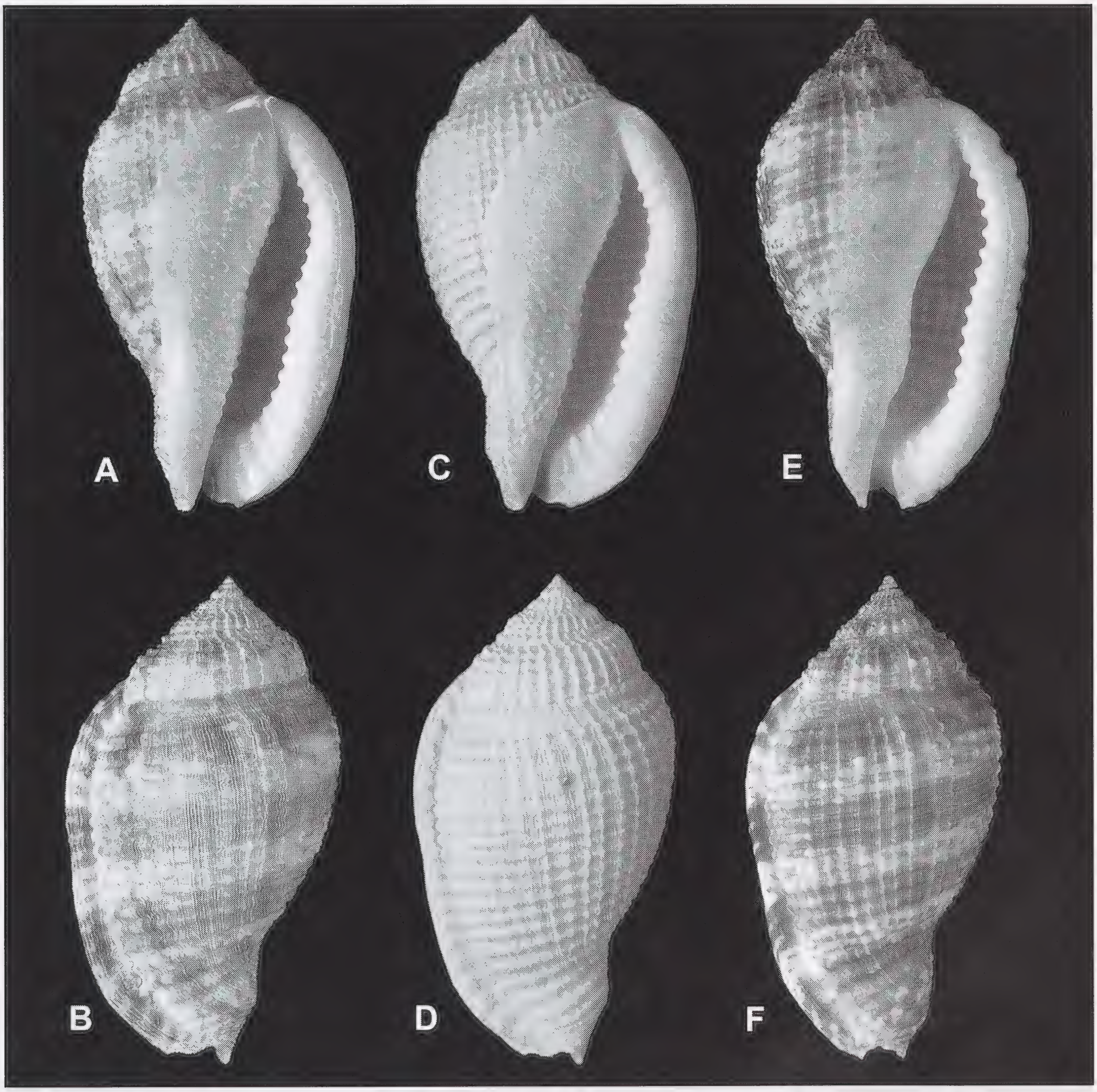

Figure 1 *Morum clatratum* n. sp. **A–D** holotype, height 60.5 mm; off Nuku Hiva, Marquesas Is., 108-112 m; **A–B** natural, **C–D** coated with magnesium chloride. **E–F** paratype, height 57.0 mm; off Fatu Hiva, Marquesas Is., 210 m.

Geographic range Known only from the Marquesas, dead in 112–210 m.

Comparisons *Morum clatratum* belongs to the species group sometimes recognized as the subgenus *Oniscidia* Mörch, 1852, and it has a general resemblance to *Morum grande* (A. Adams, 1855), *M. teramachii* Kuroda & Habe, 1961, and *M. uchiyamai* Kuroda & Habe, 1961, on the one hand, and *M. amabile* Shikama, 1973, on the other hand. *Morum clatratum, M. grande, M. teramachii*, and *M. uchiyamai* have in common a high-spired teleoconch, a sculpture of strong spiral cords and frilled axial ribs, and a colour pattern with four dark bands on a lighter ground on the last adult whorl. *Morum grande* differs by its much coarser sculpture (the last whorl of a 51 mm adult has 20 axial ribs and 15 spiral cords). The axial ribs form a spiny projection, strongest at shoulder, where it intersects the spiral cords, whereas they form only a low spineless knob in *M. clatratum*. In *M.*

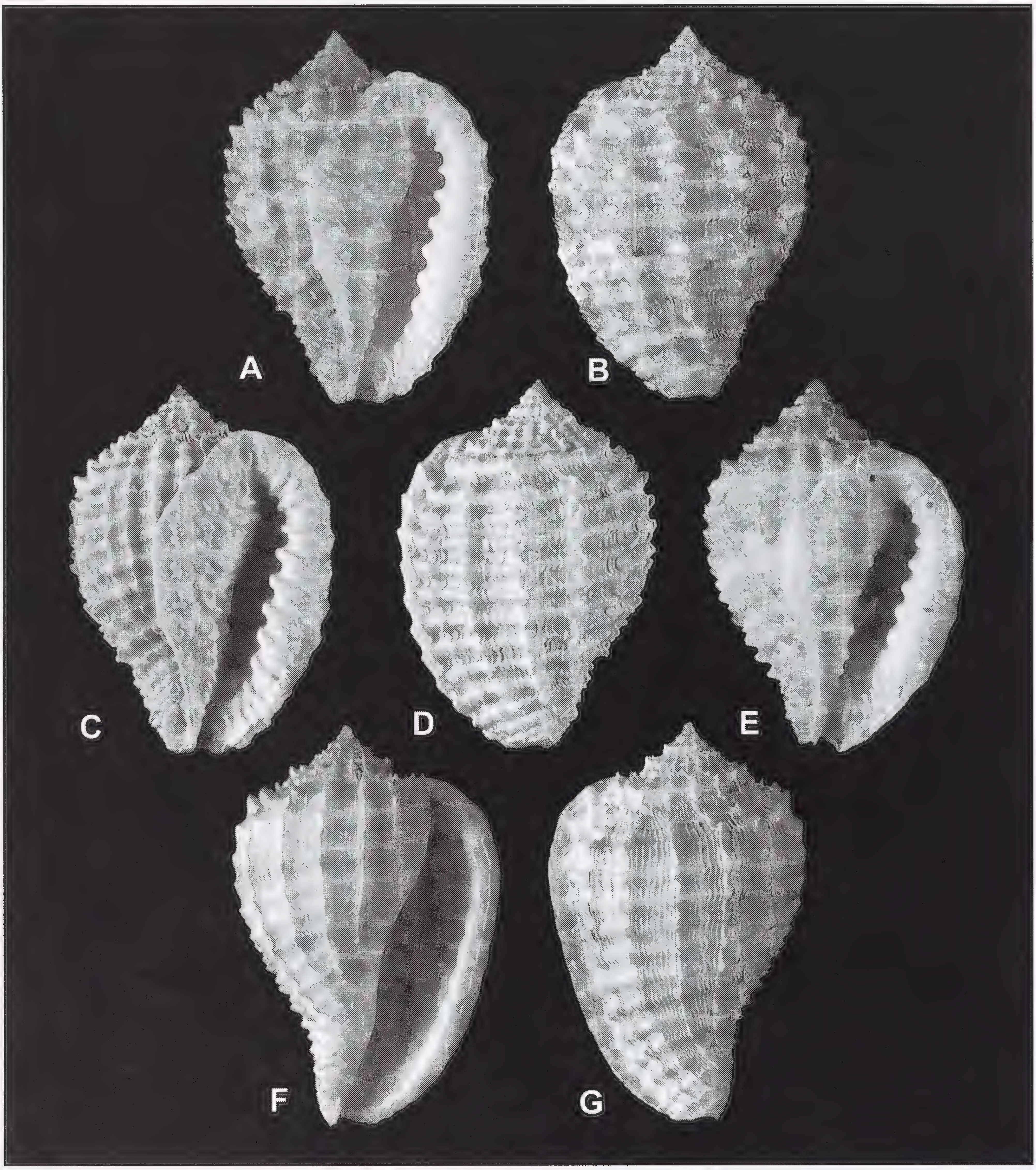

Figure 2 *Morum roseum* n. sp. (**A–E**) and *M. watanabei* (**F–G**). **A–D** holotype, height 21.5 mm; off Fatu Hiva, Marquesas Is, 115–120 m; **A–B** natural, **C–D** coated with magnesium chloride. **E** paratype, height 21.0 mm; off Hiva Oa, Marquesas Is, 105–285 m [MUSORSTOM 9 sta. DW1235]. **F–G** height 34.0 mm; south of Viti Levu, Fiji, 18°11.8′ S, 178°28.1′ E, 213 m.

grande, the outer margin of the parietal shield is elevated, and not adherent to the last adult whorl as in *M. clatratum. Morum uchiyamai* (which may be only an ecological form of *grande* - see below) also differs by its much coarser sculpture, strongly projecting spines at the intersection between the shoulder cord and the axial ribs, and very strong, widely spaced, secondary lamellae between ribs. *Morum teramachii* differs by its coarser sculpture (the last whorl of a 57 mm adult has 19 axial ribs and 14 spiral cords): except on the shoulder, the spiral cords are low and rather indistinct; the intersection of ribs and cords forms spines on the shoulder, and spineless nodules elsewhere. The parietal shield is weakly developed and appressed to the last whorl. *Morum amabile* bears a general resemblance to *M. clatratum*, but reaches a smaller adult size (31–36 mm), lacks well defined colour bands on the last whorl, and has coarser sculpture at comparable size. The other species of *Oniscidia* are more strongly dissimilar.

Remarks Two of the shells carry respectively two and three small (diameter 0.5–1 mm) borings on the spire, which appear to be octopus drill holes.

Morum roseum n. sp.
Figure 2 A–D

Type material Holotype (live taken?) and two paratypes in MNHN.

Type locality Off Fatu Hiva, Marquesas Is, 09°44.6′ S, 138°51.1′ W, 115–120 m.

Material examined (all in MNHN) Marquesas Island (collected by P. Bouchet, B. Dayrat, B. Richer de Forges and A. Warén, MUSORSTOM 9 Expedition, N.O. '*Alis*', August–September 1997): Off Nuku Hiva, 08°45.5′ S, 140°03.8′ S, 86–120 m [MUSORSTOM 9 sta. DW1183], 26 August 1997, 1 dd.— Off Hiva Oa, 09°48.9′ S, 139°09.5′ W, 117 m [MUSORSTOM 9 sta. DW1208], 28 August 1997, 5 fragments and juv.— Off Fatu Hiva, 09°44.6′ S, 138°51.1′ W, 115–120 m [MUSORSTOM 9 sta. DW1208], 30 August 1997, 1 lv(?) (holotype), 1 fragment.— Off Hiva Oa, 09°41.8′ S, 139°03.5′ W, 105–285 m [MUSORSTOM 9 sta. DW1235], 31 August 1997, 1 dd (paratype).— Off Fatu Hiva, 10°28.1′ S, 138°41.1′ W, 119–122 m [MUSORSTOM 9 sta. DW1242], 1 September 1997, 1 dd (paratype).— Off Motu One, 07°48′ S, 140°21′ W, 450–455 m [MUSORSTOM 9 sta. DW1281], 7 September 1997, 1 dd.— Off Eiao, 07°52′ S, 140°31′ W, 416–460 m [MUSORSTOM 9 sta. DW1282], 7 September 1997, 2 dd.

Wallis & Futuna Islands NE of Wallis Island (collected by P. Bouchet, B. Métivier and B. Richer de Forges, MUSORSTOM 7 Expedition, N.O. '*Alis*', May 1992): Field Bank, 12°31′ S, 174°19′ W, 469–475 m [MUSORSTOM 7 sta. DW597], 24 May 1992, 1 fragment.

Measurements Holotype height 21.5 mm, width 15.5 mm; paratypes height 21.0 mm, width 15.5 mm; height 21.0 mm, width 14.5 mm.

Description (holotype) Shell small, solid, pyriform, consisting of 4.5 teleoconch whorls, spire low, broadly conical, apical angle 80°, last whorl occupying 85% of total shell height. Protoconch multispiral, protoconch I diameter *ca.* 400 μm, protoconch II smooth, consisting of 2.5 whorls, diameter 1500 μm, protoconch / teleoconch transition sharp, marked with raised, prosocline lamellar varix. Teleoconch whorls moderately convex, first 2 whorls shouldered, last whorl with concave subsutural ramp. Sculpture of axial ribs, almost entirely orthocline except for short adapical portion, which is prosoclinely appressed to preceding whorl, sharp on spire whorls, broader but asymetrical on last adult whorl, abapertural side higher, slightly raised over adapertural side, intersecting thick raised spiral cords, each intersection forming a projecting scale, scales stronger on shoulder cord, interspaces between ribs and cords forming spirally elongate cells. One spiral cord exposed below shoulder cord on spire whorls, 11 below shoulder cord of last whorl, subsutural cord developped on last 2 whorls only, 18 axial ribs on last whorl, 18 on penultimate and 14 on antepenultimate whorls. In addition to the main axial ribs, there is a finer sculpture of thin, sharp, fragile lamellae, 4–8 crowded on the descending, adapertural side of the axial ribs, 3–7 less evenly spaced between ribs. Aperture high, narrow; siphonal canal open, very slightly recurved; outer lip thick, recurved, with 12 bulging denticles corresponding to interspaces between spiral cords, much stronger in median part of lip, with 1–2 smaller, elongated pustules between them; parietal shield broad but thin, except in columellar region where it is thicker and raised, bearing numerous wart-like, spirally elongated pustules, disposed in parallel on lower part of shield, more irregularly arranged adapically. Ground colour light pinkish brown with irregular, deep violet brown speckles on cords, tip of siphonal canal pink; 4 darker spiral bands, 1 poorly defined subsuturally, 1 on whorl periphery about two cords broad, 1 below about one cord broad, 1 poorly defined covering shell base, outer lip marked with deep violet brown dots where these bands reach aperture; parietal shield and aperture white.

Derivation of name From the Latin *roseus, -a, -um*, pinkish, with reference to the colour of the tip of the siphonal canal.

Geographic range The Marquesas and NE of Fiji, alive (?) in 115–120 m, shells to 470 m.

Comparisons *Morum roseum* is easily distinguished from the other Recent species of *Morum* by the combination of its small adult size, broadly inflated last whorl, and narrow aperture, but it resembles *M. macdonaldi* Emerson, 1981, and *M. kurzi* Petuch, 1979, more than any other species. *Morum macdonaldi* differs by its much smaller adult size (less than 17 mm: it is the smallest *Morum* species), narrower shell with higher spire, and narrow parietal callus. *Morum kurzi* reaches 27 mm, and has a thicker and broader parietal callus, and has a characteristically orange aperture. *Morum roseum* also resembles a miniature *M. praeclarum* Melvill, 1919, but is distinguished by the more complex pustulation of the parietal shield and outer lip, the shorter, almost truncated siphonal canal, the finer sculpture, and the lack of a projecting spine on the shoulder of each axial rib.

NEW RECORDS

Morum bruuni (Powell, 1958)

New records Norfolk Ridge. SMIB 4: sta. DW48, 24°46′ S, 168°09′ E, 240–245 m, 1 dd.— Sta. DW53, 23°40′ S, 168°00′ E, 250–270 m, 1 lv.— SMIB 8: sta. DW157, 24°46′ S, 168°08′ E, 251–255 m, 1 dd.— Sta. DW158, 24°47′ S, 168°08′ E, 262–290 m, 2 dd.— Sta. DW159, 24°46′ S, 168°08′ E, 241–245 m, 2 dd.— SMIB 10: sta. DW208, 24°49′ S, 168°09′ E, 270 m, 1 dd.— LITHIST: sta. DW12, 24°45.7′ S, 168°08.1′ E, 235–280 m, 2 dd.— NORFOLK 1: sta. DW1653, 23°28′ S, 167°51′ E, 328–340 m, 1 fragm.— Sta. CP1657, 23°28′ S, 167°52′ E, 305–332 m, 1 dd.— Sta. CP1676, 24°43′ S, 168°09′ E, 227–232 m, 1 dd.— Sta. CP1677, 24°44′ S, 168°09′ E, 233–259 m, 1 dd. (all MNHN).— R.V. *Tangaroa*, sta. BS882, 32°31.8′ S, 167°29.5′ E, 113–118 m, Wanganella Bank, 1 lv (NMNZ).

Kermadec Ridge. R.V. *Acheron*, sta. BS437, 29°11.9′ S, 177°56.2′ W, 154 m, off Raoul I., 1 lv.— Sta. BS571, 29°18.8′ S, 177°54.2′ W, 219–274 m, 1 dd. (both NMNZ).

North Island of New Zealand. R.V. *Tangaroa*, sta. BS719, 37°33.2′ S, 176°58.7′ E, 134–174 m, 1 fragment (NMNZ).

Distribution (Figure 6) South-West Pacific: Kermadec Ridge, northern North Island of New Zealand, Norfolk Ridge, Lord Howe Rise (Emerson, 1990), Tasman seamounts and New South Wales; alive in 120–270 m, shells to 360 m.

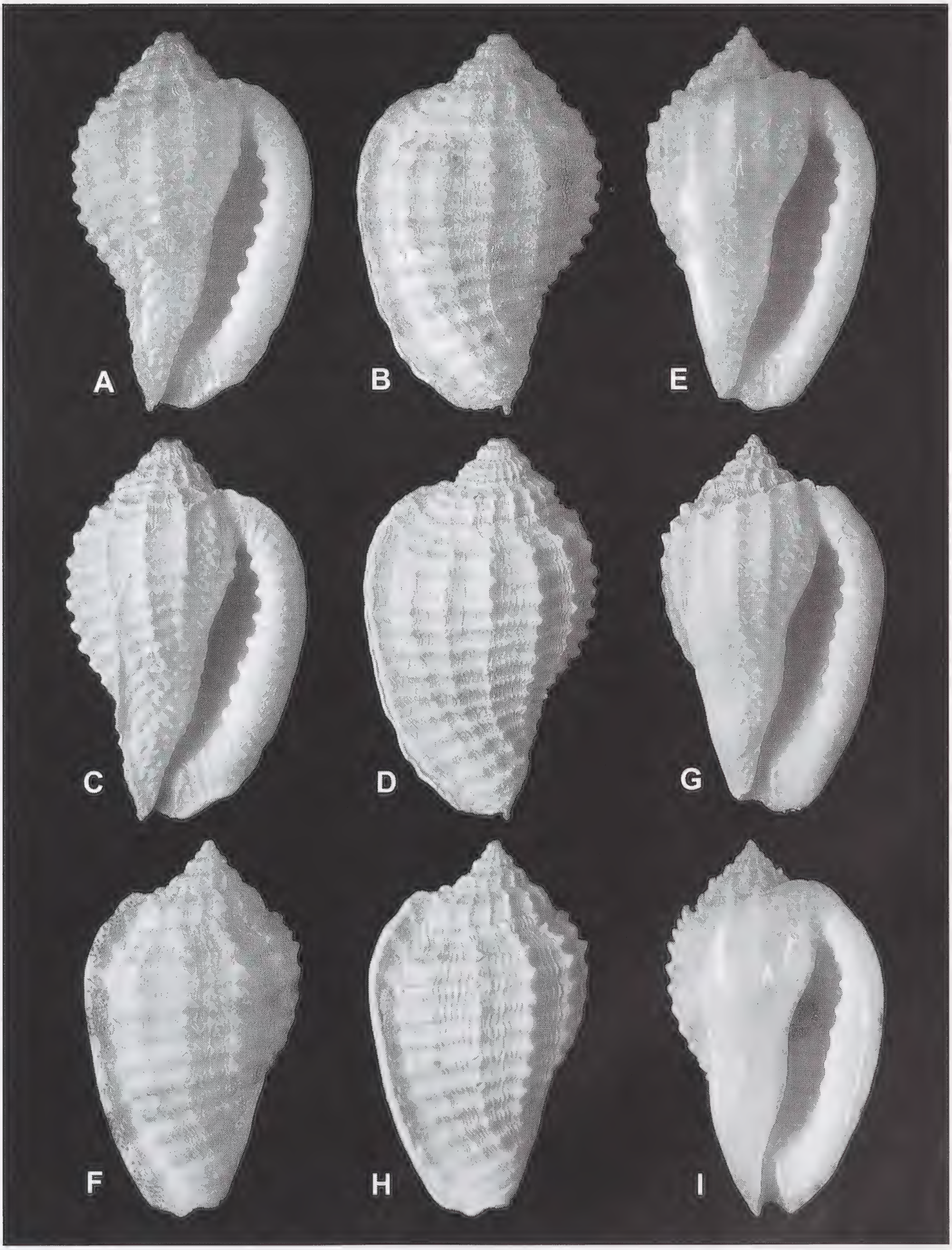

Figure 3 *Morum grande* / *Morum uchiyamai*. **A–D** *grande* form, height 41.6 mm; North of New Caledonia, 205–215 m [SMIB 6 sta. DW128]; **A–B** natural, **C–D** coated with magnesium chloride. **E–H** *uchiyamai* form, height 40.8 mm; Tonga, 216–237 m [BORDAU 2 sta. DW1610]; **E–F** natural, **G–H** coated with magnesium chloride. **I** *uchiyamai* form, height 52.0 mm; New Caledonia, Loyalty Ridge, 21°00′ S, 167°27′ E, 250 m [MUSORSTOM 6 sta. DW453].

Morum grande (A. Adams, 1855) / *Morum uchiyamai* Kuroda & Habe, 1961
Figure 3

New records (all MNHN) (*grande* type). New Caledonia. SMIB6: sta. DW128, 19° 06′ S, 163°22′ E, 205–215 m (North of New Caledonia), 1 dd.— BATHUS 4: sta. DW932, 19°08′ S, 163°29′ E, 170–190 m, 1 juv. dd.

(*uchiyamai* type). New Caledonia. MUSORSTOM 6: sta. DW399, 20°42′ S, 167°00′ E, 282 m (Loyalty Ridge), 1 juv. dd.— NORFOLK 1: sta. CP1715, 23°22′ S, 168°02′ E, 270–312 m, 1 dd.

Fiji. MUSORSTOM 10: sta. CP1387, 18°18.5′ S, 178°04.7′ E, 229–370 m (south of Viti Levu), 1 fragment (identification tentative).

Tonga. BORDAU 2: sta. CP1533, 21°44′ S, 175°20′ W, 322–329 m, 1 fragment.— Sta. DW1610, 22°59′ S, 175°47′ W, 216–237 m, 1 dd.— Sta. DW1630, 23°23′ S, 176°18′ W, 360 m, 1 lv.

Distribution West Pacific: from middle Japan (Izu peninsula) southwards to the China Sea, Philippines, Queensland, New Caledonia, Fiji and Tonga; alive in 100–360 m.

Remarks The distinction between *M. grande* and *M. uchiyamai* is problematical. Frydman (1991) separated specimens with 17–19 axial ribs and a "strongly curved siphonal canal" as *grande*, and specimens with 13–15 ribs and a "weakly curved siphonal canal" as *uchiyamai*. Dance & Poppe (in Poppe *et al.*, 1999: 11) have raised doubts as to the validity of *M. uchiyamai*, but based on their apparent sympatric occurrence in Tosa Bay, Japan, concluded that they are probably distinct. The present records of both *M. grande* and *M. uchiyamai* from New Caledonia would seem to support the latter view. However, the two forms do not occur in New Caledonia together: *M. grande* having been

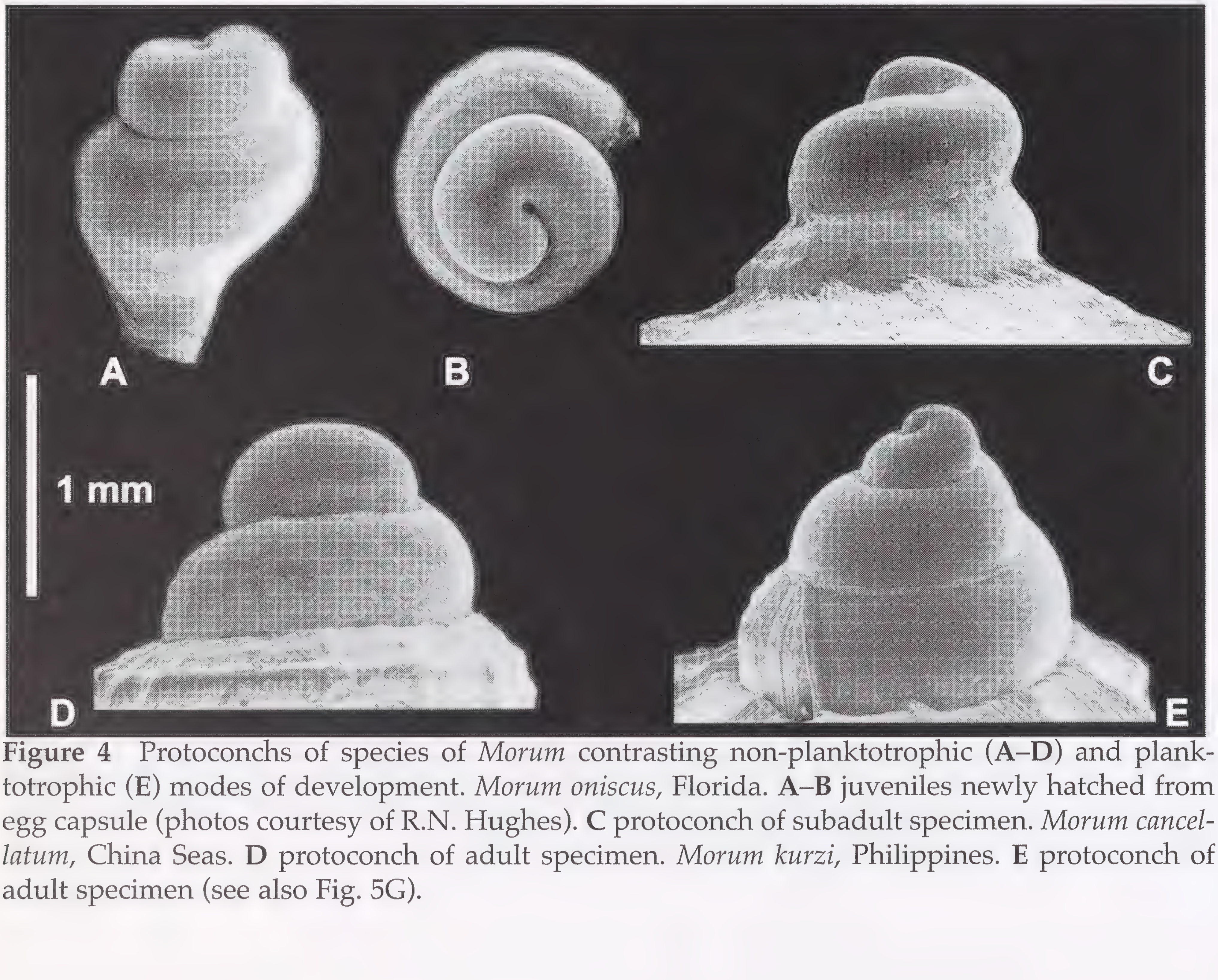

Figure 4 Protoconchs of species of *Morum* contrasting non-planktotrophic (**A**–**D**) and planktotrophic (**E**) modes of development. *Morum oniscus*, Florida. **A**–**B** juveniles newly hatched from egg capsule (photos courtesy of R.N. Hughes). **C** protoconch of subadult specimen. *Morum cancellatum*, China Seas. **D** protoconch of adult specimen. *Morum kurzi*, Philippines. **E** protoconch of adult specimen (see also Fig. 5G).

found only in the north and *M. uchiyamai* only in the south. They may prove to be soft-bottom and hard-bottom forms of a single species. A re-evaluation of these nominal species should also include *Morum watsoni* Dance & Emerson, 1967, which is evidently a juvenile of a species in the *grande/uchiyamai* complex (see also Tsuchiya [in Okutani], 2000: 532–535).

Morum kurzi Petuch, 1979

New record Fiji. BORDAU 1: sta. DW1393, 16°45′ S, 179°59′ E, 426–487 m (Somosomo Strait, between Vanua Levu and Taveuni), 1 broken shell (MNHN).

The damaged and faded specimen is a small adult, 19.5 mm high. The apertural callosity still retains the pale orange hue characteristic of Philippines specimens.

Distribution The Philippines, Solomon Islands (alive in 25–30 m; Emerson, 1990), Fiji.

Morum macdonaldi Emerson, 1981

New record Two shells (MNHN) of *M. macdonaldi* have been collected at Okukina, Takapoto Atoll, Tuamotus Archipelago, by Dr G. Richard. This locality is 5800 km south-east of the previously only known occurrence of *M. macdonaldi*, Kwajalein Atoll, in the Marshall Islands.

Morum ponderosum (Hanley, 1858)

Remarks Two shells of *M. ponderosum* have been collected at Moerai, Rurutu Island, Australes Archipelago by Mr J.P. Lefort, a collector based in Huahine, Society Islands, and are now in his collection. This is presumably the locality "Rurutua" mentioned for one of the specimens illustrated by Poppe & Brulet (in Poppe *et al.*, 1999: pl. 39, fig. 3).

Morum teramachii Kuroda & Habe in Habe, 1961

New records (all MNHN) New Caledonia, Norfolk Ridge. LITHIST: sta. CP16, 23°43.2′ S, 168°16.2′ E, 379–391 m (Banc Jumeau Ouest), 1 dd, worn.— NORFOLK 1: sta. DW1651, 23°27′ S, 167°50′ E, 276–350 m, 1 dd.— Sta. DW1704, 23°45′ S, 168°16′ E, 400–420 m (Banc Jumeau est), 1 dd.— Sta. DW1707, 23°43′ S, 168°16′ E, 381–493 m, 1 lv(?), 2 dd.— Sta. CP1708, 23°43′ S, 168°16′ E, 381–384 m, 1 dd, worn.

Distribution Previously known only from the western North Pacific: southern Japan, the Philippines and the Marianas, in 170–448 m (alive in 353 m) (Emerson 1990: 148).

Morum watanabei Kosuge, 1981
Figure 2 F–G

New record Fiji. SUVA2: sta. BS11, 18°11.8′ S, 178°28.1′ E, 213 m (south of Viti Levu), 1 dd (MNHN).

Remarks The present specimen is a young, uncallused adult, with unthickened lip. I identify it as *M. watanabei*, rather than *M. cancellatum* Sowerby, 1824, based on the numerous spiral cords, and axial ribs with a spine projecting at the shoulder. The paucispiral protoconchs are essentially similar in *M. cancellatum* and *M. watanabei*. Emerson (1990: 146, figs 6–7) has recorded as *M. cancellatum* an adult, crabbed specimen taken in a trap from a nearby station off Fiji, in 220 m. The two specimens may be conspecific.

THE *MORUM* PROTOCONCH AND MODES OF LARVAL DEVELOPMENT

The mode of development has been observed in one species of *Morum* only. The Western Atlantic *M. oniscus* (Linnaeus, 1767) has non-planktotrophic development with intracapsular metamorphosis, and hatches as a crawling snail (Work, 1969; Hughes & Emerson, 1987). It has a paucispiral protoconch (Figure 4 A–D). All other species of *Morum* are less common, some of them even quite rare, and their reproduction has remained undocumented, either in the field or in the laboratory. Their mode of development, however, can be inferred from protoconch morphology. The vast body of literature on the correlations between protoconch morphology and mode of development need not be reviewed again in the present paper. I refer to Thorson (1946), Thiriot-Quiévreux (1983), Jablonski & Lutz (1980, 1983), Rex & Warén (1982), Scheltema & Williams (1983), and references therein, for a presentation of data and discussion.

Emerson (1990) published SEM photographs of the protoconchs of *M. kurzi, M. bruuni* and *M. ponderosum* (Hanley, 1858) and presented the comments of two colleagues on these micrographs. [I have reexamined the MNHN shell of *Morum bruuni* from which he stated he had illustrated the protoconch (Emerson, 1990: figs 18–19). I find that its protoconch does not correspond with the figured specimen, and none of the other *M. bruuni* in MNHN corresponds with it. I suppose a mixing of data has occurred. Emerson's figs 18–19 could possibly represent *M. joelgreeni* Emerson, 1981]. Emerson cited a personal communication from Harasewych who stated that inference of mode of development of *M. kurzi* based on Shuto's criteria (Shuto, 1974) was inconclusive. Conversely, Scheltema (com. pers. to Emerson) concluded that *M. kurzi* and *M. ponderosum* have planktotrophic development, and suggested a planktonic phase of 1 to 2 months duration. Scheltema observed that the protoconch I of "*M. bruuni*" (probably *M. joelgreeni*: see above) has a diameter of 400 μm and from this inferred non-planktotrophic development, even suggesting intracapsular metamorphosis. Based on these comments, Emerson concluded that a planktonic larval stage is present in two species of *Morum* only, and hypothesized non-planktotrophy to be the rule in the other 14 Indo-West Pacific species then known.

Based on my own reexamination of the protoconch morphology in *Morum* and *Harpa* Röding, 1798 (Figures 4–5), I conclude the opposite, i.e. that planktotrophy is the standard condition present in the majority of the Indo-Pacific species, with non-planktotrophy being a derived character state present in a few species only. *Morum* protoconchs belong to the two categories of protoconchs classically recognised in caenogastropods (Table 1).

(a) The paucispiral type of protoconch consists of 1.1–1.2 whorls; it is smooth, has a diameter of 1150–3360 μm, and the protoconch / teleoconch transition is often sharp. Indo-Pacific species with a paucispiral protoconch are *M. cancellatum* (diameter 1200–1380 μm), *M. watanabei* (diameter 1150–1250 μm), and *M. macandrewi* Sowerby, 1889 (diameter 1180 μm). There are proportionally more western Atlantic species with a paucispiral protoconch, and *M. matthwesi* Emerson, 1967, has the largest protoconch in the genus (diameter 3360–3500 μm); although it has 1.8–2.2 whorls, it clearly belongs to

TABLE 1

Protoconch parameters for Indo-Pacific *Morum* species and inferred mode of development (P = planktotrophic; NP = non-planktotrophic). All data original.

Species	**protoconch I**	**protoconch II**		**n**	**inferred mode of development**
	diameter (µm)	**no. whorls**	**diameter (µm)**		
amabile Shikama, 1973	500-625	1.6-1.9	1375-1500	3	P
bruuni Powell, 1958	450	2.1-2.2	1525-1650	2	P
cancellatum Sowerby, 1824		1.1-1.2	1200-1380	2	NP
clatratum n. sp.					
exquisitum (A. Adams & Reeve, 1848)	700	1.2	1175	1	P
fatimae Poppe & Brulet, 1999	no data		?		
grande (A. Adams, 1855)	650-700	1.3-1.5	1250-1500	3	P
joelgreeni Emerson, 1981	575-625	1.3-1.6	1200-1350	3	P
kurzi Petuch, 1979	400-460	2.2	1325	2	P
macandrewi Sowerby, 1889		1.2	1180	1	NP
macdonaldi Emerson, 1981	350-375	2.5-2.6	1375	2	P
ninomiyai Emerson, 1986	650	1.45	1325	1	P
ponderosum (Hanley, 1858)	720	2.0	2320	1	P
praeclarum Melvill, 1919	370	2.3	1500	1	P
roseum n. sp.	400	2.5	1500	2	P
teramachii Kuroda & Habe, 1961	550-625	2.0	1425-1475	2	P
uchiyamai Kuroda & Habe, 1961	600-750	1.2-1.6	1275-1500	3	P
vicdani Emerson, 1995	no data		?		
watanabei Kosuge, 1981		1.2	1150-1250	2	NP
watsoni Dance & Emerson, 1967	525	2.0	1500	1	P

the paucispiral type, with no distinction between a protoconch I and protoconch II. Other western Atlantic species with paucispiral protoconchs are *M. lindae* Petuch, 1987 [regarded by Poppe *et al.* (1999) as a synonym of the Neogene fossil *M. dominguense* (Sowerby, 1850)] (diameter 1350–1500 μm, 1.6–1.7 whorls), *M. oniscus* (diameter 1200–1300 μm, 1.7–1.9 whorls) and *M. dennisoni* (Reeve, 1842) (diameter 1880 μm, 1.5 whorls).

(b) The multispiral type of protoconch consists of 1.8–2.8 whorls. Protoconch I is smooth or finely papillose; protoconch II is smooth except for a partly covered spiral keel exposed just above the suture. The transition between protoconchs I and II is rather discrete; that between protoconch II and teleoconch is sharp, with a slightly raised varix. Number of whorls and diameter in different Indo-Pacific species are compiled in Table 1.

For comparison with the *Morum* protoconch, I figure the protoconch of *Harpa major* Röding, 1798 (Fig. 5 A, C, E) (the identification is tentative, as the specimen is very young; it could also be *H. articularis* Lamarck, 1822). It is multispiral. Protoconch I is finely papillar and has a diameter of 500–550 μm; protoconch II is smooth with one suprasutural spiral cord, has 2.25 whorls and a diameter of 1750 μm. Based on correlations in other families of Caenogastropoda, *Morum* species with a paucispiral type of protoconch are here inferred to have non-planktotrophic larval development. The proto-

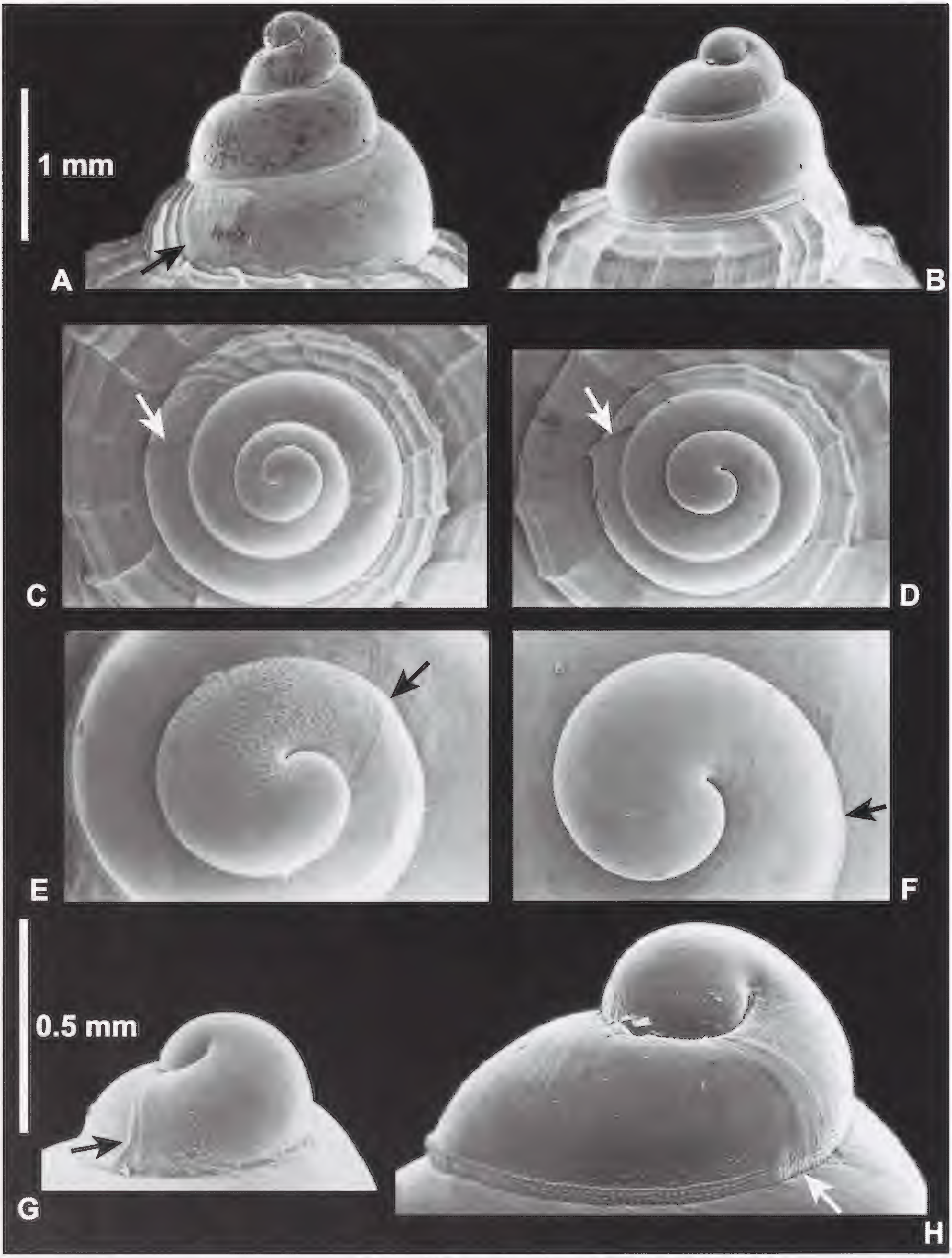

Figure 5 Protoconchs of species of *Harpa* (**A**, **C**, **E**) and *Morum* (**B**, **D**, **F–H**) from which a planktotrophic mode of development can be infered. The arrows show the protoconch II / teleoconch discontinuity (**A**, **C**, **D**) and the protoconch I / protoconch II discontinuity (**E–H**), indicating metamorphosis and hatching of the veliger larva, respectively. *Harpa major*, New Caledonia, North lagoon, 42 m. **A**, **C**, **E** protoconch of juvenile specimen. *Morum uchiyamai*, New Caledonia, Loyalty Ridge, 282 m. **B**, **D**, **F**, **H** protoconch of subadult specimen. *Morum kurzi*. **G** same specimen as in Fig. 4E. Scale lines 1 mm (A–D) and 0.5 mm (E–H).

conch / teleoconch transition is sharp in certain species (e.g. *M. oniscus*) and gradual in others (e.g. *M. matthewsi*), which probably reflects differences in the respective timings of metamorphosis and hatching. A short, non-feeding, dispersal larval stage may be present in some species, but it is almost certainly absent in *M. matthewsi*.

Conversely, those species of *Morum* with a multispiral type of protoconch are here inferred to have planktotrophic larval development. The diameter of protoconch I (range 350–700 μm) is admittedly larger than protoconch I of many caenogastropods with planktotrophic development, where a diameter of 150–300 μm is typical. However, the protoconch I of *Ranella olearia* (Linnaeus, 1758) has a diameter of 560 μm (Warén & Bouchet, 1990: fig. 88), despite the fact that it has teleplanic larvae, and protoconch I of *Harpa* is also in the same range of diameter. Evidently the diameter of protoconch I alone is not a reliable indicator of developmental mode.

Incidentally, the Caribbean *Morum lamarckii* (Deshayes, 1844), often treated as a synonym of *M. oniscus*, differs from it by multispiral, rather than paucispiral, protoconch. This difference was first noticed by Kaicher (1983: cards 3752, 3760), who treated *M. oniscus* and *M. lamarckii* as distinct species, but regrettably she illustrated the wrong protoconchs with the corresponding adults. Poppe *et al.* (1999) treated *M. lamarckii* as "a good species", while accepting that "it may be merely a subspecies or form of *M. oniscus*". The difference between the protoconchs of *M. oniscus* and *M. lamarckii* reflects non-planktotrophic (Hughes, 1990) vs. inferred planktotrophic larval development, respectively. As poecilogony remains undocumented in marine caenogastropods (Hoagland & Robertson, 1988, Bouchet, 1989), the difference in protoconch type is here interpreted as indicating specific rank.

Within the planktotrophic type, the relative duration of the feeding planktonic stage certainly varies from species to species. Species such as *M. grande* or *M. joelgreeni*, with only 1.3–1.6 protoconch II whorls, presumably have the shortest planktonic life, while *M. macdonaldi* and *M. praeclarum*, with 2.3–2.6 protoconch II whorls, presumably have the longest. While it is impossible to estimate the absolute duration of this planktonic stage from the protoconch morphology, I concur with Scheltema (cited by Emerson, 1990:149) that *Morum* veligers probably spend several weeks to a few months in the plankton.

Harasewych (cited by Emerson, 1990: 149), using Shuto's (1974) criteria, noted that he could not infer the mode of development of *M. kurzi* from its protoconch morphology. In my view, this demonstrates that Shuto's formula does not appropriately describe the correlation between protoconch morphology and mode of development, and not that it is impossible to infer *Morum* mode of development from protoconch morphology. It is appropriate to stress that the number of whorls of the protoconch has, by itself, no meaning: *M. matthewsi*, with 1.8 whorls, is inferred to have non-planktotrophic development, while *M. joelgreeni*, with the same number of whorls, is inferred to have planktotrophic development. In interpreting protoconch morphology, it is important to give attention to other characters such as the size of the initial whorl, the overall size of the protoconch, and the sharpness of the protoconch/teleoconch transition.

Based on the same correlations, mode of larval development can be inferred for fossil species. The following have been examined: *Morum chipolanum* Gardner, 1947 and *M. domingense* Sowerby, 1849 (both Chipola Formation, Lower Miocene, Florida; both non-planktotrophic), *M. harpaeformis* (Grateloup, 1847) (Lower Miocene, SW France; planktotrophic), and *M. minor* (Grateloup, 1847) (Upper Oligocene, SW France; planktotrophic).

In conclusion, planktotrophic and non-planktotrophic developmental modes are both present in Indo-Pacific representatives of *Morum*. Species inferred to have non-planktotrophic larvae are: *cancellatum*, *macandrewi*, and *watanabei*. Species inferred to have planktotrophic larvae are: *amabile*, *clatratum*, *grande*, *joelgreeni*, *kurzi*, *macdonaldi*, *ponderosum*,

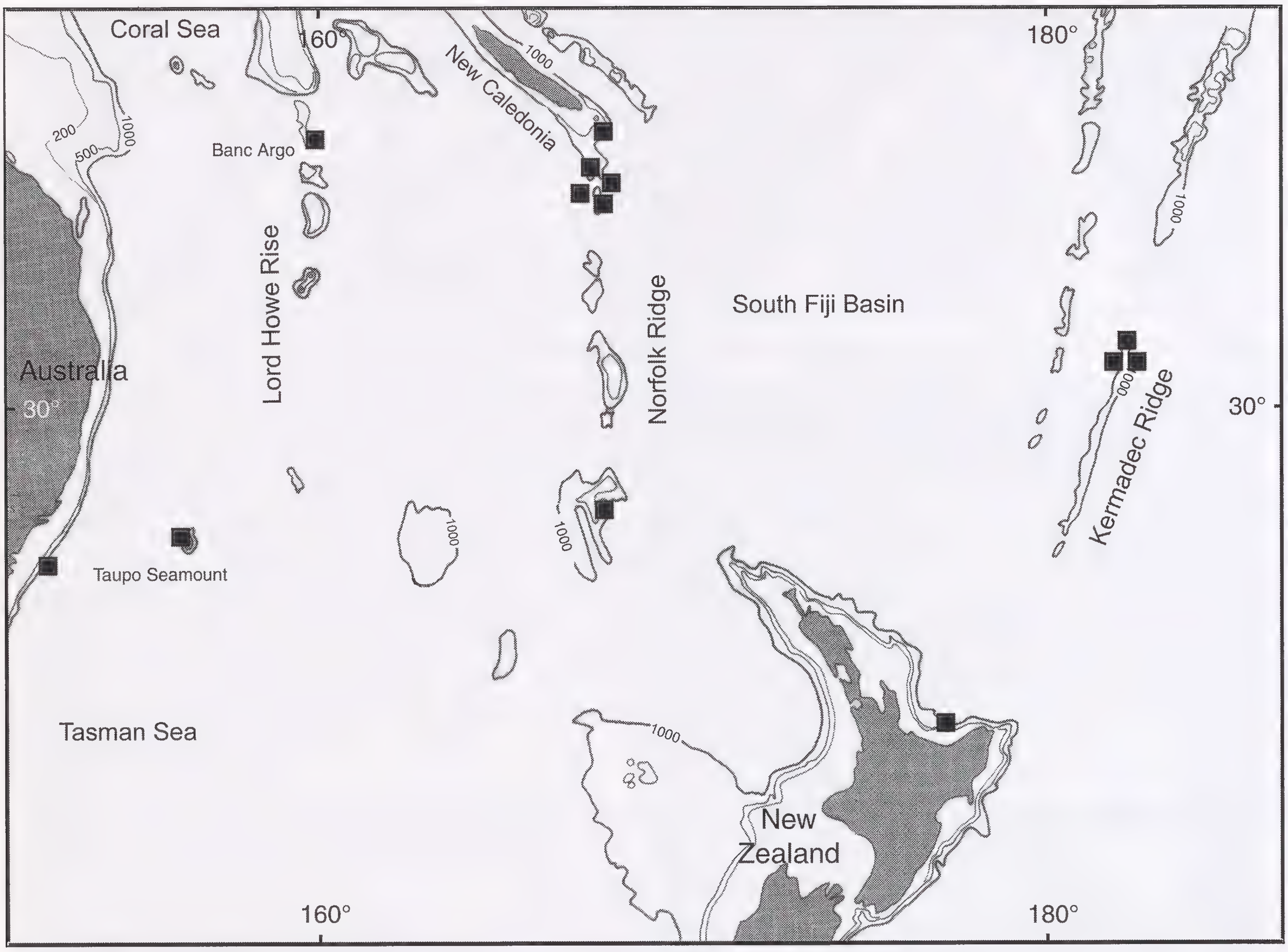

Figure 6 Distribution of *Morum bruuni*. 200, 500 and 1000 m isobaths indicated. Gene flow between the disjunct groups of populations separated by very deep water is probably maintained by planktotrophic larvae, as infered from protoconch morphology.

praeclarum, roseum, teramachii, uchiyamai, and *watsoni*. No data are available for *M. fatimae* Poppe & Brulet, 1999, and *M. vicdani* Emerson, 1995.

PLATE TECTONICS AND THE DISTRIBUTION OF SPECIES OF *MORUM*

Emerson (1990) discussed the distribution patterns of the West Pacific species of *Morum* and presented "the apparent lack of teleplanic larvae" as the single most important factor to account for what he interpreted as relict distributions. He developed a scenario of distributional patterns based on vicariant events in the tectonic history of the West Pacific region and rejected hypotheses based on dispersal of planktonic larvae. Rather than this scenario based on plate frontiers and movement of the lithospheric plates on the geological scale, I defend the view that instant larval dispersal offers a more parsimonious explanation of modern distribution patterns at the specific level.

Emerson (1990) invoked vicariant events to explain the distribution of *Morum bruuni*, which has a SW Pacific distribution consisting of several disjunct groups of populations (Figure 6): off southeastern Australia, Lord Howe Rise (Argo bank), Taupo seamount, Kaimon Maru, and Wanganella banks on Norfolk Ridge, the north of North Island of New Zealand, and the Kermadec Ridge. Records of empty shells are in the 140–360 m range, and the only live-taken specimen is from 250–270 m. These groups of populations are separated by distances of 500–2000 km with water depths in excess of 1000 m, that is 500–2000 kilometers of sea bottom where an upper slope species like *M. bruuni* is unable to live. Gondwanian relict distribution is a classic of South-West Pacific terrestrial biogeography (Stevens, 1980), with numerous taxa having vicariant distribution patterns in New Zealand, New Caledonia, and Australia. When evaluating whether the same mechanisms explain the distribution of modern marine biota, it is important to stress the time scale of the tectonic events involved in such vicariant distribution patterns. Australia, New Zealand, and New Caledonia broke up in the Cretaceous (ca. 80 MY ago) and, when the now submerged Norfolk Ridge is taken into consideration, the last vicariant event hypothesized for land vertebrates is dated from the lower Miocene (Balouet, 1990), i.e. ca. 20 MY ago. It should also be stressed that, in the terrestrial faunas and floras of these regions, vicariance following plate tectonics movements best explains disjunct distribution patterns at the generic or family level. With the exception of introduced anthropophile species, the faunas and floras of New Caledonia, New Zealand, and Australia do not have a single species in common, although the generic affinities support the hypotheses of vicariance biogeography.

At the specific level, to explain disjunct distribution between these three land masses by vicariance would require that the taxon in question is at least as old as the tectonic event being considered. In other words, explaining the disjunct SW Pacific distribution of *Morum bruuni* in terms of vicariance would require the species *M. bruuni* to be at least 20 million years old, and (i) to have remained unchanged since, or (ii) to have experienced a parallel morphological evolution in the disjunct populations (orthogenesis). Admittedly, absence of evidence is ambiguous, but, despite the fact that South Australian (Darragh, 1985) and New Zealand (Maxwell & Beu, 1990) Tertiary macromollusc faunas are relatively well studied, there are no records of fossil *M. bruuni* in the area. According to Beu (1976), the New Zealand *Morum finlayi* (Laws, 1932), which differs by having more prominent and more rounded spiral cords, may have been ancestral to *M. bruuni*. It is recorded from the lower (19–22 MY) and middle Miocene (12–15 MY) of New Zealand (Beu & Maxwell, 1990: 231). A second species of *Morum* in the lower Miocene of New Zealand is not closely related to the *finlayi-bruuni* lineage. Therefore I reject vicariance as the cause of disjunct distributions of *M. bruuni* in New Zealand and New Caledonia.

Furthermore, vicariance cannot explain the presence of *Morum bruuni* on such guyots as Argo Bank in the Coral Sea. Argo Bank is part of a chain of guyots stretching from the Chesterfield-Bellona Plateau to Lord Howe in the northern part of the Tasman Sea. The age of the volcanic structures supporting the guyots varies from 28 MY (upper Oligocene) in the North (Chesterfield-Bellona) to 6.5 MY in the South (Ball's Pyramid, off Lord Howe) (Missegue & Collot, 1987). An age of 15–20 MY is probable for Argo Bank. During this lapse of time, Argo Bank has always been separated from New Caledonia, Australia and New Zealand by expanses of deep (several thousand meters) water in the order of 500 km or more. The presence of benthic gastropods on the summit areas of these seamounts therefore requires an explanation other than the fragmentation of a former continuous distribution area. Dispersal of and colonization by planktotrophic or demersal non-planktotrophic larvae offers a reasonable hypothesis that rests on the vast corpus of literature on larval biology, population genetics and plankton ecology.

Morum has now been recorded from seven oceanic locales in the Central Pacific: Kwajalein, Marshall Islands (*M. macdonaldi*; type locality), Field Bank, north of Fiji (*M. roseum*; herein), Vanua Levu, Fiji (*M. kurzi*; herein), Takapoto, Tuamotus (*M. macdonaldi*; herein), Rurutu, Australes Islands (*M. ponderosum*; Poppe *et al.*, 1999, and herein), several islands in the Marquesas (*M. clatratum* and *M. roseum*, herein), and Oeno and Henderson, Pitcairn group, SE Polynesia (*M. ponderosum*; Preece, 1995). The mode of development of these species has been inferred from protoconch morphology to be planktotrophic. Larvae of *Morum* have not been positively identified in plankton catches from Pacific waters (see e.g. Scheltema & Williams, 1983), but this is not surprising in view of the rarity of the adults. With the Pitcairn Is and Fatu Hiva both younger than 2 MY (references cited by Preece, 1995; Duncan & McDougall, 1974), occurence of species of *Morum* on such oceanic islands is best explained by the settlement of planktonic veligers originating from other insular populations in the Pacific. The patchy records of many species on the Pacific Plate largely reflects the fact that the archipelagoes of the South Pacific are still inadequately sampled. Considering its inferred mode of development, *M. clatratum* should not be expected to be a Marquesas endemic, but to have a more extensive distribution in the West Pacific.

ACKNOWLEDGEMENTS

I am most grateful to Frank Frydman (Paris), a collector specialising in Harpidae, for placing his knowledge and material of *Morum* at my disposal. Joseph Poupin, a biologist then working for Service Mixte de Contrôle Biologique (SMCB) in Tahiti, dredged the first three specimens of *M. clatratum* on board R.V. "*Marara*", and donated this, and other molluscan specimens to MNHN. Jean Trondle (La Force, France) made available the material from the collection of J.P. Lefort (Papeete), and Georges Richard (University of La Rochelle) presented the material of *M. macdonaldi* he had collected in Takapoto. Roger Hughes (School of Biological Sciences, Bangor, UK) kindly permitted my use of his SEM photographs of newly hatched specimens of *M. oniscus*. Philippe Maestrati and Benoit Fontaine prepared and/or mounted all other original illustrations, Bruce Marshall revised the language, and Jose Leal improved the manuscript during the refereeing process.

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THE STATUS, DISTRIBUTION AND ECOLOGY OF *PALUDINELLA LITTORINA* (DELLE CHIAJE, 1828) (GASTROPODA: ASSIMINEIDAE) IN THE BRITISH ISLES

IAN J. KILLEEN[1] & JANICE M. LIGHT[2]

Abstract *Surveys over the last 15 years have revealed that the assimineid* Paludinella littorina *(delle Chiaje, 1828) is much commoner in the British Isles than previously believed. It is currently known living at 40 sites ranging from the Isles of Scilly, eastwards along the Channel coast of England as far as the eastern end of the Isle of Wight. It extends as far north as the Bristol Channel with sites on the north coast of Devon and the coast of Pembrokeshire. The west coast of the Lizard peninsula, Cornwall and the Isles of Scilly support significant numbers of* P. littorina *populations. The two principal habitats in which we have found* P. littorina *are caves, and shores with a supra-littoral zone comprising large stones and boulders with stable interstitial gravels beneath. Observations on the species' habitats, ecology and conservation are discussed.*

Key words Paludinella, *Assimineidae, British Isles, Distribution, Ecology*

INTRODUCTION

Until the late 20th century *Paludinella littorina* (delle Chiaje, 1828) was considered to be a rare species in the British Isles. The species was first noted from Weymouth as *Cingula ? globularis* (Metcalfe MS in Thorpe 1844) and was subsequently recorded living from the estuary near Portland, Dorset (i.e. The Fleet), from Whitecliff Bay, Isle of Wight by Forbes & Hanley (1853) and Exmouth (presumably living) by Clark (1855). Sykes (1890) also found living individuals in The Fleet but the species was not recorded there again until 1986 (Light 1986). All other pre-1986 records were based upon dead shells (Table 1).

Based upon The Fleet habitat, *P. littorina* was subsequently referred to, particularly in UK conservation literature, as a lagoonal species, and was attributed the vernacular name "the lagoon snail" (HMSO 1996, Downie 1996). As a result of its perceived rarity it was added to Schedule 5 of the UK Wildlife and Countryside Act 1981. Attempts to locate the species at other sites initially focused on searching habitat type similar to that in the Fleet, although such habitat would not have existed at most of the historical sites. Populations of *P. littorina* were discovered in a cave at Woody Bay, north Devon (Light 1991) and interstitially in an open marine environment at Whitecliff Bay, the site of Forbes & Hanley's 1853 record, (Light 1992). Subsequent field searching of similar habitats has revealed populations at several sites in south-west Britain (Table 1).

Paludinella littorina has a north-east Atlantic distribution from the Azores, Madeira and Canaries, northwards to the Iberian peninsula, France and south-west Britain. It also extends eastwards into the Mediterranean as far as the Adriatic, although the true distribution is unclear owing to the presence of other similar species whose taxonomic position requires further research. It is widely acknowledged amongst European malacologists that there is more than one species currently assigned to the taxon *Paludinella littorina* (Cesari 1988, Gaglini 1991, Giusti *et al.* 1995), yet hitherto, no author has fully resolved the problem. Various authors over the past 20 years (e.g. Sabelli *et al.* 1990) have expressed doubt as to whether populations found in Britain are the same species as those found in the Mediterranean. We have examined material from many NE Atlantic and Mediterranean localities. Results based on characters such as shell morphology,

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genital anatomy and radulae have shown that the snail currently referred to as *P. littorina* is an aggregate of at least 2 species which may be placed into two main groups according to the size of their protoconch. Atlantic populations all have a broad protoconch and show little difference in shell size and shape, or in genital anatomy and we therefore consider that these may be the same taxon. Populations in the Mediterranean present more difficulties with both wide- and narrow-protoconch forms present. Nomenclatural problems will also need to be addressed as delle Chiaje's Sicilian type material is no longer extant, but for the purposes of this paper we use the name *P. littorina*.

The diagnostic characters of the Atlantic form of *P. littorina* are provided by Graham (1988). The shell is very small with 3–4 moderately convex whorls, globose, glossy and semitransparent, usually of a golden horn colour, but varying from almost white through to orange-brown, with a smooth surface and fine irregular growth lines. The protoconch is relatively broad (400–430 microns), the spire is short and the last whorl is large. The aperture is oval and a small umbilicus is present, Figures 1a–d. British specimens rarely exceed 2mm in height and 1.7mm in diameter. Measurements of 30 specimens from The Fleet gave mean dimensions of 1.62 x 1.38mm. The animal is pale grey but appears whitish through the shell. The snout is broad, bifid and the tentacles are short and stubby with large black eyes at their base, Figure 2.

To provide a more accurate picture of the species' true distributional range in Britain,

Figs 1a–d *Paludinella littorina* specimens 1a, b Beer, Devon. 1c, d Tresco, Isles of Scilly.

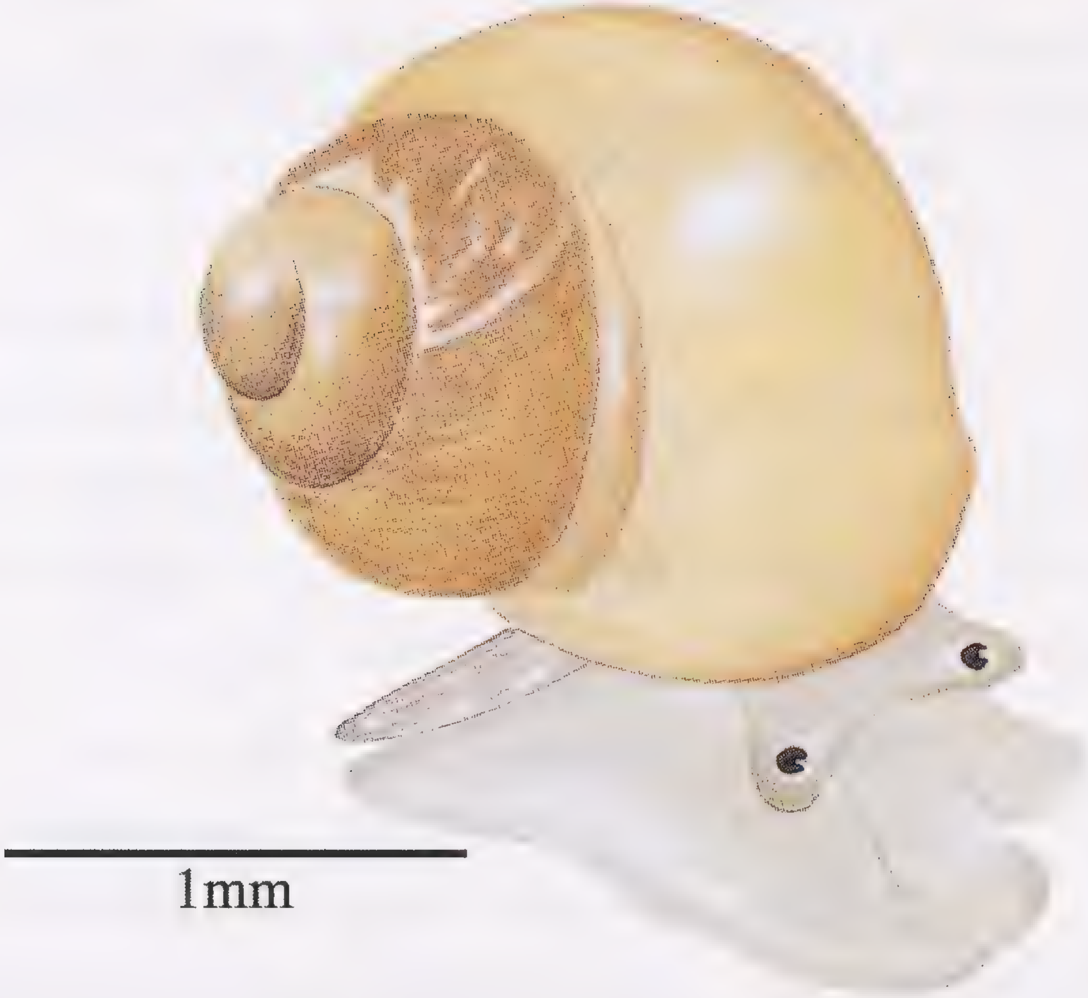

Figure 2 Live *P. littorina* from the Fleet

further surveys were carried out in 2000 with support from English Nature research funding (Light & Killeen 2001). This work has been carried out under License No. 20000819 [IJK] and No. 20000820 [JML] and representative material has been deposited in the Mollusca collections at the National Museum of Wales, Cardiff. The current paper synthesises all recent work on *P. littorina* in the British Isles.

METHODOLOGY

Fieldwork by the present authors since 1988, as part of marine molluscan biogeographical studies, has included examination of more than 250 locations on the Channel coast of England between Dover and Scilly, in addition to sites on the north coasts of Devon and Cornwall, south-west Wales and the Channel Islands. Where favourable habitat occurred, this work has included searching for *P. littorina*. Surveys in Pembrokeshire targeting *P. littorina* specifically were carried out in 1994 and 1997, and the English Nature survey in 2000 covered a further 68 sites in Scilly, south Cornwall and the Isle of Wight.

THREE PRINCIPAL HABITATS HAVE BEEN SEARCHED

Caves (figs 4 & 5)

Walls and roofs at the height estimated to coincide with upper shore/splash zone, as well as regions immediately above and below this point, were searched with particular attention focused on fissures, cavities and crevices, and their marginal areas. Artificial light is essential for searching in cave interiors, and suitable implements (fine paintbrush or soft-touch forceps) were needed to temporarily remove snails for examination. Observations at Broad Haven, Pembrokeshire and at other sites indicated that the ability to locate *P. littorina* in cave habitats may be dependent upon the length of time that has elapsed since occurrence of high tide (Light & Killeen 1997). Therefore, searches of cave habitats were attempted as soon after high tide as the cave entrance became safely accessible. It has already been observed that (particularly in caves) *P. littorina* is more likely to be found in the field in moist weather conditions (Killeen & Light, 1994).

TABLE 1
All records of *P. littorina* from the British Isles
(no reference given = Light & Killeen 2001, NGR = National Grid Reference, L = live record, S = shell only)

County	**Site**	**NGR**	**Habitat**	**L/S**	**Reference**
Sussex	Pilsey Island	SU767008	Shell drift	S	Goodchild pers. comm.
Isle of Wight	Whitecliff Bay (N)	SZ64-86-	Crevice	L	Forbes & Hanley 1853
	Whitecliff Bay (N)	SZ645865	Interstitial/crevice	L	Light 1992
	Whitecliff Bay (N)	SZ645865	Interstitial/crevice	L	
	Culver Cliff	SZ638854	Cave	L	
Dorset	Weymouth	SY66-75-	Interstitial/lagoon	?	Metcalfe in Thorpe 1844
	The Fleet	SY66-75-	Interstitial/lagoon	L	Forbes & Hanley 1853
	Weymouth (The Fleet)	SY66-75-	Interstitial/lagoon	L	Sykes 1890
	The Fleet	SY65-76-	Interstitial/lagoon	S	Seaward 1986
	The Fleet	SY654767	Interstitial/lagoon	L	Light 1986
Devon (south)	Exmouth		?	?L	Clark 1855
	Torbay	SX9--6--	? Shell drift	S	Marshall 1913
	Dartmouth		? Shell drift	S	Marshall 1913
	Beer	SY227888	Cave	L	Killeen & Light 1998
	Near Brixham	SX932555	Cave	L	Light 1998
	Hope's Nose	SX948636	Crevice	S	Killeen & Light unpub
Devon (north)	Woolacombe	SS45-43-	?	S	Conchological Society records
	Woody Bay	SS677491	Cave	L	Light 1991
Cornwall (south)	Land's End	SW34-25-	?	S	Jeffreys 1869
	Sennen Cove	SW35-26-	? Shell drift	S	Marshall 1913
	Lizard	SW70-11-	? Shell drift	S	Marshall 1913
	Mixtow	SX130530	Interstitial/crevice	S	
	Vellan Drang	SW701115	Caves	L	
	Mullion Cove	SW667178	Cave	L	
	Polurrian Cove	SW669187	Cave	L	
	N of Polbream Point	SW667189	Cave	L	
	Poldhu Cove	SW664198	Cave	L	Killeen & Light 1999
	Rinsey Head	SW590269	Interstitial/gully	L	
	Sennen Cove	SW350263	Interstitial/gully	L	
Cornwall (north)	Holywell Bay	SW76-59-	Cave	L	Llewellyn Jones pers. comm.
Scilly: Gugh	Porth Conger	SV887085	Interstitial	L	Killeen & Light 1999

County	Site	NGR	Habitat	L/S	Reference
Scilly: St Agnes	Porth Conger	SV885084	Crevice	L	Killeen & Light 1999
	Porth Conger	SV885083	Interstitial	L	
	Porth Coose	SV877087	Interstitial	L	
	Porth Killier	SV880086	Interstitial	L	
Scilly: St Mary's	Porth Cressa	SV906099	Interstitial	L	Killeen & Light 1999
	Old Town	SV914101	Interstitial	L	
	Porth Hellick	SV927107	Interstitial	L	Killeen & Light 1999
	Toll's Island	SV930120	Interstitial	L	Killeen & Light 1999
	Block House Point	SV924125	Interstitial	L	Killeen & Light 1999
	Innisidgen	SV922128	Interstitial	L	
	W of Bar Point	SV912128	Interstitial	L	
Scilly: St Martin's	W of St Martin's Head	SV937159	Interstitial	L	
	Porth Seal	SV918166	Interstitial	L	
Scilly: Tresco	Old Grimsby	SV894159	Interstitial	L	
	Gimble Porth	SV888163	Interstitial	L	
	Castle	SV882160	Interstitial	L	
	New Grimsby	SV886154	Interstitial	L	Killeen & Light 1999
Scilly: Bryher	Hangman's Island	SV880156	Interstitial	L	
	Popplestone Neck	SV873150	Interstitial	L	
	Great Porth	SV874147	Interstitial	L	
	Stony Porth	SV873142	Interstitial	L	
	N of Works Point	SV880143	Interstitial	L	
Pembrokeshire	Caldey Island	SS13-96-	? Shell drift	S	Williams Vaughan 1905
	Broad Haven	SR981939	Cave	L	Killeen & Light 1994
	Broad Haven	SR981939	Cave	L	Light & Killeen 1997
	West Angle Bay	SS85-03-	Shell drift	S	Smith pers. comm.
	Caldey Island	SS131972	Interstitial/gully	L	Killeen & Light 1994
	Caldey Island	SS128972	Caves	L	Light & Killeen 1997
Channel Islands	Sark		? Shell drift	S	Marshall 1913
	Guernsey		? Shell drift	S	Marshall 1913
	Jersey; Flicquet Bay	49°13'N, 02 °01'W	Interstitial	L	Killeen & Light unpub (1998)
	Jersey, Greve au Lançon	49°15'N, 02°14'W	Cave	L	Killeen & Light unpub (1998)

Interstices of unconsolidated substrate (figs 6–9)
Favourable *P. littorina* habitat occurs on upper shores where there are gullies, or sheltered areas on platforms with a surface deposit of stable cobbles. At more open sites, for example on Scilly where the potential habitats occur on the rugged granite boulder shores, the targeted zone is at the interface of large stable granite boulders supporting *Pelvetia canaliculata*, and the boulders slightly higher on shore colonised by lichens *Ramalina* spp., *Caloplaca* sp and *Xanthoria* sp. (fig. 7). All these habitats have lattices of varying scale and must be free-draining. There is a vertical gradation from large scoured cobble at the surface to a stable habitat of smaller pebbles with interstitial sediments and organic detritus. These cobbles and pebbles sometimes had to be removed to some depth (as much as 30cm) to reach a zone which is deep enough to be protected, but still sufficiently distant from the underlying non-interstitial water/substratum interface (fig. 8). During the excavation process the undersides and tops of the rocks were searched. Shores with large embedded, or semi-embedded slabs resting on silt and organic detritus, provide suitable *P. littorina* habitat. A similar approach was employed for tidal lagoons similar to the Fleet, where *P. littorina* lives at high water mark (HWM) buried in shingle with organic detritus, particularly below bushes of sea-blite (*Suaeda maritima* and *S. fruticosa*). The substantial population at this site lives along the seaward margin of the lagoon, but is sheltered from the high energy wave regime which prevails along the Chesil Beach (fig. 9).

Ledge systems, gullies, isolated littoral outcrop and sea walls
At sites where cliffs and rock outcrop have been undermined and shaped by wave action, but full cave development is absent, there may be overhangs, ledges and gullies, where loosening and removal of small slabs often revealed interstitial molluscs on the inner surfaces.

RESULTS & DISCUSSION

DISTRIBUTION

Since 1986 *P. littorina* has been recorded living at 40 sites in the British Isles. These are shown in Table 1 with all historical (pre-1986) records. The species has a typical south-western distribution, ranging from the Isles of Scilly, eastwards along the Channel coast of England as far as the eastern end of the Isle of Wight. It extends as far north as the Bristol Channel with sites on the north coast of Devon and the coast of Pembrokeshire (Figure 3). Based on extensive fieldwork carried out around the British Isles, we can be reasonably confident that this represents a true geographical distribution. Our fieldwork east of the Isle of Wight and surveys by Julia Nunn in Ireland and Shelagh Smith in Scotland have yielded no records. However, the species may well be living at other sites in SW Wales, north Cornwall and Devon, and may possibly occur in S/SW Ireland.

Two geographical areas support significant numbers of *P. littorina* populations: the west coast of the Lizard peninsula in Cornwall, and the Isles of Scilly. On the west coast of the Lizard, the species was found in caves at 5 sites from Vellan Drang at Lizard Point to Poldhu Cove. On the Isles of Scilly *P. littorina* was found at 22 sites on the islands of St Mary's, St Martin's, St Agnes and Gugh, Tresco and Bryher. On this basis, the Isles of Scilly is currently the species' stronghold in the British Isles.

The results have demonstrated that *P. littorina* is more widespread and common in south-west England than previously known, but we believe that the species remains under-recorded within this area. There are numerous cave sites which can be seen from the air or cliff tops, or identified from maps, which cannot be accessed from the shore

Figure 3 Distribution of *P. littorina* in the British Isles by 10km square. • = post-1986 live records, O = shell only and all pre-1986 records.

or which can only be accessed on extreme low spring tides. Several of the survey sites supported favourable habitat, for example localities on the Lizard and Land's End peninsulas, and at Freshwater Bay on the Isle of Wight, but *P. littorina* was not found. These may be genuine absences; however, unfavourable environmental factors (weather conditions, tidal regime) may also account for the failure to find the snail at those sites.

FEATURES OF *PALUDINELLA* HABITAT

The shore type, intertidal zone and morphology of *P. littorina* habitat have been described above. A range of lithologies has proved to be suitable. At Brixham, Devon the rocks are Middle Devonian thinly bedded metamorphosed limestones with cm- to meter-scale horizontal and vertical faulting which is laterally continuous, and this provides sufficient depth to allow accumulation of detritus and sediment, whilst at the same time, affording protection from water action. Similar Devonian shales are also present at some sites in Cornwall, whereas elsewhere in the county, shores of the local granite, and the serpentines of the Lizard also support populations. At Broad Haven and on Caldey Island, Pembrokeshire, Carboniferous limestone is the local rock type whereas Chalk provides suitable habitat on the Isle of Wight and in south Devon. Seepage of fresh water is also a common factor in caves, and travertine deposition may also be present. Sometimes, as at Brixham, the entrances to *P. littorina* caves are veiled by a curtain of water dripping from the cliff above.

In addition to the geomorphological character of the habitat, the species appears to demonstrate a number of rather precise biological and environmental requirements. From field observations in cave habitats the majority of individuals do not stray far from the margins of rock fissures and crevices which are laterally continuous and often appear to have some depth resulting from faulting in the rocks (Light & Killeen 1997). At cave sites where *P. littorina* is found, the associated substratum is frequently colonised by green and red algal films and soft crusts and in some cases a dull lilac-coloured crustose coralline alga. Identification of the dark red soft crustal alga requires examination of microscopic features; however, two *Hildenbrandia* spp. form extensive and ubiquitous reddish brown coatings on hard rock, of which *H. rubra* is common, (Hiscock 1986).

OTHER MOLLUSCAN FAUNA OF *P. LITTORINA* HABITAT

Species such as *Patella vulgata* L., 1758 and *Melarhaphe neritoides* (L., 1758) are characteristic of the upper eulittoral zone, but are not considered to be part of the fauna associated with *P. littorina*. *Littorina saxatilis* (Olivi, 1792) lives in caves to the limit of light penetration, and is present in interstitial habitats (with *L. compressa* in Cornwall and Scilly) but less often on the undersides of embedded rocks or deep in the interstitial lattice. The most frequently co-occurring species in caves is the pulmonate *Otina ovata* (Brown, 1827) which was present in virtually all of the cave sites which supported *P. littorina*, with the elobiid *Ovatella myosotis* (Draparnaud, 1801) occurring less frequently.

In interstitial habitats the mollusc species most usually living with *P. littorina* are the elobiids *O. myosotis* and *Leucophytia bidentata* (Montagu, 1808). Whilst these species can co-occur they show slight differences in zonation; *L. bidentata* extending further down the shore (beyond the *Ovatella* and *P. littorina* zone), where *Cingula trifasciata* (J. Adams, 1800) also occurs. Crevice habitats in rock faces and platforms support *L. bidentata*, *C. trifasciata*, *Otina ovata* and *Lasaea adansoni* (Gmelin, 1791).

In continental Europe, *P. littorina* is frequently recorded with *Truncatella subcylindrica* (L., 1767) and we have found the two species together in estuary habitat (for example, the Rance in Brittany, France), and on open coasts (Madeira). Whilst both *T. subcylindrica* and *P. littorina* live within the supralittoral zone, the only site in Britain at which the two co-occur is the Fleet in Dorset. *T. subcylindrica* is currently known from eight sites on the south coast of England all of which are sheltered, estuarine habitats, whereas most of the *P. littorina* sites are open marine habitats.

NON-MOLLUSCAN FAUNA OF *P. LITTORINA* HABITAT

Table 2 summarises the non-molluscan fauna of the habitat. In cave habitats the most frequent apparent associates are the isopod *Ligia oceanica* and the red snout mites of the family Bdellidae. Although *Ligia* is a useful zonal indicator species, some caves were found to support large numbers of individuals in upper shore/splash zone crevices. Where these crevices contained substantial amounts of organic detritus and *Ligia* faecal material, *P. littorina* was not located.

TABLE 2
Non-molluscan species occurring with *P. littorina*

Classification	**Taxon**
Platyhelminthes, Turbellaria	*Procerodes littoralis*
Crustacea, Isopoda	*Ligia oceanica*, *Sphaeroma serratum*
Crustacea, Amphipoda	*Orchestia* sp., *Talitrus saltator*
Acarina, Bdellidae	snout mites: *Bdella* sp., *Neomolgus* sp.
Chilopoda, Geophilomorpha	*Strigamia maritima*
Collembola, Neanuridae	*Anurida maritima*

Bdellid mites are also associated with *P. littorina* on the open shore, as are individuals of *Procerodes littoralis*. Neither of these organisms was observed to occur in significant numbers in *P. littorina* habitat. At open shore sites, in addition to *Ligia oceanica*, other isopod and amphipod species occupy the zone of the habitat. However, we obtained negative results for *P. littorina* where these crustaceans occurred in substantial numbers.

LIFE CYCLE, POPULATION STRUCTURE AND ABUNDANCE

Little is known about the breeding and growth of *P. littorina* (Fretter & Graham 1978). The animals are probably annuals and the relatively broad diameter of the protoconch (400–430 microns) indicates that the animals develop directly from the eggs. The eggs are likely to be laid in crevices and possibly in low numbers. All of the animals found during our 2000 surveys in July (Isle of Wight) and September (Cornwall and Scilly) had shells of adult or near adult size. However, during a previous survey of sites in Pembrokeshire carried out in early March 1997, snails at varying stages of maturity were observed (Light & Killeen 1997).

The aim of survey work was to locate new sites for *P. littorina* rather than to attempt to quantify the populations. A feature of many of the positive sites was the low numbers of individuals found. At most of the cave sites less than 5 individuals were seen, and in some cases, only one. Only occasionally was *P. littorina* seen in larger numbers, namely in caves at Broad Haven, Pembrokeshire, Beer, Devon and Culver Cliff, Isle of Wight. Given the species' cryptic habitat, and the possible effects of the tidal cycle and weather conditions on the successful outcome of searching, identifying the true extent of populations is problematic and potentially destructive. At open shore sites higher numbers of individuals were recorded from interstitial habitats on unconsolidated substrate, particularly when found on large embedded or semi-embedded rocks and slabs. For example, 20 individuals were found on a single rock in the cove on the north coast of St Martins, Scilly.

CONSERVATION

In the UK, *Paludinella littorina* is protected under Schedule 5 of the Wildlife and Countryside Act (WCA) 1981, is listed in the British Red Data Book (Bratton 1991) as RDB3, Rare, and is included within the UK Biodiversity Action Plan (HMSO 1996). A significant number of the British *P. littorina* sites are within Special Areas of Conservation (SAC) designated under the European Union Habitats & Species Directive, or in Sites of Special Scientific Interest (SSSI).

Threats to British *P. littorina* populations potentially arise from construction of sea defences, coastal developments, slipways and landclaim. However, a significant number of the sites are in relatively remote places that are less likely to come under such threats and therefore few of the populations could be considered vulnerable. The most serious potential threat is from a major oil spill or the affects of the subsequent use of dispersants. However, a survey in Pembrokeshire and Caldey Island following the *Sea Empress* spill showed that there was no obvious evidence of damage to populations, at the known sites, by oil contamination (Light & Killeen 1997). Oiling also occurred in Porth Hellick, St Mary's (Scilly) from the wreck of the *Cita* in March 1997 (Roger Covey pers. comm.). Bunkers and light fuel oil covered the beach extensively. Rocks were scrubbed manually, whilst gravel and sand material was removed for mechanical cleaning and then replaced. The survival of *P. littorina* at these impacted sites suggests that interstitial habitats, particularly those protected by large rocks or boulders may be so stable as to be unaffected by surface oil coatings.

In light of the number and location of sites, there do not appear to be any special conservation or management measures necessary to ensure the survival of *P. littorina* populations. However if, as suspected, the animal is a direct developer and lays only a few eggs, it may have poor powers of dispersal and in the event of disappearance from a site the species' chances of recolonisation from neighbouring populations are low.

Excluding the Channel Islands, *P. littorina* is known to be living in sixteen 10km squares in Britain. As such, the species no longer fulfils an important criterion for its status in the British Red Data Book as a Rare species (i.e. that a species is thought to occur in 15 or fewer 10-km squares of the National Grid). If the status of *P. littorina* were reviewed, it would be classed as nationally scarce (i.e. found in 16 to 100 10-km squares). However, statuses can be changed only by the Joint Nature Conservation Committee after undertaking a national review of a group, therefore, the published Red Data Book status for *P. littorina* stands. The continued inclusion of *P. littorina* on Schedule 5 of the Wildlife & Countryside Act may no longer be merited on the basis of rarity or specific threat, although the presence at a site of a Schedule 5 species adds significantly to SSSI protection.

ACKNOWLEDGEMENTS

Parts of this study have been carried out under contract, or with research funding from the UK statutory conservation agencies which is gratefully acknowledged. The Countryside Council for Wales funded the 1994 survey in Pembrokeshire (Contract No. FC 73-01-103) and the follow-up in 1997 arising from the 1996 *Sea Empress* oil spill (Contract No. FC 73-02-77). English Nature provided a research grant for the 2000 survey of southern England (No. MAR 02-04-01). We also thank Chris Meecham, National Museum of Wales, Cardiff for the painting of a living *P. littorina*, and the Mollusca section of that Museum for access to the collections and imaging facilities.

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Fig. 4 Culver Cliff, Isle of Wight. Caves in the Chalk, only the cave on the right supports *P. littorina*

Fig. 5 Caldey Island, Pembrokeshire. Cave in Carboniferous limestone.

Fig. 6 Whitecliff Bay (north), Isle of Wight. Gravel upper shore with embedded limestone boulders. Site of Forbes & Hanley's 1853 record.

Fig. 7 Tresco, Isles of Scilly. Granitic boulder shore. *P. littorina* is common in the habitat in the foreground, but absent from the habitat in the background.

Fig. 8 Tresco, Isles of Scilly. Granitic boulder shore. Detail of *P. littorina* habitat.

Fig. 9 The Fleet, Dorset. Interstitial gravel habitat beneath *Suada* on the lagoon side of Chesil Beach.

CERNUELLA AGINNICA CONFIRMED AS A BRITISH SPECIES

RON CARR[1]

Abstract The suspected presence of Cernuella aginnica *(Locard) in the British Isles is confirmed. Specimens collected from a roadside in Kent are shown to differ from the closely related species* C. virgata *(Da Costa) on conchological and anatomical characters, in particular the relative size of the secondary dart sac.*

Dr Michael Kerney (1976) drew attention to the possible occurrence of the Continental Helicid *Cernuella aginnica* (Locard 1894) in the British Isles following the discovery by Dr Edmund Gittenberger of shells resembling that species which had been collected in Torquay, South Devon in 1955 and are currently in the collection of Leiden Museum, The Netherlands.

Although the occurrence of *C. aginnica* in England is referred to by Clerx and Gittenberger (1977) in their revision of the genus, the Torquay record has remained unsubstantiated due to lack of anatomical evidence. Conchologically, *C. aginnica* closely resembles *C. virgata* (Da Costa 1778), the shells of both species being subject to much variation and overlap. The co-existence of the two species has been recorded in Southern France (Clerx and Gittenberger 1977).

The shell of *C. aginnica* differs from that of *C. virgata* in being depressed, with the umbilicus usually larger, illustrations being provided by Kerney and Cameron (1979). Anatomically, Clerx and Gittenberger (1977) drew attention to the size of the dart sacs, the smaller empty sac being as broad as the larger, dart-containing sac (behind which it is situated) in *C. aginnica* but much narrower than the dart-containing sac in *C. virgata.*

In October 2000, a number of snails were collected from a roadside verge at Grange Lane, Sandling, on the northern outskirts of Maidstone, Kent (TQ 762583). The shells (fig. 1) resembled *C. virgata* but were observed to be more depressed than usual and one specimen in particular had an unusually larger umbilicus. Dissected material was forwarded to Dr Gittenberger, who has confirmed the identity of *C. aginnica.*

The internal anatomy of a Maidstone specimen is illustrated in Fig. 2 (1) with that of a typical specimen of *C. virgata* from Dover (2).

Grange Lane is a quiet country road which runs roughly parallel with and partly alongside the main M20 London to Folkestone motorway. The site at which *C. aginnica* was collected is a typical habitat for the genus, being exposed, south-facing and which suffered some minor disturbance due to the widening of the adjacent motorway several years previously. Some species present included *Candidula gigaxi* (Pfeiffer 1850), *Monacha cantiana* (Montagu 1803) and *C. virgata.*

Among many other named varieties of *C. virgata* occurring in Britain, Ellis (1926) includes var. depressa Requien "shell depressed with a wider umbilicus", a description that could well refer to *C. aginnica* and which may imply that the species has been present in the country for some considerable time.

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[1] 9 The Mallows, Maidstone, Kent, ME14 2PX.

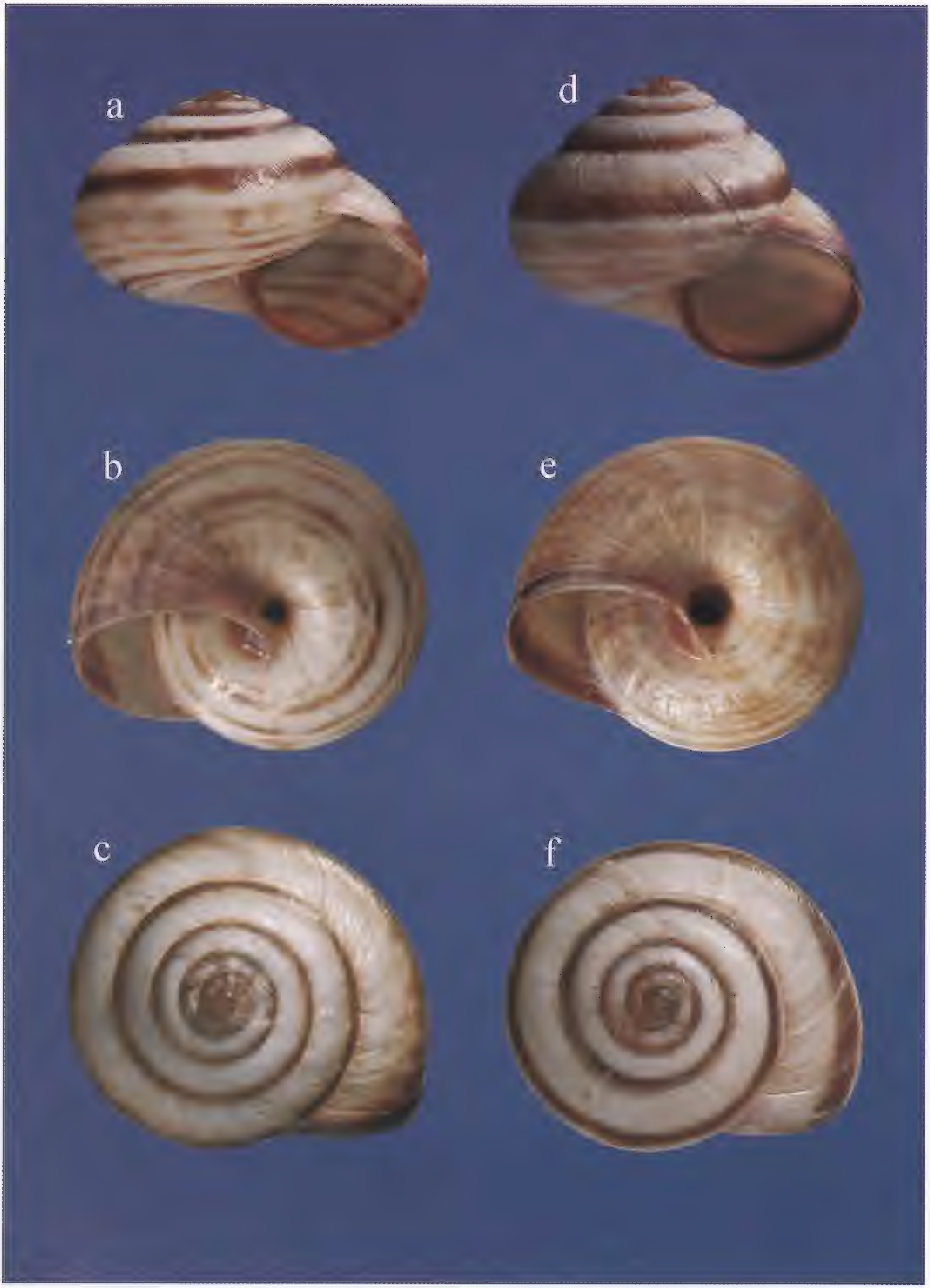

Figure 1 **a–c** *Cernuella aginnica* (Locard) Maidstone. Specimen with unusually narrow umbilicus. **d–f** *C. virgata* (Da Costa).

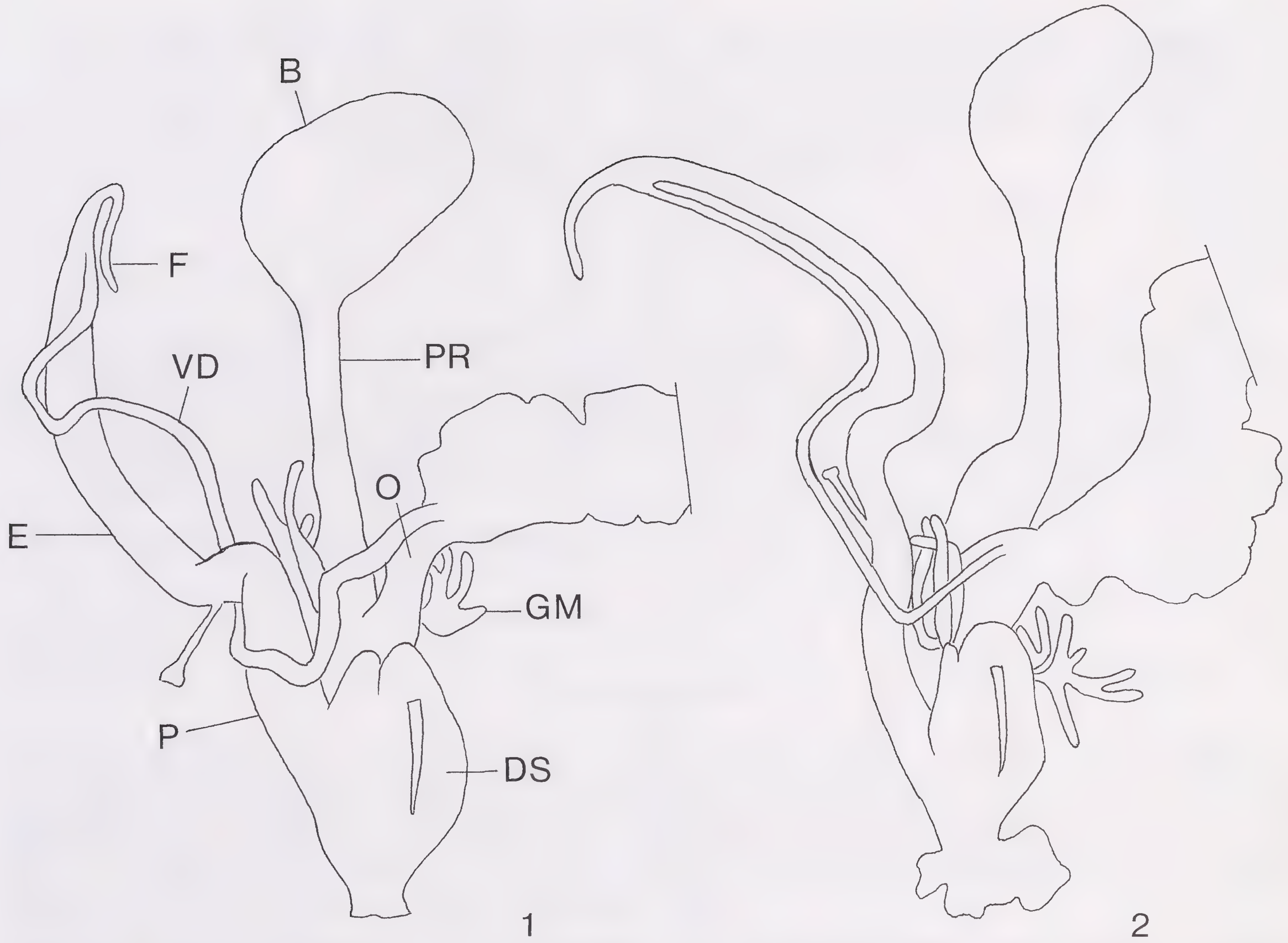

Figure 2 **1** *Cernuella aginnica* (Locard) Maidstone B=Bursa DS=Dart Sac E=Epiphallus F=Flagellum GM=Glandula Mucosa O=Oviductus P=Penis PR=Pedunculus of the Receptaculum Seminis VD=Vas Deferens **2** *C. virgata* (Da Costa) Dover

ACKNOWLEDGEMENTS

My thanks are conveyed to Dr Edmund Gittenberger for his examination of dissected material and helpful comments.

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GEOGRAPHICAL VARIATION OF TAXA IN THE GENUS *RUMINA* (GASTROPODA: SUBULINIDAE) FROM THE MEDITERRANEAN REGION.

RON CARR[1]

Abstract *Conchological data is presented showing that two different taxa can be identified in parts of the Mediterranean, supporting conclusions in previous studies. The genital anatomy of material of the genus* Rumina *from these regions has been investigated. The specimens recognised as* Rumina decollata *(Linnaeus, 1758) and* R. saharica *Pallary, 1901 show differences in the internal structure of the penis. This character requires further investigation, but indicates the need for a wider review of anatomical and molecular characters.*

Key words Rumina, *Subulinidae, Conchological, Mediterranean, Anatomy.*

INTRODUCTION

The characteristic genus *Rumina* Risso, 1926 with decollate shells is well distributed throughout the Mediterranean region and also the United States, where it had become established as recently as 1822 (Pilsbry, 1946). Prior to the nomenclatural revision by Bank and Gittenberger (1993), the genus was considered to be represented by a single species, namely *Rumina decollata* (Linnaeus, 1758).

Bank and Gittenberger (1993) reviewed the status of small, subcylindrical shells typical of the east Mediterranean region that had been given various sub-specific names and showed these taxa were similar to Pallary's "var *saharica*" from Algeria (1901). Using conchological characters they recognised two distinct species, *R. decollata* and *R. saharica,* however subsequent authors such as Giusti and Manganelli (1995) recognise only *R. decollata* as a valid taxon.

This paper provides comparative anatomical information, the study of which has hitherto been neglected. Material from a representative range of localities within the Mediterranean region has been dissected for this purpose. Scatter plots of penis/vagina width ratios and shell dimensions are also included in order to provide correlations of anatomical differentiation with shell size and the biogeography of the two species within the Mediterranean region is briefly discussed.

MATERIAL AND METHODS

Preserved spirit material was dissected and drawn using a light binocular microscope equipped with a drawing tube and micrometer eye piece. Measurements were made of the total shell length and width (across the last whorl) with a vernier caliper to the nearest 0.1mm.

ABBREVIATIONS FOR COLLECTIONS

BMNH British Museum (Natural History) CRC Collection R. Carr LMRC Leeds Museum Resource Centre NMGW National Museums & Galleries

Additional abbreviations sp = specimens preserved in spirit sh = dead shell only

Material examined Algeria 5sh (BMNH) 1sp (NMGW) Crete 17sh (CRC) Croatia 1sh

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[1] 9 The Mallows, Maidstone, Kent ME14 2PX.

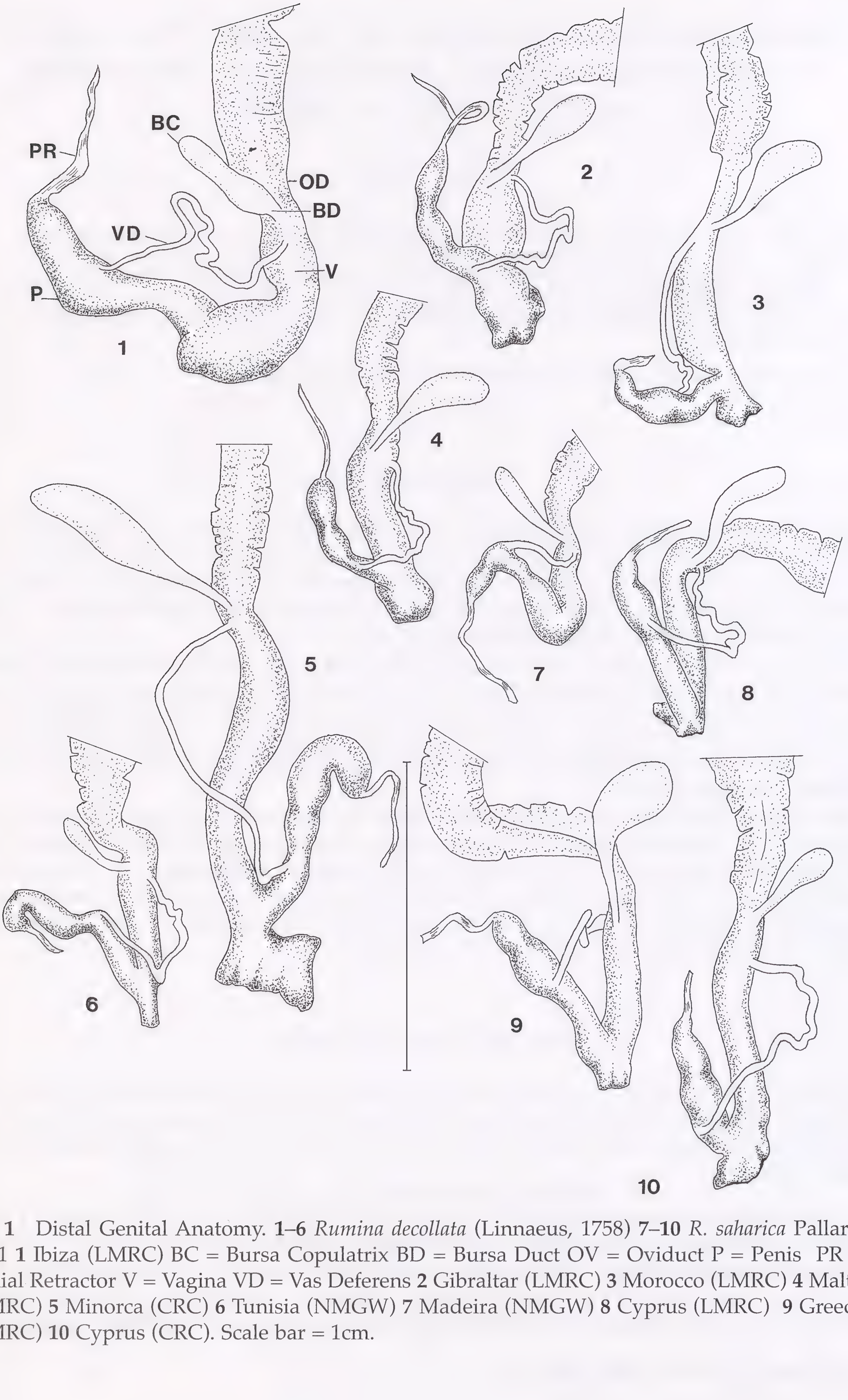

Fig 1 Distal Genital Anatomy. **1–6** *Rumina decollata* (Linnaeus, 1758) **7–10** *R. saharica* Pallary, 1901 **1** Ibiza (LMRC) BC = Bursa Copulatrix BD = Bursa Duct OV = Oviduct P = Penis PR = Penial Retractor V = Vagina VD = Vas Deferens **2** Gibraltar (LMRC) **3** Morocco (LMRC) **4** Malta (LMRC) **5** Minorca (CRC) **6** Tunisia (NMGW) **7** Madeira (NMGW) **8** Cyprus (LMRC) **9** Greece (LMRC) **10** Cyprus (CRC). Scale bar = 1cm.

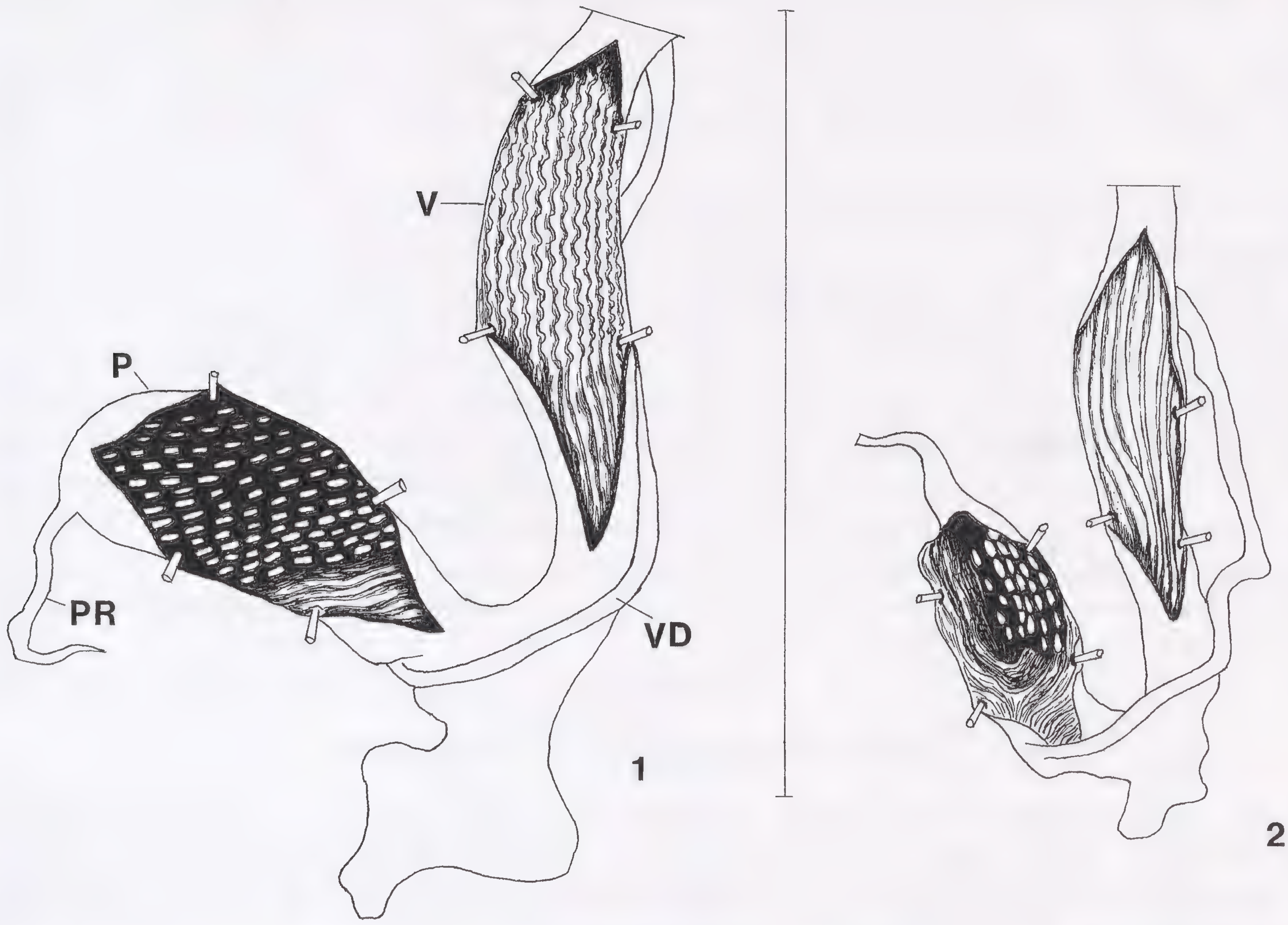

Fig 2 Internal Structure of Penis and Vagina **1** *Rumina decollata* (Linnaeus, 1758) P = Penis PR = Penial Retractor V = Vagina VD Vas Deferens **2** *R. saharica* Pallary, 1901. Scale bar = 1cm.

(LMRC) Cyprus 18sp (LMRC) 4sh 1sp (CRC) Egypt 14sh (BMNH) France 3sh (LMRC) Gibraltar 6sp 11sh (LMRC) Greece 30sp (LMRC) Ibiza 15sp (LMRC) Israel 5sh (BMNH) Italy 3sh (LMRC) Madeira 3sp (NMGW) Malta 4sp (LMRC) Majorca 3sh (CRC) Minorca 12sh 4sp (CRC) Morocco 13sp (LMRC) 45sh (NMGW) Sardinia 2sh (BMNH) Sicily 3sh (BMNH) Spain 12sh (BMNH) 8sh (CRC) Tenerife 5sp (LMRC) Tunisia 1sp (NMGW) Turkey 6sh (BMNH).

Genital anatomy This work is primarily concerned with the anatomical structures located proximal to the genital aperture, which are commonly utilised as diagnostic criteria. A comprehensive anatomical description of the Subulinidae is provided by Naggs (1994). Previous illustrations of the genital anatomy of *Rumina* are to be found in Germain (1930) Giusti (1970) and Pilsbry (1946).

The genus is known to reproduce by facultative self fertilisation (Selander and Kaufman, 1973) to which the wide variety of shell forms and also observed anatomical diversity is no doubt attributable. Dundee (1986) refers to the occurrence of cross fertilisation in *R. decollata* which has also been observed nocturnally by the author on captive snails from Minorca. Specimens of *R. decollata* from Minorca and *R. saharica* from Cyprus kept individually in containers produced eggs which failed to hatch, whereas eggs deposited in a container containing a number of *R. decollata* hatched within 59 days. It is therefore considered reasonable to assume that some degree of interspecific differentiation can be anticipated to occur within the genital system of the two species.

The genital system of *Rumina* is primitive and lacks secondary sexual appendages such as a dart sac and mucous glands (Figs 1 and 2). It consists of a muscular vagina and muscular penis which are of a similar length. The penis is swollen at its proximal end into a bean or a pear-shaped structure which is highly variable in shape and often

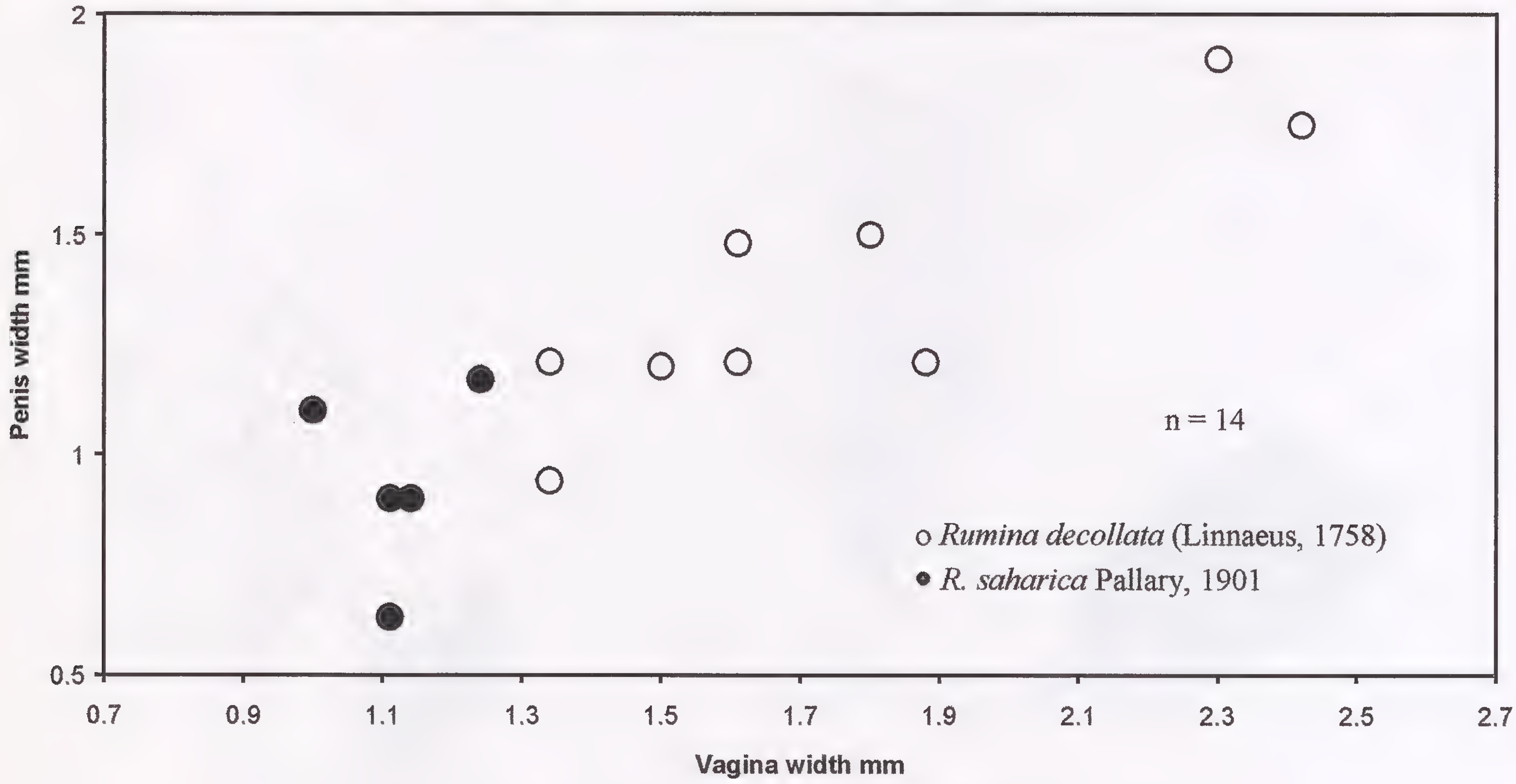

Fig. 3 Penis width plotted against Vagina width

convoluted, particularly in *R. decollata,* and to which is attached the long penial retractor muscle. Close to its point of origin, the vas deferens is located within a narrow groove situated within the muscular sheath of the penis. The bursal duct is relatively short and terminates in a sack-shaped bursa copulatrix.

Specimens (n=9) identified as *R. decollata* on conchological characters from the west Mediterranean region, Canary Islands and North Africa (Plate 1) were dissected and found to display much distortion in the swollen section of the penis, which extends approximately one half to three quarters of the total length of the structure (Fig. 1, 1–6). The most elaborate examples, which resemble the shape of a centrally constricted bean, were observed from Gibraltar (Fig. 1, 2), Morocco (Fig. 1, 3) and Tunisia (Fig. 1, 6).

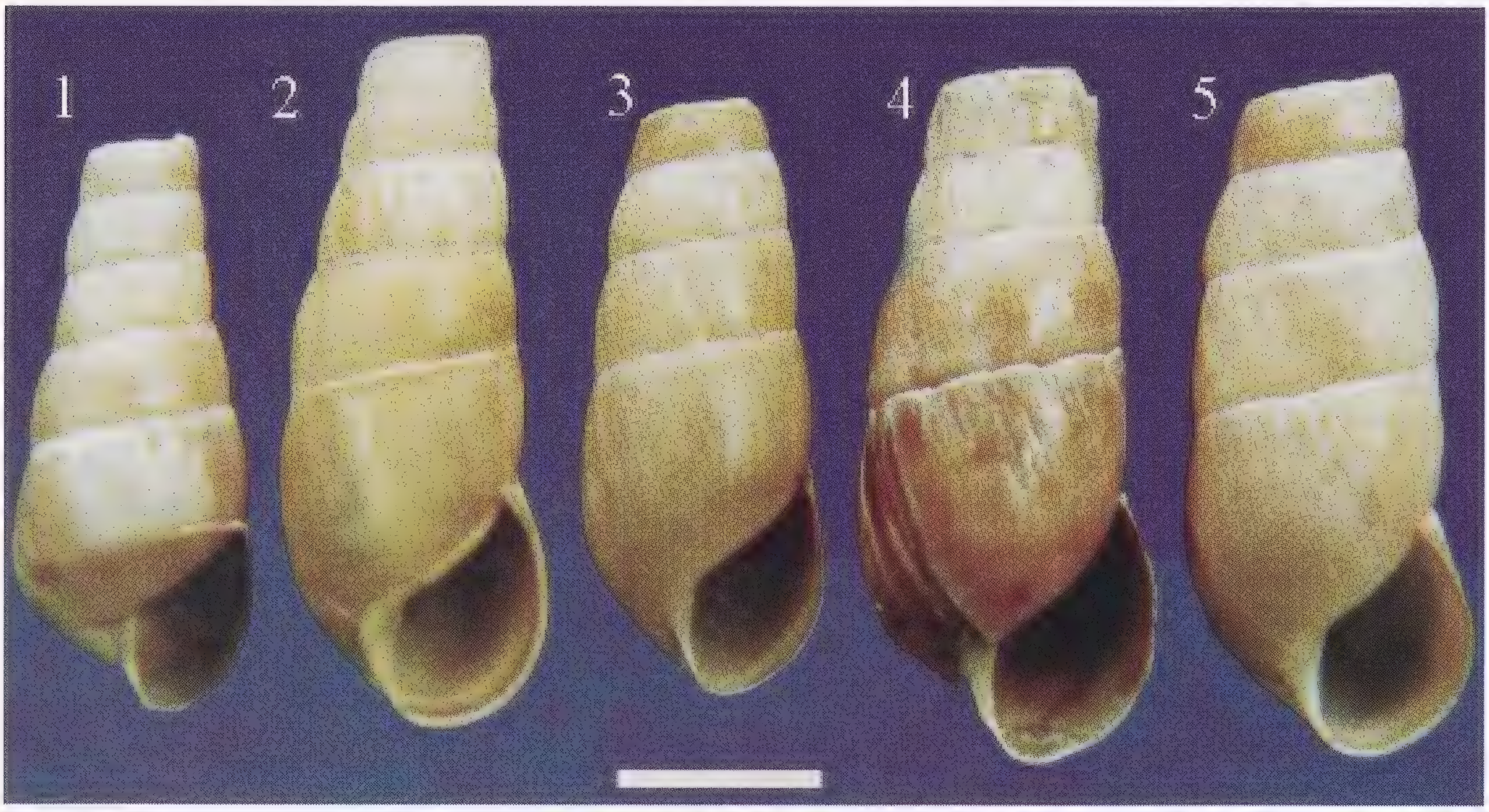

Plate 1 *Rumina decollata* (Linnaeus, 1758) **1** Malta (LMRC) slightly immature shell **2** Minorca (CRC) **3** Tenerife (LMRC) **4** Ibiza (LMRC) **5** Spain (CRC) Scale bar = 1cm.

However, one of the more distinctive differences is seen internally (Fig. 2, 1), where the distal end of the penis contains transverse lamellae which rapidly separate into abundant, prominent papillae towards the centre and proximal section. In the majority of specimens, the vagina was found to be broad and flattened, internally with longitudinal, crenulated lamellae.

Smaller, subcylindrical shells from Cyprus, Greece and Madeira (Plate 2) were identified on conchological grounds as *R. saharica*. Following dissection of their contents (n=5), these specimens were observed to display intraspecific similarities anatomically (Fig. 2, 7–10). The swollen section of the penis was found to be characteristically pear-shaped, usually extending no more than half the total length of the organ. Internally (Fig. 2, 2), the distal section of the penis contains transverse lamellae which gradually separate into sparsely distributed, obscure papillae towards the proximal end. The structure of the vagina is narrow and tubular, internally with longditudinal lamellae.

A positive correlation is demonstrated in Fig. 3 by the relationship of penis width to vagina width observed in dissected specimens, the width of each organ falling within a range of 1.24mm in *R. saharica*.

Anatomical measurements (mm)

	R. dellocata		*R. saharica*	
	range	mean	range	mean
Penis length	4.90–7.50	6.01	3.71–5.60	4.72
Penis width	0.94–1.90	1.37	0.90–1.17	0.94
Vagina length	5.07–9.40	6.24	3.84–8.00	5.32
Vagina width	1.34–2.42	1.95	1.00–1.24	1.11

Animal morphology

Body colour	dark grey	light grey
Foot colour	yellow-grey	light grey-brown

Observations were carried out on living specimens from Minorca (*R. decollata*) and Cyprus (*R. saharica*). Distinctions in body colour were evident, particularly that of the foot, though variation in body morphology should be treated with some degree of caution as it is likely to be affected by local diets of snail populations (Jordaens *et al.*, 2001).

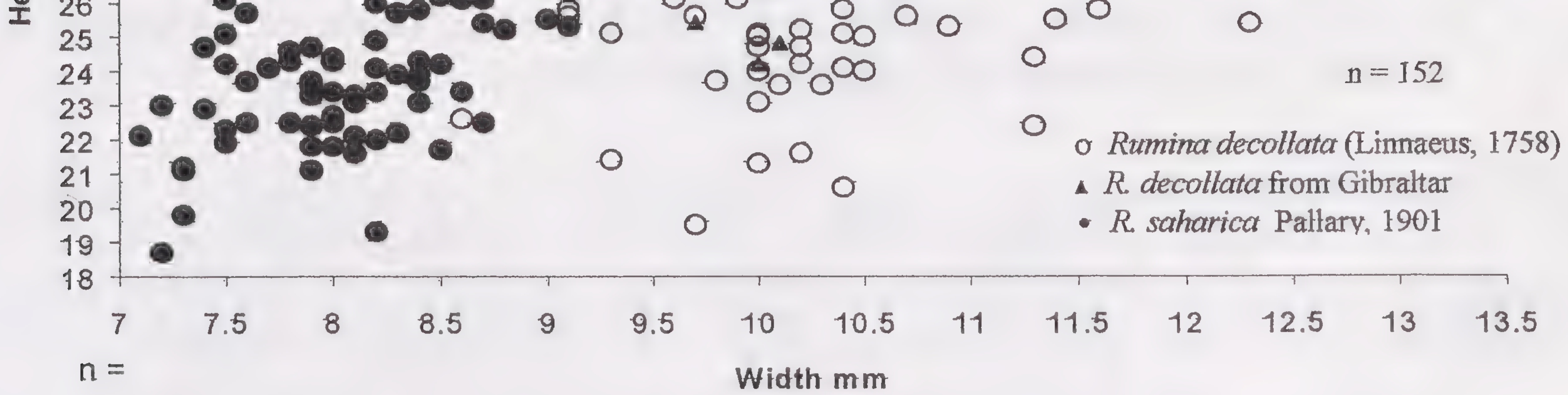

Fig. 4 Canary Islands, Europe, Israel, Madeira & Turkey

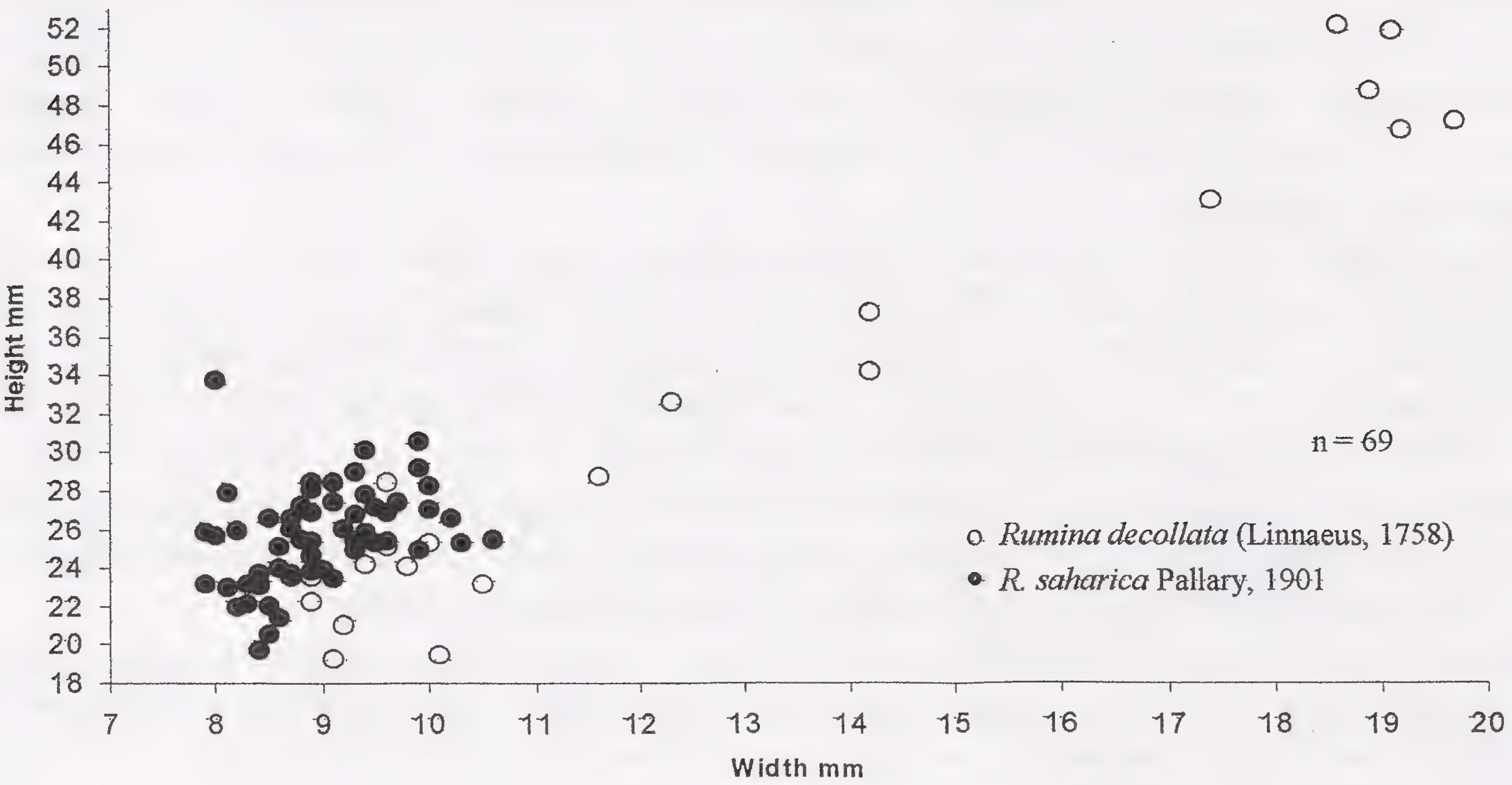

Fig. 5 North Africa

Shell measurements An extensive number (n=221) of shell specimens have been measured, the results of which are presented in Fig. 4 and Fig. 5. Conchologically distinct specimens from the west and east Mediterranean regions including the Canary Islands and Israel are presented in Fig. 4 (n=152), north African specimens are presented in Fig. 5 (n=69).

There is invariably some overlap in shell height between the two species particularly due to the decollate nature of the shell, which breaks at an early age in virtually all specimens. Shell width is therefore seen as a more reliable criterion, particularly in Fig. 4, where all east Mediterranean specimens of *R. saharica* fall below 9.5mm. Information provided by Mylonas and Vardinoyannis (1989) concurs with this viewpoint, mean dimensions for shells from the Greek island of Macronissos being cited as 21.4mm height, 7.7mm breadth.

The situation in north Africa presented in fig. 5 becomes more obscure. Shell specimens identified as *R. saharica* occasionally exceed 10mm width, though still maintain a comparatively cohesive scatter cluster when compared with the diversity of shell size displayed by *R. decollata* in that region (Plate 3, 1). Monstrous shells of the latter species up to 52mm height, 19.7mm width are well represented in the Holyoak - Seddon Collection (NMGW), the majority of these appearing to have been collected at altitudes of less than 800m above sea level, whereas *R. saharica* has been found at elevations in excess of 1400m. Shells of *R. decollata* exceeding 30mm height, 14mm width from Sardinia and Sicily are also contained within the collection of the BMNH.

Three notably cylindrical shells morphologically resembling *R. saharica* were observed within a batch of *R. decollata* collected at Europa Point, Gibraltar (LMRC) (Plate 3,3). These shells plotted well within the size range of the latter species (Fig. 4). A dissected specimen also displayed genital anatomy very similar to that of north African *R. decollata* (Fig. 1, 2) and the specimens are therefore attributed to that species.

Shell dimensions (mm)

	R. decollata		*R. saharica*	
	range	mean	range	mean
Shell height	19.3–52.2	29.7	17.7–33.7	23.2
Shell width	8.9–19.7	11.8	7.1–9.4	8.4

Plate 2 *Rumina saharica* Pallary, 1901 **1** Argos, Greece (LMRC) **2** Sparta, Greece (LMRC) **3** Cyprus (LMRC) **4** Madeira (NMGW) containing preserved snail **5** Crete (CRC) Scale bar = 1cm.

BIOGEOGRAPHY

Distributional data acquired from British museum collections supports that presented by Bank and Gittenberger (1993). Shells attributable to the current concept of *R. decollata* have been examined from the Canary Islands, throughout the Mediterranean region and Balearic islands as far east as Croatia. Specimens have also been observed from Turkey (Ephesus), Algeria, Tunisia and Morocco. Since its first introduction into the United States, the species has spread as far as Mexico and Cuba (Selander and Kaufman, 1973). *R. saharica* appears to occur mainly in the east Mediterranean region (Cyprus, Greece and Turkey), throughout north Africa, and the Middle East. Shells closely resembling *R. saharica* from Israel (Plain of Sharon) and Sicily together with sub-fossil material from southeast Spain (Paibilla Mountains) are contained within the collection of the BMNH. The occurrence of the species in Madeira is no doubt attributable to human dispersal through trade routes.

Guiller *et al*. (2001) have demonstrated genetic differentiation among populations of *Helix aspersa* Müller in North Africa with the implication that gene flows were prevented between eastern and western populations following plate tectonic activity via the Tellian Atlas Chain during the Pliocene. A similar North Africa east-west divide may well have occurred in *Rumina*, with subsequent disjunct colonisation taking place by both species due to the high dispersal ability of the genus.

DISCUSSION

Anatomical evidence presented within this study is considered generally supportive of the opinion held by Bank and Gittenberger (1993) that *R. dellocata* and *R. saharica* comprise separate taxa. Conversely, some confusion may arise if only conchological material is available, particularly from areas where the sympatric occurrence of the two species is evident, e.g. Madeira, North Africa, Spain and Turkey.

Electrophoretic analysis undertaken by Selander and Kaufman (1973) detected no

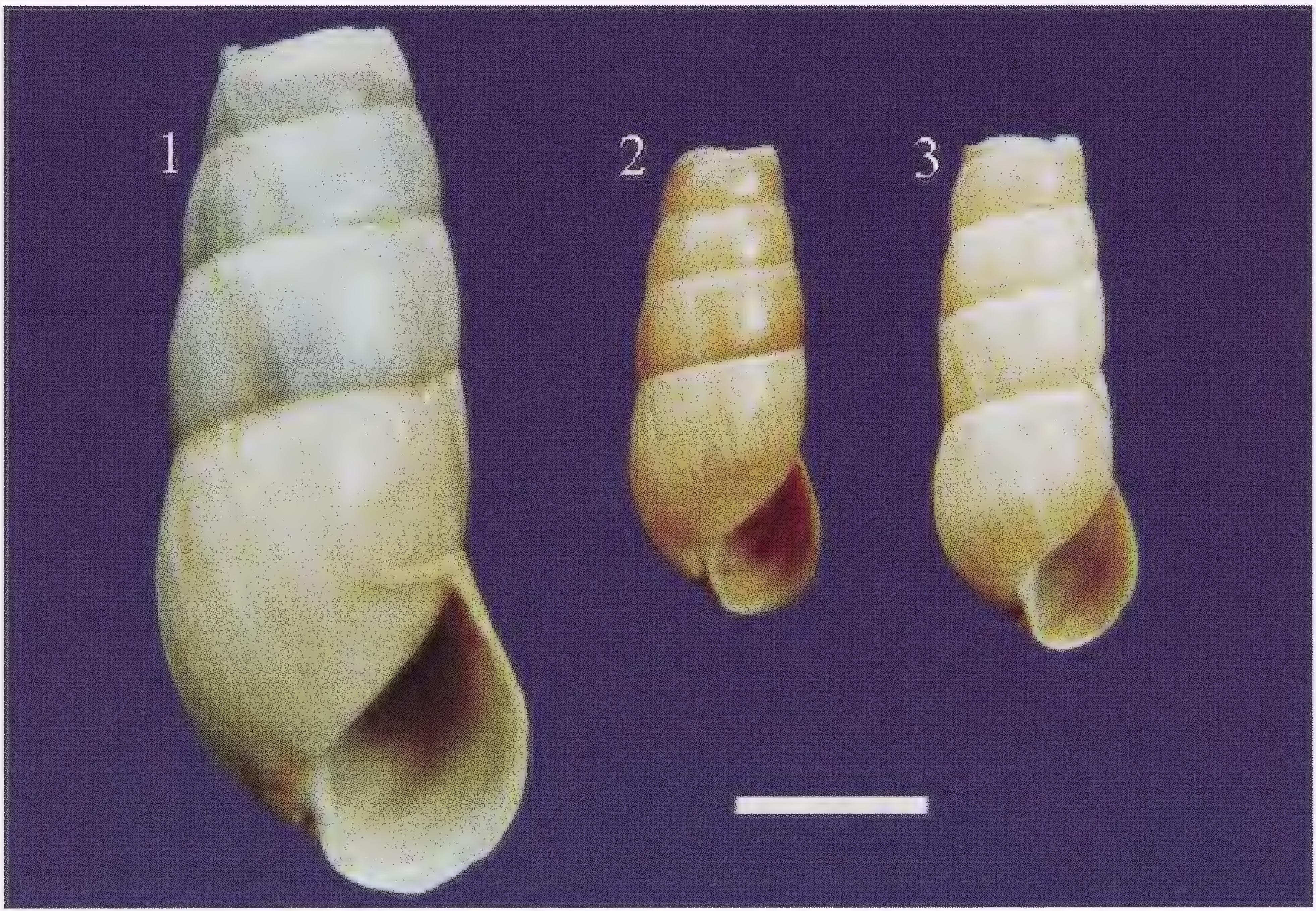

Plate 3 *Rumina decollata* (Linnaeus, 1758) **1** Algeria (NMGW) **2** Morocco (LMRC) **3** Gibraltar (LMRC) Scale bar = 1cm.

genetic variation in populations of *R. decollata* from the United States, though samples from Tunisia were found to share alleles and morphological features that distinguished them from French strains.

Although many shells of this widespread genus are available in museum collections, very little material has been preserved in spirit for anatomical study. Specimens collected in the future, particularly from north Africa, would probably repay further study at both anatomical and molecular level, with the possible discovery of additional taxa.

ACKNOWLEDGEMENTS

I am particularly indebted to Mr Adrian Norris (LMRC) who kindly provided most of the preserved spirit material examined in this study, all of which was collected by himself. I am also very grateful to Dr Mary Seddon (NMGW) for access to collections and the loan of preserved material. Sincere thanks are conveyed to Dr P. Mordan and Dr F. Naggs (BMNH) for access to collections and helpful advice with literature. Miss Eleanor Fogan and Dr Robert Angus painstakingly provided live specimens and Dr David Bilton kindly assisted with literature. Thanks are also conveyed to Jeannette Freeman for her assistance in compiling the manuscript.

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A NEW POLISH RECORD FOR *MYXAS GLUTINOSA* (MÜLLER)

The lymnaeid snail *Myxas glutinosa* (the glutinous snail) is one of Europe's most endangered freshwater molluscs and has recently been suggested as a candidate for inclusion in the European Union Habitats Directive of specially protected species (Bouchet *et al.* 1999).

Recent records for *Myxas* in Europe are extremely scarce. In the United Kingdom the only currently known population is in Llyn Tegid in Wales (Willing and Holyoak 1998). A population rediscovered in the Oxford area in the late 1980s (Walker *et al.* 1991, Whitfield *et al.* 1998) can no longer be found despite a number of searches. In Finland, Ralf Carlsson has found *Myxas* recently in four lakes out of 51 searched in the Åland Islands (Carlsson, 2001). In Ireland, animals have been found during 2000 and 2001 in the Grand Canal near Dublin (Mary Harris, pers. comm.) and in 2001 in Lough Sheelin, Co. Cavan (Willing, 2001). One other recent record has also come to light in the Netherlands where several specimens were found in the Westbroekse Zodden area near De Egelshoek on 13 May 2000 during an excursion of the Dutch Malacological Society. The location is in the central part of the Netherlands, about 30 km. southeast of Amsterdam (Robert Reuselaars, pers. comm.). A picture of a live specimen from this location has been posted at http://www.rer-swgd4u.freeler.nl/excursions.htm.

Given the rarity of *Myxas* it was, therefore, with considerable pleasure that the present authors found two fully grown *Myxas* in a small unnamed lake in the Glazowisko Rutka geological reserve on 14th June 2001, approximately 15 km north of Suwalki in north-east Poland. The snails were found amongst aquatic mosses growing on the margins of vertically sided peat cuttings in fen vegetation on the edge of the lake. The peat pools were about 100 m^2 in area and isolated from the main waterbody with clear water and a rich aquatic flora, including *Stratiotes aloides* (Water-soldier), *Utricularia* sp.(bladderwort), *Potamogeton crispus* (Curled Pondweed) and *Myriophyllum spicatum* (Spiked Water-milfoil). Water quality in the pools appeared to be good, probably reflecting the fact that the surroundings of the lake are non-intensively managed grassland. A brief search of the lake itself failed to locate any *Myxas* specimens.

Given the rarity of *Myxas glutinosa* in Europe we would be pleased to hear of any other recent records of the species.

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THE STANDARDIZATION OF ABIOTIC VARIABLE DATA COLLECTION IN LAND MOLLUSC RESEARCH

The relationships between abiotic and biotic variables can provide insights into how communities are structured and factors that affect species abundances, diversities and distributions[1,2,3]. Different research fields often follow set methods for data analysis, tending to constrain the interpretation of results[4]. In marine ecological investigations, including those involving molluscs, abiotic variables are frequently used as explanatory factors[5,6]. Land mollusc research tends to have followed a different path. A large proportion of this work has concentrated on aspects of taxonomy and species presence/absence at sites. Ecological investigations are generally limited to brief descriptions of habitats adjoined to taxonomic work.

Recently, however, there has been a marked interest in topics related to land mollusc ecology and this is influenced by current research in biodiversity[7,8]. A feature of many papers that deal with abiotic variables is that there is no, or at best very little, attempt to standardize the collection of these variables. Variables are often subjectively recorded providing little or no possibility for rigorous statistical analysis. This prevents the comparison of data from different studies to be effectively undertaken. In this paper I present a simple system for recording abiotic variables for land mollusc ecology research. Species data recording for mapping work (e.g. for distributional atlas recording) often does not require the collection of variable data as described in this paper because species presence/absence is mostly interpreted using published large-scale data including geology and climatic patterns. Abiotic data collection in these cases could hinder mapping progress because many recorders would not undertake fieldwork if the requirement for collecting this data was imposed.

Here, abiotic variables are considered to be any variables other than the species matrix. These are sometimes termed environmental variables by some authors although this is strictly incorrect as the latter term includes both biotic as well as abiotic variables[9]. It is not possible to include all variables that may influence biotic patterns and generally knowledge of the taxa under study provides an indication of those variables that may be important. The system used here covers a range of variables, which are known to influence land mollusc ecology[10,11,12,13,14,15,16]. These encompass small-scale (e.g. Condition of leaf litter) as well as large-scale (e.g. Latitude) variables. This allows the subsequent analysis of data at varying scales.

The variables (shown in the Table, with accompanying brief notes) are either obtained from published literature (e.g. Type of rock) or from measurement in the field (e.g. Area covered by vegetation). The latter are easy to measure and data collection should be within the ability of those not experienced with such work, hopefully encouraging non-ecologists to attempt the recording of abiotic data at specimen collection points.

Number of species and abundances, as well as abiotic variables, require quantification using standardized techniques. These data then allow analyses to be performed that provide objective explanatory information on patterns of number of species, abundances, diversities and distributions. There are many methods available for this including Multidimensional Scaling (MDS), Canonical Correspondence Analysis (CCA) and Cluster Analysis[1,2,6,17,18].

The collection of abiotic variables in conjunction with a quantified specimen collecting strategy[19] provides the best data for detailed ecological work but even a reduced number of variables than those proposed here is worthwhile. As an example, how much more useful would species lists be to those that want to use them for biogeographic analyses if the lists also included soil pH, vegetation type and percentage cover of rocks?

TABLE SHOWING ABIOTIC VARIABLES

VARIABLE	**NOTES**
Altitude	Using altimeter
Latitude	GPS measurement is preferable
Longitude	GPS measurement is preferable
Age of rock	
Type of rock	
Rainfall	Yearly mean[1]
Temperature	Yearly mean[1]
Sunshine hours	Yearly mean[1]
Wind speed	Yearly mean[1]
Wind duration	Yearly mean[1]
Slope angle	
Aspect	
Area covered by rocks	Percentage
Area covered by soil	Percentage
Area covered by leaf litter	Percentage
Area covered by water	Percentage
Linear distance to nearest town/village	
Road/tracts	Presence/Absence
Buildings	Presence/Absence
Domestic animals	Presence/Absence
Area covered by vegetation	Using DOMIN scale[2]
Cover of 0-5cm vegetation layer	Using DOMIN scale[2]
Cover of 5-10cm vegetation layer	Using DOMIN scale[2]
Cover of 10-15cm vegetation layer	Using DOMIN scale[2]
Cover of 15-20cm vegetation layer	Using DOMIN scale[2]
Cover of 20-50cm vegetation layer	Using DOMIN scale[2]
Cover of 50-100cm vegetation layer	Using DOMIN scale[2]
Cover of 100-1000cm vegetation layer	Using DOMIN scale[2]
Cover of >1000cm vegetation layer	Using DOMIN scale[2]
Nature of soil	Gravel/Sand/Silt/Clay/Loam[3]
pH of soil	
Moisture of soil	Dry/Moist/Wet
Moisture under rocks	Dry/Moist/Wet
Nature of leaf litter	Leaves:Small/Medium/Large/Small & Medium/Small & Large/Medium & Large/Small & Medium & Large
Condition of leaf litter	Leaves:Fragmented/Intact/Fragmented & Intact
pH of leaf litter	
Moisture of leaf litter	Dry/Moist/Wet
Erosion	None/Minimal/Moderate/Marked
Hydrochloric acid reaction of rock	Positive/Negative
Texture of rock	Smooth/Rough/Smooth & Rough
Macrotopography of rock surfaces: crevices and holes >10cm	None/Few/Moderate/Many
Microtopography of rock surfaces: crevices and holes <10cm	None/Few/Moderate/Many
1st most abundant plant	
2nd most abundant plant	
3rd most abundant plant	
4th most abundant plant	
5th most abundant plant	

FOOTNOTES:

[1] Yearly means, standard deviations and ranges are preferable if these are available.

[2] The DOMIN scale is preferable to other scales, such as the DAFOR scale, because percentage cover gives more information than measures of dominance. Here the vegetation is objectively quantified by height and concentrates on the lower levels (which may be most relevant to land molluscs) but some authors prefer to classify the vegetation into herb, shrub, tree levels etc. The main problem with this approach is that some species (e.g. *Olea europaea* L. and *Pistacia lentiscus* L.) are present in more than one class (shrub and tree in this case) both intra- and inter-site. This a priori classification of vegetation, based on species composition, also requires a good knowledge of plant identification and if this is not the case the worker is classifying by height anyway which logically leads to the approach preferred in this paper.

[3] Additional edaphic variables such as calcium, phosphate, magnesium and phosphate concentrations can also be measured.

A.E. Boycott (1934)20 was perhaps ahead of his time encouraging collectors to test the pH of soil in the field when he wrote: 'Hence a bottle of 20 per cent. Hydrochloric acid (which wrapped in a rag does no harm in the pocket) is an essential part of the collector's equipment and each locus can be tested directly.'

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GIRAUDA BGT. (GASTROPODA, THIARIDAE) A LATER HOMONYM

Whilst working through Ichneumon records for supplement 34 of the Wild Fauna and Flora of Kew I encountered the genus *Giraudia* Förster and immediately remembered there was a genus of the same name erected by Bourguignat for some thalassoid snails from Lake Tanganyika. Förster[1] proposed his name for a genus of Hymenoptera Icheumonidae in 1868 and is a valid name in use. Bourguignat's[2] homonymous name dates from 1885. David Brown[3] does not recognise this genus but Pilsbry and Bequaert[4] treat it as a subgenus of *Baizea* Bgt. 1885.

It seems worth while to point out that it cannot be used as a genus or subgenus in the Mollusca.

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B. Verdcourt

REVIEW

Atlas of the land and freshwater molluscs of Cornwall and the Isles of Scilly. Stella M. Turk, Hazel M. Meredith and Geraldine A. Holyoak. ERCCIS Publication No. 1, Environmental Records Centre for Cornwall and the Isles of Scilly, 2001. 136pp. ISBN 1-902864-01-8. Cost 17.50 pounds Sterling (12 to Conchological Society Members) plus 4.00 postage and packing.

Cornwall has been in the forefront of biological recording in the UK with the development of computerised databases long before the establishment of biological records centres in other counties. This non-marine mollusc atlas represents the first in a new series of publications and comprises a synthesis of all mollusc records to the end of 1999. This well-presented, softback A4 book has a glossy green cover with a photograph of a living *Ashfordia granulata*, six pages of introductory text, and a page each for the 122 species recorded from Cornwall. The species' pages comprise a tetrad (2 x 2km) map with records discriminated as pre- and post-1965, a smaller map showing distribution by hectad (10 x 10km), Latin and vernacular names, size, a black and white illustration, and a few lines of text on habitat, modern and sub-fossil records. The national status of species according to the criteria in the British Red Data Book is given. However, there is no mention of those (2) species legally protected under Schedule 5 of the UK Wildlife and Countryside Act 1981, for which a license is required for collection.

The non-marine malacofauna of Cornwall is impoverished compared with most of England and this is clearly seen in maps in the national Atlas, (Kerney 1999). This is largely due to absence of calcareous rocks. The freshwater fauna is especially poor; many species which are abundant further east are absent and even some otherwise ubiquitous lymnaeids and planorbiids are uncommon.

The inclusion of a map showing distribution both by hectad in addition to tetrad is very useful and reinforces the value of presenting data on a smaller scale. Distributions not evident from hectad scale are clearly revealed at tetrad scale, e.g. the almost exclusively coastal distribution of helicellids. For others e.g. *Zonitoides excavatus*, the hectad map (with 24 dots) suggests that the species is common and widespread throughout the county, yet the tetrad map with only 30 dots demonstrates the over-simplification of the larger scale. Comparison of the maps for the two *Cepaea* species shows that in Cornwall *C. nemoralis* is considerably commoner than *C. hortensis*, whereas there is good evidence from other parts of the country that *C. nemoralis* is declining and *C. hortensis* is spreading. Interpretation of the distributions would have been greatly assisted by the inclusion of a coverage map showing the number of species recorded from each tetrad. This would show which parts of the county support the most diverse molluscan fauna and highlight areas for which there is the greatest scope for further work. The areas south west of Newquay, the St Ives peninsula and the Helford river valley, appear to support the greatest diversity, but they may well also be the most intensively recorded areas. The eastern part which includes Bodmin Moor appears to be the most impoverished, but it may be that the area has received the least attention.

Regardless of the sparsity of habitats likely to support a diverse molluscan fauna, many species are clearly under-recorded and this is acknowledged by the authors. There are few segregate records for the *Arion hortensis* and *A. circumscriptus* complexes. Small species which are tolerant of poorer conditions (e.g. *Columella aspera, Vertigo substriata*) are likely to be more widespread, and with only 11 records for *Punctum pygmaeum*, there is much scope for sampling woodland leaf litter! As is often the case with mollusc data, *Pisidium* are under-recorded. However, comparison of the map for *P. personatum* (<30 records), which is a species likely to be widespread, with that for *Potamopyrgus* *antipodarum* (*c.* 175 records), suggests that *Pisidium* are neglected when aquatic habitats have been sampled.

Is there a need for a publication such as this, particularly as it does not represent the results of a detailed or a systematic survey? The opening line of the Foreword states: "This atlas is intended to stimulate interest in non-marine molluscs and is advisedly deemed provisional since there doubtless are more species and certainly more records to be discovered". This not only applies to Cornwall but to many other areas in Britain. It is fair to say that recording non-marine molluscs in this country is at a rather low ebb; a new national atlas has been published which inevitably leads to a belief that work is completed. Also, malacologists involved in county surveys find it difficult to find enough time to maintain the enthusiasm and momentum for such a major undertaking. Any such project should ultimately fulfil the requirements of the end users, i.e. the conservation agencies. These call for up-to-date information on habitats and species of local, national and international importance. Whilst county surveys for their own sake may have less value, systematic small-scale surveying can enable those species and habitats in need of conservation to be identified. In addition to work by malacologists, we need to involve and enthuse the local naturalist community. For example, Cornwall supports a significant number of sites for *Lymnaea glabra*, a species in severe decline elsewhere - why not organise a targeted survey? Similarly, most of the British populations of *Ponentina subvirescens* are in Cornwall and are therefore of national importance. Detailed distributional and ecological surveys would have immense value. Another species, *Hygromia cinctella*, was not recorded in Cornwall until 1993 and is now spreading. An excellent opportunity exists to initiate work to monitor the rate of spread. Such a project is successfully underway in Cardiff, involving local schools. So yes, there is a need for such a work; this atlas should act as a stimulus, not only to continue general non-marine mollusc recording, but also to carry out fieldwork structured towards specific projects.

Ian Killeen

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Journal of Conchology
Vol. 37, Part 5, May 2002

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ISSN 0022-0019

Journal of Conchology

(Established 1874)

Vol. 37, Part 6, November 2002

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SYSTEMATICS OF *MELANOPSIS* FROM THE COASTAL PLAIN OF ISRAEL (GASTROPODA: CERITHIOIDEA)

JOSEPH HELLER[1], NAOMI SIVAN[1] & FRIDA BEN-AMI[1]

Abstract Based on conchiometrics of 161 snails of the freshwater genus Melanopsis *collected from six sites in the Coastal Plain of Israel, three species were identified:* buccinoidea *(Olivier),* costata *(Olivier) and* saulcyi *Bourguignat. Species previously described from this region* (lampra *Bourguignat,* phoeneciaca *Bourguignat,* belusi *Bourguignat and* hebraica *Bourguignat) are placed as synonyms. Within* buccinoidea, *the slim, elongate shells of the northern Coastal Plain differ from Jordan Valley ones in their fewer ribs, shallower notch and more conic shape. While most samples of the Coastal Plain fall into clearly distinct species, in Sa'adia ribbed shells gradually merge into smooth ones. The frequency of intermediates is high, but the mechanism maintaining these possible hybrids is unknown.*

Key words Melanopsis, *systematics, distribution, hybrids, variation, Israel.*

INTRODUCTION

The freshwater snail *Melanopsis* (Melanopsidae) is very widespread and abundant in the Near East. The first descriptions of *Melanopsis* from the Levant are those of Olivier (1801, 1804). Today, 200 years after these first descriptions and many revisions, intra-generic taxonomy is still not stable. In the southern Levant alone and over the last seventy years only, Pallary (1939) described 18 species, which Tchernov (1973, 1975) Burch (1985) and Glaubrecht (1993, 1996) considered as one species (or super-species) with several phenotypes (or subspecies), Mienis (1983) as three species, and Mienis & Ortal (1994) as five species. In their conchiometric study, Heller, Sivan & Motro (1999) found three recent species in the Jordan Valley, *M. buccinoidea* (Olivier), *M. costata* (Olivier) and *M. saulcyi* Bourguignat; intermediates, interpreted as hybrids, were found in narrow zones of sympatry, at low frequencies and over short distances. A new species, *M. meiostoma,* was later described from the Golan Heights (Heller & Sivan, 2000). A study of the sperm confirmed the conchometric species-level distinctness of these four taxa (Hodgson & Heller, 1997, 2000), as did also a study of their radula (Mazan-Mamczarz, Heller & Szwarowska, 2001). In a study of fossil *Melanopsis* from the Mid Pleistocene of the Upper Jordan Valley, seven species were found (Heller & Sivan, 2001). Bandel (2000) described seven Recent (and several Pleistocene) *Melanopsis* species from the Kingdom of Jordan and suggested that hybridization may play an important part in the appearance of new species.

From the Coastal Plain of Israel, Bourguignat (1884) described four endemic species, which he named *M. lampra, M. belusi, M. phoeneciaca* and *M. hebraica*. However, Glaubrecht (1996, fig. 56) illustrated from the coastal plain only two *Melanopsis* taxa, which he named *praemorsa buccinoidea* (from the Yarqon) and *praemorsa costata* (from the environs of the Na'aman). On the other hand Mienis & Ortal (1997, table 1; also fig. 3) recognized from the Taninim River two species, *praemorsa buccinoidea* and *saulcyi*; and they recognized *buccinoidea* and *lampra*, from the Na'aman catchment area (Mienis & Ortal 2001). In this study we describe the *Melanopsis* species of the Coastal Plain of Israel. In particular, we test whether only one ribbed species is present in the Coastal Plain (as Glaubrecht suggests).

Israel's coastal plain is 160 km long and up to 25 km wide. A series of dunes (and hardened dunes named 'kurkar' ridges) stretch parallel to the coast. Few springs are

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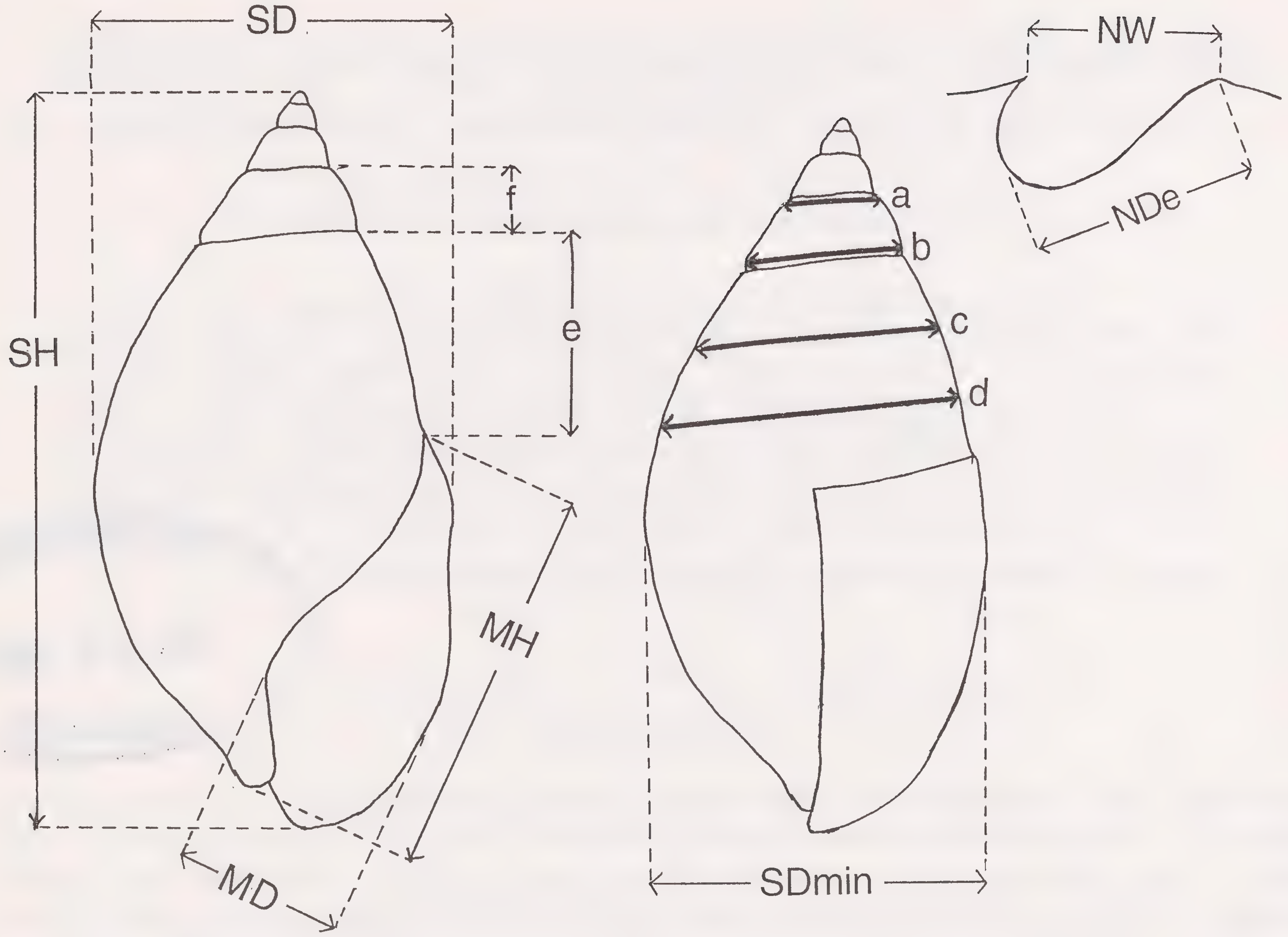


Fig. 1 Measurements used in this study. Left: Shell viewed from front. Middle: Shell viewed from side. Upper right: Notch viewed from below. SH - shell height; SD - maximal shell diameter; SDmin - minimal shell diameter; MH - mouth height; MD - mouth diameter (the widest diameter at a right angle to mouth height); a, b, c, d - diameter of shell at different points; e, f - whorl heights; NDe - notch depth; NW - notch width.

found in the plain, but rivers and streams that carry water from hinterland mountains cut across it and, to enter the sea, must break their way through the dunes and/or kurkar ridges. Consequently, in Israel's coastal plain several small swamps used to exist behind the dunes and ridges, until the 1920's. None of these swamps exceeded 2 km^2 and they were drained about eighty years ago. The gastropods of two sites along the Coastal Plain were described by Mienis & Ortal (1997, 2001).

Today many aquatic ecosystems of the coastal plain are heavily polluted, to such an extent that much of their fauna has disappeared (Yom-Tov and Mendelssohn, 1988; Heller, 2001). Further, water from Lake Kinneret (100 km north-east) is routinely pumped into the Yarqon, as part of a national policy of water resources. Mienis & Ortal (1997) have reviewed changes in the mollusc fauna of Nahal Taninim over a period of 120 years. They found that not less than ten species (maybe even thirteen) seem to have disappeared; and that the remaining fauna is under heavy pressure from agrochemical and industrial pollution. The deteriorating condition of the aquatic ecosystems of Israel's Coastal Plain gives this taxonomic study some urgency.

It might perhaps be argued that in focusing only upon the Coastal Plain our approach is not comprehensive in geographical terms; and that it would be more advisable to study the taxonomy of *Melanopsis* simultaneously throughout its entire distribution area. However, we believe that taxonomic analysis may get out of hand when shell variation of a very large geographic region is considered simultaneously. A more cautious approach may be to start by collecting snails from many sites within one small area, analyzing their conchiometrics and developing a taxonomy that concerns only that small region; and only later to extend research into further regions. One small region is the Jordan Valley, which we have recently studied (Heller *et al*. 1999). Our next step, presented here, is the Coastal Plain of Israel. The aim of this paper is to describe, through shell morphometry, the systematics and extent of hybridization of recent *Melanopsis* of the Coastal Plain of Israel.

METHODS

Our study is based upon conchiometrics of 161 snails, collected from six sites; and another 400 shells from these sites, which we inspected but did not measure.

General conchiometrics (Fig. 1) include shell-height, shell-diameter (maximal), mouth-height, mouth-diameter, notch-width and notch-depth; all measured with a caliper accurate to 0.1 mm or under the binocular, using an eye-piece micrometer. From these measurements nine ratios were calculated: shell-diameter/shell-height; mouth-height/shell-height; mouth-diameter/mouth-height, mouth-height/shell-diameter, notch-width/notch-depth, notch-width/mouth-diameter, notch-depth/mouth-diameter.

To enable future comparisons with fossil material (in which maximal shell diameter frequently cannot be taken because shells are broken) we present also minimal shell diameter, and the ratios shell-diameter (min)/shell-height, and mouth-height/shell-diameter (min). However, these two ratios were not used in the statistical analysis, because they are closely similar to shell-diameter (max) /shell-height and to mouth-height/shell-diameter (max). The term shell-diameter by itself refers, in this study, to maximal shell diameter.

In addition, the diameter of the shell was measured at four different points under the binocular, using an eye-piece micrometer (a, b, c and d, see Fig. 1; c is two thirds above the point of insertion of the lip, d is one third). From these measurements, to quantitatively express the extent of whorl shouldering that may sometimes occur in *Melanopsis* species (e.g. *M. dufouri*, see Bandel 2000, Figs 139–142; *M. obediensis*, see Heller & Sivan 2001, Fig. 3–D) we calculated the ratio b/c. To express the extent of shell figurativity ('waist') that may sometimes occur (e.g. *M. vincta*, see Heller & Sivan 2001, Fig. 3F), we calculated the ratio c/d. To express the extent to which whorls are conic ('conicality', e.g *M. buccinoidea* versus *M. costata* -Allenby, Heller *et al*. 1999, Figs 4A and 4C) we calculated the ratio a/b.

Whorl height was measured at two points: e - height of penultimate whorl, from the aperture to nearest point on the suture above; and f - height of the previous whorl (Fig. 1). From these measurements we calculated two relative whorl heights, the ratios e/mouth-height and f/mouth-height.

To measure rib characteristics, each shell was scored for presence or absence of ribs. When ribs were present, at first three rib characteristics were scored: a) Rib number, from uppermost point of insertion of the aperture on the penultimate whorl rightways, to the corresponding point on the previous whorl. b) Rib density, as the number of ribs from uppermost point of insertion of aperture 5 mm leftwards (from the point of insertion of the outer lip on the whorl) counted under the micrometer of the binocular. c) Rib length, examined on the ultimate whorl close to the aperture. This characteristic is continuous. To describe increasing rib length four categories were erected: ribs very short, do not reach the shell aperture (1); ribs reach from the suture down to the aperture (2); ribs reach beyond the aperture but do not extend the entire height of the ultimate whorl (3); ribs reach the entire height of the ultimate whorl (4). Rib index combines

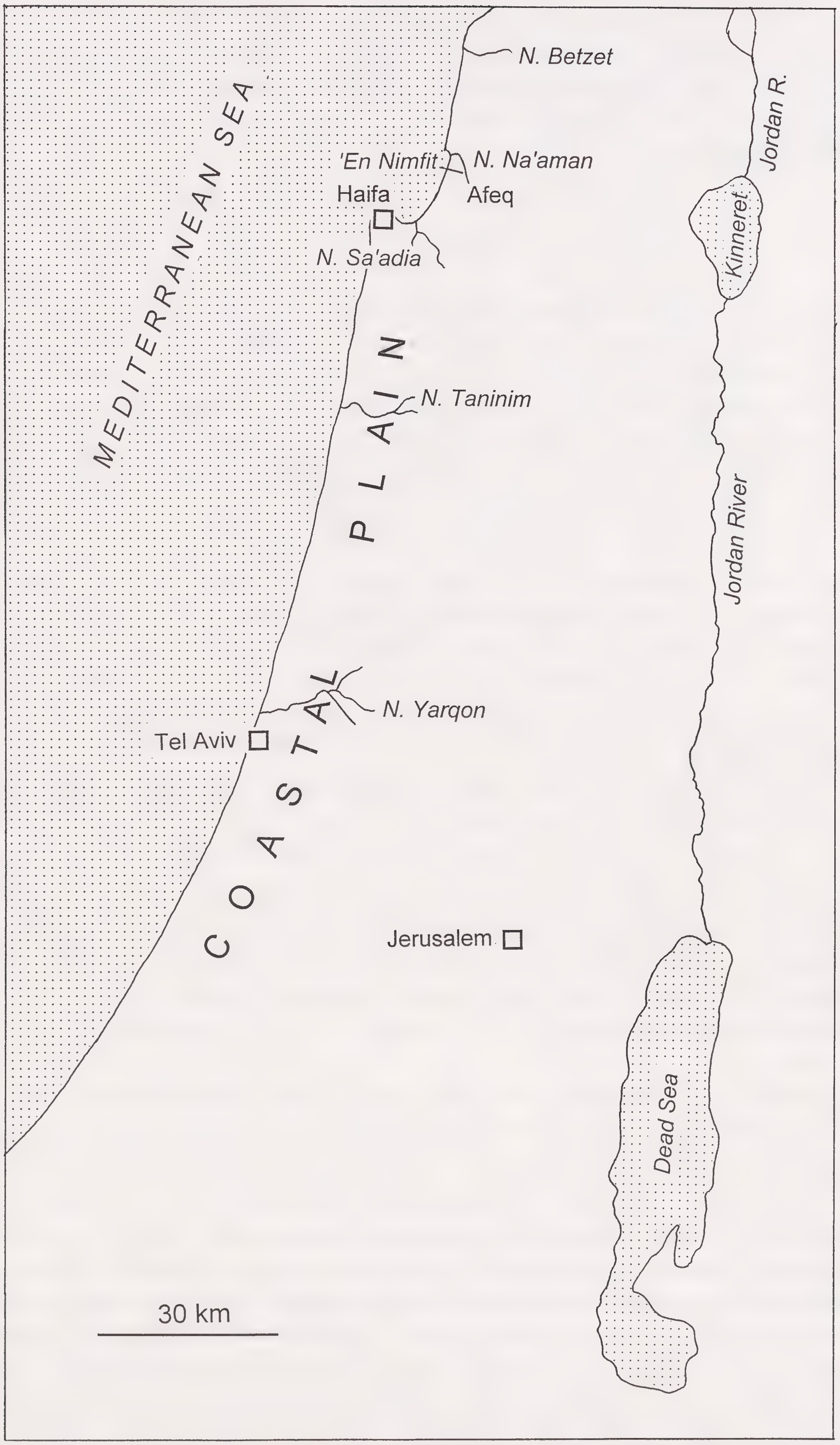


Fig. 2 Sites along the Coastal Plain where *Melanopsis* was found in this study.

shell conchiometry and rib number and was defined as the ratio

$$\frac{\text{Shell-diameter/shell-height}}{\text{number of ribs}}$$

Statistical comparisons between different taxonomic groups were done with t-test. Significance levels were set at $0.01<P<0.05$ or $P<0.01$ as indicated. Cluster analysis of sample means was performed by UPGMA based on Canberra distances, by use of the multivariate statistical package MVSP.

RESULTS

We found *Melanopsis* in six sites along the Coastal Plain: Nahal Betzet, 'En Nimfit and Afeq (these two together represent the Na'aman area), Nahal Sa'adia, Nahal Taninim and Nahal Yarqon (Fig. 2).

Melanopsis buccinoidea (Olivier, 1801)

Fig. 3A

Mélanie buccinoide, *M. buccinoidea* Olivier, 1801, pl. 17 Fig. 8.
Melanopsis praemorsa buccinoidea, Mienis & Ortal, 1997.
Melanopsis buccinoidea, Heller, Sivan & Motro 1999.

Holotype and Type locality "de Scio". (Olivier 1801, explanations to pl. 17 Fig. 8).

Diagnosis *M. buccinoidea* differs from *M. praemorsa* L., the type species of *Melanopsis* (from Spain) in that it is larger and less ventricose.

Description The shell has up to seven whorls. It has a pointed spire, flattened whorls separated by very shallow sutures, and is smooth. Shell color is almost always uniform black, or reddish brown; when not completely black, the upper half of the shell is darker than the lower half. In some shells the white callus of the upper parietal wall merges with the white columella. Shell measurements and ratios of the three Coastal Plain sites of *M. buccinoidea* are in Table 1.

Geographic range and habitat In the Coastal Plain *M. buccinoidea* occupies silty mud (and stones where available). Beyond the Coastal Plain it is found in Israel throughout the Jordan Valley, from the tributaries of the Jordan River down to the vicinity north of the Dead Sea; it is absent from the Jordan River and Lake Kinneret.

Comparisions Two of our Coastal Plain samples, from Taninim and Yarqon, are broadly similar to those of the Jordan Valley (Table 1) but they have slightly more ventricose shells and have larger apertures relative to shell-diameter. However, the shells from Betzet differ, from the above and also from the Jordan Valley in their taller, slimmer and more elongate shell, in which the whorls are taller (higher ratios e/mouth-height and f/mouth-height) and the aperture is smaller (lower mouth-height/shell-height ratios; Figs. 3–4). Conchiometrics are given in Table 1. Shell differences between *M. buccinoidea* of Bezet and those of the Jordan Valley are illustrated in Fig. 4. These *buccinoidea* of Betzet are similar to *M. buccinoidea* illustrated by Olivier (1801), to *M. buccinoidea* illustrated by Pallary (1939 Pl. 6, Figs. 3, 64, 65) from south of Sidon (Sin el Fil), and to his

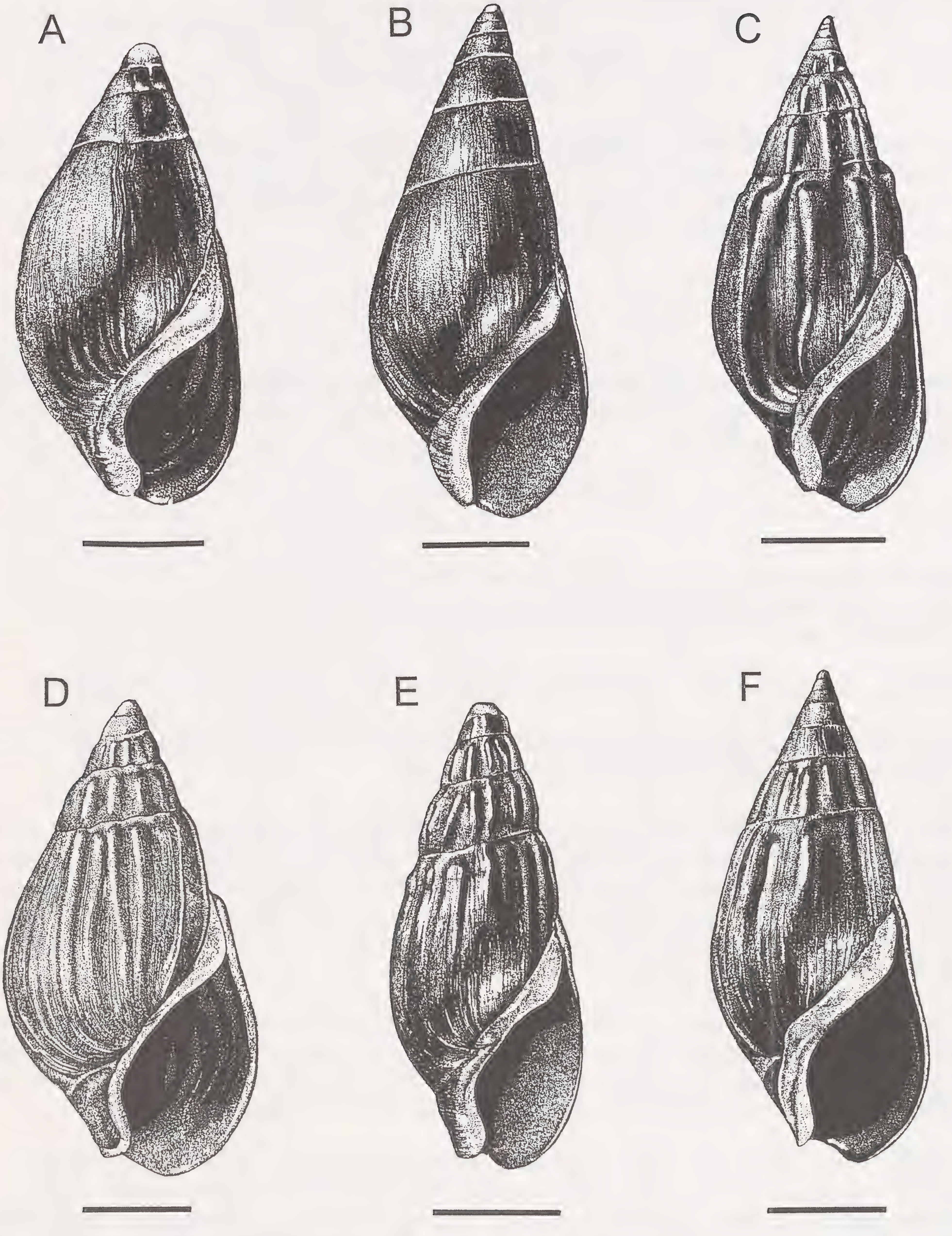


Fig. 3 *Melanopsis* taxa of the Coastal Plain. **A** - *buccinoidea* (Nahal Taninim) **B** - *buccinoidea* (Nahal Betzet) **C** - *costata* ('En Nimfit) **D** - Ribbed shell from Nahal Yarqon **E** - *saulcyi* (Nahal Taninim) **F** - Vaguely ribbed shell from Nahal Sa'adia.

M. buccinoidea var. *stricta* from Beirut. Illustrations in the literature suggest that similarly elongate smooth *Melanopsis* are not found in Turkey (Germain, 1936, Figs 26-28; Bilgin, 1983, Figs 1-2), Syria (Germain, 1921-22, Pl. 19-20), the Lebanese coastal plain south to Tripoli (Schütt, 1983, Pl. 2 Figs 42, 44, 45) or Jordan (Bandel & Salameh, 1981, Fig. 23;

TABLE 1

Conchiometrics (mean ± SD and observed range) of *buccinoidea* from the northern (Nahal Bezet) and southern (Nahal Taninim and Nahal Yarqon) Coastal Plain. Statistics: comparisons of each population are to *buccinoidea* from the Jordan Valley (part of the data from Heller *et al.* 1999), (*$0.01<P<0.05$, ** $P<0.01$).

	COASTAL PLAIN			JORDAN VALLEY
	Nahal Bezet n=16	Nahal Taninim n=9	Nahal Yarqon n=15	n=240
Max. shell-height	35.1 mm	19.2 mm	20.4 mm	26.0 mm
Shell-diameter/ shell-height	0.44 ± 0.02** 0.39 – 0.46	0.47 ± 0.02** 0.45 – 0.49	0.46 ± 0.02** 0.42 – 0.49	0.50 ± 0.02 0.45 – 0.56
Mouth-height/ shell-height	0.51 ± 0.04** 0.44 – 0.56	0.62 ± 0.04* 0.55 – 0.67	0.58 ± 0.03 0.52 – 0.62	0.60 ± 0.04 0.48 – 0.68
Mouth-diameter/ mouth-height	0.42 ± 0.02** 0.39 – 0.45	0.37 ± 0.03** 0.33 – 0.40	0.39 – 0.01 0.36 – 0.41	0.40 ± 0.03 0.33 – 0.48
Mouth-height/ shell-diameter	1.17 ± 0.05 1.07 – 1.29	1.32 ± 0.10** 1.22 – 1.49	1.27 ± 0.05** 1.17 – 1.34	1.20 ± 0.07 0.97 – 1.36
Notch-width/ notch-depth	0.88 ± 0.10 0.71 – 1.00	0.79 ± 0.03** 0.74 – 0.84	0.86 ± 0.04 0.75 – 0.90	0.92 ± 0.11 0.60 – 1.33
Notch-width/ mouth-diameter	0.55 ± 0.06 0.44 – 0.62	0.49 ± 0.51 0.43 – 0.56	0.55 ± 0.05* 0.47 – 0.62	0.47 ± 0.07 0.30 – 0.68
Notch-depth/ mouth-diameter	0.62 ± 0.04** 0.56 – 0.69	0.62 ± 0.55** 0.56 – 0.69	0.64 ± 0.05** 0.54 – 0.71	0.51 ± 0.07 0.29 – 0.75
e/mouth-height	0.36 ± 0.05** 0.30 – 0.47	0.26 ± 0.04 0.20 – 0.30	0.28 ± 0.03 0.24 – 0.33	0.29 ± 0.05 0.21 – 0.40
f/mouth-height	0.23 ± 0.03** 0.18 – 0.31	0.14 ± 0.02** 0.11 – 0.17	0.17 ± 0.02 0.14 – 0.21	0.17 ± 0.02 0.13 – 0.22
Conicality (a/b)	0.72 ± 0.04 0.67 – 0.81	0.72 ± 0.03 0.66 – 0.76	0.69 ± 0.05 0.56 – 0.75	0.71 ± 0.04 0.63 – 0.82
Figurativity (c/d)	0.89 ± 0.02 0.85 – 0.93	0.86 ± 0.02 0.84 – 0.90	0.90 ± 0.06 0.84 – 1.08	0.88 ± 0.03 0.76 – 0.94
Shouldering (b/c)	0.82 ± 0.03** 0.18 – 0.31	0.80 ± 0.03 0.75 – 0.83	0.80 ± 0.05 0.65 – 0.85	0.78 ± 0.05 0.64 – 0.85
Shell-diameter (small)/ shell-height	0.41 ± 0.02 0.36 – 0.41	0.44 ± 0.03 0.40 – 0.51	0.43 ± 0.01 0.40 – 0.45	0.46 ± 0.02 0.42 – 0.50
Mouth-height/shell-diameter (small)	1.28 ± 0.08 1.19 – 1.53	1.43 ± 0.15 1.18 – 1.62	1.40 ± 0.05 1.30 – 1.48	1.26 ± 0.11 0.97 – 1.45

Glaubrecht, 1993, Pl. 2 Fig. 1; 1996, Pl. 8 Fig. 1). The Betzet population of *M. buccinoidea* may be a separate taxon, consisting of slim, elongate, smooth-shelled snails; perhaps ranging along the southern coastal plain of the Near East, somewhere between Beirut and northern Israel. It seems different from the more ventricose smooth-shelled *M. buccinoidea* of the Jordan Valley. Further data from Lebanon would enable more decisive statements on this question.

Melanopsis costata (Olivier, 1804)
Fig. 3C

Melania costata Olivier, 1804, pl. 31 Fig. 3.
Melanopsis lampra Bourguignat, 1884.
Melanopsis belusi Bourguignat, 1884.
Melanopsis phoeneciaca Bourguignat, 1884.
Melanopsis costata, Heller, Sivan & Motro 1999.

Holotype and type locality "de l'Ororonte". (Olivier 1804, explanations to pl. 31 Fig. 3).

Diagnosis *Melanopsis costata* differs from *Melanopsis buccinoidea* in that it is ribbed.

Description The two to four upper whorls are smooth, the 3–6 lower whorls are ribbed. Ribs extend the entire height of each whorl and most of them descend vertically; usually however, two–four ribs above the shell aperture bend leftwards (from the point of insertion of the outer lip on the whorl) towards the base of the columella. In some shells only the lower part of these ribs bend, in others the entire rib tends diagonally in a leftward direction (from the point of insertion of the aperture). The upper section of each rib (near the suture) is almost always rounded.

Shell color is uniform, very dark brown, or black. No shells are banded. The white callus of the upper parietal wall merges with the white columella, so the entire inner lip is white.

Measurements of 40 shells from the Na'aman area ('En Nimfit and near Afeq) are given in Table 2, which also gives data of *M. c. costata* s. str. from the Jordan Valley for comparison (some of the data of the latter are from Heller *et al.* 1999).

Geographic range and habitat In the Coastal Plain of Israel we found *M. costata* only in 'En Nimfit, 'En Afeq nature reserve and in a small stream near 'En Afeq. The snails were found on muddy substrates, submerged plants and floating bits of vegetation. Beyond the Coastal Plain *M. costata* is found in Israel in the Upper Jordan River, Lake Kinneret and the lower Jordan River (Heller *et al.*, 1999).

Comparisons *M. costata* of the Coastal Plain differs from *M. c. costata* of the Upper Jordan Valley in that it has fewer ribs (Fig. 5); a more shallow notch (lower notch-width/notch-depth) which is also larger (higher notch-width/mouth-diameter and notch-depth/mouth-diameter); a higher rib index; and is more conic. These differences are significant but not diagnostic, and the extent of overlap between the Coastal Plain and Jordan Valley populations is so considerable to that we consider them con-specific.

Synonyms From "Bélus, prés de Saint-Jean-d'Acre" (environs of the Na'aman of today) Bourguignat (1884) described *Melanopsis lampra* as a species in which each rib is short (usually not reaching the basis), diagonal, and with a nodosity in its upper part. The Bourguignat collection contains two lots (together 90 shells) defined by Bourguignat as *M. lampra*. Table 2 presents measurements and ratios of ten of these shells. These shells

TABLE 2

Ratios and rib characters (mean ± SD and observed range) of *costata* from the northern Coastal Plain (Na'aman area); *lampra, belusi* and *phoeneciana* described by Bourguignat from the Na'aman area, ribbed shells from Nahal Yarqon and *c. costata* from the Jordan Valley. Statistics: comparisons are with *costata* from the Na'aman area (* 0.01<P<0.05, ** P<0.01).

	costata Na'aman area n=40	*lampra* n=10	*belusi* n=3	*phoeneciana* n=15	? Nahal Yarqon n=14	*c. costata* Jordan Valley n=140
Max. shell-height	22.4 mm	19.2 mm	17.3 mm	20.7 mm	20.0 mm	29.2 mm
Shell-diameter/ shell-height	0.46 ± 0.02 0.41 – 0.50	0.48 ± 0.02** 0.46 – 0.52	0.48	0.47 ± 0.03 0.42 – 0.52	0.49 ± 0.03** 0.44 – 0.52	0.48 ± 0.03* 0.39 – 0.56
Mouth-height/ shell-height	0.52 ± 0.03 0.47 – 0.58	0.55 ± 0.02** 0.53 – 0.59	0.55 – 0.58*	0.55 ± 0.04* 0.51 – 0.63	0.58 ± 0.04** 0.46 – 0.63	0.54 ± 0.03 0.44 – 0.63
Mouth-diameter/ mouth-height	0.43 ± 0.02 0.38 – 0.48	0.44 ± 0.02 0.41- 0.48	0.41 – 0.44	0.42±0.03 0.38 – 0.46	0.43 ± 0.03 0.38 – 0.51	0.44 ± 0.02 0.38 – 0.52
Mouth-height/ shell-diameter	1.14 ± 0.04 1.05 – 1.22	1.14 ± 0.03 1.09 – 1.20	1.14 – 1.20	1.16 ± 0.08 0.99 – 1.29	1.19 ± 0.07* 1.05 – 1.30	1.14 ± 0.06 1.01 – 1.30
Notch-width/ notch-depth	0.86 ± 0.07 0.74 – 1.00	0.86 ± 0.07 0.75 – 1.00	0.80 – 0.85	0.91 ± 0.04* 0.86 – 0.96	0.88 ± 0.07 0.79 – 1.00	0.91 ± 0.07** 0.76 – 1.11
Notch-width/ mouth-diameter	0.57 ± 0.06 0.44 – 0.68	0.54 ± 0.04 0.49 – 0.58	0.38 – 0.63	0.63 ± 0.05** 0.56 – 0.73	0.56 ± 0.05 0.50 – 0.63	0.52 ± 0.06** 0.39 – 0.76
Notch-depth/ mouth-diameter	0.67 ± 0.06 0.52 – 0.79	0.63 ± 0.04 0.58 – 0.67	0.47 – 0.74	0.69 ± 0.05 0.63 – 0.81	0.63 ± 0.06 0.53 – 0.70	0.58 ± 0.07** 0.40 – 0.76
e/mouth-height	0.36 ± 0.04 0.25 – 0.49	0.34 ± 0.02 0.30 – 0.37	0.29 – 0.39	0.36 ± 0.02 0.33 – 0.38	0.30 ± 0.08** 0.24 – 0.54	0.36 ± 0.04 0.28 – 0.44
f/mouth-height	0.21 ± 0.03 0.15 – 0.28	0.21 ± 0.02 0.19 – 0.24	0.19 – 0.24	0.24 ± 0.01** 0.22 – 0.26	0.17 ± 0.03** 0.13 – 0.24	0.22 ± 0.03 0.16 – 0.34
Conicality (a/b)	0.79 ± 0.04 0.68 – 0.88	0.79 ± 0.03 0.75 – 0.85	0.76 – 0.77	0.74 ± 0.01** 0.73 – 0.75	0.77 ± 0.05 0.68 – 0.83	0.86 ± 0.05** 0.76 – 1.00
Figurativity (c/d)	0.92 ± 0.03 0.77 – 0.96	0.93 ± 0.04 0.89 – 1.00	0.93 – 0.94	0.91 ± 0.03 0.87 – 0.94	0.92 ± 0.05 0.88 – 1.06	0.92 ± 0.05 0.76 – 1.00
Shouldering (b/c)	0.78 ± 0.02 0.74 – 0.83	0.68 ± 0.04 0.68 – 0.82	0.78 – 0.81	0.82 ± 0.05** 0.72 – 0.86	0.76 ± 0.05 0.62 – 0.82	0.77 ± 0.05 0.60 – 0.98
Number of ribs	9.15 ± 1.08 8 - 12	10.7 ± 1.6* 9 - 14	11 – 15**	11.1 ± 1.8** 9 - 15	13.3 ± 1.6** 11 - 16	11.1 ± 1.14** 9 - 14
Rib length	3.38 ± 0.39 2.5 – 4.0	3.45 ± 0.28 3.0 – 4.0	3.0 – 4.0	3.21 ± 0.43 2.5 – 4.0	3.89 ± 0.22* 3.5 – 4.0	3.55 ± 0.43 3 - 4
Rib index	5.01 ± 0.71 3.30 – 6.12	4.56 ± 0.77 3.28 – 5.80	3.42–4.36**	4.43 ± 0.59* 3.30 – 5.10	3.71 ± 0.42** 3.19 – 4.36	4.35 ± 0.54** 3.29 – 6.12
Rib density	2.63 ± 0.55 2.0 – 4.0	3.05 ± 0.37* 2.5 – 3.5	3.5 – 4.0**	3.54 ± 0.80** 2.5 – 5.0	4.25 ± 0.42** 3.5 – 5.0	2.85 ± 0.53* 2.0 – 4.0
Shell-diameter (small)/shell-height	0.43 ± 0.02 0.38 – 0.46	0.46 ± 0.02** 0.44 – 0.48	0.46 – 0.48*	0.43 ± 0.02 0.40 – 0.45	0.45 ± 0.04 0.39 – 0.56	0.44 ± 0.02** 0.39 – 0.50
Mouth-height/ shell-diameter (small)	1.26 ± 0.06 1.14 – 1.38	1.24 ± 0.04 1.17 – 1.30	1.15 – 1.30	1.29 ± 0.09 1.17 – 1.48	1.34 ± 0.07 1.21 – 1.45	1.21 ± 0.06** 1.08 – 1.37

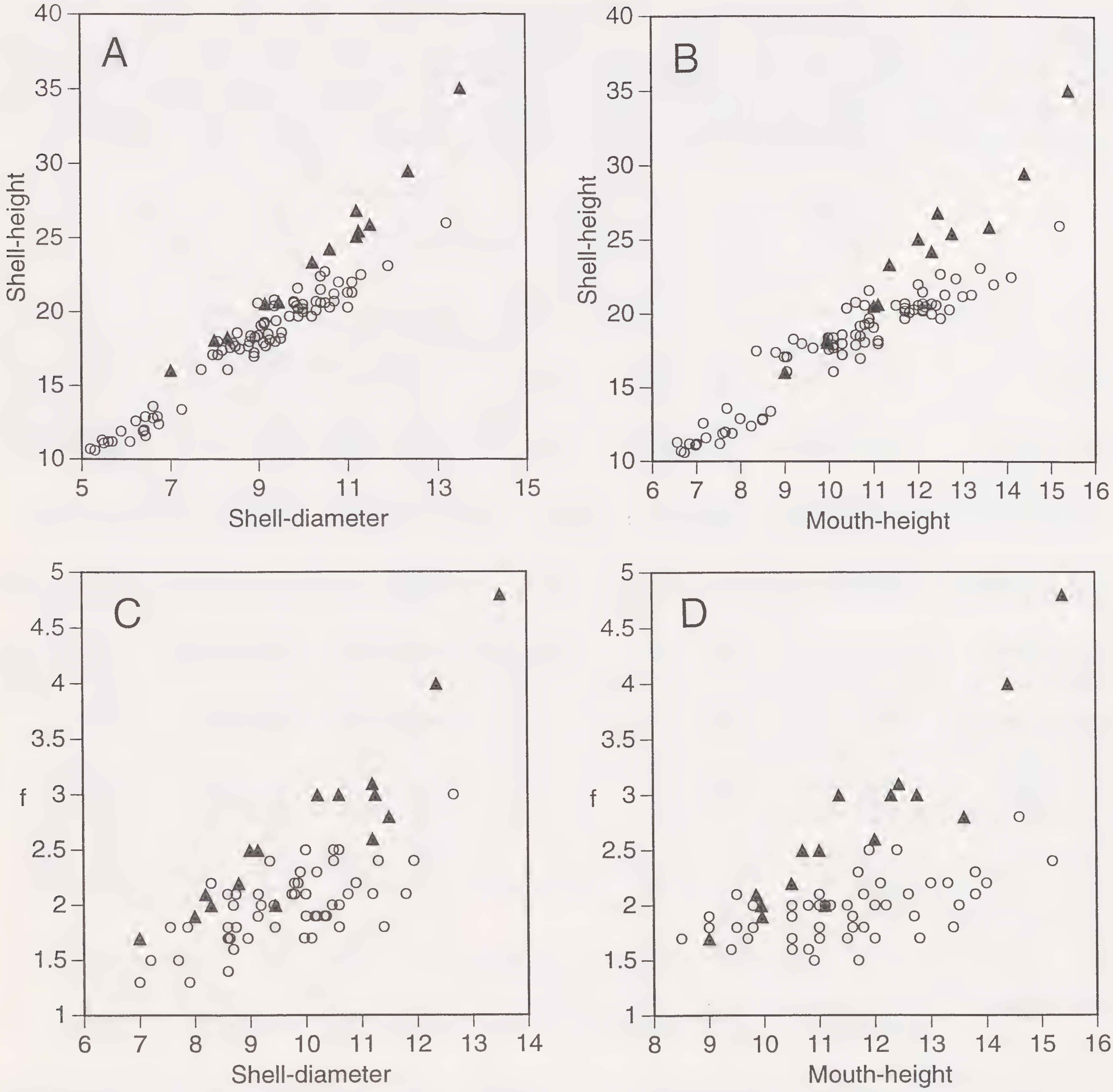


Fig. 4 *Melanopsis buccinoidea* from Nahal Betzet (full triangles) compared with *M. buccinoidea* (open circles) from the Jordan Valley. **A** - shell-height versus maximal shell-diameter **B** - shell-height versus mouth-height **C** - f versus maximal shell-diameter **D** - f versus mouth height.

are similar to our *M. costata* from the Na'aman area in their conchiometrics, including their diagonal ribs which reach the lower part of the ultimate whorl; they differ in that the shell is very thin and horny brown, and in that most shells have a slight nodosity at the top of the ribs. However, such nodosities occur also in several of our own shells from the Na'aman area. There are no significant differences between *M. lampra* and our *M. costata* samples of the Na'aman area. The ribbed *Melanopsis* of the Na'aman have been assigned by Mienis & Ortal (2001) to *lampra* Bourguignat. However, as they neither describe this species, nor present any consistent differences between it and *costata*, it is difficult to accept their opinion. We therefore place *M. lampra* as a synonym of *M. costata*.

Bourguignat (1884) considered *Melanopsis belusi* Leterneux, 1882 from the Belus swamp as differing from *M. lampra* in its dense, straight ribs and also in its shell notch that is deeper than in *M. lampra* and *M. phoeneciaca*. We could not find any description of *M. belusi* by Leterneux 1882 and we could not trace any specimens labeled by him to *M. belusi*. The Bourguignat collection contains one lot (with three adult shells) determined by Bourguignat as *M. belusi*. The measurements of these three specimens are presented in Table 2. These shells do not differ significantly from the shells determined by Bourguignat as *M. lampra* or from our *M. costata*. In rib number they fall in the higher range of *M. lampra*. One shell has higher rib density than *M. lampra*, but it falls in the range of *M. costata*. One shell has an extremely small notch as compared to mouth width. Two of the shells have straight ribs, and in this character they are similar to *M. phoeneciaca* (see below). We therefore consider *belusi* a synonym of *costata*.

Bourguignat (1884) also described from Belus *Melanopsis phoeneciaca*, which he noted as differing from *M. lampra* mainly in its narrower shell, with straighter ribs (that tend to disappear on the last whorl). We express the extent to which a shell is ventricose versus narrow by two ratios, shell-diameter/shell-height and mouth-diameter/mouth-height. We measured 15 specimens of Bourguignat's type material of *M. phoeneciaca*. As concerns the ratio shell-diameter/shell-height, all except one of the *M. phoeneciaca* specimens fall within the range of *lampra*; both except two specimens fall within the range of our *M. costata* from the Na'aman area. Similarly as concerns the ratio mouth-diameter/mouth-height, of the fifteen specimens, eleven fall within the range of *M. lampra*; and both are within the range of our material from the Na'aman area (Table 2). As concerns the extent to which the ribs are straight (versus diagonal), most of the shells defined as *M. phoeneciaca* and *M. belusi* have straight ribs, and most of those defined as *M. lampra* have diagonal ribs. This is a very variable character, and both straight and diagonal ribs are present, both in our *M. costata* from the Na'aman area, and in our *M. costata* from the Jordan Valley. There is no point in separating the Belus *Melanopsis* into three species, based on this character alone. We therefore consider *phoeneciaca* a synonym of *costata*.

Variation In the samples of 'En Nimfit and near 'En Afeq most shells have well-developed ribs that extend the entire length of the whorl, as in 85% of the shells of 'En Afeq (n=175). However, in 14% of the 'En Afeq shells the ribs are so weak that they seem to be no more than slight folds that extend only to about the middle of each whorl. About 1 % of the shells are smooth. In the Jordan Valley intermediates, interpreted as hybrids between *M. buccinoidea* and *M. costata*, were found in a river system where both species are present in considerable numbers, often at the same site (Heller *et al.*, 1999). Their conchiometrics are intermediate between *M. buccinoidea* and *M. costata*. For example, the ratio e/mouth-height averages 0.32 in hybrids of the Jordan Valley - intermediate between *M. buccinoidea* (0.25) and *M. c. costata* (0.36). In Afeq the smooth and the slightly ribbed shells do not differ significantly from the ribbed shells in any of their conchiometrics ($P<0.01$). In addition, the proportion of smooth shells is very low (much lower even than the slightly ribbed shells). This rules out a scenario of two separate taxa (smooth-shelled and ribbed) hybridizing with each other. We consider both the weakly ribbed shells and the few smooth shells in the Afeq area as variations of *M. costata*.

Ribbed shells from the Yarqon River
Fig. 3D

A sample of 14 ribbed *Melanopsis* shells from the Yarqon River (dam 40), were collected in December 1998. No *Melanopsis* have been found since in this river.

The Yarqon shells have a large aperture relative to shell height. The 2–5 upper whorls are smooth, the 3–6 lower whorls are ribbed. The ribs are weak and dense. Ribs usually extend the entire height of each whorl and most of them descend vertically. The upper section of each rib (near the suture) is almost always rounded. Shell color is uniform, dark brown (or black). No shells are banded. The columella is white, gray or beige. Conchiometrics are presented in Table 2.

TABLE 3

Ratios and rib characters (mean ± SD and observed range) of *saulcyi* from the southern Coastal Plain (Nahal Taninim), *hebraica* described by Bourguignat from Ain Saadi, *saulcyi-buccinoidea* intermediates from Nahal Sa'adia and *saulcyi* from the Jordan Valley. Statistics: comparisons are with *saulcyi* from the Jordan Valley (* 0.01<P<0.05, ** P<0.01).

	saulcyi Nahal Taninim n=20	*hebraica* Ain Sa'adia n=11	*intermediates* Nahal Sa'adia n=36	*saulcyi* Jordan Valley n=160
Max. shell-height	20.5 mm		31.0 mm	26.0 mm
Shell-diameter/ shell-height	0.44 ± 0.02 0.38 – 0.47		0.44 ± 0.02 0.40 – 0.50	0.45 ± 0.03 0.37 – 0.55
Mouth-height/ shell-height	0.51 ± 0.03 0.45 – 0.56		0.51 ± 0.03 0.44 – 0.61	0.51 ± 0.04 0.38 – 0.60
Mouth-diameter/ mouth-height	0.42 ± 0.02** 0.37 – 0.46	0.42 ± 0.02* 0.40 – 0.45	0.43 ± 0.03 0.36 – 0.50	0.45 ± 0.03 0.37 – 0.51
Mouth-height/ shell-diameter	1.18 ± 0.06** 1.09 – 1.32	1.18 ± 0.04* 1.14 – 1.26	1.16 ± 0.05 1.04 – 1.27	1.13 ± 0.07 0.86 – 1.33
Notch-width/ notch-depth	0.84 ± 0.06 0.73 – 0.95	0.81 ± 0.10 0.68 – 1.00	0.89 ± 0.06** 0.72 – 1.09	0.81 ± 0.08 0.50 – 1.14
Notch-width/ mouth-diameter	0.59 ± 0.06** 0.41 – 0.69	0.49 ± 0.07** 0.42 – 0.62	0.54 ± 0.05** 0.44 – 0.68	0.48 ± 0.07 0.27 – 0.68
Notch-depth/ mouth-diameter	0.70 ± 0.08** 0.54 – 0.84	0.62 ± 0.10** 0.46 – 0.76	0.61 ± 0.06** 0.53 – 0.73	0.60 ± 0.07 0.41 – 0.79
e/mouth-height	0.36 ± 0.04** 0.30 – 0.45	0.35 ± 0.03** 0.31 – 0.40	0.38 ± 0.03 0.33 – 0.48	0.40 ± 0.05 0.29 – 0.48
f/mouth-height	0.23 ± 0.03 0.18 – 0.27	0.23 ± 0.02 0.17 – 0.25	0.22 ± 0.03 0.15 – 0.27	0.24 ± 0.03 0.19 – 0.32
Conicality (a/b)	0.82 ± 0.05* 0.72 – 0.90	0.80 – 0.87	0.76 ± 0.04** 0.68 – 0.91	0.85 ± 0.04 0.78 – 0.96
Figurativity (c/d)	0.94 ± 0.02** 0.89 – 1.00	0.91 – 0.95	0.91 ± 0.02 0.86 – 0.96	0.92 ± 0.02 0.88 – 0.96
Shouldering (b/c)	0.79 ± 0.03** 0.74 – 0.9	0.81 – 0.82	0.82 ± 0.04 0.67 – 0.89	0.82 ± 0.04 0.73 – 0.89
Number of ribs	12.3 ± 2.2 10 – 18	13.3 ± 1.6 10 – 15	12.2 ± 1.21 10 – 14	12.7 ± 1.54 9 – 19
Rib length	1.98 ± 0.5 ** 1.0 – 3.0	2.05 ± 0.47** 1.0 – 3.0	1.90 ± 0.32** 1.0 – 2.0	2.92 ± 0.66 2.0 – 4.0
Rib index	3.66 ± 0.71 2.39 – 4.70		3.65 ± 0.20 3.31 – 4.00	3.57 ± 0.49 2.42 – 5.00
Rib density	4.22 ± 0.90 3.0 – 6.0	4.12 ± 0.63 3.5 – 5.0	3.27 ± 0.35** 2.5 – 4.0	4.22 ± 0.90 3.0 – 6.0
Shell-diameter (small)/shell-height	0.41 ± 0.01 0.37 – 0.49		0.40 ± 0.02 0.38 – 0.44	0.42 ± 0.02 0.39 – 0.45
Mouth-height/ shell-diameter (small)	1.30 ± 0.07** 1.14 – 1.41	1.35 ± 0.05** 1.30 – 1.39	1.32 ± 0.05** 1.25 – 1.44	1.21 ± 0.06 1.08 – 1.29

Comparisons This Yarqon sample differs from *M. c. costata* of the Jordan Valley in the ratios mouth-height/shell-height, mouth-height/shell-diameter, e/mouth-height, f/mouth-height, number of ribs, rib index and rib density (Table 2).

They differ from *M. costata* of the Northern Coastal Plain (Na'aman area) in the ratios shell-diameter/shell-height, mouth-height/shell-height, mouth-height/shell-diameter, e/mouth-height, f/mouth-height, number of ribs, rib index, rib density and rib length (Table 2).

From the vicinity of Iskenderun, Schütt (1983, Pl. 1 Fig. 43) illustrated a shell that he named *Melanopsis praemorsa ferussaci*. The Yarqon *M. costata* are similar to the Iskenderun shell.

We postpone further taxonomic treatment of this sample until more material becomes available.

Melanopsis saulcyi Bourguignat, 1853
Fig. 3E

Melanopsis saulcyi Bourguignat, 1853.
Melanopsis hebraica Bourguignat,1884.
Melanopsis saulcyi, Mienis & Ortal 1997.
Melanopsis saulcyi, Heller, Sivan & Motro 1999.

Holotype and type locality "Artouse, en Syrie" (Bourguignat 1853: 66, pl. 2 Figs 53 and 54).

Description The shell is usually elongate and slim and its aperture is small, in relation to shell-height. The 3–4 upper whorls are smooth (in our samples, very frequently they are eroded), the 2–3 lower ones are either smooth or with slightly pronounced ribs. The ribs descend from the suture till about the middle of the lowest whorl, and often have an upper ridge; they are usually straight. The notch is usually deep. Shell color varies from uniform dark brown to uniform black. On the inner lip the pale callus of the upper parietal wall merges with the white columella, so the entire inner lip is pale. The taxonomy of *saulcyi* has been discussed in detail by Heller *et al.* (1999).

Measurements and ratios of 20 shells from Nahal Taninim are presented in Table 3, which also contains data of *M. saulcyi* from the Jordan Valley.

Synonyms The type shells of *M. hebraica* Bourguignat from "Ain Saadi" are eroded, and not all characters could be measured; those that were measurable are presented in Table 3. *M. hebraica* differs from *M. saulcyi* of the Jordan Valley in its slightly more elongate aperture; this is expressed in slightly lower values of the ratio mouth-diameter/mouth-height and higher values of the ratio mouth-height/shell diameter. Also the ratio e/mouth-height is smaller, and the rib-length is shorter. These differences are not diagnostic. *M. hebraica* is similar to *M. saulcyi* of Nahal Taninim in most of its conchiometrics. It differs only in its smaller notch (lower ratio notch-width/mouth-diameter and notch-depth/mouth-diameter).

Habitat and Geographic range In the Coastal Plain of Israel we found *M. saulcyi* in Nahal Taninim (on boulders). Beyond the Coastal Plain *M. saulcyi* is found in Israel in springs in the Bet She'an Valley (Heller *et al.*, 1999); in the beginning of the twentieth century it was found also in the Hula Valley. Glaubrecht (1993, 1996, 2000) in his reviews of Recent *Melanopsis*, did not mention *M. saulcyi*.

Comparisons In Nahal Taninim *M. saulcyi* occurs together with *M. buccinoidea*, which is

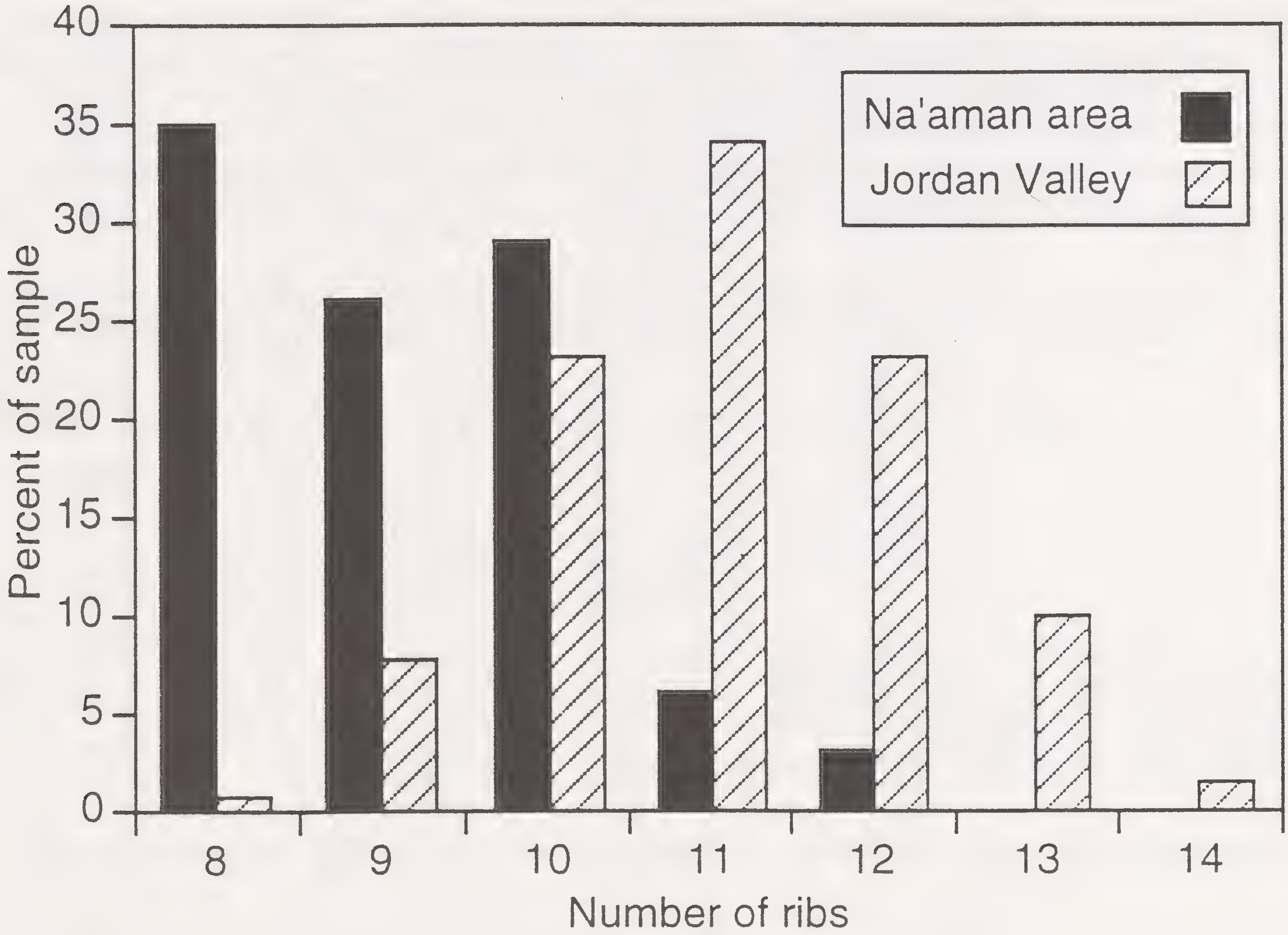
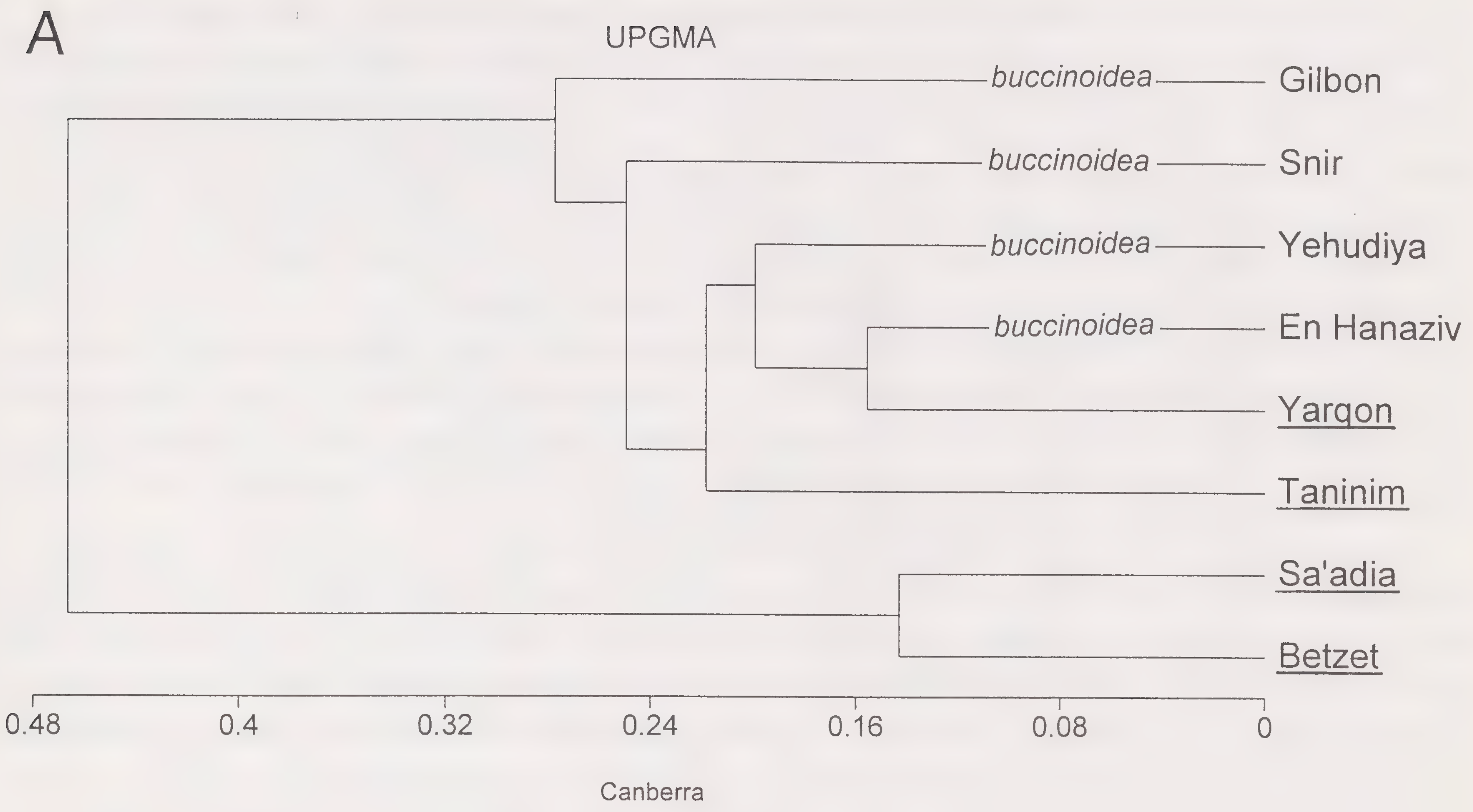


Fig. 5 *Melanopsis costata* from the Coastal Plain (Na'aman area) versus *M. c. costata* from the Jordan Valley: number of ribs.

smooth. Of a sample of 150 snails, 87 % were *M. saulcyi*, 9 % were *M. buccinoidea* and 4% intermediates between the two.

The Taninim *M. saulcyi* differ from *M. c. costata* in being slimmer (as expressed by their smaller shell-diameter/shell-height); and their ribs are shorter. They further differ in that (as with *M. saulcyi* of the Jordan Valley) they have a smaller aperture (the ratio mouth-height/shell-height is lower); the ratio shell-diameter/shell-height is lower; the ratio notch-width/notch-depth is lower, number of ribs higher, rib length and the rib index lower (all differences significant at $P < 0.01$). In addition, the Taninim *M. saulcyi* (in contrast to those of the Jordan Valley) differ from *M. c. costata* in that their ratios notch-width/mouth-diameter and notch-depth/mouth-diameter are higher ($P<0.01$).

When considering all Jordan Valley samples of *M. saulcyi* together as one (Table 3), then the Taninim *M. saulcyi* differs from the Jordan Valley average in that it almost never has long ribs and the ribs are less tubercular; the mouth diameter is narrower (lower ratio mouth-diameter/mouth-height, the whorls are lower (lower e/mouth height) ; higher ratio mouth-height/shell-diameter); they also have a larger notch (higher notch-width/mouth-diameter and notch-depth/mouth-diameter). However, within *M. saulcyi* of the Jordan Valley, considerable variation was found in rib length and form: some shells have short ribs and others long ones, some have uniform ribs and others distinct tubercles (Heller *et al.*, 1999). The Taninim sample is similar to En Hamma of the Jordan Valley in its rib form; to Enot Huga in rib length; to En Hanatziv and Hammat Gader in its mouth-diameter/mouth-height, and to Enot Huga in its ratio e/mouth-height. In the remaining significantly different ratios (mouth-height/shell-diameter, notch-width/mouth-diameter and notch-depth/mouth-diameter) the extent of overlap between Taninim and the Jordan Valley is such that we do not split the Coastal Plain *M. saulcyi* taxonomically from the Jordan Valley ones.



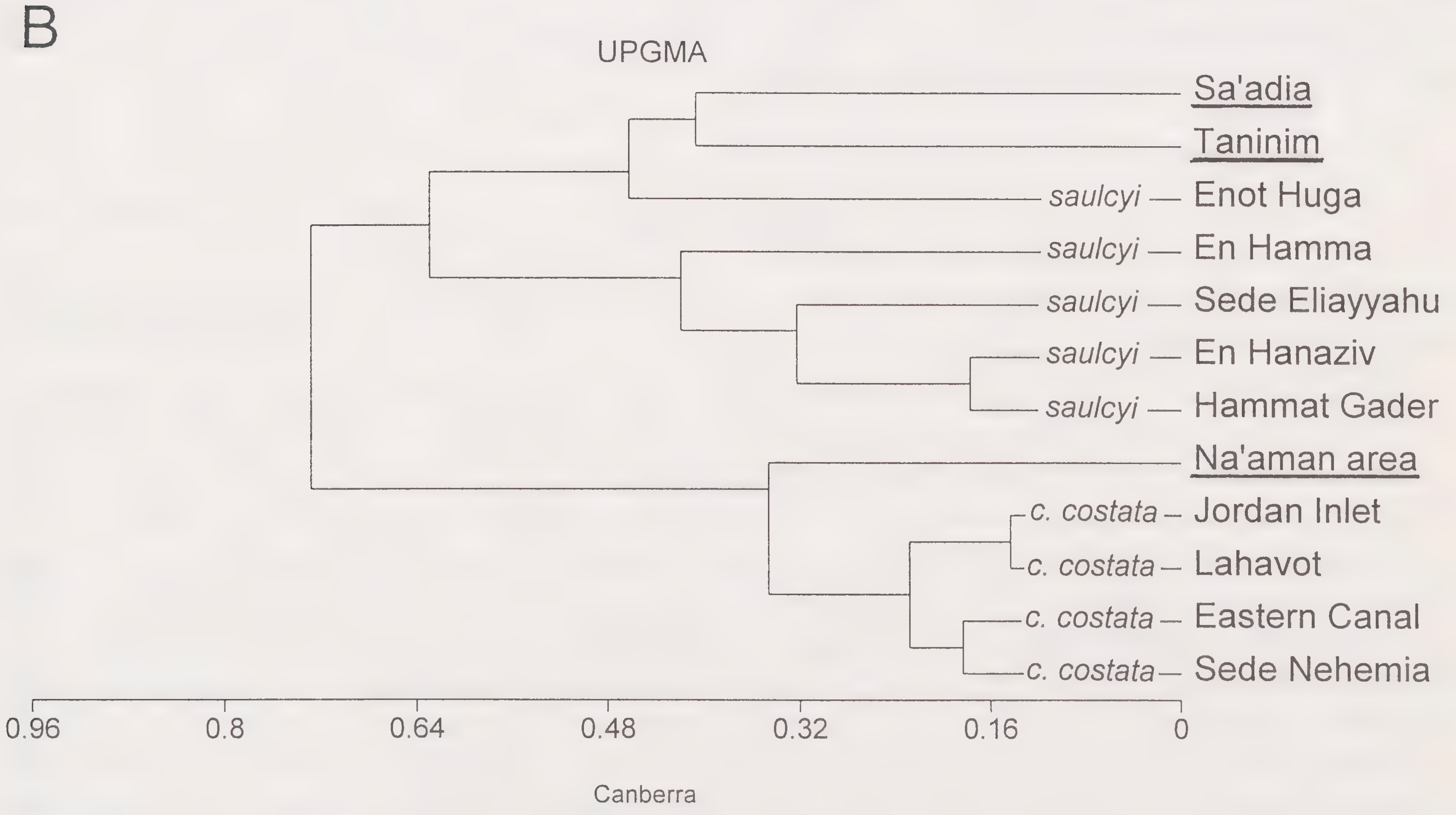


Fig. 6 Dendrograms of Coastal Plain (underlined) and Jordan Valley samples.
A. Samples of smooth shells and the Sa'adia sample.
B. Samples of ribbed shells and the Sa'adia sample.

Melanopsis cf. *saulcyi*
Fig. 3F

In Nahal Sa'adia, on a (mainly) muddy substratum, moderately ribbed, faintly ribbed and smooth shells are found together, over a stretch of 300 m. Of the 54 specimens, 48% were smooth, 26 % faintly ribbed and 26 % moderately ribbed. In conchometrics other than ribs (Table 3), these shells (found in the same three squares of 3 * 3 m) are sufficiently similar that we do not doubt that they are of one breeding population.

Dendrograms based upon conchiometric similarity present relationships among the samples of smooth shells (Fig. 6A), and the samples of ribbed shells (Fig. 6B) from the Coastal Plain and the Jordan Valley. In Fig. 6A (based upon the ratios shell-diameter/shell-height, mouth-height/shell-height, mouth-height/shell-diameter, notch depth, relative whorl height, conicality, figurativity and shouldering) all four samples of the Jordan Valley fall into one group, together with the Coastal Plain samples from Yarqon and Taninim. The Betzet population is more separate.

In Fig. 6B (based upon the same ratios and number of ribs, rib length and rib index) the Na'aman sample falls close to the *M. c. costata* samples of the Jordan Valley, and is clearly separated from other ribbed samples of the Coastal Plain. The Taninim *M. saulcyi* falls close to the *M. saulcyi* samples from the Jordan Valley, and separate from the *M. costata* samples of the Coastal Plain and Jordan Valley.

In the dendrograms presented in Fig. 6, the Sa'adia sample is placed, once among the smooth shells of other sites and once among the ribbed ones. When placing Sa'adia among the smooth shells and applying conchiometrics other than ribs (Fig. 6A), they fall close to the Betzet population; they differ from *M. buccinoidea* from Nahal Betzet only in that they are less conic. When placed among the ribbed shells, and applying also rib characters (Fig. 6B) they fall close to *saulcyi* of Taninim, from which they differ only in that they have a shallower notch, are more conic and have lower rib density (Table 3).

M. cf. *saulcyi* may represent the evolutionary stable lineage of a hybrid swarm, between smooth *buccinoidea* and ribbed *saulcyi*; or it may be a *saulcyi* population which is highly variable in the presence-absence of ribs; or perhaps it may be a separate species. We return to these points in the discussion.

DISCUSSION

This study reveals three morphologically distinct *Melanopsis* taxa in the Coastal Plain of Israel, *M. buccinoidea*, *M. costata* and *M. saulcyi*.

M. buccinoidea, *M. costata* and *M. saulcyi* are found also in the Jordan Valley (Heller *et al.*, 1999). The Coastal Plain differs in that it has an elongate smooth-shelled *M. buccinoidea* not found in the Jordan Valley; and in that its *costata* has fewer ribs. Of the three Recent subspecies of *costata* that occur in the Jordan Valley, *c. costata* is very close to the Na'aman *costata*; the other two (*M. c. jordani* and *M. c. noetlingi*) do not occur in the Coastal Plain. Two of the ribbed Coastal Plain populations (Taninim and Sa'adia) fall among Jordan Valley *saulcyi* whereas another one (Na'aman area) does not (it falls close to the Jordan Valley *costata*, fig. 6). This does not support Glaubrecht's suggestion of only one ribbed *Melanopsis* taxon in the Coastal Plain.

Most shells in our Coastal Plain samples fall into clearly distinct species. In Nahal Taninim however, where (ribbed) *saulcyi* occurs together with (smooth) *M. buccinoidea*, 4 % of the sample were *saulcyi-buccinoidea* intermediates. As isozyme distances between *M. buccinoidea* and *M. saulcyi* are low (Falniowski *et al.*, in prep), it could well be that the Taninim intermediates are hybrids. Similarly, occasional occurrence of the *vincta-corrugata* intermediates among mid-Pleistocene *Melanopsis* of the Jordan Valley suggests that they are unfit hybrids (Heller & Sivan, 2001). Many authors have concluded that hybrids, in general, are unfit relative to their progenitors (see Arnold & Hodges, 1995; Arnold, 1997 and references therein).

Also in Sa'adia ribbed shells gradually merge into smooth ones. While collecting the snails we searched for, we did not observe any habitat transition zone along Nahal Sa'adia, such as occurs in the Jordan Valley where *Melanopsis* hybrids are found between

M. costata and *M. buccinoidea*, in zones of contact between stream and lake (Heller *et al.*, 1999). Further, the frequency of the Sa'adia intermediates is high, whereas in the Jordan Valley intermediates occur at low frequencies (Heller *et al.*, 1999), suggesting that they are unfit relative to their progenitors.

In Sa'adia however, the high frequency of intermediates, combined with the lack of any habitat transition, does not suggest hybrid unfitness. The Sa'adia population may perhaps be a hybrid swarm between smooth *M. buccinoidea* of the elongate type and *M. saulcyi*. Coastal rivers are disconnected habitats. It is likely that once a swarm is formed by initial hybridization, it could persist as an evolutionary stable lineage without substantial immigration of the parental species. Alternatively, the Sa'adia population may perhaps be a *saulcyi* population that is highly variable in the presence-absence of ribs. It is odd however that no other population in Israel shows such extreme variation in ribbing. Finally, the Sa'adia population may perhaps be a separate species.

Our study is based upon shell variation. To quantitatively capture fine differences among taxa we used fifteen measurements, from which we calculated thirteen ratios. We are aware that conchiometrics might not always be sufficient to solve such complicated taxonomic situations, and that they should preferably be supplemented by further studies into variation, at such levels as anatomy, proteins and molecules. In our present study such an expansion was not possible. However, we emphasize that the detailed protein-level study of Falniowski *et al.* (submitted) supports the validation of our conchiometric methods: In the Jordan Valley, *M. costata costata, M. c. jordanica* and *M. saulcyi*, each of them distinct in their shell (Heller *et al.* 1999), appeared as distinct units also in their allozymes (*M. buccinoidea* was scattered in each of the big clusters, suggesting that it is a distinct species but with some level of hybridization with the other species). Further, a study of spermatozoon structure in *buccinoidea, costata, saulcyi* and *meiostoma* from the Jordan Valley and Golan Heights has revealed significant differences in the length of the nucleus, acrosome and midpiece between the species, supporting the results obtained from shell conchiometrics (Hodgson and Heller, 2000). We therefore tend to consider our taxonomic conclusions, drawn in this study from shell variation, as reasonably reliable.

ACKNOWLEDGEMENTS

Snails for this research were collected by permit 2000 / 8578 of the Israel Nature and National Parks Authority. Dr. Y. Finet, of Muséum d'histoire naturelle in Genève, kindly entrusted us with the types described by Bourguignat. We thank Ra'aya Shuraki, chief warden of the 'En Afeq nature reserve, for her cooperation; and Sarah Erlich of the Geological Institute for chemical analysis of the water of Nahal Sa'adia. A. Gasith kindly introduced us to the Sa'adia site and gave us the Yarqon sample. The shells in Fig. 3 were illustrated by Tuvia Kurz, who has illustrated all *Melanopsis* shells in our studies. This study was funded by the American Friends of the Hebrew University; and by a Horwitz scholarship to Frida Ben Ami.

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MELANOPSIS FROM THE PLIOCENE SITE OF 'ERQ EL-AHMAR, JORDAN VALLEY (GASTROPODA: CERITHIOIDEA)

JOSEPH HELLER[1] & NAOMI SIVAN[1]

Abstract *'Erq el-Ahmar is a 2 myr old Upper Pliocene site in the Jordan Valley (Israel). Its Melanopsis fauna was found to include five species, which are described:* M. buccinoidea *Olivier,* M. praecursor *Schütt & Ortal,* M. multiformis *Blanckenhorn,* M. aaronsohni *Blanckenhorn and* M. tchernovi *sp. nov. The latter, a keeled species, is similar to Recent* M. dufouri *Ferussac, of Morocco and it is suggested that keels may perhaps appear independently in different* Melanopsis *species. A sixth species,* M. saulcyi *Bourguignat, is present in only a single vial, which may well be mislabeled.*

A gap seems to exist, in the Jordan Valley, between the aquatic fauna of the late Pliocene on the one hand and the early Pleistocene on the other. The 'Erq el-Ahmar faunal assemblage suggests that during the upper Pliocene faunal connections between the Jordan and the Orontes were weak.

The Melanopsis *fauna suggests that the Palaeo-environment of 'Erq el-Ahmar consisted of a shallow, non-turbulent, well-aerated lake with a slow current and a nearby stream.*

Key words *Gastropods, Jordan Valley,* Melanopsis, *systematics, 'Erq el-Ahmar.*

INTRODUCTION

The freshwater snail *Melanopsis* (Melanopsidae) has a broadly circum-Mediterranean distribution. The systematics of Recent *Melanopsis* of the Jordan Valley have been described by Heller, Sivan & Motro (1999), of 780,000 yr old mid-Pleistocene ones by Heller & Sivan (2001) and of early-Pleistocene (1.4 myr) ones by Heller & Sivan (2002). This present paper concerns fossil *Melanopsis* from 'Erq el-Ahmar (Fig. 1), a 2 myr old site in the Jordan Valley, 7 km south of Lake Kinneret (Braun, 1992; Tchernov, in Schütt & Ortal, 1993). The 'Erq el-Ahmar series consists of twenty layers (Braun, 1992) of which the lowermost (at IG 20272-22575) is rich in gastropod shells.

'Erq el-Ahmar was a shallow, low-energy lake in which a north-to-south current prevailed. It was supplied by carbonate and basaltic waters, in approximately equal proportions (Rosenthal, Katz & Tchernov, 1989). The lake existed for 20,000–30,000 years, occasionally drying out due to climatic fluctuations or tectonic movements. Remains of ash *Fraxinus syriaca* indicate a cool riparian forest, while pollen remains reveal a nearby oak community containing also spruce *Picea*, as found today in certain parts of Turkey and Europe (Braun, 1992). Faunal remains and cultural artifacts suggest that elephant, deer and tool-creating hominids roamed the lake's shores; mollusc (and fish) remains suggest that it was aerobic (Braun, 1992).

The first to describe *Melanopsis* from 'Erq el-Ahmar were Blanckenhorn & Oppenheim (1927; they named the site Jisr el Medjami); they found four species (*noetlingi, aaronsohni, laevigata, oblonga* var. *torosa*). Later, Picard (1934) described five species (*costata, noetlingi, aaronsohni, hammamensis, cylindrata*). Further investigations were by Tchernov (1975) who assigned most of the 'Erq el-Ahmar *Melanopsis* to one single highly variable species, *praemorsa*; and a few to *Melanopsis* cf. *doriae*. More recently, Schütt & Ortal (1993) suggested four *Melanopsis* taxa (*praecursor, aaronsohni, obediensis obediensis* and *obediensis coroniformis*). There is thus considerable disagreement as to the species-level systematics of the 'Erq el-Ahmar *Melanopsis*.

This present paper re-describes the *Melanopsis* species of 'Erq el-Ahmar; and compares them with Recent and Pleistocene *Melanopsis* of the Jordan Valley.

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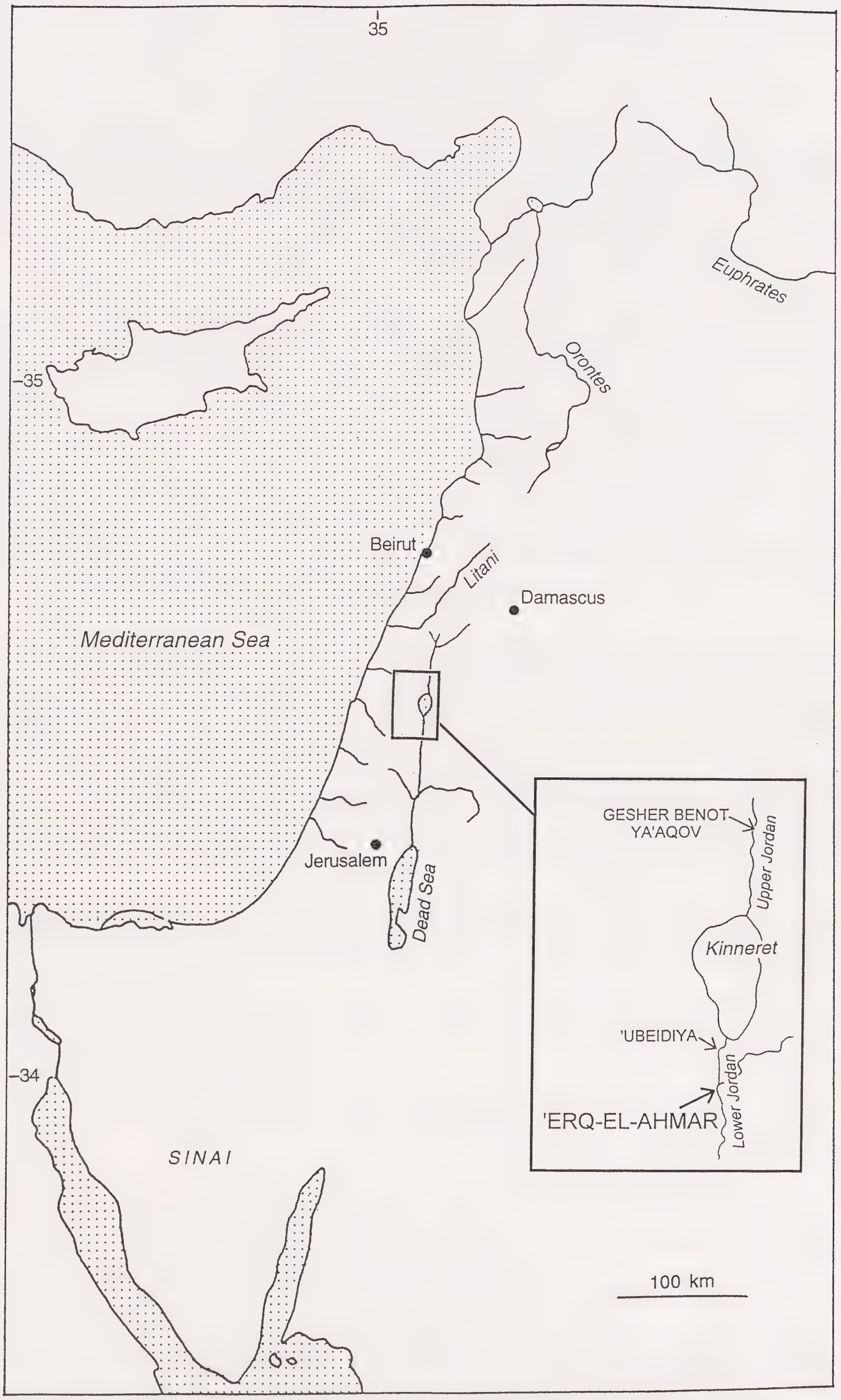


Fig. 1 The Levant, with ʻErq el-Ahmar and two additional prehistoric sites of the Jordan Valley.

METHODS

All 'Erq el-Ahmar *Melanopsis* available in the Paleontology collection of the Hebrew University were inspected. As the sub-division into layers was not always clear from data on the label, we pooled all data.

Raanan (1986: 75), in population studies of *M. costata* in Lake Kinneret, found that individuals beyond 7 mm shell-height were adult. Shohat (1995: 43) carried out histological sections of the gonad of *M. buccinoidea* throughout the year; she found that well-developed gonads can be found in snails with a shell-height beyond 10 mm. In this study, accordingly, we consider as adult any shell with a height of at least 10 mm; and conchiometrics were taken only of adults. The scatter diagrams in this study thus represent only variation among adults, and serve to illustrate gaps between taxa; they do not refer to aspects of allometric growth.

General conchiometrics (Fig. 2) include shell-height, shell-diameter (minimal) and mouth-height; all measured with a caliper accurate to 0.1 mm. From these measurements three ratios were calculated: shell-diameter (min) / shell-height; mouth-height / shell-height; and mouth-height / shell-diameter (min).

In addition, the diameter of the shell was measured at four different points under the binocular, using an eye-piece micrometer (a, b, c and d, see Fig. 2; c is two thirds above the point of insertion of the lip, d is one third). From these measurements, to quantitatively express the extent of whorl shouldering that may sometimes occur in *Melanopsis* species (e.g. *M. dufouri*, see Bandel 2000, Figs 139–142; *M. obediensis*, see Heller & Sivan 2001, Fig. 3D) we calculated the ratio b/c, as the index of shouldering. To express the extent of shell figurativity ('waist') that may sometimes occur (e.g. *M. vincta*, see Heller & Sivan 2001, Fig. 3F), we calculated the ratio c/d, as the index of figurativity. To express the extent to which whorls are conic ('conicality', e.g. *M. buccinoidea* versus *M. costata* - Allenby, Heller *et al.* 1999 Figs 4A and 4C) we calculated the ratio a/b, as the index of conicality.

Whorl height was measured at two points: e - height of penultimate whorl, from the aperture to nearest point on the suture above; and f - height of the previous whorl. From these measurements we calculated two relative whorl heights, the ratios e/mouth-height and f/mouth-height.

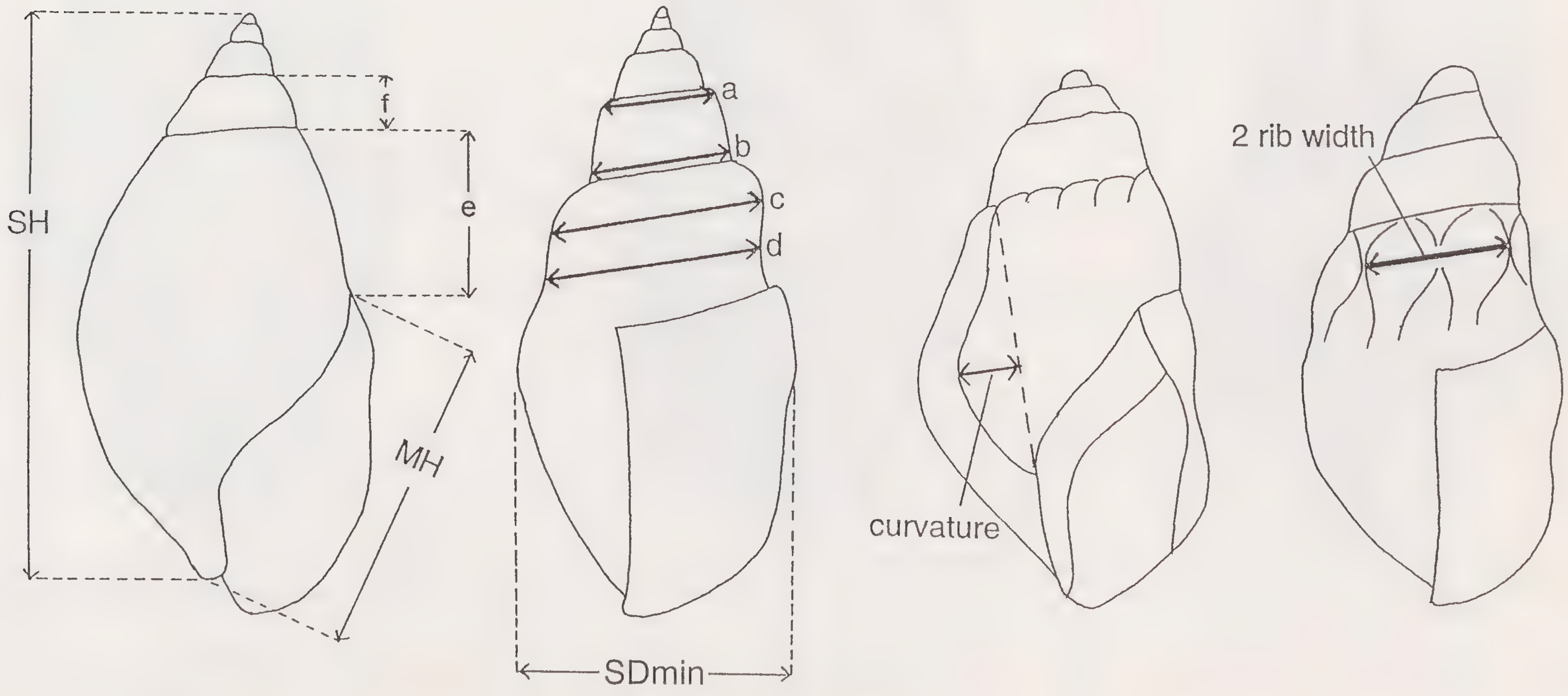


Fig. 2 Measurements used in this study. SH - shell-height; SDmin - minimal shell-diameter; MH - mouth-height.

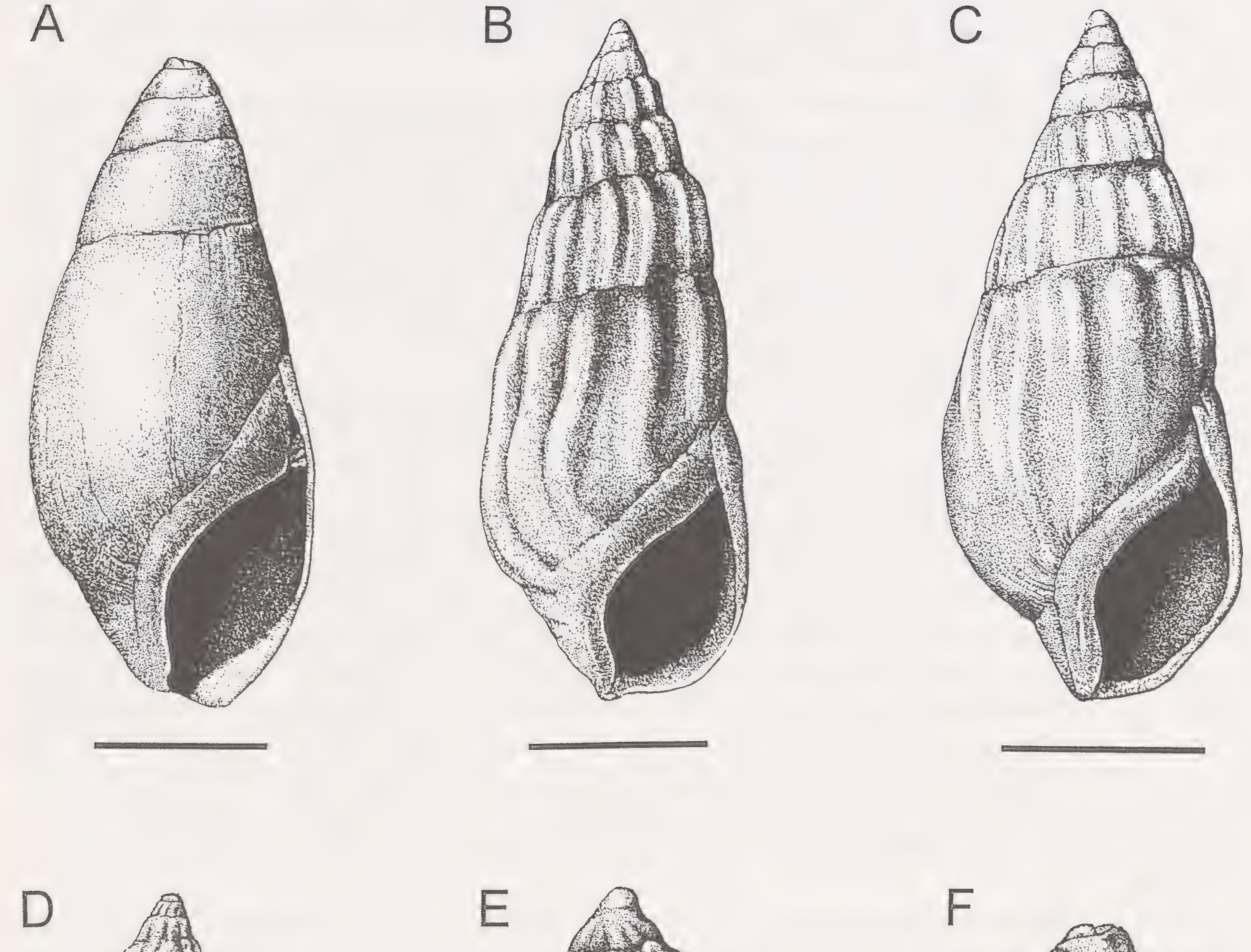


Fig. 3 *Melanopsis* species of 'Erq el-Ahmar. **A** - *M. buccinoidea;* **B** - *M. praecursor;* **C** - *M.saulcyi,* **D** - *M. multiformis* **E** - *M. aaronsohni* **F** - *M. tchernovi*. Scale bar = 5 mm.

To measure rib characteristics, each shell was scored for presence or absence of ribs. When ribs were present, at first three rib characteristics were scored: a) Rib number, from uppermost point of insertion of the aperture on the body whorl rightways, to the corresponding point on the previous whorl. b) Rib density, as the number of ribs from uppermost point of insertion of aperture 5 mm leftwards (from the point of insertion of the outer lip on the whorl), counted under the micrometer of the binocular. c) Rib length, examined on the body whorl. This characteristic is continuous. To describe increasing rib length four categories were erected: ribs very short, do not reach the shell aperture (1); ribs reach from the suture down to the aperture (2); ribs reach beyond the aperture but do not extend the entire height of the body whorl (3); ribs reach the entire height of the body whorl (4).

To measure (when relevant) the extent to which ribs are wavy (rather than straight) curvature was measured on the fifth rib of the body whorl (to the left of the aperture) using the eye-piece micrometer of the binocular (Fig. 2). Curvature is the distance (mm) to which a wavy rib deviates from an imaginary straight line that connects the upper and lower part of the rib. We distinguished ribs that curve to the left from those that curve to the right. On the shells from 'Erq el-Ahmar only left curvature was measured.

To express (when relevant) the width of the ribs at the tubercle (or at similar level in ribs without tubercle), the width of two ribs (on the body whorl, above the aperture) was measured (Fig. 2).

Statistical comparisons between different taxonomic groups were done with the non-parametric Kolmogorov-Smirnov test. Significance level was set at P= 0.05. For multivariate analysis we carried out Principal Coordinate Analysis (by use of the multivariate statistical package MVSP). Specimens with lacking data were excluded from this analysis.

The *Melanopsis* of 'Erq el-Ahmar are deposited, together with other molluscan remains of this site, in the Paleontology Collection of the Hebrew University of Jerusalem.

RESULTS

We found six species, which we hereby describe.

Melanopsis buccinoidea (Olivier 1801)

Fig. 3A

Mélanie buccinoide, M. buccinoidea Olivier 1801, pl. 17 fig. 8.
Melanopsis buccinoidea, Heller, Sivan & Motro 1999.
Melanopsis buccinoidea, Heller and Sivan 2001.

Holotype and Type locality '*Melanie buccinoide, M. buccinoidea* de Scio.' (Olivier 1801, pl. 17 fig. 8).

Description The shell has up to seven whorls. It has a pointed spire, flattened whorls separated by very shallow sutures, and is smooth (Heller *et al.* 1999).

Measurements Measurements and ratios of *M. buccinoidea* from 'Erq el-Ahmar (n=10):

Shell Characters	**Range**	**Mean ± SD**
shell-height	up to 18.5 mm	
shell-diameter (min) / shell-height	0.41– 0.52	0.45 ± 0.03
mouth-height / shell-height	0.54 – 0.66	0.61 ± 0.04

mouth-height / shell-diameter (min)	1.11– 1.46	1.36 ± 0.11
conicality	0.64 – 0.78	0.70 ± 0.04
figurativity	0.86 – 0.90	0.88 ± 0.02
shouldering	0.80 – 0.86	0.84 ± 0.02

Material 92 shell remains.

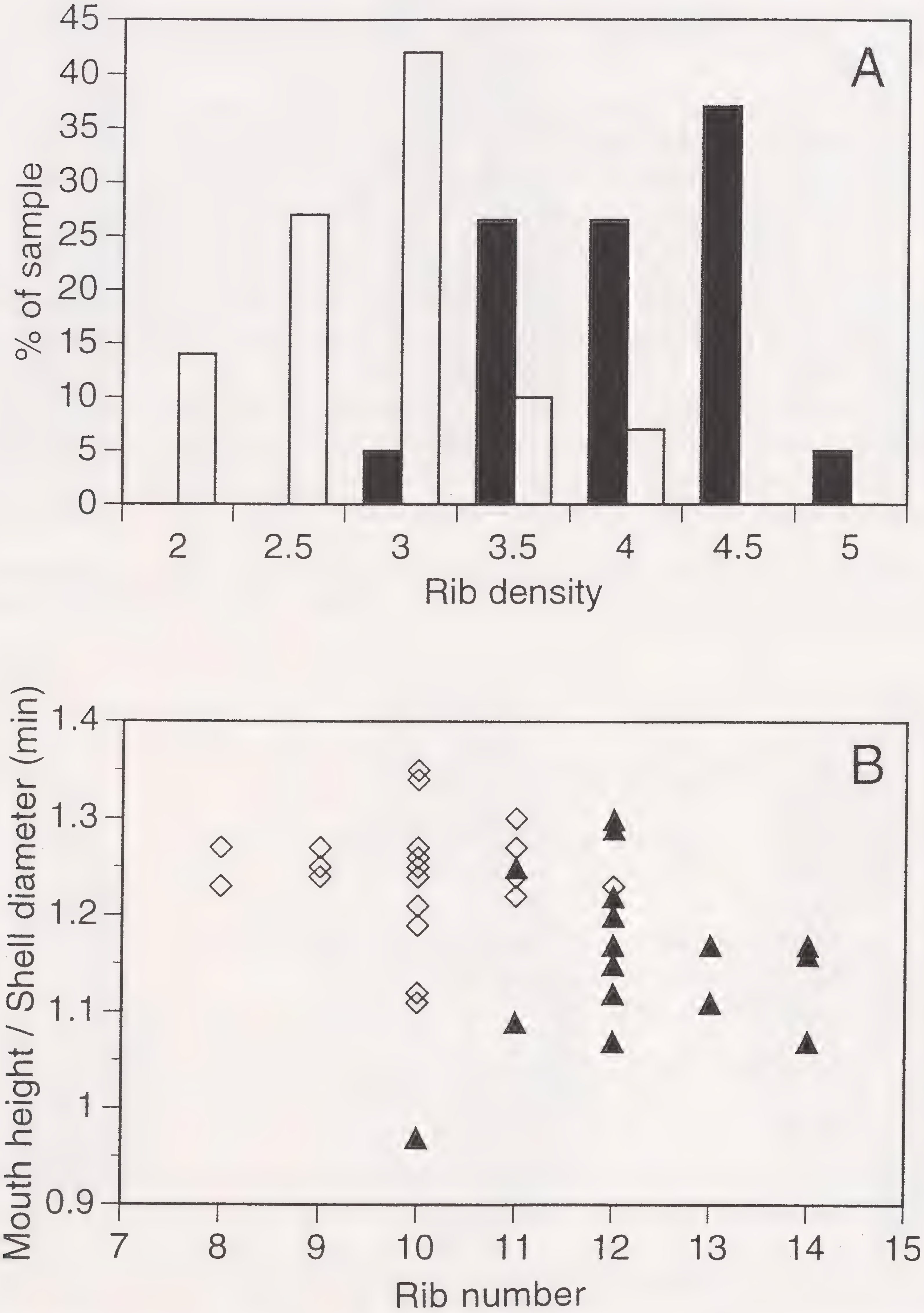


Fig. 4 Conchiometric differences between A. *Melanopsis praecursor* of 'Erq el-Ahmar (black) and Recent *M. c. costata* of the Upper Jordan Valley (white): Rib density. *B. Melanopsis praecursor* of 'Erq el-Ahmar (full triangles) and Recent *M. costata*: of the Lower Jordan Valley (open rhombi): Mouth-height / shell-diameter (min) versus rib number.

Distribution Recent in the Levant (Israel, Syria, Lebanon, Jordan and Turkey). Fossil (material we have inspected) in Gesher Benot Ya'aqov and 'Ubeidiya.

Comparisons The 'Erq el-Ahmar *buccinoidea* does not differ significantly from the Recent *buccinoidea* of the Jordan Valley and Coastal Plain, from the Upper-Pleistocene *buccinoidea* of Gesher Benot Ya'aqov, or from the Lower Pleistocene of 'Ubeidiya, in any of our conchiometric ratios (compare with Heller *et al.*, 1999: 57 and Appendix 1A; with Heller and Sivan, 2001; Heller and Sivan, 2002).

Melanopsis praecursor Schütt & Ortal 1993
Fig. 3B

Melanopsis praecursor Schütt & Ortal 1993, pl. 2 fig. 30.
Melanopsis praemorsa, Tchernov 1975, pl. 2 fig. 4.

Holotype and Type locality The type, from 'Erq el-Ahmar, is in the Paleontology Collection of the Hebrew University of Jerusalem.

Diagnosis *Melanopsis praecursor* differs from *M. c. costata* in that rib density is almost always more than 3.5.

Description The shell is tall and elongate. The 2–4 upper whorls are smooth, the 3–6 lower whorls are ribbed. Mildly to moderately-pronounced ribs extend the entire height of each whorl and most of them descend vertically.

Measurements Measurements and ratios of *M. praecursor* from 'Erq el-Ahmar (n=23):

Shell Character	**Range**	**Mean ± SD**
shell-height	up to 21.0 mm	
shell-diameter (min) / shell-height	0.38 – 0.45	0.41 ± 0.02
mouth-height / shell-height	0.41 – 0.54	0.48 ± 0.03
mouth-height / shell-diameter (min)	0.97 – 1.30	1.16 ± 0.08
conicality	0.75 – 0.92	0.86 ± 0.05
figurativity	0.89 – 1.00	0.96 ± 0.03
shouldering	0.67 – 0.89	0.80 ± 0.05
rib number	10 – 16	12.61 ± 1.36
rib density	3 – 6	4.21 ± 0.65
rib length	2 – 4	3.63 ± 0.75
2 rib width (mm)	1.8 – 3.5	2.45 ± 0.45

Material examined 420 shell remains.

Distribution Fossil in 'Erq el-Ahmar.

Comparisons From 'Erq el-Ahmar Schütt & Ortal (1993: 93 and pl. 2 fig. 30) described *Melanopsis praecursor*, as a possible genealogical precursor of *aaronsohni*. They diagnosed it as a species of small size, a turreted shell with few ribs at large intervals, the ribs thickened and knot-like at their uppermost ends. Upon examining the type we could not find knot-like upper parts of the ribs; but this shell clearly differs from *aaronsohni* in its turreted shell, with fewer and more widely inter-spaced ribs.

As compared to Recent *M. c. costata* of the Jordan Valley, *M. praecursor* differs in that it has more ribs that are denser (Fig. 4A), a mouth-height that is smaller in relation to shell-height, and a shell that is narrower.

Geographically, among recent *Melanopsis*, *M. praecursor* is closest to *costata* of the lower reaches of the Jordan River (Glaubrecht 1996, pl. 7, fig. 13; Heller & Sivan, 2001: 133). It differs significantly from it in that it has more ribs that are denser, the shell is slightly more stout and the ratio mouth-height / shell-diameter (min) is lower (Fig. 4B). Its pronounced ribs may perhaps place *M. praecursor* close to *noetlingi* Bourguignat of the Yarmouk, which is however more stout. Fossil *noetlingi* have been described by Picard (1934) from 'Erq el-Ahmar.

Among fossils, as compared to *costata* of 'Ubeidiya, *M. praecursor* differs in that it has more ribs which are denser, the shell is slimmer, the mouth is smaller as compared to shell-height, and the shell is less conic. As compared to *M. turriformis* of 'Ubeidiya, *M. praecursor* differs in that it is slimmer, has less ribs and is less conic.

Tchernov (in Schütt & Ortal, 1993) suggests that *M. praecursor* is an element of Miocene Sarmatian origin.

Melanopsis saulcyi Bourguignat 1853
Fig. 3C

Melanopsis saulcyi Bourguignat, 1853.
Melanopsis saulcyi, Heller, Sivan & Motro 1999.

Holotype *Melanopsis saulcyi* Bourguignat is from "Artouse, en Syrie" (Bourguignat 1853: 66, pl. 2 figs 53 and 54).

Measurements Measurements and ratios of *M. saulcyi* from 'Erq el-Ahmar (n=9):

Shell Character	Range	Mean ± SD
shell-height	up to 18.0 mm	
shell-diameter (min) / shell-height	0.38 – 0.43	0.41 ± 0.02
mouth-height / shell-height	0.46 – 0.47	0.46 ± 0.01
mouth-height / shell-diameter (min)	1.06 – 1.23	1.14 ± 0.06
conicality	0.75– 0.83	0.80 ± 0.03
figurativity	0.89 – 0.97	0.93 ± 0.03
shouldering	0.84 – 0.89	0.86 ± 0.02
rib number	10 – 16	13.11 ± 1.62
rib density	4 – 6	4.83 ± 0.68
rib length	2 – 3	2.21 ± 0.39

Material Nine shells.

Distribution Recent in the Levant (Israel, Syria, Lebanon and Jordan). Fossil in 'Erq el-Ahmar.

Comparisons The *saulcyi* of 'Erq el-Ahmar differs from recent *saulcyi* from the Jordan Valley in its smaller mouth, and in that its ribs do not have an upper tubercle. Among recent *saulcyi* the presence of tubercles varies from well-pronounced to very weak.

The *M. saulcyi* of 'Erq el-Ahmar differs from *M. praecursor*, the most common species of 'Erq el Ahmar, in its shorter ribs that reach only half the length of the last whorl.

All *M. saulcyi* specimens were found in a single vial. *M. saulcyi* is not known from Pleistocene sites of the Jordan Valley (Heller & Sivan 2001, 2002). As the 'Erq el Ahmar collection has, in previous years, several times been shuffled from one building in Jerusalem to another; and also as it was kept in open boxes for some while, we suspect that this vial is mislabeled.

Melanopsis multiformis Blanckenhorn 1897
Fig. 3D

Melanopsis multiformis Blanckenhorn 1897:116–117, pl. 9 figs 8–17.
Melanopsis noetlingi, Picard 1934, pl. 7 figs 28–29.
Melanopsis multiformis, Heller & Sivan 2002.

Diagnosis A fossil species of *Melanopsis, M. multiformis* differs from *costata* in the very thickened, broad tubercle in the upper part of each rib.

Type locality Clay layers in the banks of the Orontes (Blankenhorn, 1897).

Description The shell is usually cylindrical to elongate. It has up to eight whorls. The first three whorls are smooth (in our samples, very frequently they are eroded); the three-five lower whorls are ribbed. The ribs are widely spaced, well pronounced and usually reach vertically, from the suture straight down to the base of the whorl. In further detail, each rib frequently consists of an upper tubercle that is thickened and broad. This tubercle is fused to a well-pronounced lower ridge that descends vertically, or almost vertically. The sutures are wavy. On the inner lip, the well-pronounced callus of the upper parietal wall merges with the columella.

Measurements Measurements and ratios of *M. multiformis* from ‘Erq el-Ahmar (n=26):

Shell Character	**Range**	**Mean ± SD**
shell-height	up to 19.6 mm	
shell-diameter (min) / shell-height	0.44 – 0.52	0.47 ± 0.02
mouth-height / shell-height	0.41 – 0.56	0.48 ± 0.05
mouth-height / shell-diameter (min)	0.88 – 1.15	1.04 ± 0.08
conicality	0.85 – 0.98	0.92 ± 0.04
figurativity	0.94 – 1.02	0.98 ± 0.02
shouldering	0.68 – 0.83	0.75 ± 0.03
rib number	8 – 13	10.25 ± 1.32
rib density	2 – 4	3.10 ± 0.50
rib length	2 – 4	3.88 ± 0.43
2 rib width (mm)	2.5 – 3.9	3.16 ± 0.36

Material examined 30 shells.

Distribution Lowermost clay strata of the Orontes bank (Blankenhorn, 1897); ‘Ubeidiya (Heller & Sivan, 2002); ‘Erq el-Ahmar (this present study).

Comparisons *M. multiformis* of ‘Erq el-Ahmar differs from *M. praecursor* of ‘Erq el-Ahmar in that it has (almost diagnostically) less ribs, that are more tuberculated (2 rib width is bigger) (Fig. 5). It further differs in that it is stouter, the mouth is smaller relative to shell-diameter, and rib density is lower. As compared to *M. multiformis* from ‘Ubeidiya, the ‘Erq el-Ahmar *multiformis* has more ribs, is less stepped and has lower figurativity; these differences are slight ($0.01 < P < 0.05$).

Among Recent *Melanopsis* of the Jordan Valley, the ‘Erq el-Ahmar *multiformis* is most similar to *M. c. noetlingi* from the mouth of the Yarmouk (Heller et al. 1999). As compared to *M. c. noetlingi*, the *multiformis* of ‘Erq el-Ahmar differs in that the mouth is smaller relative to shell-height, it is less conical, figurativity is higher, and the tubercles are not as prominent.

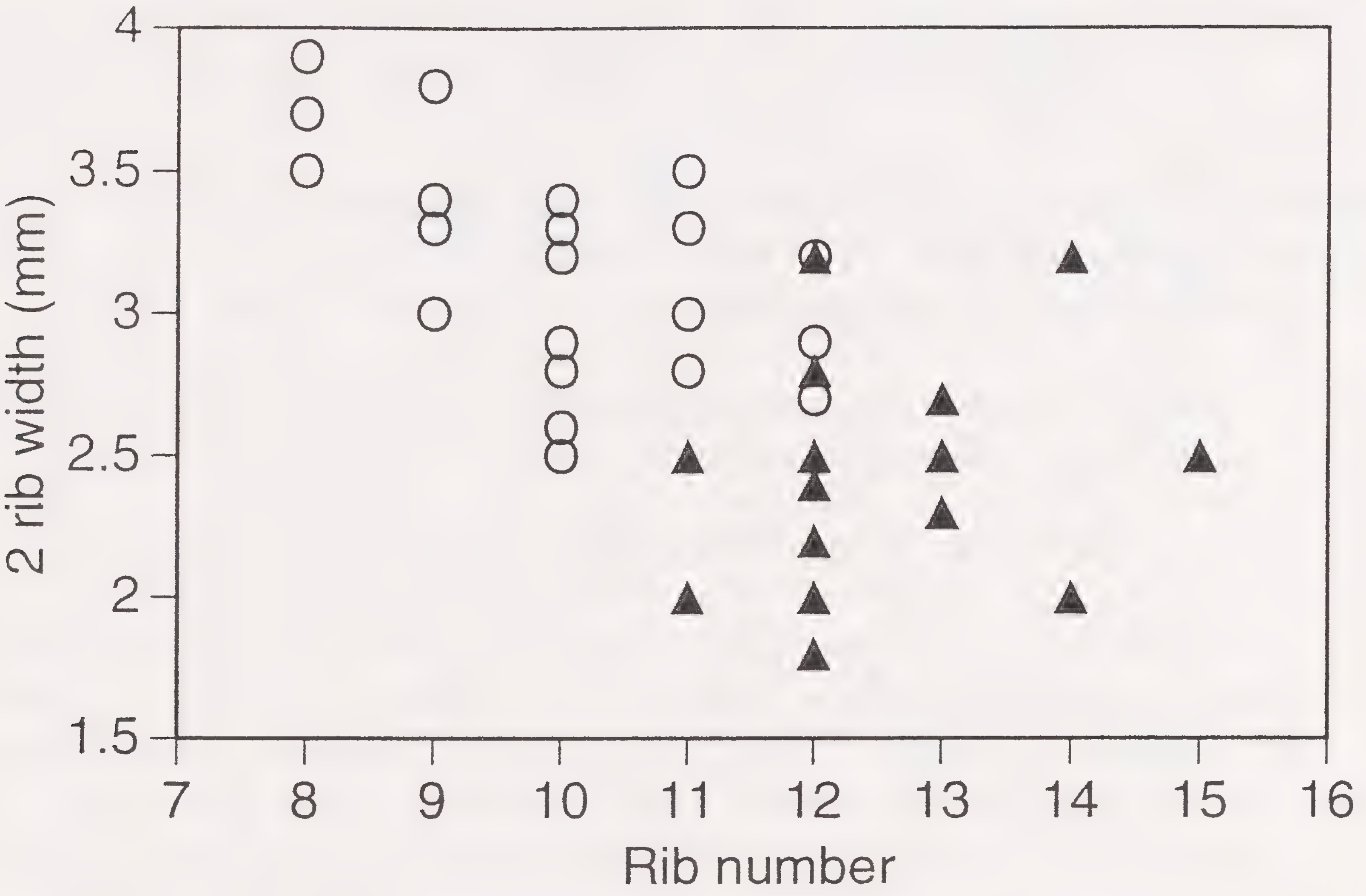


Fig. 5 Conchiometric differences between *Melanopsis praecursor* (full triangles) and *M. multiformis* (open circles), both from 'Erq el-Ahmar: rib width versus rib number.

Melanopsis aaronsohni Blanckenhorn 1927
Fig 3E

Melanopsis aaronsohni Blanckenhorn 1927: 37; pl. 1 figs 14–15.
Melanopsis aaronsohni, Picard 1934, pl. 8 figs 1–14.
Melanopsis praemorsa, Tchernov 1975, pl. 2 fig. 5.
Melanopsis aaronsohni, Schütt & Ortal 1993, pl. 2 figs 27–29.

Holotype and Type locality The holotype of *Melanopsis aaronsohni*, from 'Djisr el-Medjami' (= 'Erq el-Ahmar) is in the Paleontology Collection of the Hebrew University of Jerusalem.

Diagnosis A fossil species of *Melanopsis, M. aaronsohni* differs from *costata* in its very large aperture, as compared to shell-height.

Description The shell is ovoid, with a short spire and shouldered whorls. The 2–3 upper whorls are smooth and (when not eroded) form a small cone on top of the shell, the 3–4 lower whorls are ribbed. Many moderately pronounced ribs extend the entire height of each whorl, they are uniform in breadth, and lack tubercles. The lower part of each rib bends leftward. The callus is usually very bulky.

Measurements Measurements and ratios of *M. aaronsohni* from 'Erq el-Ahmar (n = 28, including eight specimens determined by Picard):

Shell Character	**Range**	**Mean ± SD**
shell-height	up to 16.3 mm	
shell-diameter (min) / shell-height	0.44 – 0.55	0.48 ± 0.03
mouth-height / shell-height	0.55 – 0.70	0.62 ± 0.05
mouth-height / shell-diameter (min)	1.03 – 1.42	1.25 ± 0.12
conicality	0.81– 0.91	0.87 ± 0.03

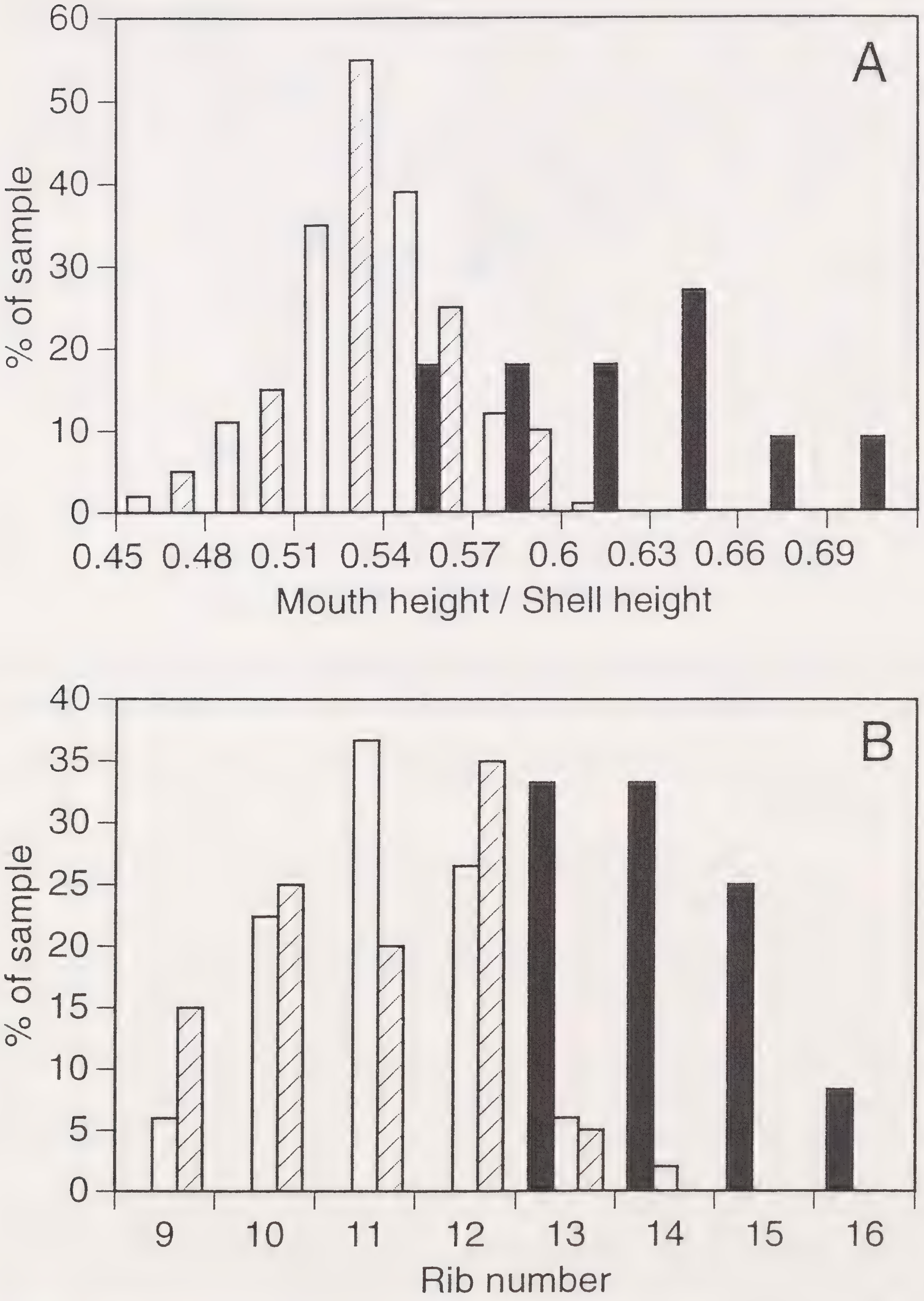


Fig. 6 Conchiometric differences between *Melanopsis aaronsohni* of 'Erq el-Ahmar (black), Recent *M. c. costata* (white) and Recent *M. c. noetlingi* (hatched) of the Jordan Valley: A. Mouth-height / shell-height. B. Rib number.

figurativity	0.88 – 0.98	0.94 ± 0.01
shouldering	0.55 – 0.79	0.70± 0.06
rib number	10 – 16	13.45 ± 1.39
rib density	3.5 – 6	4.48 ± 0.93
rib length	All 4	
rib curvature (left) (mm)	0.6 – 1.2	0.87± 0.18

Material examined 322 shell remains.

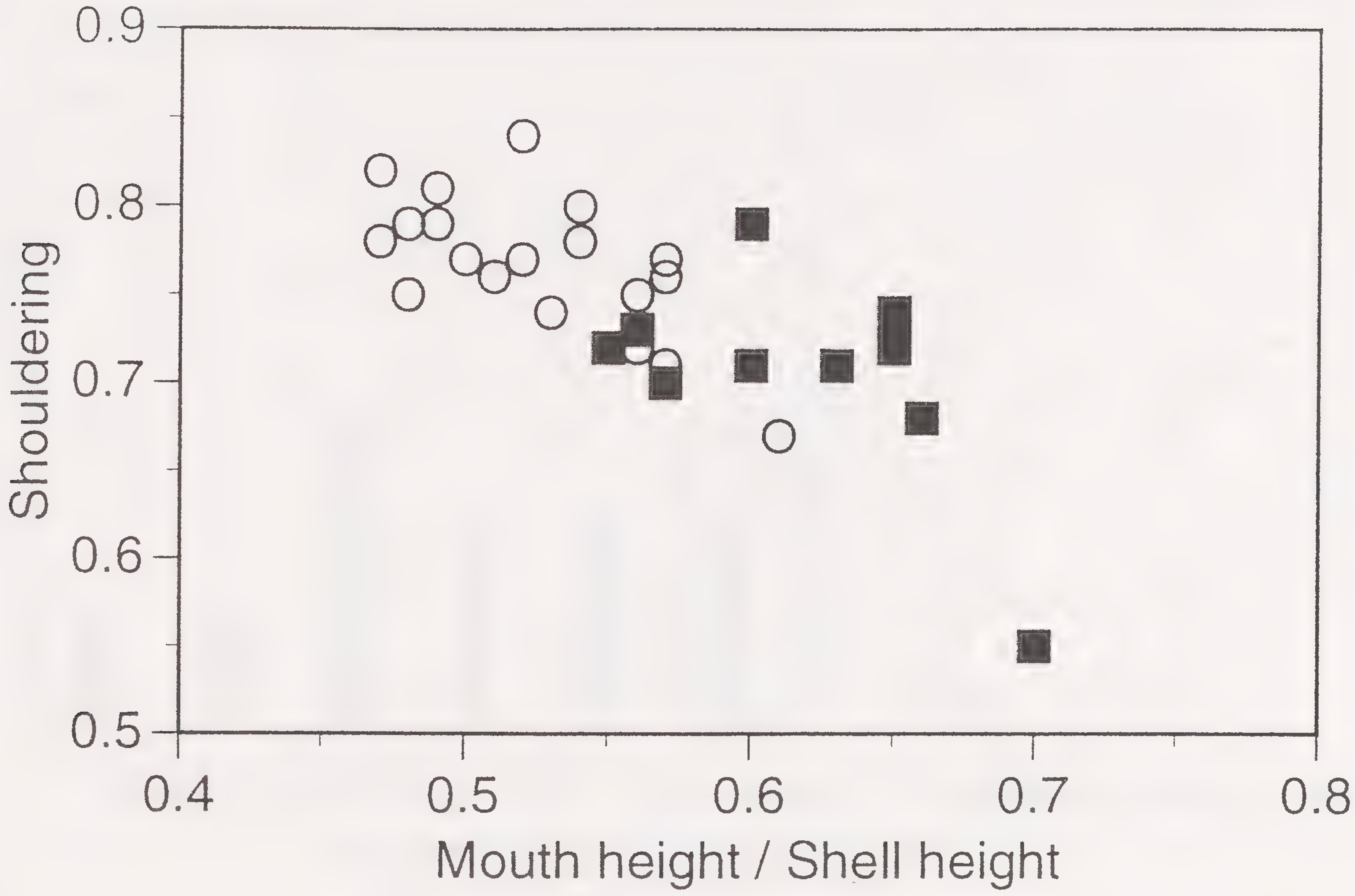


Fig. 7 Conchiometric differences between *Melanopsis aaronsohni* of 'Erq el-Ahmar (full squares) and *M. turriformis* of 'Ubeidiya (open circles): Shouldering versus mouth-height / shell-height.

Distribution 'Erq el-Ahmar (Blanckenhorn & Oppenheim, 1927; Picard, 1934; Tchernov, 1975; this present study).

Comparisons *M. aaronsohni* differs from *M. precursor* in that it is stouter, has a bigger mouth relative to shell-height and is more stepped.

M. aaronsohni differs from Recent *c. costata* of the Jordan Valley in that it is stouter, has a shorter spire (as expressed in a higher mouth-height / shell-height, Fig. 6A) and has denser ribs. Also, *aaronsohni* almost always has 13 ribs or more, whereas in *costata* most shells have less (Fig. 6B); and in *aaronsohni* the whorls are almost always more stepped: the index of shouldering is usually less than 0.73, whereas in costata it is usually more.

Blanckenhorn & Oppenheim (1927) suggested that *aaronsohni* is close to *noetlingi*, perhaps only a variety within the latter. However (as in costata) *aaronsohni* differs from Recent *noetlingi* in that it has a shorter spire (Fig. 6A), is more stepped, and almost always has more ribs (Fig. 6B) that are denser. In addition, it does not have a prominent upper tubercle (Fig. 3E). These differences do not support Blanckenhorn & Oppenheim's suggestion. Picard (1934) suggested that *aaronsohni* is close to *obediensis*. However, *aaronsohni* differs from *obediensis* of 'Ubeidiya in that it has a shorter spire, and has more ribs that are denser. These differences do not support Picard's suggestion. Tchernov (1975) suggested that *Melanopsis* consists of a vast numbers of ecotypes, all belonging to a single circum-Mediterranean species; consequently he considered *aaronsohni* as synonymous with *costata* (and other forms, all of which he placed in a single species, *praemorsa*). The distinct conchiometric gaps between *aaronsohni, costata* and *buccinoidea* do not support Tchernov's suggestion.

Of the fossil *Melanopsis* species of Israel *aaronsohni* may seem close to *turriformis*, in its general appearance and delicate ribs. However, *aaronsohni* differs from *turriformis* of 'Ubeidiya in that it has a shorter spire, its ribs curve to the left (Fig. 3E), its index of conicality is usually more than 0.85 and it's index of shouldering is usually less than 0.73 (Fig. 7).

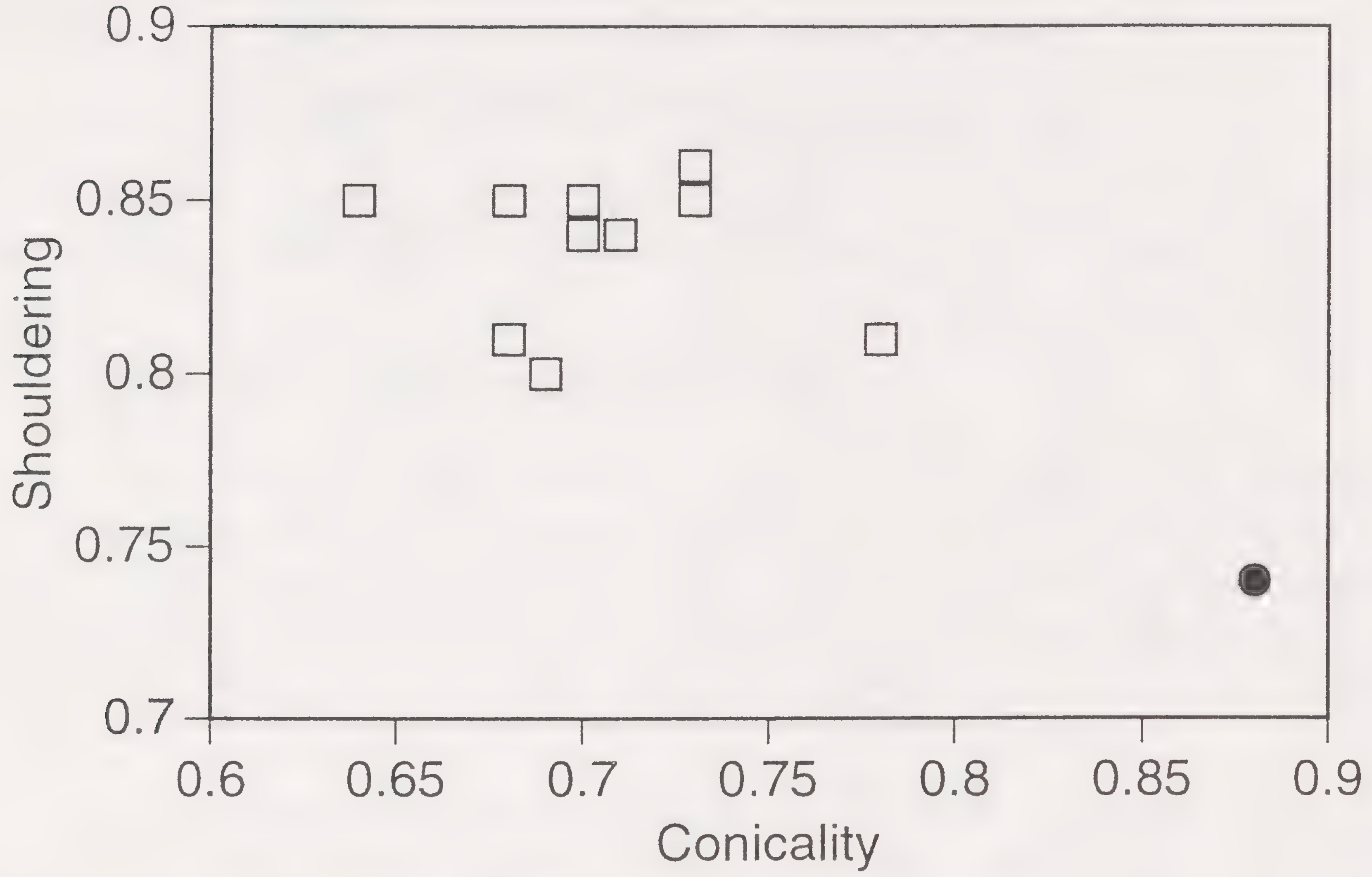


Fig. 8 Conchiometric differences between *Melanopsis tchernovi* (full circles) and *M. buccinoidea* (open squares), both from 'Erq el-Ahmar: Shouldering versus conicality.

Melanopsis tchernovi sp. nov.
Fig. 3F

Melanopsis hammamensis, Picard 1934, pl. 8 figs 44, 45 (non 46).
Melanopsis cf. *doriae*, Tchernov 1975, pl. 2 fig. 6.

Holotype and Type locality The holotype of *Melanopsis tchernovi*, from 'Erq el-Ahmar, is in the Paleontology Collection of the Hebrew University of Jerusalem (HUJ 9016).

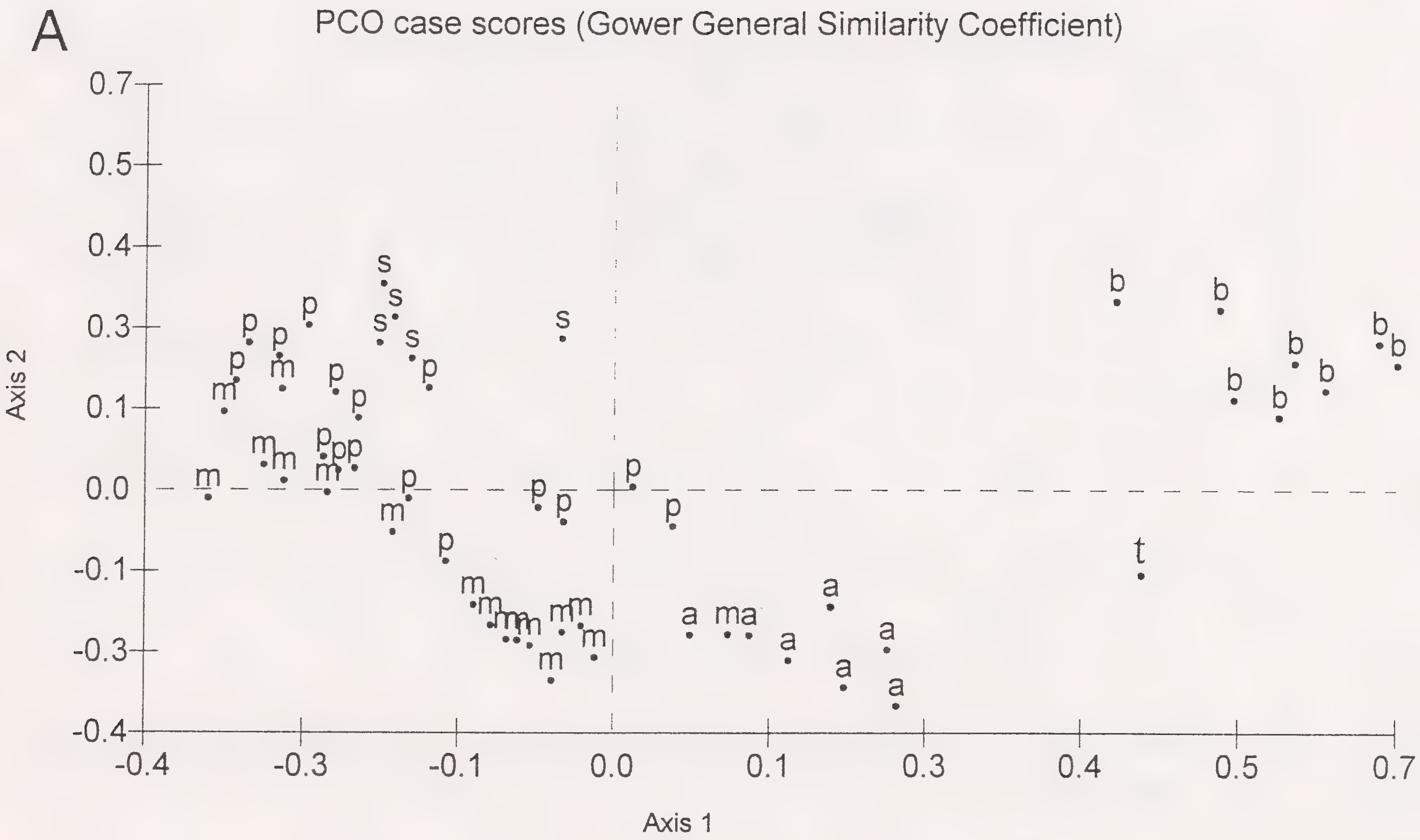
Diagnosis A fossil species of the genus *Melanopsis, M. tchernovi* differs from *M. buccinoidea* Olivier, the smooth-shelled *Melanopsis* that occurs today in the Jordan River, in that the last whorls posses a distinct keel that protrudes from the shell.

Description The shells available are heavily eroded, to such an extent that the number of whorls could not be determined. The three lowermost whorls are cylindrical and heavily scalariform, with a distinct keel protruding beyond the suture above it.

Material Two shells in the Picard collection; ten shell remains in the Palaeontology Collection of the Hebrew University of Jerusalem, nine of which are badly eroded.

Measurements Measurements are given of one specimen of *M. tchernovi* from 'Erq el-Ahmar (Picard's shells are partly embedded in hard matrix):

Shell characters	
shell-height	18.3 mm
shell-diameter (min) / shell-height	0.47
mouth-height / shell-height	0.63
mouth-height / shell-diameter (min)	1.34
conicality	0.88
figurativity	0.74



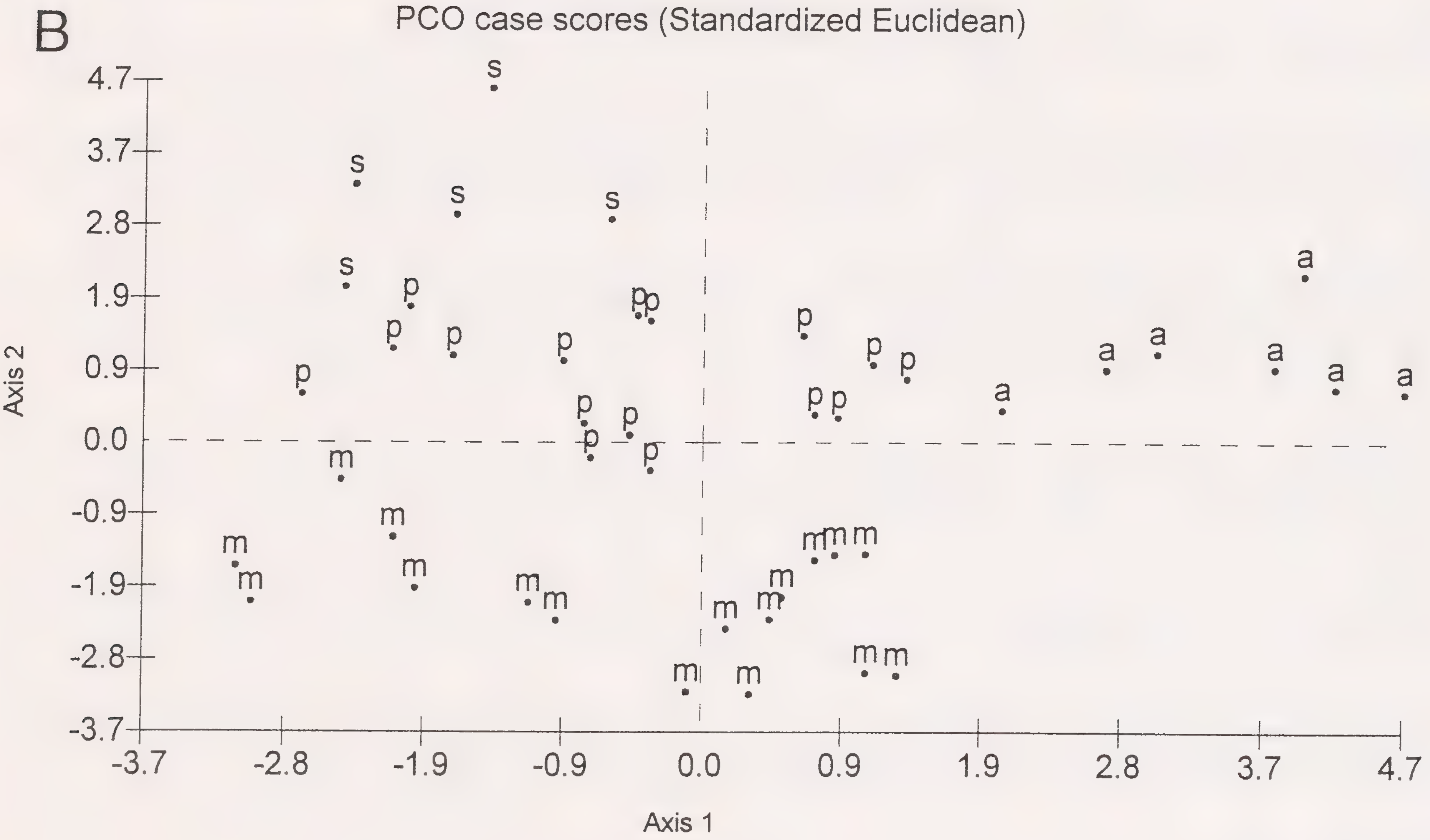


Fig. 9 Principal Coordinate Analysis of the *Melanopsis* species of 'Erq el-Ahmar; each point represents one specimen. **b** *M. buccinoidea* **p** *M. praecursor* **s** *M. saulcyi* **m** *M. multiformis* **a** *M. aaronsohni* **t** *M. tchernovi*. **A** Shell proportions and presence / absence of ribs; all six species. (Axis 1 = 34.8 %, Axis 2 = 17.4 %). **B** Shell proportions and rib characters; four ribbed species only. (Axis 1 = 33.0 %, Axis 2 = 30.5 %).

shouldering	0.93
e/MH	0.39
f/MH	0.16

Derivation of name In name of Prof. Eitan Tchernov of the Hebrew University of Jerusalem, eminent researcher of the Recent and Quarternary fauna of Israel.

Distribution *M. tchernovi* is a fossil species known only from 'Erq el-Ahmar, and perhaps also from Abu Habil, in the Jordan Valley.

Comparisons *M. tchernovi* falls beyond the range of *buccinoidea* (the smooth-shelled species that occurs today in the Jordan Valley) in conicality, figurativity and shouldering (Fig. 8). It differs from *vincta* of the mid Pleistocene site of Gesher Benot Ya'aqov (upper Jordan Valley; see Heller & Sivan, 2001) in that shell conicality is diagnostically higher (the ratio a/b is lower); shouldering is significantly smaller (the ratio b/c is higher), and figurativity (ratio c/d) is significantly lower.

Remarks Several scalariform-to-keeled species have been described from Morocco; their synonymy is so entangled that before comparing them to *Melanopsis tchernovi*, a brief review seems appropriate. Chemnitz (1795: 285, pl. 210 figs 2078– 2083) described from Morocco six shells that he named *Buccina moroccana*. Of these six specimens two (no. 2080–1) were keeled, and assigned by Deshayes (1838, in Richardson, Tucker Abbot & Davis, 1979) to *Melanopsis dufouri* Ferussac (see Richardson *et al.*, 1979: 413). Pallary (1920: 147, pl. 4 fig. 1) described *M. fasensis* from Morocco, a smooth-shelled species with a transverse keel close below the suture. He commented that this species, first illustrated by Chemnitz (1795, figs 2080–1) as *moroccana*, is somewhat similar to *scalaris* Bourguignat, *hammamensis* Gassies, *scalaris* Gassies and *subscalaris* var. *major* Bourguignat. Pallary (1920: 149, pl. 4 figs 23–25) further described from Morocco *M. torquilla*, a species with a strongly transverse keel close below which there is a depression; and with a short, pointed spire. He commented that *torquilla* seems close to *M. guiraoi* Bourguignat from southern Spain, and to *M. cylindrica* Stroliczka from the Neogene of Hungary. Pérès (1939; pl. IV–V) reviewed the *Melanopsis* of Morocco. He found so many transitional intermediates between *scalaris, subscalaris, hammamensis, fasensis, torquilla* and a new variety (*arbalensis*) that he placed them all under one heading, *scalaris* Gassies. Later however, Pérès (1945, pl. 1 figs 11–14) assigned all these forms to *dufouri* Ferussac.

From the Levant, Blankenhorn (1897: 124, pl. 10 fig. 4) mentioned *Melanopsis moroccana* Chemnitz var. *media* Bourguignat, both as a fossil from the mid-Pliocene of the lower Orontes and also as a recent species, from the (now drained) Lake Hula and from Lebanon. He figured a non-keeled shell, so it is obvious that he was not referring to Chemnitz's keeled *moroccana*. Picard (1934) considered *hammamensis* as a species separate from *moroccana*, and commented that differences between it and *torquilla* are negligible. From Jisr el-Medjami (= 'Erq el-Ahmar) he described two keeled shells as *M. aff. hammamensis* Gassies 1856, that differ from typical *M. hammamensis* in their more cylindrical shape and more pronounced keel. Later, Tchernov (1975) considered these keeled shells as very similar to *M. doriae* Issel, a species occurring today in Iran. Tchernov commented that *M. doriae* is at present endemic to Mesopotamia, but its geographical distribution during the late Neogene to early Pleistocene was far wider, including the Jordan Valley. In referring to the similarity of the 'Erq el-Ahmar shells to the Moroccan species, Tchernov commented that in certain environmental conditions, similar shell textures may appear in any of the *Melanopsis* species. We could not find any close resemblance between the Jisr el-Medjami shells on the one hand and any of the keeled *M.*

doriae shells illustrated by Starmühlner & Edlauer (1957: 443) on the other. Further, we inspected the *M. doriae* deposited by Starmühlner & Edlauer in the Naturwissenschaften Museum in Vienna, and could not find any keeled specimens. Also the *doriae* illustrated by Bandel (2000, figs 26–29) are not keeled. We therefore do not accept the assignment of the 'Erq el-Ahmar specimens to *doriae*.

From Abu Habil, a Lower Pleistocene site in the Jordan Valley broadly time-equivalent to 'Erq el-Ahmar, Bandel (2000, pp. 147–148 and 180, figs 139–142) illustrated several shells which he assigned to *M. dufouri* Ferussac, a species with up to three weakly developed spiral ribs. He described the Abu Habil *dufouri* as having two low, rounded ridges along the body whorl, and as being more stout and cylindrical than the *dufouri* from Morocco. Bandel further commented that in Abu Habil, *dufouri* probably formed hybrids with *buccinoidea* and with *orientalis;* and that *dufouri* from the Pleistocene of Granada is so extremely similar to *M. delessei* Tournouer 1876 from the Neogene of Greece (p. 148) that *dufouri* and *delessei* are identical (p. 180). We have measured both *dufouri* from Abu Habil and *delessei* from Greece (Kos), and found that they differ statistically in the ratio shell-diameter (min) / shell-height (Abu Habil is thinner); shouldering (Abu Habil is more stepped) and in the ratio f/MH (Abu Habil has higher whorls). We therefore consider Bandel's *dufouri* and *delessei* as different species (Heller & Sivan, in prep.). *M. tchernovi* is similar to Bandel's *dufouri* in shell proportions. However, none of Bandel's dufouri has the very prominent ridge that is characteristic of *M. tchernovi.*

Melanopsis dufouri, found in Morocco, is large (shell-height up to 35 mm, see Pérès, 1945 Pl. 1, Figs 11–14) as compared to the 'Erq el-Ahmar specimens that reach only 18.3 mm. Otherwise we do not see differences between the 'Erq el-Ahmar specimens and the *dufouri* illustrated by Pérès (1945, pl. 1 fig. 12), the *hammamensis* illustrated by Pallary (1920) and the various forms of *scalaris* as illustrated by Pérès (1939) (his figs 1–3 as *M. scalaris,* his fig. 4 as *M. torquilla,* his figs 26, 37 as *M. fasensis*).

However, it is noteworthy that *M. dufouri* occurs today only in northwestern Africa and Spain. We know of no Recent species, animal or plant, that occurs in the Levant on the one hand and the Maghreb on the other, yet not in between (see also Tchernov 1975).

The possibility that *dufouri* once ranged from Morocco-Spain to the Levant via Libya and Egypt is not likely, in view of total lack of fossil evidence of any *Melanopsis* in these regions (van Damme, 1984).

Another possibility is that *dufouri* was once widespread throughout parts of Europe, with a south-eastern extension into the Levant on the one hand, and a southwestern one into the Maghreb on the other; that eventually *dufouri* became extinct in the center of its range, lingered on in the Levant until about 2 myr ago when it became extinct; but survives in Spain and the Maghreb. The only evidence to support such a scenario are Bandel's (2000) statements (not conchiometric evidence) that *dufouri* of the Pleistocene of Spain is extremely similar to *M. delessei* from the Late Neogene of Greece; and that *Melanopsis vincta* Blanckenhorn from the Pliocene of Syria is a *M. dufouri.*

A third possibility should also be considered: that keels may appear independently in shells of different *Melanopsis* species, and that the keeled *Melanopsis* of 'Erq el-Ahmar (as well as that of Abu Habil) is not *dufouri.* In support of this possibility we note that among recent *Melanopsis,* ribbed *costata* of the eastern Mediterranean is convergent in shape with ribbed *cariosa* of the western Mediterranean; and smooth *buccinoidea* of the eastern Mediterranean is convergent in shape with smooth *praemorsa* of the western Mediterranean. The possibility that also keeled species evolved in convergence, in the eastern separately from the western Mediterranean, should not be discarded. Accordingly, we assign the 'Erq el-Ahmar specimens to a separate species, *M. tchernovi.*

MULTIVARIATE COMPARISONS BETWEEN TAXA

Fig. 9 presents Principal Coordinate Analysis of the Melanopsis taxa found at 'Erq el-Ahmar. For Fig. 9A, which includes both the ribbed and smooth taxa, shell ratios were used, and also presence/absence of ribs. For Fig. 9B, which includes only the ribbed taxa, rib characters were added. Fig. 9A clearly separates the one specimen of *tchernovi* from the other smooth species, *buccinoidea*. Some grouping of the ribbed shells can also be seen. Fig. 9B separates the ribbed shells into the four ribbed taxa.

DISCUSSION

PALAEO-BIOGEOGRAPHY

The 'Erq el-Ahmar fauna suggests that *Melanopsis* is an early inhabitant of the Jordan Valley, for at least 2 myr. Of the five *Melanopsis* taxa definitely found at 'Erq el-Ahmar, four are extinct (*M. praecursor, multiformis, aaronsohni, tchernovi*); one occurs in the Levant also today (*buccinoidea). M. saulcyi* is excluded from the discussion, since its status is unclear.

Within the Jordan Valley, in both geographic and in chronological terms, 'Erq el-Ahmar (2 myr) is close to the lower- Pleistocene lake of 'Ubeidiya (4 km further north, 1.4 myr old). Only two of the 'Erq el-Ahmar *Melanopsis* taxa (*M. buccinoidea, multiformis*) occur also in 'Ubeidiya whereas *M. praecursor, M. aaronsohni*, and *M. tchernovi* do not; and two of the 'Ubeidiya *Melanopsis* do not occur in 'Erq el-Ahmar (*turriformis; phanesiana obediensis*; Heller and Sivan, 2002). A gap thus seems to exist in the Jordan Valley, between the aquatic fauna of the late Pliocene on the one hand and that of the early Pleistocene on the other (see also Tchernov, 1975, and 1993 in Schütt & Ortal).

In both space and time, 'Erq el-Ahmar is more distant from the mid-Pleistocene lake of Gesher Benot Ya'aqov (45 km further north, 780,000 yr). Only one species is common to these two sites (*M. buccinoidea*). Hydrological connections between the Upper and Central sectors of the Jordan systems thus seem to have been poor during the late Pliocene and early Pleistocene; it was only during the later Middle Pleistocene that firm links were established between both Jordan basins, following the secondary tectonic movements along the Rift Valley (see also Tchernov, 1975).

Beyond the Jordan Valley, 'Erq el-Ahmar is broadly contemporaneous with the Pliocene aquatic fauna of the Orontes (Blanckenhorn, 1897; Picard, 1934). Of the five *Melanopsis* taxa of 'Erq el-Ahmar, only *buccinoidea* and *multiformis* occur also in the Pliocene of the Orontes (Blanckenhorn, 1897; Blankenhorn & Oppenheimer, 1927). Both Picard (1934), and Tchernov (in Schütt & Ortal, 1993) suggested that during the Upper Pliocene the fauna of the Jordan was largely independent of the Orontes, and that during the late Pliocene, faunal connections between the Jordan and Orontes catchment areas were not extensive (see also Heller & Sivan, 2002).

PALAEO-ENVIRONMENTS

In general, freshwater molluscan death assemblages show strong fidelity to relative abundances in the live community (Kidwell and Flessa, 1995; Kidwell, 1998). Relative abundances of the *Melanopsis* species' in 'Erq el-Ahmar are therefore likely to be in good agreement with the live community of that period. Combining shell numbers of the two Recent species of 'Erq el-Ahmar (n = 510) reveals that about four fifths of the shell remains are *costata*, one fifth *buccinoidea*.

Among recent *Melanopsis*, *costata* with a large, elongate, small-mouthed shell *(c. costata*) correlates with non-turbulent habitats, such as river banks where the current is weak, silty mud and submerged vegetation, as used to exist in the Hula Lake until forty years ago (Heller *et al.*, 1999). Among the fossils of 'Erq el-Ahmar, *costata* is elongate and with a small aperture. It is reasonable to speculate that the *costata* of 'Erq el-Ahmar represent a shallow (1–2 m), non-turbulent, well-aerated lake with a slow current, similar to sub-recent Lake Hula. This speculation agrees with the conclusion, reached by Braun (1992) on sedimentary evidence, that 'Erq el-Ahmar was a shallow, low-energy lake.

Among recent *Melanopsis* of the Jordan Valley, *buccinoidea* occurs in springs and streams rather than in rivers and lakes (Heller *et al.*, 1999). It occupies both hard substrates and silty mud. It is reasonable to speculate that the *buccinoidea* of 'Erq el-Ahmar represents a spring or stream, flowing into the 'Erq el-Ahmar lake.

ACKNOWLEDGEMENTS

We thank Eitan Tchernov for entrusting us with the *Melanopsis* of 'Erq el-Ahmar, and for commenting on an early draft of this paper. Tuvia Kurz carried out the illustrations of Fig. 3. This study was funded by the American Friends of the Hebrew University.

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A REVIEW OF THE PLEISTOCENE OCCURRENCE OF THE EXTINCT LAND SNAIL *ZONITOIDES SEPULTUS* IN EUROPE, INCLUDING THE FIRST RECORDS FROM BRITAIN AND FRANCE

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Abstract The Pleistocene occurrence of Zonitoides sepultus, *an extinct zonitid land snail, is reviewed. The species is now known from 23 sites, ranging from Hungary and Poland in the east to northern France and eastern England in the west. The four British records, from Beeches Pit, West Stow (Suffolk), Barnfield Pit, Swanscombe (Kent), Clacton-on-Sea (Essex) and Barling (Essex), and the French record from St Pierre-les-Elbeuf (Normandy) are new. Stratigraphically, the oldest records date from the Early Pleistocene of Poland and The Netherlands, where* Z. sepultus *occurs in sediments of Tiglian age. However, it appears to have been widespread in central Europe during the Middle Pleistocene, especially in calcareous tufas of Holsteinian (=Hoxnian) age. This suggests that the species may have had an ecological preference for damp woodland habitats. The new sites in Britain and France are all Middle Pleistocene in age and, apart from Barling, appear to date from the same interglacial (the Hoxnian). The Barling record seems to be younger, probably dating from the subsequent interglacial stage, and is therefore likely to be the same age as that from Belvédère in The Netherlands. These two late Middle Pleistocene records from western Europe therefore represent the last known occurrence of the species.*

Key words Zonitoides sepultus, *Pleistocene, Holsteinian, Hoxnian, calcareous tufa*

Extinct species of land snail form a relatively high proportion of the molluscan assemblages from the Early Pleistocene of Europe but by the Middle Pleistocene the number of species had fallen sharply and they are represented by only a handful of taxa. This paper is concerned with one of these rare extinct taxa that persisted into the Middle Pleistocene.

Zonitoides sepultus is an extinct species of zonitid (Fig. 1), distinguished from other species of *Zonitoides* by its more compressed shell and especially by its marked peripheral angulation, so that in profile it resembles *Discus rotundatus*. The angulation is particularly obvious in juvenile shells. Its umbilicus is also wide, usually about a quarter of the width of the shell, but not as broad as in *Z. excavatus*. The upper surface bears fine but irregular transverse sculpture but the underside is almost smooth, except for some weak spiral lines. Adult shells are typically 6.1–7.2 mm in breadth and 3–3.5 mm in height and have 4 ¾ slowly but regularly increasing whorls. Unlike fossil shells of *Z. nitidus* and *Z. excavatus*, which usually retain some of their original brown colour, those of *Z. sepultus* are almost invariably pure white.

Zonitoides sepultus was originally described by Ložek (1964) from deposits of 'Cromerian' age from Stránská skála near Brno in the former Czechoslovakia. Here it occurred as part of a fully interglacial Middle Pleistocene fauna with other extinct species such as *Helicigona capeki* and the biostratigraphically important vole *Mimomys savini* (=intermedius). *Z. sepultus* was subsequently reported from other Middle Pleistocene deposits in Czechoslovakia (Ložek, 1964), Hungary (Krolopp, 1978), Germany (Dehm, 1969), The Netherlands (Meijer, 1985) and from Early Pleistocene deposits in Poland (Stworzewicz, 1981). We have been able to trace 18 records of *Z. sepultus* in the literature, to which we can now add four records from Britain, one from France, two from Germany, and one from The Netherlands (Fig. 2). Details about each of these localities, including the nature of the host sediment, its stratigraphical context and the associated fauna are given in Tables 1 and 2, together with information on the present whereabouts of each specimen (where known).

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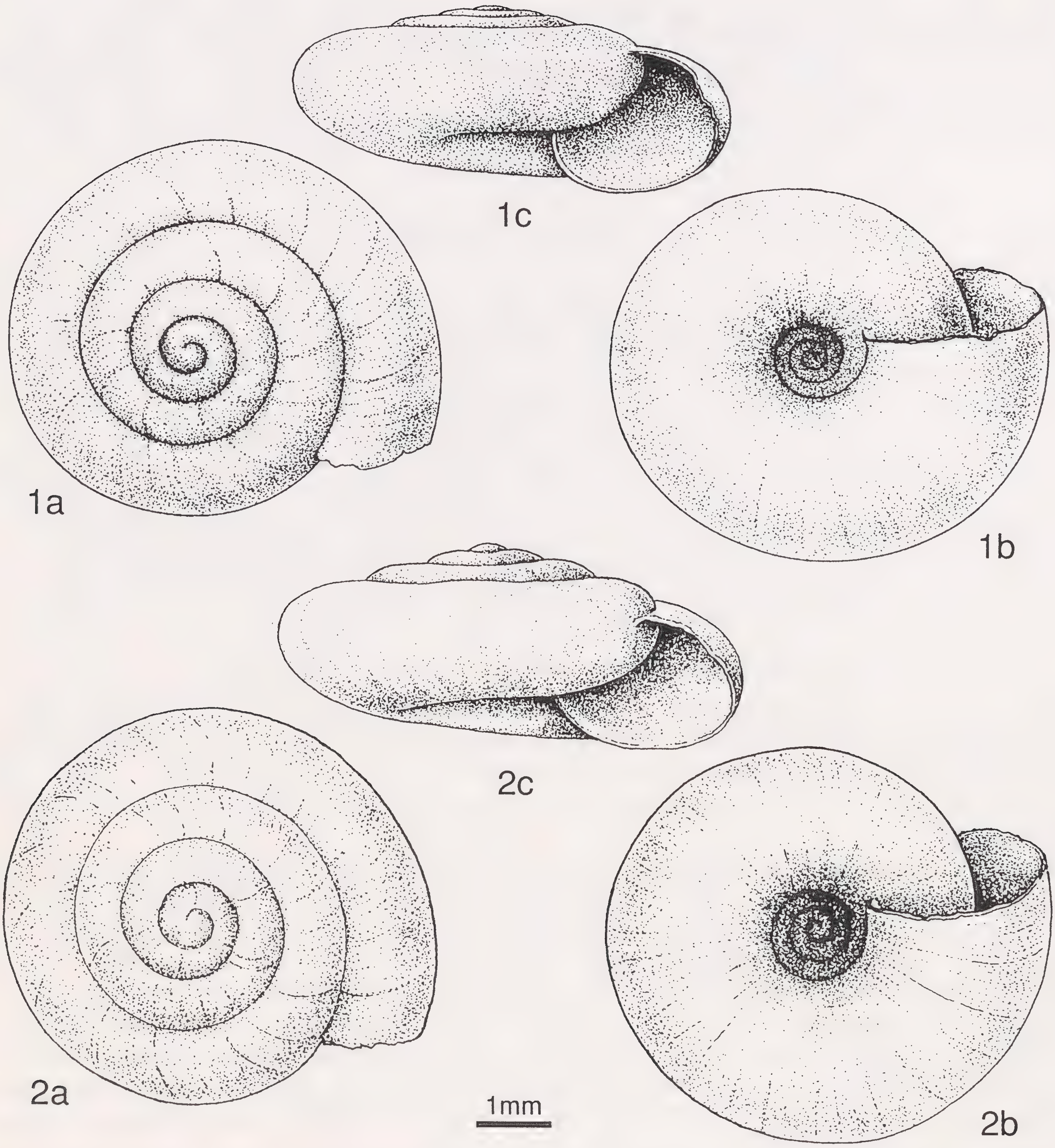

Fig. 1 *Zonitoides sepultus* from the British Pleistocene. 1a-c Specimen from Barling, Essex; 2a-c Specimen from Beeches Pit, West Stow, Suffolk.

Z. sepultus, hitherto unknown from Britain, has recently been recognized at four Middle Pleistocene sites in southern England. At Beeches Pit at West Stow, Suffolk (National grid reference TL 798719) several specimens (Fig. 1) were recovered from an interglacial tufa (the so called Icklingham tufa), that has yielded a rich woodland fauna including other extinct taxa such as *Retinella (Lyrodiscus) skertchlyi* (Kerney, 1976; Preece *et al.*, 2000)*. The tufa overlies Anglian glacial deposits and there is good biostratigraphical and geochronometric dating evidence to suggest that the tufa here formed during the Hoxnian (approximately equivalent to marine isotope stage 11), one of the warmest interglacials of the Middle Pleistocene (Preece *et al.*, 2000). A single sub-adult shell was also identified amongst material in the Natural History Museum, London, collected by A.S. Kennard from the Lower Loam at Barnfield Pit, Swanscombe, Kent (TQ 597742).

* *Retinella (Lyrodiscus) skertchlyi* Kerney, 1976 is probably a junior synonym of *R. (Lyrodiscus) elephantinum* (Bourguignat, 1869) described from Joinville, France.

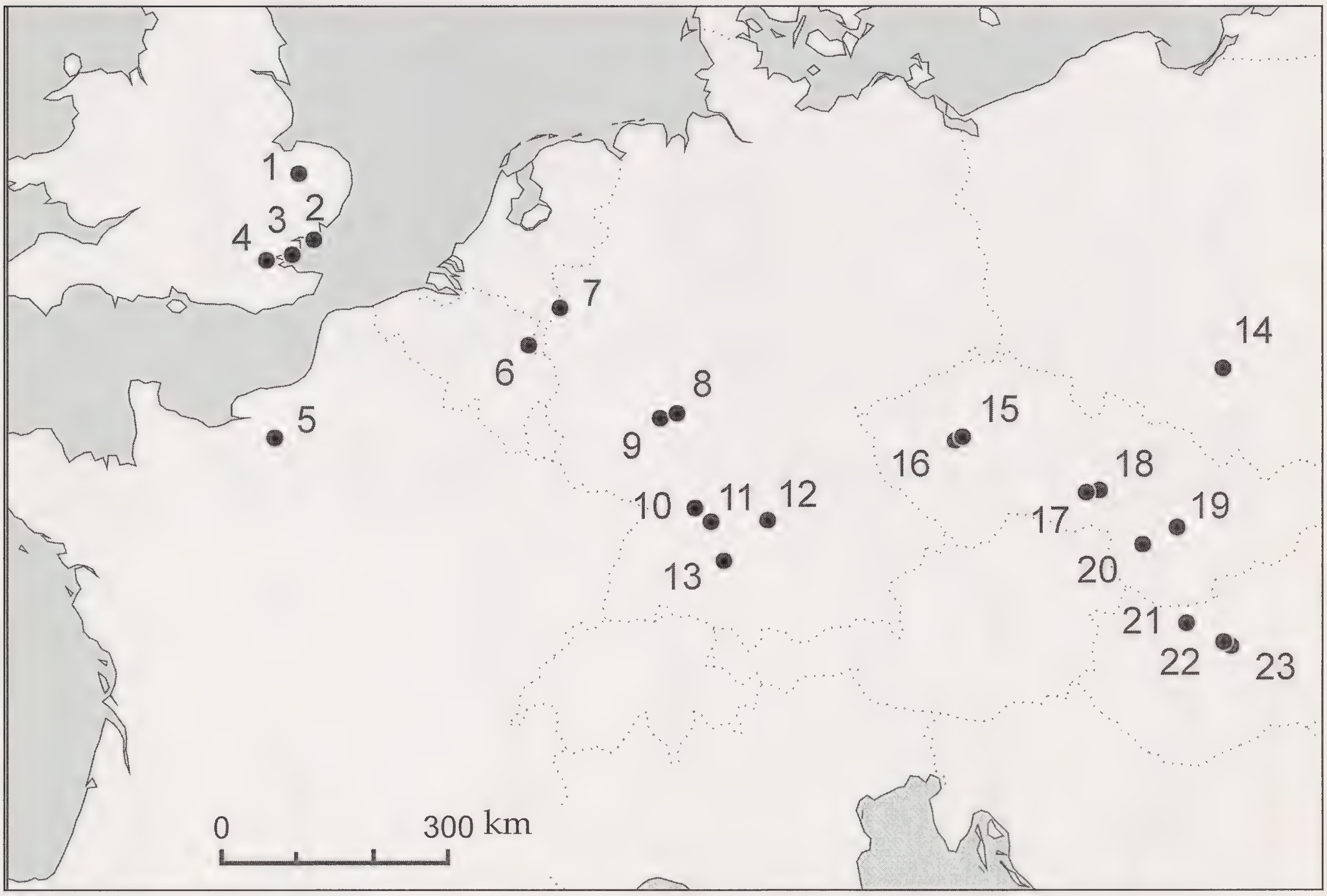

Fig. 2 Map plotting the Pleistocene records of *Z. sepultus* in Europe. Site numbers are explained in table 1.

The Lower Loam, a floodplain deposit of the River Thames, contains a rich molluscan fauna and is thought to have accumulated during the early temperate sub-stage of the Hoxnian (Kerney, 1971). Another shell, also discovered in the Kennard collection, was collected at Clacton-on-Sea, Essex (TM 171141) from deposits belonging to the same interglacial stage. The fourth British record is from Barling, Essex (TQ 935899) and is again based on a single shell (Fig. 1) from fluvial deposits in the Thames valley. The specimen came from silts that accumulated in a channel during an early temperate sub-stage, but these deposits appear to be somewhat younger than those at the other three British sites. The available evidence suggests that the deposits at Barling may have formed during the subsequent interglacial stage, perhaps that equivalent to MIS 9 (Bridgland *et al*., 2001).

The French record is also based on two specimens in the Kennard collection in the Natural History Museum, London, although they were actually collected by Abbé Breuil. They came from St Pierre-les-Elbeuf in the Seine Valley in Normandy, almost certainly from the well known interglacial tufa that formerly occurred at the base of the thick loess sequence at this site. This tufa, now completely removed, has yielded a distinctive molluscan fauna remarkably similar to that from Beeches Pit. Exotic species such as *Platyla polita, Laminifera pauli, Ruthenica filograna* and *Retinella (Lyrodiscus) skertchlyi* occur at both sites (Rousseau *et al*., 1992). The tufa at St Pierre-les-Elbeuf occurred immediately above a weathered soil horizon (Elbeuf IV) that has been correlated with the Holsteinian. It is therefore the same age as the three Hoxnian sites in Britain discussed above. The occurrence of *Z. sepultus* in both these tufas strengthens the correlation between them. The omission of *Z. sepultus* from published faunal lists from St Pierre-les-Elbeuf suggests that it may have been overlooked.

From Germany the species was recognized in old collections from the Senckenberg

TABLE 1

Details of localities where *Zonitoides sepultus* has been found

nr on Map	Site	Context	Collection	References
1	West Stow, Beeches Pit (Suffolk, UK)	Calcareous tufa, ('Icklingham Tufa'), Hoxnian; 390-400 ka (U/Th) & 471 ± 51 ka (TL burnt flint)	UMZC	Preece *et al.*, 2000
2	Barling, (Essex, UK)	Fluvial sediments of River Thames, late Middle Pleistocene Interglacial	UMZC	Bridgland *et al.*, 2001
3	Clacton-on-Sea, (Essex, UK)	Fluvial sediments of River Thames, Hoxnian.	NHM	Warren, 1955
4	Swanscombe, Barnfield pit (Kent, UK)	Floodplain sediment of River Thames, Lower Loam; Hoxnian.	NHM	Kerney, 1971
5	Saint Pierre-les-Elbeuf (F)	Calcareous tufa; Hoxnian/Holsteinian	NHM	Lautridou *et al.*, 1974; Rousseau *et al.*, 1992
6	Maastricht-Belvédère (Nl)	Calcareous mud; late Middle Pleistocene, Interglacial of Belvédère, 250 ± 20 ka [TL burnt flint] & 220 ± 40 ka [ESR shells]	TNO-NITG	Meijer, 1985
7	Tegelen, Pit Russel-Tiglia, 'Egypte' (Nl)	Fine fluvial sands of River Rhine; Tegelen Formation, Late Tiglian, Palynozone TC5/6; Mammals: Kislangian/Villanyan	TM	Freudenthal *et al.*, 1976
8	Wiesbaden, Elisabethen Höhle, (G)	Fluvial sands of River Rhine, 'Mosbacher Sande', early Middle Pleistocene	SMF	Geissert, 1970
9	Wiesbaden-Biebrich, Dyckerhof pit, (G)	Fluvial sands of River Rhine, 'Mosbacher Sande', early Middle Pleistocene	BSPG	Geissert, 1970
10	Stuttgart, Bad Münster, (G)	Calcareous tufa, Middle Pleistocene	BSPG	Dehm, 1969
11	Stuttgart, Bad Canstatt, (G)	Calcareous tufa, Middle Pleistocene	BSPG	Dehm, 1969
12	Adlerberg near Nördlingen im Ries (G)	Fissure fill, Middle Pleistocene	BSPG	Dehm, 1969
13	Schmiechen near Blaubeuren (G)	Calcareous tufa, Middle Pleistocene	BSPG	Dehm, 1951, 1969; Ložek, 1964
14	Kielniki (Poland)	Cave, karst fissure fill, Late Middle Villanyan mammal zone	ISEZ	Stworzewicz, 1981
15	Chlum near Sbrsko, Berounka valley (Bohemia, CR)	Soil material intercalated in loess deposits, Upper Templomhegy mammal zone	GUAVC	Horáček & Ložek, 1988; Ložek, 1989.
16a	Koňeprusi, Zlatý Kůň Karstpocket C718 (Bohemia, CR)	Karst fill	GUAVC	Ložek, 1964; Horáček & Ložek, 1988
16b	Koňeprusi, Zlatý Kůň Cave at Prošek Dom, (Bohemia, CR)	Cave	GUAVC	Ložek, 1964; Horáček & Ložek, 1988
17	Brno, Červený kopec (Moravia, CR)	Loess deposits, Base of pedocomplex X, Late Biharian mammal zone	GUAVC	Horáček & Ložek, 1988; Ložek,1989.
18a	Brno, Stránská skála I (Moravia, CR)	Hillwash	GUAVC	Ložek, 1964; Horáček & Ložek, 1988
18b	Brno, Stránská skála II (Moravia, CR)	Hillwash	GUAVC	Ložek, 1964; Horáček & Ložek, 1988
18c	Brno, Stránská skála (Moravia, CR)	Hillwash	GUAVC	Kovanda, 1995; Horácek & Ložek, 1988
19	Bojnice-Úbočie (SR)	Travertine	GUAVC	Ložek, 1964; Horáček & Ložek, 1988
20	Hradište pod Vrátnom (SR)	'Lower Travertine', Cromerian Complex	GUAVC	Ložek, 1964, 1989; Horáček & Ložek, 1988
21	Vérteszöllös (H)	Early Middle Pleistocene Interglacial; Upper Biharian mammal stage; 350 ± 87.5 ka [U/Th]	MAFI	Krolopp, 1978
22	Budapest, Ürömhegy (H)	Middle Pleistocene	MAFI	Krolopp, 1978
23	Budapest - Buda Hill (H)	Calcareous tufa, Middle Pleistocene	MAFI	Krolopp, 1958; Ložek, 1964

Abbreviations

CR - Czech Republic, **F** - France, **G** - Germany, **H** - Hungary, **Nl** - The Netherlands, **P** - Poland, **SR** - Slovakian Republic, **UK** - United Kingdom

BSPG Bayerische Staatssammlung für Paläontologie und Geologie (Bavarian State Collection for Palaeontology and Geology), Munich, Germany; **GUAVC** Geologický ústav Akademie věd České republiky (Geological Institute of the Academy of Science of the Czech Republic) Prague, Czech Republic; **ISEZ** Instytut Systematyki i Ewolucji Zwierząt (Institute of Systematics and Evolution of Animals), Kraków, Poland.; **MAFI** Magyar Állami Földtani Intézet (Geological Institute of Hungary) Budapest, Hungary.; **TM** T. Meijer (Alkmaar, The Netherlands); **TNO-NITG TNO** Nederlands Instituut voor Toegepaste Geowetenschappen (TNO Netherlands Institute of Applied Geosciences – National Geological Survey), Utrecht, The Netherlands.; **SMF** Senckenberg Museum, Frankfurt, Germany.; **UMZC** University Museum of Zoology, Cambridge, United Kingdom.

TABLE 2

Significant species associated with *Zonitoides sepultus*.

Taxa	Sites (see Table 1)																									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16A	16B	17	18A	18B	18C	19	20	21	22	23
molluscs:																										
Aegopinella bourdieri Rousseau & Puisségur,1989	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aegopis acieformis (Klein, 1913)	-	-	-	-	x	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aegopis klemmi Schlickum & Ložek, 1965	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-
Aegopis verticillus (Lamarck, 1822)	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	x	x	-	-	x	x	x	-	x	-	-
Azeca goodalli (Férussac, 1821)	x	-	x	x	-	x	-	-	-	x	x	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-
Bradybaena chouquetiana (Tournouër, 1877)	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Candidula crayfordensis Kennard & Woodward, 1915	-	x	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carychium mariae Paulucci, 1878	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cochlicopa nitens (Von Gallenstein, 1848)	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-
Cochlostoma salomoni Geyer, 1914	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cochlostoma scalarinum saueri Geyer, 1914	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	x	x	-	-	-
Discus perspectivus (Megerle von Mühlfeld, 1816)	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	x	-	x	x	-	-	-	-
Drobacia banatica (Rossmässler, 1838)	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	-	-	x	x	x	x	-	-	-	-
Fusulus interruptus (Pfeiffer, 1828)	-	-	-	-	-	-	-	-	-	x	x	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-
Gastrocopta sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-
Helicigona capeki (Petrbok, 1922)	-	-	-	-	-	-	x	-	-	-	-	-	-	-	x	x	-	-	x	-	x	-	x	-	-	-
Helicigona vertesi Krolopp, 1977	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-
Hygromia cinctella (Draparnaud, 1801)	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Laminifera pauli (Mabille, 1865)	x	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Leiostyla anglica (Wood, 1828)	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Retinella (Lyrodiscus) skertchlyi Kerney, 1976	x	-	x	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Platyla dupuyi (Paladilhe, 1868)	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Platyla polita (Hartmann, 1840)	x	-	x	x	x	-	-	-	-	-	x	-	x	-	-	-	-	-	x	-	x	x	x	-	-	-
Platyla similis (Reinhardt, 1880)	x	-	-	-	-	-	-	-	-	x	-	x	x	-	-	-	-	-	x	-	x	-	-	-	-	-
Riedeliella jourdani (Michaud, 1862)	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ruthenica filograna (Rossmässler, 1836)	x	-	-	-	-	-	-	-	-	-	-	-	x	x	-	x	x	-	x	-	x	x	x	-	-	x
Soosia diodonta (Férussac, 1822)	-	-	-	-	-	-	-	-	-	-	-	x	-	x	-	x	-	-	x	-	x	-	-	-	-	-
Soosia sp.	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Spermodea lamellata (Jeffreys, 1830)	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vallonia enniensis (Gredler, 1856)	-	-	-	-	-	x	-	x	x	-	x	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-
vertebrate biostratigraphy	D	?	D	D	?	D	A	D	D	?	?	?	?	A	C	C	b	?	C	C	?	?	D	D	D	D

x=present; -=absent, A=Villanyian; B=Early Biharian; b=as B, but less certain; C=Late Biharian; D=Toringian; ?=No information or uncertainty about association

Museum (Frankfurt) and the Bayerische Staatssammlung für Paläontologie und Geologie (Munich). The species was not mentioned by Geissert (1970) who reviewed the molluscs from the various Mosbach sites. *Z. sepultus* occurs at two sites near Wiesbaden in the fluvial 'Mosbacher Sande', which dates to the later part of the 'Cromerian Complex'. The exact bed yielding the *Z. sepultus* within the 'Mosbacher Sande' is uncertain, so it is not possible to constrain the dating any further.

From The Netherlands an inventory of the molluscs known at the Tiglian type locality at Egypt Pit, Russel Tiglia near Tegelen was published by Freudenthal *et al.* (1976). Investigations made after this publication yielded one juvenile specimen of *Z. sepultus*. The palaeoenvironment in which it occurred can be described as a fluvial backswamp deposit. The age of this site is similar to that of the Polish site at Kielniki, which makes both the oldest known occurrences of the species.

This brief review of the occurrence of *Z. sepultus* shows that it occupied a large part of central Europe, from Poland and Hungary in the east to northern France and southern England in the west, although not all these records belong to the same period. The stratigraphical range of *Z. sepultus* extends from the Early Pleistocene (Tiglian) in The Netherlands and Poland to the late Middle Pleistocene at Barling (England) and Belvédère (The Netherlands), which are probably similar in age, but it is unknown after the Saalian cold stage. In terms of its ecology, *Z. sepultus* appears to have been most common in woodland assemblages, particularly those living in the vicinity of calcareous springs, although it is known from fluvial contexts and caves. *Z. sepultus* is now known from 23 sites but it has probably been overlooked. Any white medium-sized zonitid with a distinctly angulated periphery should be scrutinized carefully.

ACKNOWLEDGEMENTS

We thank various curators for access to collections in their care, especially J. Cooper (Natural History Museum, London), R. Janssen (Senckenberg Museum, Frankfurt) and G. Falkner (Institut für Paläontologie und Historische Geologie, München). Simon Parfitt provided information about the associated vertebrates. John Rodford kindly provided the illustrations for Fig. 1.

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B. B. WOODWARD AND THE '*PISIDIUM* AFFAIR'

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Abstract *In 1913 B. B. Woodward published his* Catalogue of the British species of *Pisidium, a work he hoped would stabilise the nomenclature of a poorly understood genus of freshwater bivalves and place its study on a firm footing. Copiously illustrated with photos based on specimens housed in the Natural History Museum, London, and in other collections, the book was studied minutely by three malacologists with considerable experience of British freshwater molluscs, A. W. Stelfox, C. Oldham and R. A. Phillips. They proved that Woodward's book was full of misunderstandings and erroneous identifications. Stelfox, in various publications, took him to task and the two men became engaged in a drawn out and contentious war of words. The '*Pisidium *Affair' ended after Woodward's death in 1930 and was soon forgotten by all but a few. In 1960 the two authors of this article joined forces and examined the specimens illustrated in the book, intending to publish a revision of Woodward's identifications. That intention was not realised and now, some 40 years later, would serve no useful purpose. Instead, they have attempted to place Woodward's pioneering work and the controversy it engendered in a historical perspective. Their analysis of Woodward's contribution to the study of* Pisidium *shows that he had an imperfect understanding of the genus, due principally to his lack of field experience. Consequently, they support the views expressed by Woodward's three principal critics, Stelfox in particular, while at the same time giving due credit to Woodward for his laborious and partially successful attempt to make sense of a notoriously difficult genus of freshwater bivalves.*

Key words Pisidium, *Woodward.*

INTRODUCTION

In 1913 B. B. Woodward published his *Catalogue of the British species of Pisidium* (Woodward, 1913), a book devoted to a detailed and fully illustrated study of a genus of bivalves, popularly known as Pea mussels, belonging to the family Sphaeriidae. The genus *Pisidium* contains some of the smallest of all freshwater bivalves, is present in large and small bodies of freshwater worldwide, occurs plentifully throughout Europe, and comprises a significant part of the freshwater molluscan fauna of the British Isles. Members of the genus also occur, often abundantly, in Pleistocene deposits. Woodward's book deals with diminutive and dull-coloured bivalve shells that have never been popular with students and collectors, but it was widely distributed, many copies being presented to learned institutions and libraries. No-one seriously interested in the non-marine bivalves of Britain and Europe was likely to overlook it.

Some of those who had sent material to Woodward awaited the book's publication with keen interest. When it did appear three enthusiastic students of British non-marine molluscs agreed unanimously that it contained fundamental mistakes concerning the identification and nomenclature of certain common species. Soon Woodward became engaged in an exchange of views with this trio, an exchange that continued, often acrimoniously, for several years. When he died, in 1930, the '*Pisidium* Affair' fizzled out and was soon forgotten by all but a few.

Most of the specimens illustrated in Woodward's book are preserved in the Natural History Museum, London. In 1957, when one of us (SPD) examined them cursorily, it seemed as though no specialist had looked at them since 1913. In correspondence we both agreed that the specimens would repay closer study. In 1960 we joined forces in the museum for several days and examined them critically, intending to publish a revision of all Woodward's identifications. We did not do so and the notes we made then have remained virtually unpublished since.

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Returning to the subject after a lengthy interval we consider that a complete revision of this material would have little relevance now, the study of *Pisidium* in Britain and Europe having progressed steadily in the century since Woodward began compiling the information for his *Catalogue*. Instead, we have used the extensive notes we made 40 years ago to help us tell the sometimes amusing, sometimes pathetic story of a man who wrote a book that he hoped would ameliorate the study of a difficult genus but which brought him into conflict with three men who had contributed materially to his researches. We want to tell the story because of its intrinsic interest, because the principal players have all gone to their rest, and because, if we do not do so now, it may never be told.

WOODWARD AND THE HISTORY OF EUROPEAN *PISIDIUM* STUDIES

Bernard Barham Woodward (1853–1930) is well known as the compiler of the *Catalogue of the books in the British Museum (Natural History)*, the monumental publication that crowned his career as Librarian of that institution, since renamed the Natural History Museum, London (Woodward, 1903–15). He is less well known for his spare-time studies of the Mollusca, recent and fossil, although the resulting publications are numerous and authoritative. It is easy to understand why he became a librarian and why he took up the study of the Mollusca in his spare time. His father, Bernard Bolingbroke Woodward (1816–69), was Librarian of the Royal Library at Windsor Castle. He also had two illustrious uncles, Samuel Pickworth Woodward (1821–65) who wrote the celebrated *Manual of the Mollusca* (1851–56), and Henry Woodward (1832–1921), Keeper of Geology at the British Museum (Natural History) towards the end of the nineteenth century. It comes as no surprise, therefore, to learn that he formed a small collection of shells at the age of ten, or that he served as Curator to the Geological Society from 1873, or that, in 1881, he was placed in charge of the General Library in the museum where, at one time or another, his two uncles were employed (Kennard, 1931).

From the 1880s onwards he contributed numerous articles to popular and scientific journals, concentrating his attention on British non-marine molluscs. He took a keen interest in the study of non-marine shells found in Pleistocene deposits, enthusiastically exploring the changes in the British fauna, tracing the introduction and extinction of species, their distribution and - a favourite theme - their nomenclature. His publications on these subjects were usually written in collaboration with Alfred Santer Kennard (1870–1948), a man who, it is said, 'looked much towards the past, so his studies naturally took that direction' (Wrigley, 1949). To some extent this outlook seems to have been true of Woodward also. His long association with Kennard meant that he would have spent a great deal of time studying fossilised molluscan shells - and fossilised molluscan names. The study of molluscs and other living things in their natural habitats seemed to occupy little of his time. Circumstances and personal inclination helped turn Woodward into a closet naturalist, content to delve into books and identify preserved specimens.

'Very early in our joint work on the post-tertiary Mollusca', says Woodward, in the Introduction to his *Pisidium* book, 'Mr. A. S. Kennard and I were led to see that the group must be dealt with, whilst the late Dr. O. Böttger had urged me to study it more closely. It was not, however, till Dr. A. C. Johansen visited this country in 1901 that any serious start was made. Dr. Johansen it was who directed my attention to the hinge-characters as the only sure means of identification of the species, and by his intimate knowledge of the Scandinavian forms he was able to point out that we had species present in Britain hitherto unrecognised.' (Woodward 1913: vii).

Throughout the second half of the nineteenth century the leading authority on British molluscs was John Gwyn Jeffreys (1809–85), his *British Conchology*, published in five volumes between 1862 and 1869, being the standard text. In the first volume, devoted entirely to non-marine species, Jeffreys said of *Pisidium*: 'The general shape and appearance of the shells, as well as the position of their beaks, appear to offer almost the only reliable grounds of distinction' (Jeffreys, 1862:18). He claimed to have examined thousands of specimens from Britain and many parts of Europe and to have studied all the relevant literature. Of the 41 different species that had been proposed by European writers, he said he could recognise no more than six as distinct. He classified the five he recognised as British into four groups, according to their shape, as follows: 1. Triangular - *amnicum, fontinale*. 2. Oval - *pusillum*. 3. Round - *nitidum*. 4. Oblong - *roseum*.

The names chosen to designate the five species seldom agree with the names adopted by those who preceded him in this narrow field. Among the more important of his predecessors was the English naturalist, the Rev. Leonard Jenyns (1800–93), who published a monograph in 1832 that laid the foundations of our knowledge of the British species of *Pisidium* (Jenyns, 1832). Much later he published a short article on the smaller British species that was virtually a supplement to his pioneering memoir (Jenyns, 1858). Meanwhile, in 1855, the Swedish naturalist, August Wilhelm Malm (1821–82), had published an article on Swedish non-marine molluscs in which he enumerated nine species of *Pisidium* (Malm, 1855). Among them were two he described as new to science, *subtruncatum* and *personatum*, concerning which Woodward wrote, 'it was failure to recognize these two forms that led to much of the confusion into which the work of British and other authors had been thrown' (Woodward, 1913: 9).

In 1854 the young Jules René Bourguignat (1829–82) published a note advocating the utility of the hinge as a basis for broadly classifying the species of *Pisidium* (Bourguignat, 1854). Fortunately, perhaps, the arch species-monger did not follow this then novel idea to its logical conclusion, that the hinge could also be used to help distinguish one species from another. Auguste-Adolphe Baudon (1821–1905), described by Woodward as 'the French Jenyns', published a monograph on *Pisidium* in 1857 in which he made partial use of the hinge for classification but, like Bourguignat, failed to use it to help differentiate the species (Baudon, 1857). It was Stefan Clessin (1833–1911) who first utilised the hinge characters of *Pisidium* to discriminate species in a work notable for its typographical errors and execrable figures (Clessin, 1874–79). As far as British students were concerned, the first volume of Jeffreys' *British Conchology* still reigned supreme in 1901, when Woodward began his study of *Pisidium*. Its supremacy, in this respect, did not last for much longer.

WOODWARD'S *CATALOGUE* (1913)

'Of all the genera of British non-marine Mollusca none has presented more difficulties to the student than *Pisidium*. The small size of the shells, their great variability, the lack in most cases of any striking external characteristics, as well as the confusion in which the subject has been left by the various authorities, have all contributed to these difficulties, with the result that the genus has been largely neglected.' Few would have disagreed with this first paragraph of Woodward's Introduction to his book when it appeared in 1913. 'In the course of the present investigations', he continued, 'it was found that each species varied in outline from what came to impress itself as the normal form, towards a more rounded shape on the one hand and a more elongate on the other, as well as to assume sometimes a more swollen, sometimes a more flattened condition; whilst the hinges of those taken in quiet waters are feeble and weak, in comparison with the hinges of those habitually dwelling in running water.' (Woodward, 1913: 4).These observations sounded the death knell of Jeffreys' system of classification by shell shape.

In 1913, having spent ten years examining many thousands of specimens, Woodward published his study of the genus *Pisidium*. His densely factual text is accompanied by 30 illustrative plates. Four of them show diagrammatic enlargements and camera lucida drawings of hinges, the remaining 26 showing enlarged photos of specimens from the collections contained in the museum where he worked and in other collections public and private. He claimed to be able to discriminate seventeen well-marked forms. Two of these were extinct (*vincentianum* and *astartoides*) and one he said had yet to be found in Britain, either recent or fossil (for which he employed the name *parvulum*). This left the following fourteen so-called species that he said were known to be present in Britain: *amnicum* (Müller), *astartoides* Sandberger, *casertanum* (Poli), *henslowanum* Sheppard, *hibernicum* Westerlund, *lilljeborgii* Clessin, *milium* Held, *nitidum* Jenyns, *obtusale* Lamarck, *parvulum* Clessin, *personatum* Malm, *pulchellum* Jenyns, *pusillum* (Gmelin), *steenbuchii* (Möller), *subtruncatum* Malm, *supinum* A. Schmidt, *vincentianum* B. B.Woodward.

The list contains thirteen *Pisidium* names still in use today, including *vincentianum*, a taxon introduced and described by Woodward in his *Catalogue* but which is now considered the extinct analogue of the living *stewarti*, described in 1909 by Preston (Kuiper, 1962). Two names, *astartoides* and *parvulum*, are now recognised as junior synonyms respectively of *clessini* Neumayr, and *moitessierianum* Paladilhe. Two other names, *pusillum* and *steenbuchii*, have dropped out of use altogether. Since 1913 other specific names have been applied to members of the genus occurring in Britain but only three are now in use: *conventus* Clessin, *tenuilineatum* Stelfox, and *pseudosphaerium* Favre.

Woodward did not provide a key to facilitate identification of the thirteen species he recognised as British and this did not make his book any easier to use in a practical sense. It did not help, either, that he gave no more than the original description (usually in Latin) to describe the shape of the shell. The Latin diagnoses include no less than fifteen different terms defining shell shape in *Pisidium*, sixteen describing the shape of the umbones, six describing sculptural differences, and another six describing insignificant differences of colour. Rather than provide information in a form that could be understood by potential users of his book he seemed to be engaged on a private academic exercise. On the other hand he was the first to give detailed descriptions of the hinge characters. Resulting from his close scrutiny of these characters he was also the first to point out the singular diagnostic feature of *personatum*, 'the hallmark of the species, the peculiar callus that lies in either valve between the umbonal ends of the posterior lateral teeth and the ligament-pit' (Woodward, 1913: 55).

WOODWARD VERSUS THE '*PISIDIUM* CLUB'

Although a book-length study of *Pisidium* was unlikely to have wide appeal its publication had been eagerly awaited by enthusiastic students of freshwater molluscs. This genus, after all, is well represented throughout Europe and the book held out the promise of simplifying the identification of a dozen species, a significant proportion of the entire British freshwater molluscan fauna. Woodward had been generously assisted by many men and women who had sent him hundreds of specimens, not just from Britain but also from localities all over Europe. One of his more enthusiastic helpers was Arthur Wilson Stelfox (1883–1972), then a young student of non-marine molluscs in Ireland who was hoping to make a career for himself as an architect. For this young man identifying *Pisidium* was no easier than it was for everyone else and so he was happy to help someone who promised to make sense of the genus.

At the tender age of 28 Stelfox published '*A list of the land and freshwater molluscs of Ireland*', a substantial publication that was much more than a mere list (Stelfox, 1911). This publication showed that he knew a lot about non-marine molluscs in the field. It did not prove that he knew much about the identification of *Pisidium*. In a letter to Woodward mostly concerning *hibernicum*, dated 9 May 1911, he wrote, 'The hinge means nothing to me until I see your monograph' (Woodward, Linn. Soc. MS 317, item 259). This is a significant comment because it shows he had been in the habit of distinguishing species of *Pisidium* entirely, or mostly, on the basis of their external form and ornament, á la Jeffreys. Indeed, he admitted in print that Jeffreys' views on *Pisidium* were accepted generally when he began studying molluscs (Stelfox, 1918a).

Stelfox often referred to *hibernicum* in the letters he wrote to Woodward before the 'monograph' was published, sublimely unaware that this species would prove to be controversial and lead to a permanent rift between them. When the *Catalogue of the British species of Pisidium* was published Woodward sent a copy to Stelfox who acknowledged its receipt on 25 August 1913: 'Dear Mr. Woodward', he wrote, 'It is very remiss of me not to have written you long ago & thank you for a copy of your beautiful monograph of the Pisidia.' (Woodward MS 317, item 268). The thanks were genuine, but Woodward would soon be regretting that he had presented him with a copy of his 'beautiful monograph'. The young man for whom the hinge had meant nothing was soon to prove that the hinge could mean everything.

Among others acknowledged in the *Catalogue* were two men who, like Stelfox, had been unstinting with their help, Charles Oldham (1865–1942) and Robert Albert Phillips (1866–1945). Oldham, who settled in Hertfordshire and was employed by an insurance firm, was a field naturalist of rare attainment, the British non-marine Mollusca being just one of several branches of natural history to which he made valuable contributions. Phillips, a travelling salesman with a firm of stationers, was another excellent field naturalist. Both became good friends and colleagues of Stelfox, the three of them pooling their abilities and checking each other's identifications. Each was actively interested in *Pisidium*, Oldham in particular being prepared to hunt down specimens all over the place, especially in remote mountain lochs and tarns. Phillips was more reticent and retiring than the other two but his opinions were valued highly by them. Shortly after the publication of the *Catalogue* the three of them became convinced that Woodward's book was seriously flawed. It looked an efficient piece of work, superficially, but closer inspection showed that it was full of errors, its shortcomings becoming more obvious when specimens identified by Woodward were studied. So they took him to task, often disagreeing with him radically and opening a rift between him and them.

One version of the disagreement and its consequences occurs in Stelfox's Preface to a projected monograph on *Pisidium*, a work that was never published and may never have been written. This Preface, dated 26 September 1922, was published as an appendage to an obituary notice of Stelfox (McMillan, 1972). In it Stelfox refers to differences of opinion between himself and Woodward that arose in 1916 about the correct identification of shells of *parvulum* (= *moitessierianum*). Woodward had misidentified juvenile examples of *supinum* as *parvulum** and Stelfox had told him so. The differences, Stelfox writes, 'led to the breaking down of direct communication between myself and Mr. Woodward, who considered it was impertinent on my part not to accept his verdict'. Stelfox also says that it led to the formation of a 'small but exclusive *Pisidium* Club', comprising himself, Phillips and Oldham.

Another version of the story behind the breaking down of direct communication between Woodward and Stelfox was given by the latter in an unpublished letter he wrote to one of us in 1955. The letter accompanied a loan of examples of *Pisidium*, including some *hibernicum*, labelled 'From one of the lower N. Wales tarns at only 920 feet, Llyn Dwythwch near Llanberis, C. O. 19.7.16' (C. O., of course, was Charles

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* The specimens of *moitessierianum* that Woodward misidentified as other species, including *supinum*, are illustrated on Plates 23–27 of his *Catalogue*. A list of Woodward's figures of these specimens, with commentary, has been published recently (Zettler & Kuiper, 2002).

Oldham). Stelfox had this to say about them: 'These are historic specimens & began the "differences" which I had with B. B. W. The story is worth telling as C. O., & B. B. W. are dead & only I know it. These were amongst the first Pisidia on which C. O. had asked my opinion. He had got them identified by B. B. W. who had named them *nitidum* (i.e. B. B. W's "*nitidum*", which might have been anything!). Evidently C. O. was so cross that he removed the locality label & sent them back to B. B. W. not telling the latter he had seen them & most innocently asked "Could these be *hibernicum*?" & B. B. W. fell into the trap & sent C. O. a hurried p.c. which read "Congratulations! Typical *hibernicum*!!!!" & added "It is unlike you not to say where they come from", to which p.c. Oldham, still more angry, replied by sending the original label with "*P. nitidum* Jen." written across it in B. B. W's handwriting. I knew nothing about this & was perfectly innocent, but was blamed for it nevertheless & had to bear the brunt of B. B. W's anger. It also explains why ever afterwards B. B. W. walked in fear of C. O. & went to no end of trouble to please him, but C. O. was not deceived.' (Stelfox in litt. to S. P. Dance, 22 July 1955).

Some of the observations and criticisms voiced by Stelfox and Oldham are encapsulated in another unpublished letter, written in 1939 by Oldham to Arthur Erskine Ellis (1902–83), the biology teacher and authority on British snails, who was then planning to write an identification guide to the British species of *Pisidium*: 'There is no doubt that Woodward's *pusillum* (and later *pusillulum*) are really the *nitidum* of Jenyns. I have many sets of *nitidum* which were identified by Woodward as *pusillum*. What Woodward called *nitidum* is a strange hotch-potch. I have many shells of *hibernicum* and *cinereum* [i.e. *casertanum*] among others which Woodward attributed to *nitidum*. The shell that Woodward called *parvulum* is *torquatum* of Stelfox whose name however was antedated by *moitessierianum*. Clessin's *steenbuchii* was apparently one of the protean forms of *cinereum*, but Woodward attributed to *steenbuchii* specimens of *obtusale* which I sent him. Anyhow *steenbuchii* is not recognized as a species nowadays*. Woodward was constantly driven to error by his failure to appreciate the importance of the ligament-pit, which indeed never figures in his diagnoses. His long, wordy descriptions of the hinged teeth do very often fit several species indifferently and a study of his catalogue is not likely to help you much; indeed rather the reverse.' (Oldham in litt. to A. E. Ellis, 15 November 1939).

In various publications Stelfox and Oldham criticised many of Woodward's identifications, not only of specimens illustrated or mentioned in his book but also of other specimens he identified. Many of the criticisms concerned Woodward's misapplication of the names *nitidum* Jenyns and *pusillum* Jenyns, a problem dealt with by Stelfox (1918a). In essence Stelfox maintained a) that Woodward misidentified *nitidum* of Jenyns as *pusillum* of Jenyns; b) that shells identified as *pusillum* by Woodward were really specimens of *personatum* Malm. He advocated dropping the name *pusillum* because he had examined specimens so named by Jenyns and these were referable to *personatum* Malm. A recent attempt to establish the identity of the nominal taxon *Pisidium pusillum* in the sense of Jenyns confirmed Stelfox's findings (Falkner & Korniushin, 2000).

In a reply to Stelfox's article Woodward made the following frank admission: 'Complaint has also reached me, from various sources, that some of my past determinations, on comparison, will not always agree with later ones. It would be surprising if they did. So soon as it became known that I was working at the group, and before I had been able really to settle the various forms, my aid in determining specimens was invoked, and with more wishfulness to oblige than, perhaps wisdom, I complied. Many hours did I devote to various gatherings received from different correspondents; but, naturally, many of these early determinations have proved to need revision. Papal infallibility was never claimed for them, and many correspondents have courteously, when in doubt, referred such doubtful cases back to me.' (Woodward, 1918).

In his masterly account of the *Pisidium* fauna of the Grand Junction Canal Stelfox

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*The syntypes of *Pisidium steenbuchii* (Möller, 1842), collected in Greenland, are preserved in the Naturhistoriska Museet, Göteborg, Sweden, where they were examined by one of us (JGJK) in 1965 and identified as *casertanum*.

pointed out that Woodward not only consistently misidentified adult *parvulum* (= *moitessierianum*) as the fry (i.e. juveniles) of *supinum* but even mistook a specimen of *nitidum* var. *crassa* Stelfox for one (Stelfox, 1918b). In the same publication Stelfox delivered a speedy riposte to Woodward's reply and produced further evidence to bolster his case against the closet naturalist. He criticised the illustrations in Woodward's book, saying that photography had failed to reproduce recognisable representations of the hinges of *Pisidium*. With true prescience he also said that he believed it would only be by a close study of their ecology that the secrets of *Pisidium* would be revealed.

In 1957 Stelfox sent to one of us an unpublished manuscript about *steenbuchii*, a taxon accepted by Woodward but not by Stelfox (and since rejected by the scientific community). In a covering letter he wrote: 'Whenever we did anything to annoy B. B. W. the latter took it out of A. S. K. [A. S. Kennard] at their next weekly meeting, because he was unable to get any change out of me or R. A. P. [R. A. Phillips] Of C. O. he was afraid, but just why I don't know. He tried to choke me off the Pisidia but of course it only made me keener & Kennard warned me that if I wrote to B. B. W. & told him he was wrong the old boy would probably have a stroke, so we thought it better not to put the enclosed in print, though every word of it is true & amply justified.' (Stelfox in litt. to S. P. Dance, 15 February 1957). This extract, perhaps, is enough to show how serious were the differences between Woodward and the *Pisidium* Club. It may also serve to draw a line under the less savoury aspects of an otherwise interesting and in some ways fruitful episode in the history of malacology.

ANALYSIS OF WOODWARD'S CONTRIBUTION TO THE STUDY OF *PISIDIUM*

In 1960 we had the opportunity to study the specimens illustrated in Woodward's book. They are preserved in the Palaeontology Department of the Natural History Museum, London, with the Registration numbers: 1914.9. 1–1135. Glued to wooden tablets, they were (and still are) exactly as they appear in the book. A total of 44 specimens were missing, some having been returned to their owners many years previously (including the 14 specimens forming part of the type series of *vincentianum*), and six specimens were broken beyond recall. This still left more than a thousand specimens intact (regarding each figure, whether it shows a single valve or a complete shell, as representing a specimen). We had intended to check the identities of all the remaining specimens but did not do so because it would have been necessary to unglue many that were brittle and fragile, inevitably damaging some in the process. Examining the hinge characters wherever possible, we were still able to identify a sufficient number of specimens to draw certain conclusions. Occasionally we considered shells that are not illustrated in the book but are mentioned in the text or had been sent to Woodward for his opinion.

Woodward emphasised the importance of the hinge characters in species identification, provided enlarged views of the 'Topography of the hinge' (p.3) and stated that he was 'taking the details of the hinge-structure as a guide' (p.5). Unfortunately, the diagrammatic enlargements of the hinges shown on Pls I and II have all been retouched (not, as Woodward states, only figs 2 and 3 on Pl. I), significantly affecting their clarity. Many of the photographs, too, are very indistinct, the hinge characters being seldom clear enough for identification purposes. Throughout the book he describes these characters in great detail, his descriptions giving the impression that they are constant within a species and not subject to variation.

Except when describing his new species, *vincentianum*, in which it is the most obvious diagnostic feature, he never refers to the ligament-pit, nor does it show up clearly in his diagrammatic enlargements of the hinges (Pls I and II). This suggests that he failed to recognise the diagnostic significance of a feature to which later workers came to attach great importance. It also helps to explain why he had difficulty separating *supinum* from *casertanum* var. *ponderosa*, a difficulty noted by the proposer of that variety, Stelfox (1918b: 293). The following specimens referred to *supinum* are all *casertanum* var. *ponderosa*: Pl. XXV (1a,b 5a,b 16a,c,e–h); Pl. XXVI (8c,d 10a, 11a,b 12g); Pl. XXVII (2a–h). Moreover, the supposed diagrammatic enlargement of the hinge of *supinum* shown on Pl. II (repeated on Pl. XXVI) clearly shows the hinge of *casertanum* var. *ponderosa*!

He had some difficulty separating *lilljeborgii* from *pulchellum*, the explanation for which may be the incorrect description of the ligament-pit of the former by its describer, Clessin, who described it as 'kurz, stark' (i.e. short, strong). The ligament-pit in *lilljeborgii* is actually long and narrow, whereas in *pulchellum* it is broad and crescent-shaped. Stelfox referred to Woodward's incorrect understanding of the two species in a trenchant note to one of us: 'You will remember that on his Plate XXIII there are two figures of *lilljeborgi* [sic] from Silverdale shoved in "for comparison" with *pulchellum*, because *lilljeborgi* [sic] "has sometimes been mistaken" for *pulchellum*! The truth was, of course, that he had mistaken the former for *pulchellum* & only found out his error after the plate was made & he could not alter it. Hence the "comparison" story. Several English collections contained the Silverdale shells labelled "*pulchellum*" by B. B. W." (Stelfox in litt. to S. P. Dance, 1 March 1960).

Woodward, unable to recognise the immature forms of some species for what they were, misidentified mature shells of *moitessierianum* (the diminutive species he called *parvulum*) as immature *supinum*, thereby missing the opportunity to record the former for the first time as occurring in Britain. Here it may be noted that the retouching of the diagrammatic enlargement of the hinge, shown on Pl. II (6) and repeated on Pl. XXVII (7), has obscured the outer posterior lateral tooth so characteristic of *moitessierianum*. He also missed the opportunity to be the first to record *conventus* from the British Isles, the well-developed, mature example in the collection, illustrated on Pl. XXVIII (25a, b), having been misidentified by him as an immature *lilljeborgii*. Ironically, it had been collected in 1909 in Lough Aguse, Fermanagh, by Stelfox! Our discovery of this misidentification has been published elsewhere (Kerney, 1969). Similarly, some specimens dredged from deep water in Loch Ness and listed under the name *pusillum* (Woodward, 1913: 65) turned out to be referable to *conventus*. In 1921 they were sent to Oldham who also misidentified them, as *cinereum* (i.e. *casertanum*), but who was later responsible for adding the species to the British list (Oldham, 1932). There is no good reason to censure Woodward for failing to recognise this rare species.

We have already seen that Woodward misidentified shells of two or three species as *hibernicum*, a species then known only from the west of Ireland. Most of the specimens illustrated on Pl. XXIX have been removed, those remaining (1 and 2a,b) having been identified correctly. A large number of the shells he has identified as *milium* belong to other species, including *obtusale, nitidum* and *subtruncatum*. The distinctive shape of the shell of *milium* should have led him to a correct appreciation of this species and it is possible that his insistence on the overriding importance of the hinge characters led him astray.

Woodward referred a number of shells to *steenbuchii*, a taxon we have already indicated is a junior synonym of *casertanum*. The specimens illustrated on his Pl. XXVIII are nearly all referable to *casertanum*. The shells identified as *obtusale* on his Pl. XXX, on the other hand, seem to be correctly named for the most part, two specimens only (1e and 16e,f) being referable to *personatum*.

His most intractable problem, however, concerned the identities of *pusillum* and *nitidum*. Ever since Jeffreys' time 'the common practice was to refer any small *Pisidium* in which the umbones were more or less central to *P. nitidum* if the shell were clean, and to *P. pusillum* if it were encrusted, whilst if the umbones were nearer to the posterior end

P. fontinale was available as a dumping-ground for it' (Stelfox, 1918a). When he came to regard the different species from an ecological standpoint Stelfox realised that the Jeffreysian approach to the identification of *Pisidium* did not work. Gradually it dawned on him that Woodward, too, was on the wrong track with his interpretation of *pusillum* and *nitidum*. Four years after the publication of Woodward's *Catalogue* Stelfox, aided and abetted by Oldham and Phillips, showed how Woodward had misapplied the two specific names (Stelfox, 1918a). Significantly, perhaps, Stelfox's important article is omitted from the otherwise comprehensive book on the synonymy of the British non-marine Mollusca co-authored by Kennard and Woodward (1926).

Stelfox's argument is too tortuous to follow in its entirety here but its main points may be stated briefly. Shells belonging to the species now universally accepted as *nitidum* are characteristically very shiny and have well-marked umbonal striae. This concept of *nitidum* was subscribed to by Stelfox. Woodward's conception of *nitidum* was quite different, as Stelfox discovered when he examined some shells owned by other collectors, including Phillips. Woodward had identified as *nitidum* shells that proved to be normal forms of *obtusale*. Woodward's *pusillum*, by contrast, proved to be the true *nitidum*, as is clear from his description of the hinge of *pusillum*!

An analysis of the 66 specimens Woodward illustrated as *nitidum* on Pl. XIX shows that they belong to at least five species, as follows:

nitidum	14
subtruncatum	18
obtusale	12
casertanum	13
personatum	2
uncertain	7

An analysis of the 110 specimens Woodward illustrated as his idea of *pusillum* on Pl. XXI shows that they belong to at least four species, as follows:

nitidum	14
subtruncatum	6
casertanum	4
hibernicum	11
uncertain	20

In brief, Woodward's *nitidum* comprises at least five species, of which *subtruncatum* is quantitatively dominant and includes the specimen from Lough Fern, Co. Donegal, shown on Pl. XIX (11), that he said 'may be taken as an example of the typical form' of *nitidum*! About 77% of the specimens he has identified as *nitidum* belong to other species. The specimens illustrating his idea of *pusillum* comprise at least four species, of which *nitidum* is quantitatively dominant.

CONCLUSION

Up to the end of the nineteenth century, those wanting to identify the British species of *Pisidium* did so according to the first volume of Jeffreys' *British Conchology*, published in 1862. In 1901 Woodward, realising the shortcomings of that volume (and of most other writings on the genus), made a fresh start by returning to first principles, which meant discarding preconceived ideas. A dozen years and thousands of specimens later he produced his *Catalogue of the British species of Pisidium*, a work of considerable scholarship and industry.

The *Catalogue* soon came under fire from a small group of students, principally A. W. Stelfox, C. Oldham and R. A. Phillips, who criticised its author privately and in print for several years because of the many errors they perceived in his work and because of the apparently insensitive way he handled their criticisms. Time has shown that most of their criticisms of his work have been substantiated, as may be seen when the *Catalogue* is compared with more recent publications on the subject, such as that of Ellis (1962). It cannot be denied that the diagrammatic representations of the hinges and the photographs of the specimens that illustrate the book are disappointing or misleading, sometimes both. Unfortunately for Woodward they were still good enough to enable his critics to see what was wrong with them, which is more than can be said for those published by most of his predecessors in this narrow field.

There is a valid reason why most of the critical comments about Woodward's text, his identifications and misidentifications were justified: he was not a field naturalist. His main interest was in fossil non-marine molluscs and, as a museum man whose duties anchored him indoors, he had only limited opportunities to study living molluscs in their natural environment. It was a different situation with the members of the *Pisidium* Club. Stelfox, Oldham and Phillips were all, by temperament, field naturalists and their professional activities often gave them the liberty to indulge their private enthusiasm for outdoor activities. This gave them advantages denied to Woodward who never seemed to understand how environment could affect the appearance of the shell of a *Pisidium*. His curious misconceptions about *nitidum* and *pusillum*, in particular, may be attributed largely to his lack of field experience, although in a futile attempt to refute Stelfox's criticisms he also dug himself into a hole from which there was no escape.

Our examination of Woodward's illustrated specimens showed that he did, indeed, misidentify many specimens. The reasons for this seem to be threefold: a) because his main interest was in fossil specimens, b) because he did not study the ecology of living *Pisidium* species, c) because he placed too much reliance on the value of hinge characters for separating the species. Why, though, did he illustrate the outside of so many valves if he valued hinge characters so highly? Why, too, did he fail to identify *milium* correctly, this species usually displaying a diagnostic quadrilateral or rhomboidal outline? These are unanswered – possibly unanswerable – questions.

Judging from the comments of his contemporaries, it seems as though Woodward was a difficult man to deal with, sensitive to criticism and easily offended. It should be borne in mind, however, that he was a pioneer, never an easy position to hold without criticism, and that he had to defend himself on his own (his trusty lieutenant, Kennard, was a passive individual and no match for the members of the *Pisidium* Club). According to one published account Woodward was known latterly as 'the "Bumble Bee" because of his burly, bustling habit and his quarrelsome nature.' (Norman, 1944: 68). What part his 'quarrelsome nature' played in this saga is now difficult to assess but it would not have helped. Reading some of the published and unpublished comments of Stelfox and Oldham they, too, may be accused of unbecoming behaviour, seeming to derive pleasure from antagonising him. These all-too-human failings add piquancy to the '*Pisidium* Affair' but they should not influence our judgment of those who were caught up in it.

Woodward's attempt to place the study of a difficult genus on a sure footing was not as successful as he would have wished. In several ways, however, it had positive results, not least as a catalyst for other studies of the genus by workers who were more field-based. His critics won the day and their views are now accepted in preference to his, but it should not be assumed that they always acted with mature deliberation or that they deserve to be remembered with more respect than he. If B. B. Woodward had not published his *Catalogue* the *Pisidium* Club may not have made important and lasting contributions to the study of *Pisidium*.

ACKNOWLEDGEMENTS

More than forty years after the event we are grateful to the Keeper of Zoology at the Natural History Museum, London, for allowing us to study the specimens on which Woodward's *Catalogue* was based. Recently one of us (SPD) was allowed to look over them again and for this we are grateful to the Collections Manager of the Mollusca Section, Miss Kathie Way. JGJK is indebted to the Netherlands Organisation for Scientific Research, NWO (formerly known as ZWO) for a grant supporting his studies of the *Pisidium* collections at the Natural History Museum, London, in 1960. Photocopies of certain scientific articles were kindly made available by the Keeper of the Department of Biodiversity, National Museum of Wales, Cardiff, and for this service we wish to express our gratitude. Dr Michael P. Kerney kindly provided the signature of A.S. Kennard. The correspondence between A.W. Stelfox and SPD, held by the Ulster Museum, Belfast, was kindly made available by Mr Brian Nelson of that institution

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B. B. Woodward (left) and A. S. Kennard in conversation 22 July 1927. (Photo J.G.J. Kuiper collection.) Also signatures of both.

B B Woodwa

Yours ever
A S Kennard

Yours sincerely
A. W. Stelfox.

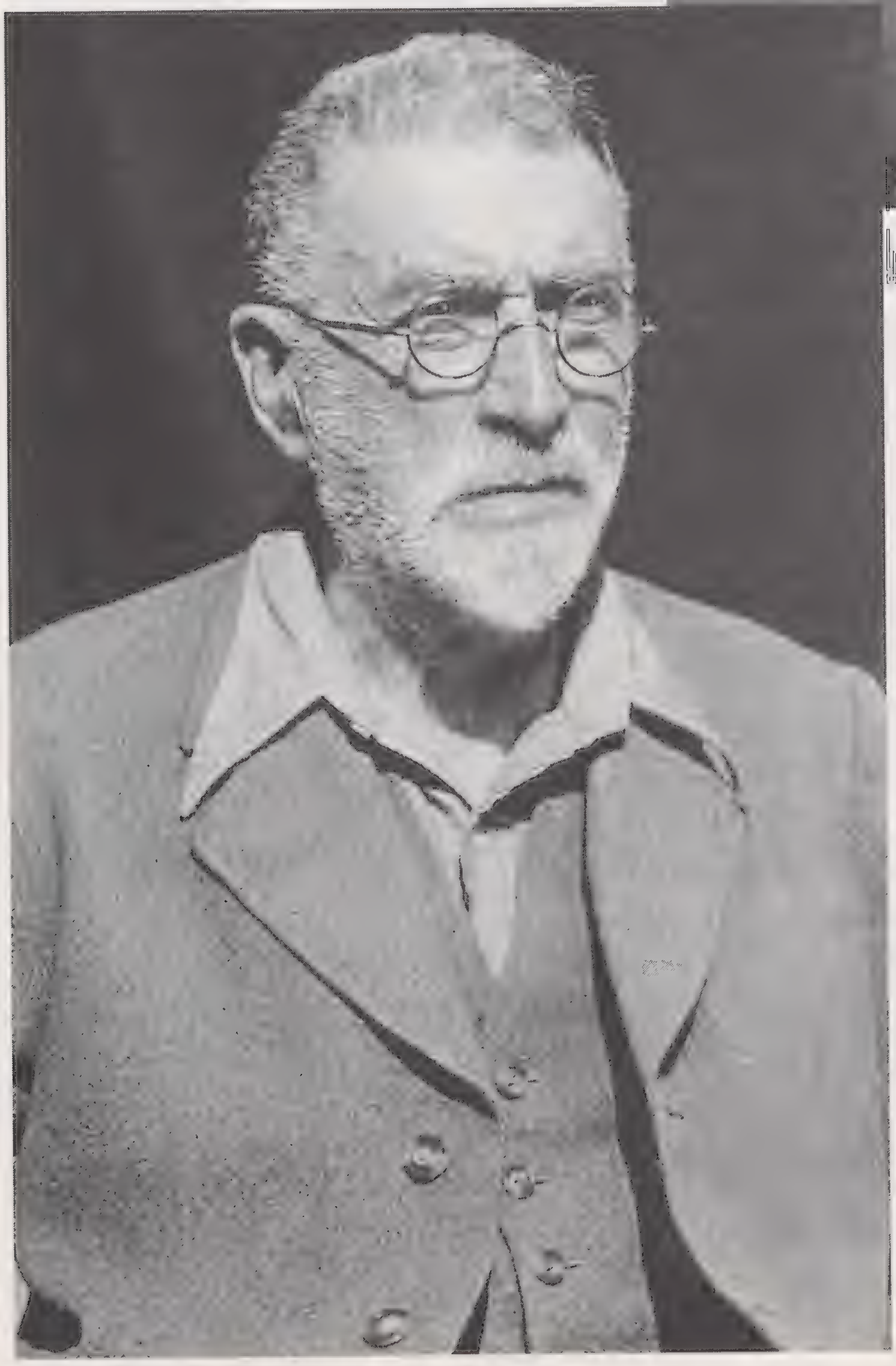
Signed photo of A.W. Stelfox. (Photo by J.G.J. Kuiper, 1971.)

Photo and signature of R. A. Phillips. By kind permission from the *Irish Naturalists' Journal.*

Yours sincerely R. A. Phillips.

Signed postcard showing C. Oldham as an elderly man scooping for *Pisidium*. Photo possibly taken in the English Lake District. (S.P. Dance collection.)

from Chas. Oldham



Charles Oldham, about 1938. (S.P. Dance collection.)

Plate XIX from the Catalogue of the British species of *Pisidium*, 1913. According to Woodward all the illustrations are of *nitidum*. In reality, only 14 out of a total of 66 specimens are referable to that species. At least four other species account for the remainder: *subtruncatum*, *personatum*, *casertanum* and *obtusale*. The diagrammatic enlargement of the hinge (shown as 16a, b) clearly represents *personatum*!

THE ENDEMIC *OXYCHILUS* SPECIES OF LAMPEDUSA (PELAGIAN ISLANDS, ITALY): *O. DIDUCTUS* (WESTERLUND, 1886) (PULMONATA, ZONITIDAE)

G. MANGANELLI[1], S. CIANFANELLI[2] & F. GIUSTI[1]

Abstract Oxychilus diductus *(Westerlund, 1886) is redescribed. The species is the only one of the genus* Oxychilus *living in the Pelagian Islands, an archipelago off the northern coast of Tunisia, and is endemic to Lampedusa.* O. diductus *can be identified by* draparnaudi-*like anatomy and shell depressed, discoidal, not "polygyrate", with umbilicus wide and external surface irregularly striated, opaque and with finely granulated microsculpture.*

Key words Oxychilus diductus, *taxonomy, systematics, distribution, Lampedusa, Pelagian Islands.*

INTRODUCTION

Many *Oxychilus* species live in Sicily and the surrounding islands (Riedel, 1980, 1998; Manganelli *et al.*, 1995); six have a reduced distribution, limited to one island, or in one case, two islands (Table 1). The taxonomy of these species is rather inadequate especially in the case of those of mainland Sicily which are anatomically uniform and very close to *O. draparnaudi* (Beck, 1837), but vary dramatically in shell shape and size. It will therefore presumably require many years of field and laboratory research to revise their status and to establish nomenclature, taxonomy and systematics. More is known about species with very reduced distribution (those endemic to single peri-Sicilian islands) thanks to papers by Giusti (1973) and Riedel (1973). However, important data on peculiar anatomical details (e.g. internal structure of penis; presence or absence of mid-penis bottle-neck) is still not available, rendering uncertain the significance of the subgenera *Hyalocornea* and *Hyalofusca* used by Riedel (1973) for some of them.

As a first contribution to the revision of the Sicilian *Oxychilus*, we start with *O. diductus* (Westerlund, 1886) endemic to Lampedusa. Lampedusa, Linosa and the islet of Lampione constitute the Pelagian Islands, an archipelago in the Mediterranean, between Sicily and Tunisia, south of Pantelleria and southwest of Maltese Islands.

Two shells of this species, collected on Lampedusa by E.H. Giglioli in August 1882, were studied by Marchesa M. Paulucci and assigned to a new species: *Hyalinia diducta*. However, Paulucci did not publish it, but sent her shells to C.A. Westerlund who confirmed that they belonged to a new species. Westerlund also assigned some other shells he had to this species and finally described it in his compendium on Palaearctic non-marine molluscs (Westerlund, 1886). Although this species has repeatedly been accepted as distinct (Alzona, 1971; Riedel, 1980, 1998; Beckmann, 1992; Manganelli *et al.*, 1995; Cianfanelli, in press), little is known about it and a redescription is therefore required.

While this paper was under editorial processing, Beckmann & Riedel (2001) published a paper on the anatomy and subgeneric status of *O. diductus*. They concluded that this species is similar to *O. gardinii* Manganelli, Bodon & Giusti, 1991, from the Ligurian Apennnines (northern Italy) by virtue of penis size and shape, but differs because it has rows of papillae inside the proximal penis instead of pleats. Consequently, they concluded that if the classical distinction of *Oxychilus* into the subgenera *Oxychilus* s.str. and *Ortizius* is maintained, *O. diductus* belongs to the former and *O. gardinii* to the latter.

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MATERIAL AND METHODS

Whole shells were photographed under the light microscope (Wild M5A). All dimensions (NW number of whorls, SD shell diameter, SH shell height, UD umbilicus diameter) were measured using a micrometer.

Live specimens were drowned in water, then fixed and preserved in 75% ethanol buffered with $NaHCO_3$. The bodies were isolated after crushing the shells and dissected under the light microscope (Wild M5A) using thin pointed watchmaker's tweezers. Anatomical details were drawn using a Wild camera lucida. Some parts of the genital organs (e.g. duct of bursa copulatrix, distal vagina, epiphallus, flagellum, proximal portion of penis, 'bottle-neck' caliber and distal penis) were measured by micrometer.

Radulae were manually extracted from the buccal bulbs, washed in pure 75% ethanol, mounted on copper stubs with electronconductive glue, sputter-coated with gold and photographed using a Philips 505 SEM.

The material examined is listed as follows: locality, UTM reference, collector(s), date, number of specimens in parenthesis. Locality names and UTM references are according to the sheet 256 II NO "Lampedusa" of the 1:25,000 scale map of Italy (Series M 891).

Key to museum and collection acronyms: FGC F. Giusti, Dipartimento di Scienze Ambientali, University of Siena, Italy, GNM Göteborg Naturhistoriska Museum, Göteborg, Sweden, MZUF Museo Zoologico "La Specola", Sezione del Museo di Storia Naturale dell'Università di Firenze, Italy, SCC S. Cianfanelli collection, Firenze, Italy, SNMNH Swedish National Museum of Natural History, Department of Invertebrate Zoology, Stockholm, Sweden.

Key to acronyms used in Figs 7-11: B "bottle-neck", BC bursa copulatrix, BS "bottle-neck" sheath, BW body wall, DBC duct of bursa copulatrix, DP distal portion of penis, E epiphallus, EO epiphallus opening, F flagellum, FO free oviduct, POS prostatic portion of ovispermiduct, PP proximal portion of penis, PR penial retractor, PS penial sheath, UOS uterine portion of ovispermiduct, V vagina, VD vas deferens, VG vaginal gland.

Oxychilus diductus (Westerlund, 1886)

H[yalinia]. diducta Paul. in schedis Westerlund, 1886: 49.

Type series Eight syntypes: two are in the Paulucci collection at the Museo Zoologico de "La Specola", Florence, Italy (no. 808), three are in the Westerlund collection at Göteborg Naturhistoriska Museum, Göteborg, Sweden (no. 127) and three are in the Westerlund collection at the Swedish National Museum of Natural History, Department of Invertebrate Zoology, Stockholm, Sweden (no. 5383). According to T. von Proschwitz (personal communication) other syntypes were possibly kept at the Finnish Museum of Natural History (Helsinki, Finland), but a search there failed to locate them (I. Valovirta personal communication).

Beckmann & Riedel (2001) selected the largest of the three syntypes kept at the Göteborg Naturhistoriska Museum as the lectotype, claiming that it was necessary to render recognition of the species unambiguous (ICZN, 1999: Art. 74.7.3). We accept their statement, although in our opinion designation of the lectotype was not necessary because all the syntypes belong to a single species collected on Lampedusa, and *O. diductus* is the only *Oxychilus* species on Lampedusa; there is consequently no uncertainty about its identity.

Type locality "Italien, Ins. Lampedusa".

TABLE 1

Oxychilus species reported from Sicily and peri-Sicilian Islands. Endemic species are marked with asterisk.

species	**geographical distribution**	**main references**
**O. (Oxychilus) diductus* (Westerlund, 1886)	Lampedusa (Pelagian Islands)	Riedel (1980, 1998), Manganelli *et al.* (1995)
O. (Oxychilus) draparnaudi (Beck, 1837)	Sicily, Lipari, Panarea, Salina (Eolian Islands), Comino, Gozo and Malta (Maltese Islands	Giusti (1973), Giusti *et al.* (1995), Manganelli *et al.* (1995)
**O. (Oxychilus) fuscosus* (Rossmässler, 1838)	Sicily	Riedel (1980), Manganelli *et al.* (1995)
**O. (Oxychilus) lagrecai* Giusti, 1973	Filicudi (Eolian Islands)	Giusti (1973), Riedel (1980), Manganelli *et al.* (1995)
**O. (Hyalocornea) alicurenis* (Benoit, 1857)	Alicudi (Eolian Islands)	Giusti (1973), Riedel (1980), Manganelli *et al.* (1995)
**O. (Hyalocornea) canini* (Benoit, 1843)	NW Sicily	Riedel (1973, 1980), Manganelli *et al.* (1995)
**O. (Hyalocornea) egadiensis* Riedel, 1973	Favignana and Levanzo (Egadian Islands)	Riedel (1973, 1980), Manganelli *et al.* (1995)
**O. (Hyalocornea) nortoni* (Calcara, 1843)	Ustica	Riedel (1973, 1980), Manganelli *et al.* (1995)
**O. (Hyalofusca) denatale* (Pfeiffer, 1857)	Marettimo (Egadian Islands)	Riedel (1973, 1980), Manganelli *et al.* (1995)
O. (Mediterranea) hydatinus (Rossmässler, 1838)	Sicily, Lipari (Eolian Islands), Favignana, Levanzo, Marettimo (Egadian Islands), Gozo and Malta (Maltese Islands)	Giusti (1973), Giusti *et al.* (1995), Manganelli *et al.* (1995)
O. (Morlina) ercicus (Benoit, 1859)	Sicily and Pantelleria I.	Riedel (1980), Manganelli *et al.* (1990, 1995)

Identification A medium-sized species of *Oxychilus* endemic to Lampedusa (one of the Pelagian Islands), characterized by *draparnaudi*-like anatomy and shell depressed, discoidal, not "polygyrate", with umbilicus wide and external surface irregularly striated, opaque and with finely granulated microsculpture.

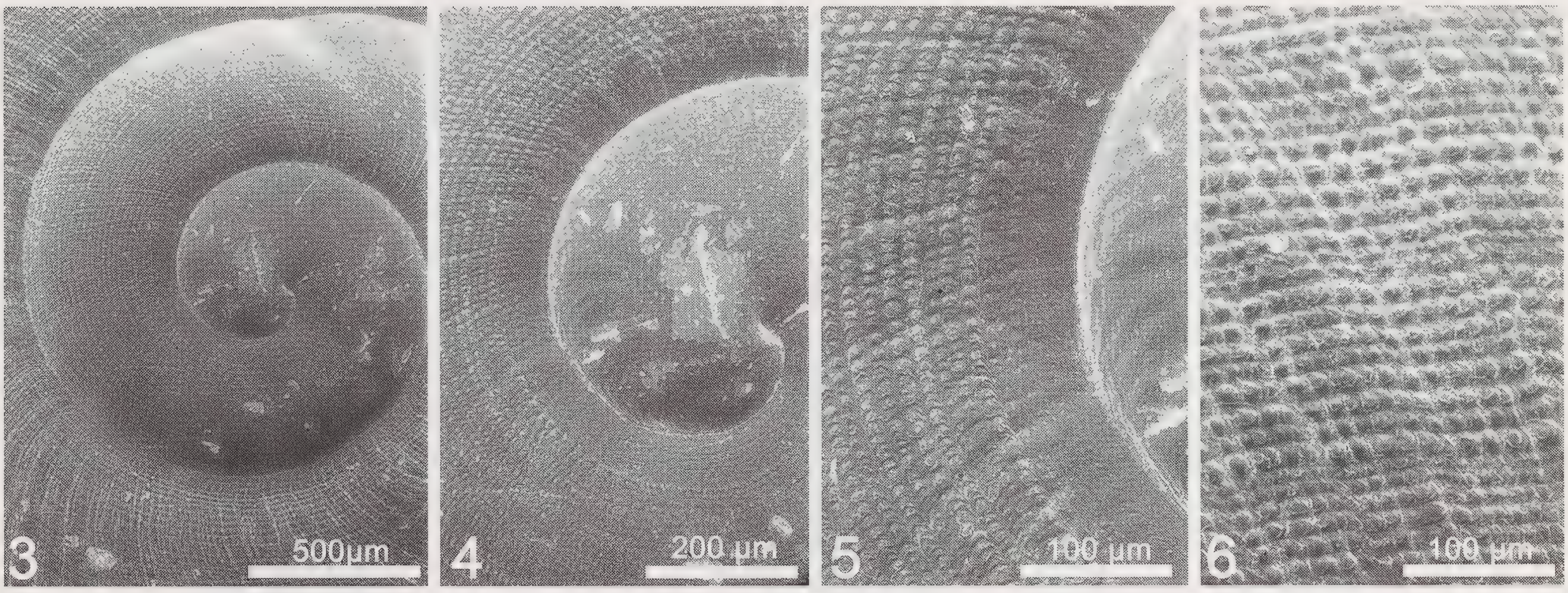
Description Body slate-blue in colour; neck and upper part of sides with variably wide areas with conspicuous pits (with phylacites); foot slender, of aulacopod type, pale slate-grey, sole longitudinally tripartite; sigmurethrous kidney; jaw of oxygnathous type.

Shell (Figs 1-6) dextral, medium-sized, depressed, discoidal (last whorl rather angled at periphery, but not keeled), usually tectiform, occasionally flat above, rather flat below, thin, fragile, subtransparent, opaque, with marked and irregularly spaced growth lines, more evident immediately before end of last whorl, yellowish to pale brownish-yellow in colour when fresh, paler and opalescent below; external surface of initial protoconch with fine longitudinal furrows, that of distal protoconch and teleoconch with increasingly evident, finely granulated microsculpture (crossing of longitudinal and transverse furrows divides the surface into very small squares, each containing a globular relief or granulum); spire with 4 $^3/_4$ to 5 $^7/_8$ whorls, rather slowly (not as slowly as in the "polygyrate" *Oxychilus* from Sicily and some Sicilian islands; Riedel, 1973) and regularly increasing in size, last whorl slightly dilated near aperture, its last quarter descending slightly or not at all; sutures shallow; umbilicus wide, about $^1/_4$–$^1/_5$ of maximum shell

Figs 1-2 Two shells of *Oxychilus diductus* (Westerlund, 1886) from Valle di Cala Galera, 50 m asl, 33STV7932, S. Cianfanelli & E. Talenti leg. 09.05.2000.

diameter; aperture oval to rhomboidal, oblique; peristome interrupted, simple, not thickened nor reflected, its superior vertex starting at or slightly above periphery of last whorl. Dimensions (40 shells measured). Shell diameter: 10.8 ± 1.17 mm (9.1-15.00), height: 4.0 ± 0.41 mm (3.3-5.5), umbilicus diameter: 2.3 ± 0.29 mm (1.9-3.2), number of whorls: 5 ⅓ ± ⅕ (4 ¾–5 ⅞).

Genitalia (Figs 7-11). General scheme of genitalia as in *Oxychilus* (s.str.), we only describe the distal genitalia. Female distal genitalia include free oviduct, bursa copulatrix and its duct, and vagina. Proximal vagina and base of duct of bursa copulatrix fully enveloped by well developed layer of spongy glandular tissue forming vaginal gland; duct of bursa copulatrix cylindrical and rather long (2.1-2.7 mm); bursa copulatrix oval



Figs 3-6 Detail of shell microsculpture of specimens of *Oxychilus diductus* (Westerlund, 1886) from Valle di Cala Galera, 50 m asl, 33STV7932, S. Cianfanelli & E. Talenti leg. 09.05.2000.

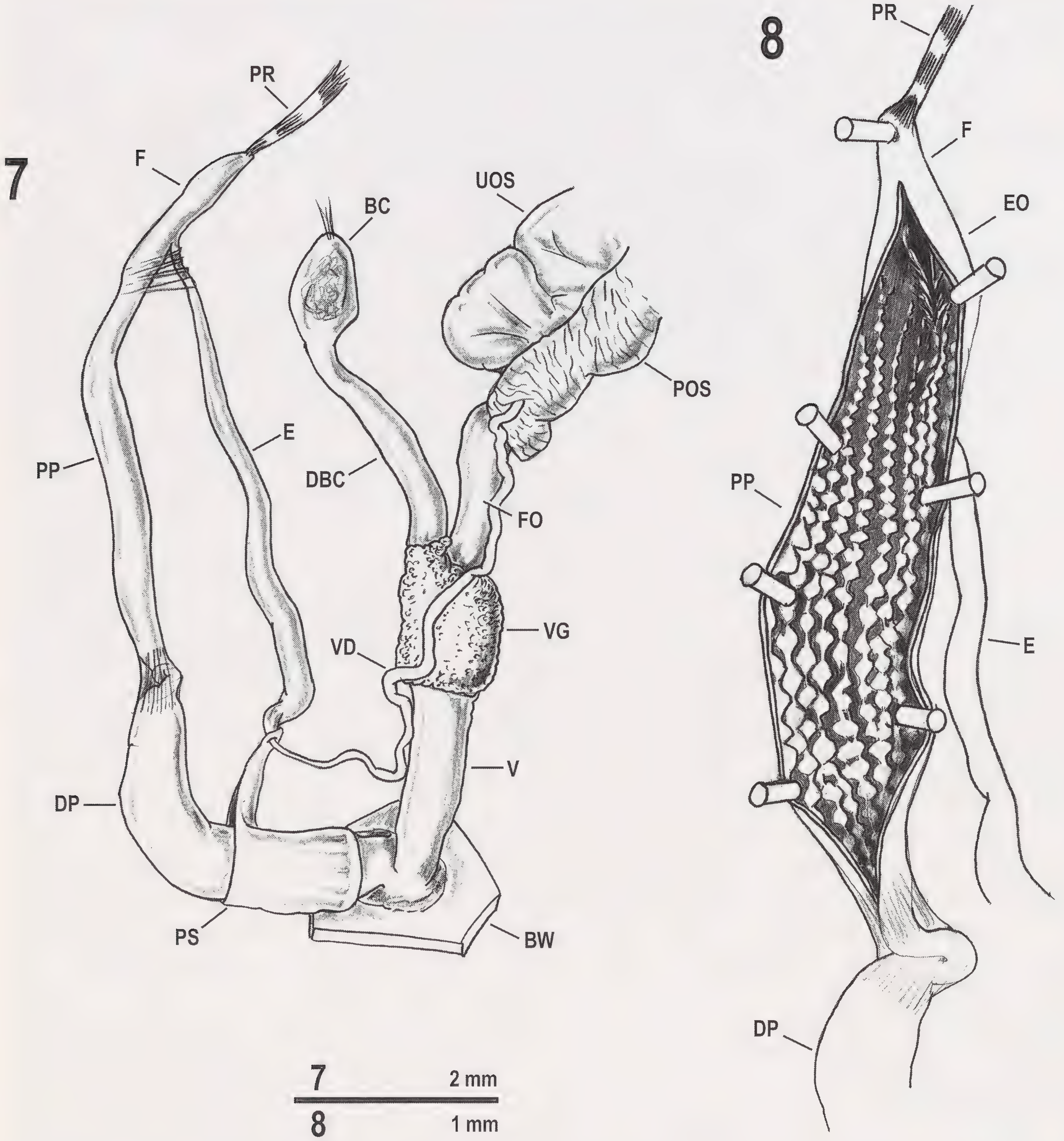
or pyriform; distal vagina (from end of vaginal gland to genital atrium) relatively wide and short (1.5-1.9 mm).

Male distal genitalia include vas deferens, epiphallus and penial complex (flagellum and penis). Epiphallus long (4.5-5.3 mm), initially relatively wide (where vas deferens ends) then narrowing, its slender final portion (before entering penis) attached to external wall of proximal penis by thin strips of tissue. Flagellum rather short (0.9 mm), with penial retractor muscle ending at its apex. Penis divided into distal and proximal portions by evident constriction. Proximal penis (3.6-5.1 mm) longer (PP/DP: 1.3-1.5) than distal (2.7-3.3 mm), initially slender, slightly wider at about half its length, then progressively reducing in caliber to form 'bottle-neck'; 'bottle-neck' (caliber: 0.1-0.2 mm), enveloped in very thin, transparent sheath, straight or occasionally slightly bent, gradually narrowing, then gradually widening before continuing into distal penis. Distal penis begins where 'bottle-neck' ends and ends close to genital atrium; distal penis enveloped by sheath; penial sheath much shorter than distal penis, extending on one side to reach and envelop proximal apex of epiphallus (and consequently traversed by vas deferens). Very short, thin walled tube connects distal penis (level with where penis sheath originates) to genital atrium.

Internal wall of proximal penis with approximately 8-9 rows of papillae; papillae very numerous and small, their number and size varying in different rows (smaller near opening of epiphallus into proximal penis and just before 'bottle-neck'); papillae variable in shape and outline (polygonal, pyramidal or conical), distinct but with bases connected by thin, raised, root-like crests; small, elongated, closely spaced, wavy papillae bordering rim of epiphallus opening into proximal penis. Wall of distal penis thick, with 5-6 continuous internal pleats having jagged sides.

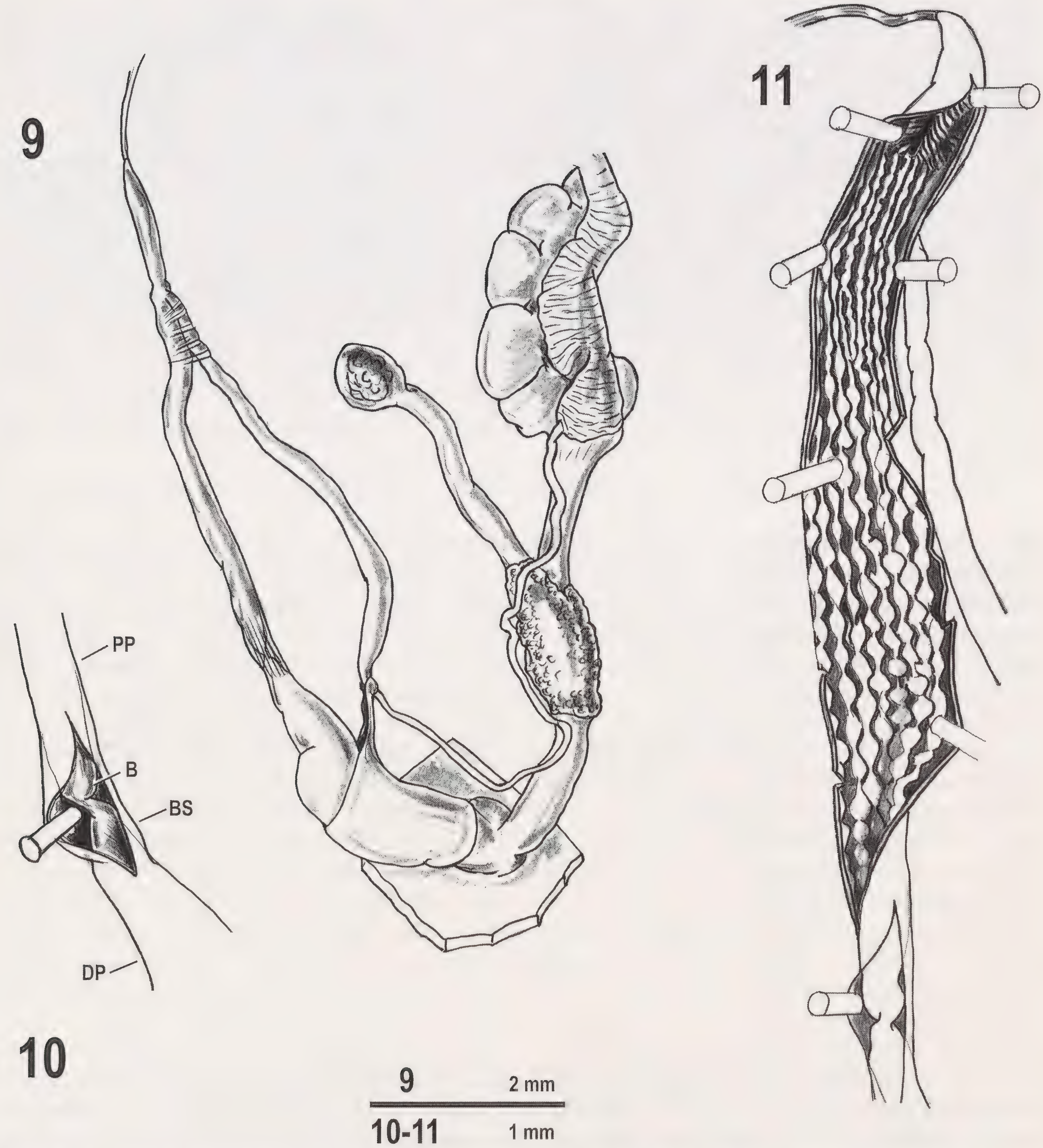
Radula (Figs 12-13). Each row with 25-27 teeth according to the formula: 9-10 M/1 + 1 LM/2 + 2 L/3 + C/3 + 2 L/3 + 1 LM/2 + 9-10 M/1; central tooth with robust basal plate from which tricuspid crown arises, crown with long, slender, pointed mesocone and two small, pointed ectocones; lateral teeth (two on each side) with tricuspid crown formed by long, robust mesocone, small endocone (⅔ way up mesocone side) and small ectocone (about half-way up mesocone side); lateromarginal teeth, one on each side, with inwardly curved crown having mesocone, very small endocone and sometimes a trace of ectocone; marginal teeth monocuspid, thorn-like, progressively reducing in size.

Material examined Lampedusa (1 sh det. "Hy. sp.", Paulucci collection, MZUF 17572; 3 sh [syntypes], Westerlund collection, GNM 127; 3 sh [syntypes], Westerlund collection,



Figs 7-9 Distal genitalia (Fig. 7) and internal ornamentation of flagellum and proximal penis (Fig. 8) in a specimen of *Oxychilus diductus* (Westerlund, 1886) from Valle di Cala Galera, 50 m asl, 33STV7932, S. Cianfanelli & E. Talenti leg. 09.05.2000.

SNMNH 5383), E.H. Giglioli leg. 12.08.1882 (2 sh [syntypes]; Paulucci collection, MZUF 808). Valle dell'Acqua, 25 m asl, 33STV7533, S. Cianfanelli & E. Talenti leg. 12.05.2000 (1 sh, MZUF 17573). Valle dell'Acqua, 90 m asl, 33STV7533, S. Cianfanelli & E. Talenti leg. 12.05.2000 (1 sh, 2 sp. MZUF 17580). Valle della Forbice (debris of spring), 0.5 m asl, 33STV7732, S. Cianfanelli & E. Talenti leg. 14.05.2000 (8 sh, MZUF 17577). Valle della Forbice, 5 m asl, 33STV7732, S. Cianfanelli & E. Talenti leg. 14.05.2000 (18 sh, MZUF 17575; 2 sh FGC). Valle della Forbice (debris talus), 5 m asl, 33STV7732, S. Cianfanelli & E. Talenti leg. 14.05.2000 (1 sh ? Holocene - Recent, MZUF 17579). Valle della Forbice, 10 m asl, 33STV7732, S. Cianfanelli & E. Talenti leg. 14.05.2000 (40 sh, MZUF 17576). Valle della Forbice, 33STV7733, R. Noto La Diega, 02.11.2000 (1 sh, FGC). Isola dei



Figs 9-11 Distal genitalia (Fig. 9), mid-penis region (Fig. 10) and internal ornamentation of flagellum and proximal penis (Fig. 11) in a specimen of *Oxychilus diductus* (Westerlund, 1886) from Valle di Cala Galera, 50 m asl, 33STV7932, S. Cianfanelli & E. Talenti leg. 09.05.2000.

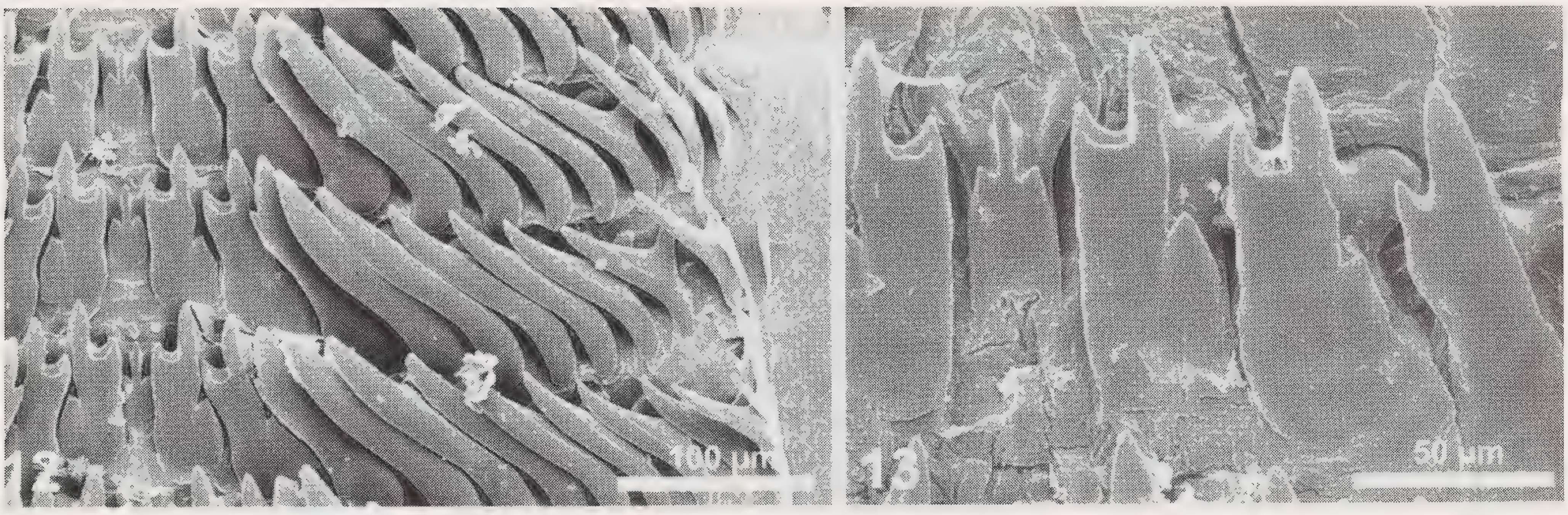
Conigli, 27 m asl, 33STV7832, S. Cianfanelli & E. Talenti leg. 13.05.2000 (28 sh, MZUF 17574). Arja Rossa, 33STV7833, R. Noto La Diega, 18.02.2000 (1 sh; FGC). Valle di Cala Galera, 50 m asl, 33STV7932, S. Cianfanelli & E. Talenti leg. 09.05.2000 (19 sp, MZUF 17503; 4 sp, FGC; 105 sh, MZUF 17578; 52 sh, 7 sp, MZUF 17581; 5 sh, FGC). 250 m SW of Punta Cappellone, 80 m asl, 33STV7933, , S. Cianfanelli & E. Talenti leg. 10.05.2000 (3 sh, MZUF 17596). 250 m SW of Punta Cappellone (carbonate lithoclast breccias with terra rossa), 80 m asl, 33STV7933, S. Cianfanelli & E. Talenti leg. 10.05.2000 (1 sh ? Holocene - Recent, MZUF 17587). Casa di S. Fratello, 45 m asl, 33STV8032, S. Cianfanelli & E. Talenti leg. 13.05.2000 (4 sh, MZUF 17585). Santuario della Madonna di Porto Salvo,

TABLE 2

Taxa and main character-states cited in Discussion. **1** – Penial flagellum (PF) and penial retractor (PR): PF present with PR inserted at its apex (0); PF absent, PR inserted where epiphallus ends and proximal penis begins (1). **2** – Internal ornamentation of proximal penis consisting of: rows of papillae (0); rows of thorned papillae (1); rows of flat, hardly visible papillae, each row continuing as a wavy wrinkled segmented pleat (2); longitudinal pleats (3). **3** – Epiphallus: long, usually as long as proximal penis, its internal wall with slender longitudinal pleats (0); short, with series of transverse crests on one side and a few slender longitudinal pleats on the others (1). **4** – Mucous gland: mainly vaginal (0); forming muff of glandular tissue, denser and more intensely yellowish, around distal portion of free oviduct, only rarely extending as thin, whitish layer to cover part of surface of proximal vagina (1). **5** – Mesocone of central tooth: long (0); short (1). **6** – Mid-penis region: narrow ("bottle-neck") and enveloped by thin sheath (0); not narrow and without thin sheath (1). **7** – Shell: discoidal (0); markedly discoidal (1); lenticular (2). **8** – Shell: not polygyrate (0); polygyrate (1). **9** – Shell microsculpture: absent or consisting of barely evident, fine wavy spiral lines (0); consisting of evident fine wavy spiral lines (1); consisting of spiral rows of small granules (2).

	1	2	3	4	5	6	7	8	9
Oxychilus alicurenis (Benoit, 1857)	0	0	0	0	0	?	0	1	1
Oxychilus canini (Benoit, 1843)	0	0	? 0	0	0	?	0	1	1
Oxychilus denatale (Pfeiffer, 1857)	0	?2	? 0	0	0	?	0	1	2
Oxychilus diductus (Westerlund, 1886)	0	0	0	0	0	0	1	0	2
Oxychilus draparnaudi (Beck, 1837)	0	0	0	0	0	0	0	0	0
Oxychilus egadiensis Riedel, 1973	0	0	? 0	0	0	?	0	1	1
Oxychilus fuscosus (Rossmässler, 1838)	0	0	? 0	0	0	0	0	0	0
Oxychilus gardinii Manganelli, Bodon, Giusti, 1991	0	3 (0)	? 0	0	0	0	0	0	0
Oxychilus lagrecai Giusti, 1973	0	0	? 0	0	0	?	0	1	1
Oxychilus majori (Westerlund, 1886)	0	2	0	0	0	0	1	0	0
Oxychilus mortilleti (Pfeiffer, 1859)	0	0	? 0	0	0	0	0	0	0
Oxychilus nortoni (Calcara, 1843)	0	?	0	0	?	?	0	1	1
Oxychilus oglasicola Giusti, 1968	0	0	0	0	0	0	2	0	0
Oxychilus oppressus (Shuttleworth, 1878)	0	0	0	0	0	0	0-1	0	2
Mediterranea species	0-1	1	1	1	1	1	0	0	0
"*Pseudopolita*" species	0-1	1	? 1	? 1	? 1	? 1	0	0	2

25 m asl, 33STV8131, S. Cianfanelli & E. Talenti leg. 09.05.2000 (6 sh, MZUF 17582). Village of Lampedusa, 3 m asl, 33STV8231, S. Cianfanelli & E. Talenti leg. 14.05.2000 (10 sh, 1 sp, MZUF 17589). Valle Imbriacole, 35 m asl, 33STV8232, V. Billeci, S. Cianfanelli, B. Maraventano & E. Talenti leg. 13.05.2000 (11 sh, MZUF 17592). Valle Imbriacole, 40 m asl, 33STV8232, S. Cianfanelli & E. Talenti leg. 11.05.2000 (10 sh, 6 sp, MZUF 17593; 74 sh, MZUF 17586). Valle Imbriacole (carbonate lithoclast breccias with terra rossa), 40 m asl, 33STV8232, V. Billeci, S. Cianfanelli, B. Maraventano & E. Talenti leg. 14.05.2000 (16 sh ? Holocene - Recent, MZUF 17588). Cala Maluk, 2 m asl, 33STV8330, S. Cianfanelli & E. Talenti leg. 15.05.2000 (121 sh, MZUF 17751; 6 sh, FGC). Cavallo Bianco, 10 m asl, 33STV8331, S. Cianfanelli & E. Talenti leg. 15.05.2000 (2 sh, MZUF 17583). Between Punta Sottile and Capo Uccello, 20 m asl, 33STV8430, S. Cianfanelli & E. Talenti leg. 11.05.2000 (2 sh, MZUF 17591). Cala Francesca, 10 m asl, 33STV8430, S. Cianfanelli & E. Talenti leg. 11.05.2000 (1 sh, MZUF 17594). Cala Pisana, 5 m asl, 33STV8431, S. Cianfanelli & E. Talenti leg. 09.05.2000 (6 sh, 4 sp, MZUF 17595). Cala Creta (debris of spring), 10 m asl, 33STV8432, S. Cianfanelli & E. Talenti leg. 10.05.2000 (4 sh, MZUF 17590). Capo Grecale, 40 m asl, 33STV8532, S. Cianfanelli & E. Talenti leg. 11.05.2000 (2



Figs 12-13 The radula of a specimen of *Oxychilus diductus* (Westerlund, 1886) from Valle di Cala Galera, 50 m asl, 33STV7932, S. Cianfanelli & E. Talenti leg. 09.05.2000.

sh, MZUF 17584).

Derivation of name *"diductus"*, Latin adjective meaning "distinct", "separate".

Taxonomy *Oxychilus diductus* belongs to *Oxychilus* (s.str.) sensu Giusti & Manganelli (1999). Indeed it has the same anatomical organization as the *Oxychilus* (s.str.) species: penis with flagellum; penial retractor inserted at apex of flagellum; internal ornamentation of penis consisting of pleats and rows of papillae; epiphallus long, usually longer than proximal penis; internal wall of epiphallus with slender longitudinal pleats; mucous gland mainly vaginal; long mesocone of central tooth. Among the *Oxychilus* (s.str.) species, it shares narrow mid-penial region ("bottle-neck") enveloped in a thin sheath with *O. draparnaudi* (Beck, 1837), *O. majori* (Paulucci, 1986), *O. mortilleti* (Pfeiffer, 1859), *O. oglasicola* Giusti, 1968, and *O. oppressus* (Shuttleworth, 1878) and internal ornamentation of proximal penis consisting of rows of evident papillae which stop level with mid-penial constriction, with *O. draparnaudi, O. mortilleti, O. oglasicola* and *O. oppressus* (for *O. draparnaudi*, see Giusti & Manganelli, 1997: Figs 15-30, Manganelli & Giusti, 1998: Figs 19-22; for *O. majori*, see Manganelli *et al.*, 2000: Figs 4-8; for *O. mortilleti*, see Manganelli & Giusti, 1998: Figs 5-17; for *O. oglasicola*, see Manganelli *et al.*, 2000: Figs 12-14; for *O. oppressus*, see Riedel, 1967: Figs 1-2; personal unpublished data).

O. diductus is readily distinguished from *O. draparnaudi* and *O. mortilleti* by its markedly discoidal shell with external surface striated, opaque and with granulated microsculpture, and from *O. oglasicola* by its smaller shell, not keeled at periphery and with granulated microsculpture (shell not markedly angled and without microsculpture in *O. draparnaudi* and *O. mortilleti*; shell larger (17.8 ± 2.0 mm), lenticular, not granulated and with the last whorl markedly carinate in *O. oglasicola*; for *O. draparnaudi*, see Giusti & Manganelli, 1997: Fig. 1; for *O. mortilleti*, see Manganelli & Giusti, 1998: Figs 1-4; for *O. oglasicola*, see Manganelli *et al.*, 2000: Figs 10-11). *O. diductus* is distinguished from the Sardinian *O. oppressus* – with which it shares similar shell microsculpture – by its smaller, more discoidal shell, with smaller protoconch and larger umbilicus and longer slender proximal penis (for *O. oppressus*, see Riedel, 1967: Figs 1-2; personal unpublished data)

O. diductus is also readily distinguished from the many species of *Oxychilus* (s.str.) sensu Giusti & Manganelli (1999) living in Sicily and the surrounding islands. None of these species has a depressed-discoidal, well-umbilicated shell like *O. diductus*. Moreover, *O. alicurensis* (Benoit, 1857), *O. canini* (Benoit, 1843), *O. denatale* (Pfeiffer, 1857), *O. egadiensis* Riedel, 1973, *O. nortoni* (Calcara, 1843) have a shell without or with less evident granulated microsculpture (microsculpture consisting in very fine wavy spiral lines in *O. alicurenisis, O. canini, O. egadiensis, O. nortoni*, or smaller granula in *O. dena-*

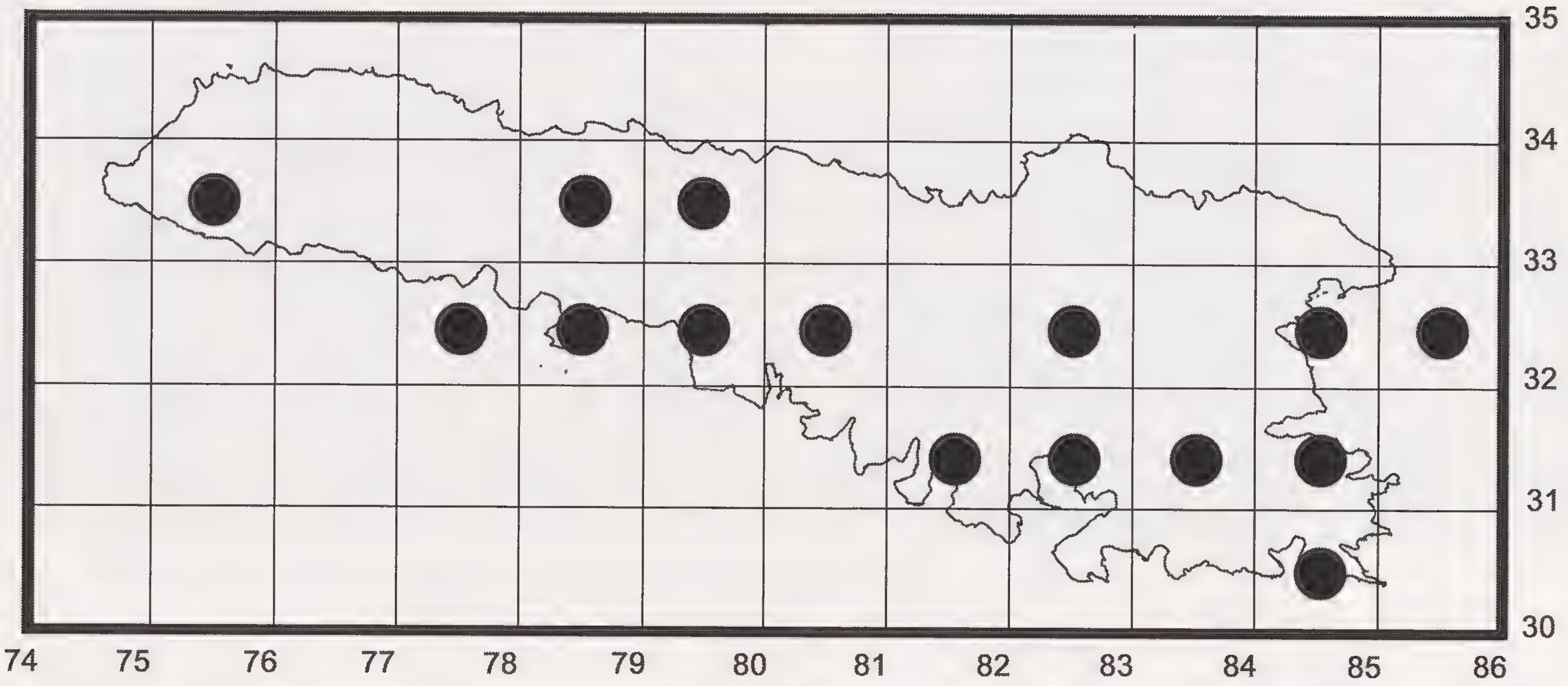


Fig. 14 The distribution of *Oxychilus diductus* (Westerlund, 1886) on a UTM map (1 x 1 km squares) of Lampedusa.

tale) and a proportionally larger number of whorls for a given size shell (whence the Italian name of "ossichili poligirati" [polygyrate *Oxychilus*], for these species) and *O. fuscosus* (Rossmässler, 1838) has a very large shell, smooth, glossy and without granulated microsculpture (for *O. alicurenis*, see Riedel, 1973: Pl. 2, figs 20-25; for *O. canini*, see Riedel, 1973: Figs 1-4, Pl. 1, figs 1-3, 7-11; for *O. denatale*, see Riedel, 1973: Figs 16-17, Pl. 2, figs 26-31; for *O. egadiensis*, see Riedel, 1973: Figs 8-10, Pl. 1, figs 4-6; for *O. fuscosus*, see Giusti, 1973, Pl. 16, figs, 8, 10 [as *O. draparnaudi*]; for *O. lagrecai*, see Giusti, 1973: Pl. 16, figs 12-14; for *O. nortoni*, see Riedel, 1973: Pl. 2, figs 14-19).

O. diductus shares a shell granulated microsculpture with other West Mediterranean *Oxychilus* species (*O. oppressus*, Sardinia; *O. denatale*, Marettimo, Egadian Islands; some species of *Pseudopolita*, North Africa; Riedel, 1975, 1980). The first three species belong to *Oxychilus* (s.str.) sensu Giusti & Manganelli (1999) whereas the species of *Pseudopolita* are related to *Mediterranea* Clessin, 1880 (Giusti & Manganelli, 1999). This character therefore presumably arose independently in the two groups.

Beckmann & Riedel (2001) stated that *O. diductus* is similar to the Ligurian *O. gardini*, by virtue of the very slender proximal penis. The specimens examined by us have a slender proximal penis, as do other *Oxychilus* species (e.g. *O. draparnaudi*, see Giusti & Manganelli, 1997: Figs 15-18; *O. mortilleti*, see Manganelli & Giusti, 1998: Figs 13-14; *O. majori*, see Manganelli *et al.*, 1999: Fig. 4), but not quite as slender as *O. gardinii* (in *O. gardinii* the proximal penis has the same caliber as the vas deferens, see Manganelli *et al.*, 1991: Figs 7-10, 17). Moreover, as stated by Beckmann & Riedel (2001), there are important differences in internal ornamentation of the proximal penis (pleats in *O. gardinii*; rows of papillae in *O. diductus*) and in shell shape and external microsculpture (*O. gardinii* has more rapidly growing whorls and a smooth external surface).

Geographical distribution *Oxychilus diductus* has a reduced distribution, limited to Lampedusa island, including the islet "Scoglio dei Conigli".

Status and Conservation Although *Oxychilus diductus* is a common species, its narrow distribution is a clear factor of risk. It must therefore be considered a "Lower risk (near threatened)" [LR, nt] species.

ACKNOWLEDGMENTS

We thank Antonella Daviddi, Leonardo Gamberucci and Eugenio Paccagnini for technical assistance, Helen Ampt for revising the English, Vincenzo Billeci, Giuseppina Nicolini, Beppino Maraventano, Ruggero Noto La Diega and Enrico Talenti for helping in field collection and Ted von Proschwitz (Göteborg, Sweden), K. Sindemark (Stockholm, Sweden) and I. Valovirta (Helsinki, Finland) for information about or loan of material from their respective museums.

Research financed by MURST (grant no. 9905317452 "Aspetti descrittivi e metodologici della biodiversità animale in Italia") and Museo Zoologico de "La Specola", Sezione del Museo di Storia Naturale dell'Università di Firenze (Italy).

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A SECOND LOCALITY FOR *HELICELLA (H.) VALDEONA* (HYGROMIIDAE)

EDMUND GITTENBERGER[1] & RON CARR[2]

Abstract The taxonomic validity of Helicella (H.) valdeona *(Gittenberger and Manga 1977) is confirmed, following the discovery of further specimens from a second locality to the south of the Picos de Europa, northern Spain.*

A quarter of a century ago, Gittenberger & Manga (1977) descried some hygromiid species from the northern Spanish province of León as new to science. By far the largest of these species was *Helicella (H.) valdeona*, known only from its type locality and characterised by both conchological and anatomical characteristics of a quantitative nature. No further data on this nominal species has been acquired until now. Its validity as more than only a local form of *H. (H.) itala* (L., 1758) *sensu lato* was doubted and Manga González (1983) did not refer to it in her monograph on the helicid snails of the province of León.

In August, 1999, RC collected samples of terrestrial snails at Fuente Dé, province of Cantabria, northern Spain, some of which were studied by EG. It was observed that these shells were strikingly similar to *H. (H.) valdeona*. The proximity of the collection site to that of the type locality indicated the necessity for anatomical investigation and two snails were subsequently dissected.

The shells (Fig. 1) are fragile and somewhat transparent, with pale corneous spiral bands on a creamy white background with some irregular, radial, darker streaks. They cannot be distinguished from shells of the type series of *H. (H.) valdeona*, differing from

Figure 1 *Helicella (H.) valdeona*

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[2] 9 The Mallows, Maidstone, Kent ME14 2PX.

H. (H.) itala nubigena (De Saulcy, 1852) in exactly the same way as the types. They have a slightly narrower, more roundish umbilicus, measuring ⅙ of the total shell width. The umbilicus is not unproportionally enlarged by the last section of the body whorl, since the columellar insertion of the apertural lip is in line with the umbilical suture and not shifted further sideways. Shell dimension: Height 8.5-11.2mm, width 14.3-18.6mm (n=9).

In both dissected specimens (Fig. 2, 1) the flagellum was found to be slightly longer than the epiphallus instead of clearly shorter, whereas the bursa of the bursa copulatrix is triangular in shape (Fig. 2, 2). These characteristics were referred to as diagnostic for *H. (H.) valdeona* against *H. (H.) itala sensu lato*. The shape of the bursa depends at least partly on its contents and may vary for that reason, but not so the relative length of the flagellum.

The luminal structure of the male organ has been examined and the proximal half of the penis has been found to contain a simple, cylindrical, blunt penial papilla, which reaches into the genital atrium. In the distal half of the penis, there is a conspicuous twist within the penis sheath in both specimens (Fig. 2, 3); this may result from the functional state of the organ, since such a twist is not present in the holotype (slide RMNH 883).

H. (H.) valdeona is now known from the two localities in a restricted area of northern Spain, south of the Picos de Europa: Province of León (1) Marina de Valdeon (=8.5km E of Espinama), type locality, UTM UN4977 (Gittenberger and Manga 1977: 185). Province of Cantabria (2) Fuente Dé (=3km NW of Espinama), UTM UN5278 (CRC).

The species was locally abundant on the lower south facing mountain slopes of Fuente Dé where it was collected from low herbage.

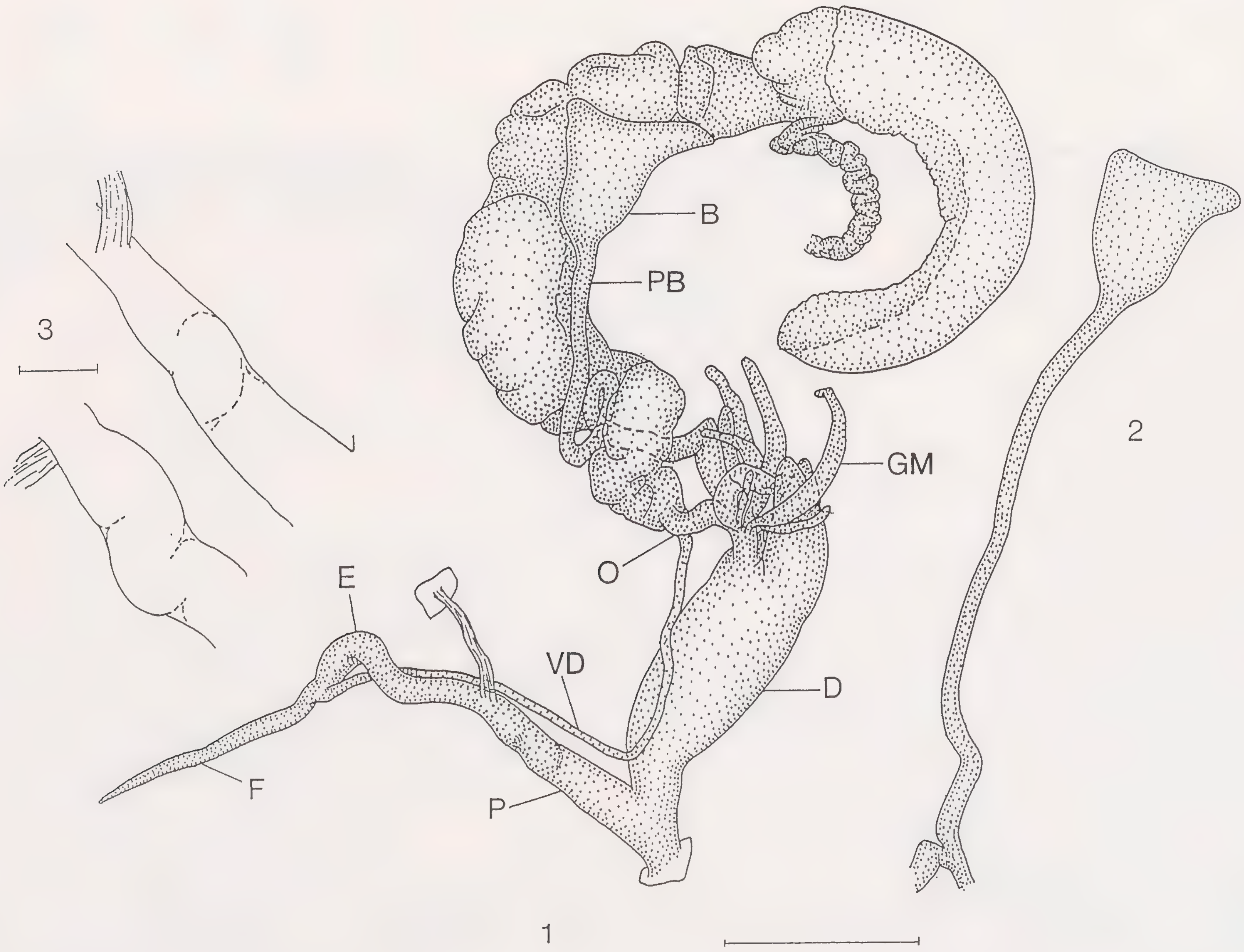

Figure 2 *Helicella (H.) valdeona* (Gittenberger & Manga) B=Bursa copulatrix D=Dart Sac E=Epiphallus F=Flagellum GM=Glandula mucosa O=Oviductus P=Penis PB=Pedunculus of the bursa copulatrix VD=Vas deferens 2 Detached Bursa and Pedunculus 3 Distal section of penis. Scale bar 1&2=5mm, 3=1mm.

Abbreviations: RMNH, National Museum of Natural History (formerly Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands. CRC collection of R. Carr.

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THE LAND SNAILS OF THE ALDABRA ISLANDS, WESTERN INDIAN OCEAN

JUSTIN GERLACH[1] & OWEN GRIFFITHS[2]

Abstract *Collections of Aldabran land snails made since 1895 are reviewed to provide a list of species recorded on the atoll. 31 extant species are recorded, of which 5 (16%) are endemic species, 1 (3%) endemic subspecies and 1–2 (3–6%) possibly introduced. 4 of the species believed to be endemic are represented by insufficient material to allow formal taxonomic description. One species,* Gulella gwendolinae *is suggested to have changed morphology significantly over the last 100 years. Further priorities for land snail research on Aldabra are identified.*

Key words *Aldabra, Assumption, Gastropoda, Mollusca, Seychelles.*

INTRODUCTION

The land snails of the high islands of the western Indian Ocean are notable for the high proportion of island endemics and their varied biogeographical affinities. Those of Madagascar and the granitic Seychelles islands have a mixture of Gondwanan and recent African origins (Emberton & Rakotomalala, 1996; Gerlach, 1999; Gerlach & Bruggen, 1999), whilst those of the Comores and Mascarenes are colonists from Africa and Madagascar respectively. The low coral islands are very poorly known from a biogeographical perspective. Studies of Aldabra atoll suggest a largely African (Peake, 1971) derived fauna although some groups show a strong Malagasy influence (Cogan, 1984). Published data for snails of the coral islands of the Aldabra and Amirante groups are restricted to incomplete collections from Aldabra, Assumption, Cosmoledo, D'Arros, Desroches and Poivre. These mostly represent isolated shells or small collections made during visits of a few hours only.

The Aldabra group of islands in the western Indian Ocean comprise the atolls of Aldabra, Astove, Cosmoledo, Farquhar and the island of Assumption (Fig. 1). Only the first of these has been studied in any detail and is notable for the high degree of endemism in its fauna (Cogan, 1984) which demonstrate largely Afro-Malagasy affinities. Comparatively few introduced species have been recorded on the atoll and the ecosystem is considered one of the most natural in the region (Stoddart, 1979). The biogeography of much of the fauna has been studied, most notably birds, reptiles and insects but the terrestrial molluscs have been largely overlooked, with only five taxonomic publications for the islands (Martens, 1898; Connolly, 1925; Bruggen, 1975 & 1986; Patterson, 1975).

Small collections of snails have been made on a number of occasions; Thomasset in 1907, J.G. Lionnet in 1966 (specimens in Seychelles Natural History Museum), J.F. Peake in 1967 (specimens in British Museum (Natural History) [BM(NH)]), V. Spaull 1974 (specimens in BM(NH) and Aldabra Research Station), K. Beaver in 1989 (specimens in Nature Protection Trust of Seychelles [NPTS]), R. Chapman in 1997 (specimens in O. Griffiths colln. and NPTS) and J. Gerlach in 2000 (specimens in NPTS). In addition single specimens of *Rhachistia aldabrae* have been collected by Wilson in 1895 and R. Fanchette in 1999 (specimen in Aldabra Research Station). The present paper summarises the records made to the present. Only terrestrial species are considered and emphasis is placed on the fully terrestrial species, without marine larvae.

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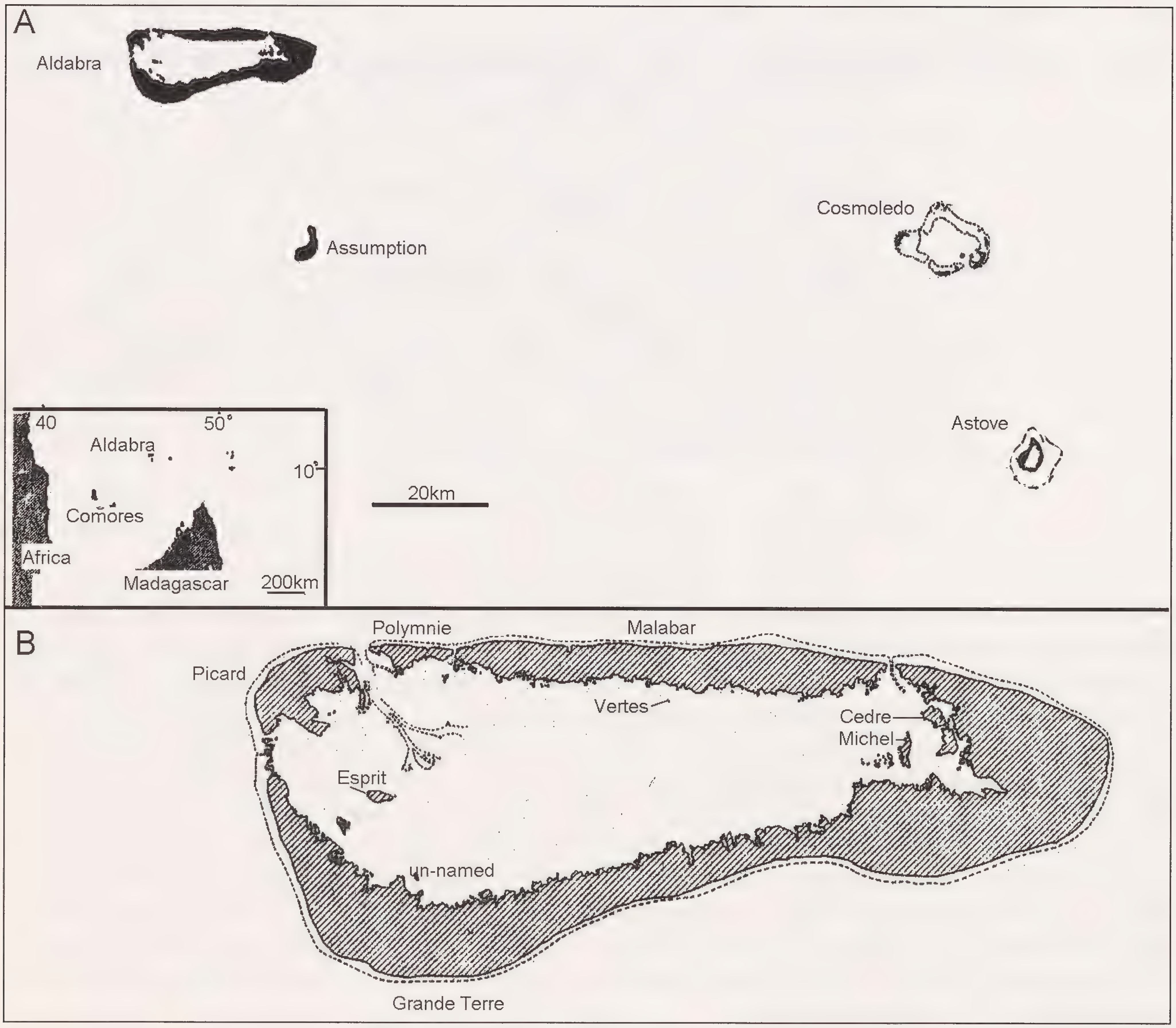

Fig. 1 Islands of the Aldabra group

PROSOBRANCHIA

LITTORINIDAE

Littorina glabrata Philippi, 1846 (Plate 1a, NMW.Z.2002.027.00025)

Widespread in the Indo-Pacific.

Aldabra: Picard (islet near La Gigi) 9/12/2000; Malabar (islet off Gionnet) 11/12/2000.

Littorina scabra (Linnaeus, 1758) (Plate 1b, NMW.Z.2002.027.00016)

Widespread in the Indo-Pacific.

Aldabra: Picard (La Gigi mangroves) 9/12/2000, (Bassin Lubine) 12/12/2000; Grande Terre (Bras Deux Cedres) 10/12/2000.

ELLOBIIDAE

Auriculastra cf. *radiolata* (Morelet, 1860)

A genus of several very similar species, widespread in the Indo-Pacific, *A. radiolata* is found in east and southern Africa.

Aldabra: Picard (400m east of camp) 1/11/97; Grande Terre (Takamaka) 3/11/97; Un-named island 1/7/97.

Melampus caffra (Küster, 1844) (Plate 1c, NMW.Z.2002.027.00013)

Widespread in the Indo-Pacific.

Aldabra: Picard (islet near La Gigi) 9/12/2000, (Bassin Lubine) 12/12/2000; Grande Terre (Cinq Cases) 6/89.

Melampus graniferus (Mousson, 1849) (Plate 1d, NMW.Z.2002.027.00006)

Widespread in the Indo-Pacific.

Aldabra: Grande Terre (Anse Mais) 17/4/97; Un-named island 1/7/97.

Melampus lividus (Deshayes, 1830) (Plate 1e, NMW.Z.2002.027.00010)

Recorded from the western Indian Ocean: Mascarenes, Seychelles, South Africa, Chagos and the Nicobars.

Aldabra: unknown locality 1907; Picard 20/4/97, (Bassin Cabris) 8/12/2000, (islet near La Gigi) 9/12/2000; Malabar (rail trail) 10/97, (Gionnet) 27/11/97; Grande Terre (Anse Mais) 17/4/97, (Bras deux Cedres) 10/12/2000; Ile Michel (Casuarina woodland) 29/6/97.

Astove: west side of lagoon 3/12/97.

Melampus (Tralia) semiplicatus Pease, 1869

Widespread in the Indo-Pacific.

Aldabra: Picard (Anse Mais) 17/4/97; Un-named island 1/7/97.

Pedipes affinis Férussac, 1821 (Plate 1f, NMW.Z.2002.027.00014)

Widespread in the western Indian Ocean: Mauritius, Reunion, Chagos, Seychelles, Andamans, Arabia and South Africa.

Aldabra: Malabar (Gionnet) 27/11/97; Grande Terre (10m east of camp Cinq Cases) 8/10/97.

ASSIMINEIDAE

Assiminea parvula Morelet, 1877 (Plate 2g, NMW.1955.158.02424)

Widespread in the Indo-Pacific.

Aldabra: 1907, 1966; Picard 6/89, 3/3/97 & 11/97, (islet near La Gigi) 9/12/2000; Malabar 6/89; Grande Terre (Anse Tambalico) 1974, (Cinq Cases) 1974, (Bassin Flamant) 6/89, (Takamaka) 6/89 & 3/11/97, (Dune d'Messe) 23/6/97 & 27/9/97, (Anse Mais) 17/4/97, (Bras Deux Cedres) 10/12/2000; Orchid island 1974; Ile Michel 29/16/97; Esprit 1974 & 16/12/2000.

Assumption: 18/12/2000.

Cosmoledo: Menai 1907 & 3/12/97.

Astove: Cocos woodland 3/12/97.

Assiminea (Syncera) nitida (Pease, 1864) (Plate 2h, NMW.Z.2002.027.00001)

Recorded from Seychelles, Rodriguez and Mauritius.

Aldabra: Picard 11/97, 12/12/2000; Malabar (coral pit at Middle camp) 9–10/10/97, (200m east of camp) 11/10/97, (Gionnet) 27/11/97; Grande Terre (Anse Tambalico) 1974, (Bassin Fregate) 7/7/97, (Anse Mais) 17/4/97, (Bras Deux Cedres) 10/12/2000; Un-named island 1/7/97.

TRUNCATELLIDAE

Truncatella guerini Villa, 1841 (Plate 2i, NMW.Z.2002.027.00029)

This is a large *Truncatella* with coarse ribs, widespread in the Indo-Pacific.

Aldabra: 1907, 1966; Picard 1907, 6/89, 20/4/97, 11/97, (400m east of camp) 1/11/97, (Bassin Cabris) 8/12/2000, (Anse Var) 8/12/2000, (Pte. dans Nord) 12/12/2000, (islet near La Gigi) 9/12/2000, (Bassin Lubine) 12/12/2000; Malabar 6/89, (coral pit at Middle camp) 9/10/97, (rail trail) 10/97, (200m east of camp) 11/10/97, (Gionnet) 27/11/97 & 11/12/2000, (islet off Gionnet) 11/12/2000; Grande Terre (Anse Tambalico) 1974, (Dune Jean Louis) 1975 & 19/10/97, (Dune d'Messe) 23/6/97, (Cinq Cases) 18/2/97 & 8/10/97, (Anse Mais) 17/4/97, (Takamaka) 3/11/97, (Anse Anglais) 10/12/2000, (Bras Deux Cedres) 10/12/2000,

Plate 1 **a** *Littorina glabrata* **b** *Littorina scabra* **c** *Melampus caffra* **d** *Melampus graniferus* **e** *Melampus lividus* **f** *Pedipes affinis* **k** *Tropidophora* sp. *'gardineri'* **m** *Rhachistia aldabrae* **p** *Quickia aldabrensis* (Aldabra and Assumption specimens).

(Anse Mais) 13/12/2000 (not coll.); Orchid island 1974; Esprit 1974 & 16/12/2000; Ile Michel 29/16/97; Un-named island 1/7/97.

Cosmoledo: Menai 3/12/97.

Astove: Cocos woodland 3/12/97.

Truncatella cf. *valida* Pfeiffer, 1846 var. minor Nevill 1878 (Plate 2j, NMW.Z.2002.027.00011)

This is very similar to *T. guerini* but is much smaller and smoother. It appears to be the same species as was recorded by Nevill (1878) as *T. valida* var. *minor* from the Mascares, Seychelles, Sri Lanka and Andamans. It has not been recorded subsequently and it is not clear whether this is a distinct taxon or a small variety of *T. guerini*.

Astove: west side of lagoon 3/12/97.

POMATIASIDAE

Tropidophora sp. *'gardineri'* (Plate 1k, NMW.Z.2002.027.00023)

Tropidophora gardineri	Barnacle, 1968
	Lionnet, 1984
	Gerlach, 1987

An Aldabra endemic species, presently undescribed. Further material, especially spirit material, is required for comparison with species from Madagscar.

Aldabra: 1966; Picard (back path) 12/12/2000; Grande Terre (Dune d'Messe) 1975 & 23/6/97, (Bassin Fregate) 7/7/97; Esprit 16/12/2000.

Tropidophora sp.

A large subfossil species. Subfossil *Tropidophora* have been recorded from a number of fossil deposits on Aldabra.

Aldabra: Malabar (rail trail) 10/97.

Tropidophora (Ligatella) ligata (Müller, 1774) var. *affine* (Sowerby, 1847)

The species has been recorded from Mauritius, Madagascar and South Africa. Var. *affine* has been reported from Mauritius and South Africa.

Cosmoledo: Menai 1907.

CYCLOPHORIDAE

Cyathopoma sp. (Plate 2l, NMW.Z.2002.027.00009)

Cyathopoma picardense	Barnacle, 1968
	Lionnet, 1984
	Gerlach, 1987

An Aldabra endemic species, presently undescribed. Further material is required before this species can be described.

Aldabra: 1966; Picard 1907 (1 specimen); Malabar (rail trail) 10/97; Grande Terre (Takamaka) 3/11/97.

PULMONATA

CERASTIDAE

Rhachistia aldabrae (Martens, 1898) (Plate 1m, NMW.Z.2002.027.00004)

Bulinus (Rhachis) Aldabrae	Martens, 1898; 28
Rachis aldabrae	Barnacle, 1968
	Lionnet, 1984
	Gerlach, 1987

An Aldabra endemic species.

Aldabra: 1907, 1966; Picard 11/1895, 11/97, (back path) 12/2/99 & 12/12/2000;

Malabar (Gionnet) 11/12/2000; Grande Terre (Anse Tambalico) 1974, (Dune d'Messe) 23/6/97 & 27/9/97; Ile Michel 29/16/97; Esprit 16/12/2000; Un-named island 1/7/97.

STREPTAXIDAE

Gulella gwendolinae aldabrae Bruggen, 1975 (Plate 2n, NMW.Z.2002.027.00012 & 17)
Ennea alauda Barnacle, 1968
Lionnet, 1984
Gerlach, 1987

An African species represented by an Aldabra group endemic subspecies. This is also known from fossils from Aldabra (Aldabra limestone on Malabar; >125,000bp, Takamaka limestone on Grande Terre; <125,000bp). Measurements of *G. gwendolinae aldabrae* are significantly different from those of the nominate African subspecies in shell length ($t=3.1906$, $P<0.05$), diameter ($t=2.6198$, $P<0.05$), relative proportions (H/D) ($t=3.1576$, $P<0.05$) and aperture width ($t=2.9321$, $P<0.05$), but not aperture height ($t=0.6933$, $P>0.05$). Within *G. gwendolinae aldabrae* there appears to be little significant inter-island differentiation; shells from Assumption and Aldabra are virtually identical in size and proportion. The shells from Cosmoledo appear to be smaller, although only two shells are available at present. Interestingly, the differences within Aldabra are more pronounced; shells from Ile Michel are shorter but do not differ from the main Aldabra populations in any other respect, whilst those from Ile Esprit are narrower in proportion and the aperture is narrower. Unfortunately there is insufficient material from both these islands for reliable statistical significance testing and, although the Esprit population would appear to be distinct at varietal level at lest, it is inappropriate to describe it as a distinct form on the available material. These differences are all in the direction of smaller shells on smaller and more isolated islands, this is what would be expected from wind or bird-dispersed species with strong founder effects on the more isolated islands. It is also notable that comparison of historical collections from Aldabra indicate a statistically significant reduction in shell size over the last 100 years (Fig. 2). This change is probably not due to simple adaptation to small islands as the form on the small island of Esprit is notably larger than the form currently inhabiting the main islands of

TABLE 1
Morphometrics of *Streptostele acicula* populations

Population		**Height (mm)**	**Diameter (mm)**	**H/D**	**n**
granitic Seychelles	mean (sd)	5.3±0.57	1.7±0.05	3.16±0.43	22
Madagascar	mean (sd)	5.3±0	1.5±0	3.53±0	2
Comores	mean (sd)	4.9±0.42	1.4±0.05	3.61±0.24	5
Mascarenes	mean (sd)	4.6±0.42	1.4±0.27	3.4±0.42	13
Aldabra	mean (sd)	4.4±0.34	1.3±0.15	3.60±0.32	14
	range	3.9-5.1	1-1.8	3.33-4.19	

TABLE 2
Quickia aldabrensis morphometrics

Population	**Form**	**Shell (mm)**			**Aperture (mm)**			**Whorls**	**N**
		Height	**Diameter**	**H/D**	**Height**	**Width**	**H/W**		
Aldabra	ovate	7.4-9	5-6	1.48-1.55	5.2-6	4	1.3-1.5	3	(Patterson, 1975)
	attenuate	8.5-9	4.5-5	1.8-1.9	5.75-6	4	1.44-1.5	3	(Patterson, 1975)
Assumption	large	8.6-9.6	5.1-5.2	1.8-1.9	4.7-5.3	3.2-3.4	1.59-2.64	3.5-4	8
	small	4.8	3.3	1.44	2.9	2.5	1.16	2	7

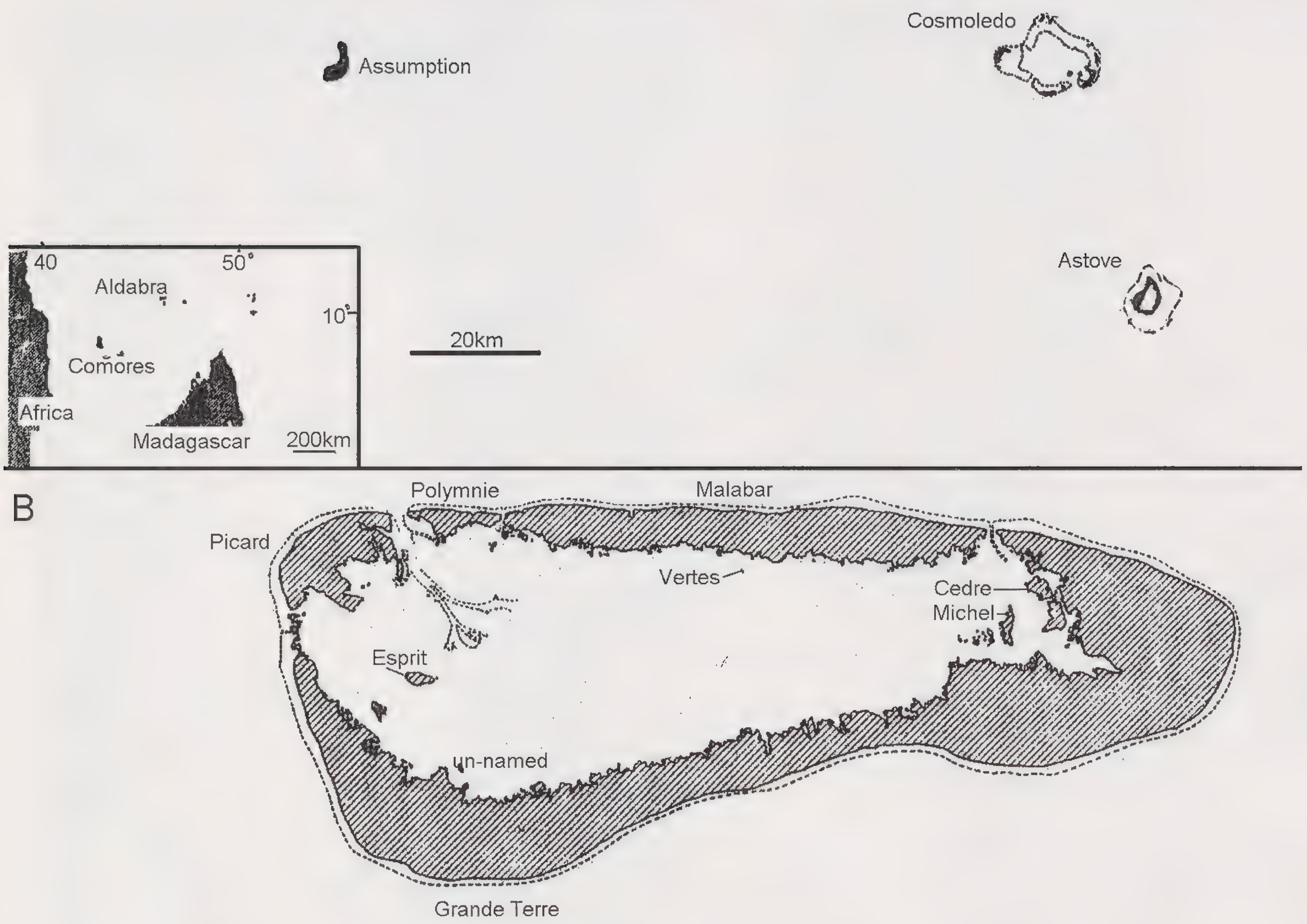

Fig. 2 Change in length of *Gulella gwendolinae aldabrae* since 1905. Esprit population shown as filled circles.

Aldabra. The size reduction may be due to a decline in the abundance of potential prey species over the last 100 years; potential prey such as Euconulidae are largely restricted to Esprit and the Takamaka area of Grande Terre, over the rest of the range of *G. gwendolinae aldabrae* prey are restricted to the much smaller *Gastrocopta* and *Nesopupa* species. Thus only smaller forms may be able to survive over most of Aldabra whilst large forms remain on Esprit. Further specimens from other parts of Aldabra (especially Takamaka) are needed to test this hypothesis.

Aldabra: Picard 1907, 7/9/67, 3/3/97, 11/97, (400m east of camp) 1/11/97, (Bassin Lubine) 12/12/2000; Malabar 6/89, (coral pit) 10/10/97, (Gionnet) 27/11/97; 11/12/2000, (Polymnie) 9/12/2000; Grande Terre 9&11/9/67, (Anse Cedres) 2/9/67, (Anse Tambalico) 1974, (Cinq Cases) 1974 & 6/89, (Dune D'Messe) 23/6/97, (Takamaka) 3/11/97; Ile Michel 14/9/67. Esprit 1974; 16/12/2000. Reported from Verte (Smith, 1909).

Assumption: 16/9/67.

Cosmoldeo: Wizard island 1/4/83 (Schileyko coll., RMNH, Leiden).

Streptostele acicula (Morelet, 1877) (Plate 2o, NMW.Z.2002.027.00021)

Recorded from Seychelles (Mahé, Silhouette), Amirantes (Poivre), Comores (Anjouan, Mayotte), Madagascar (Nossi Bé) and Mascarenes (Mauritius, Reunion, Rodriguez). The population on the granitic Seychelles islands represents a distinct subspecies, *S. acicula maheensis* (Connolly, 1925). The Aldabran and Amirante specimens have been suggested to be closer to the Comoros specimens than those from the granitic Seychelles (Gerlach & Bruggen, 1999). The larger series available here confirms that these islands support the nominate subspecies (Table 1).

Aldabra: Picard (back path) 11/97 & 12/12/2000; Grande Terre (Takamaka) 3/11/97.

Plate 2 **g** *Assiminea parvula* **h** *Assiminea (Syncera) nitida* **i** *Truncatella guerini* **j** *Truncatella* cf. *valida* var. *minor* **l** *Cyathopoma* sp. **n** *Gulella gwendolinae aldabrae* (Picard and Esprit specimens) **o** *Streptostele acicula*.

SUCCINEIDAE

Quickia aldabrensis Patterson, 1975 (Plate 1p, NMW.Z.2002.027.00003 & 8)

An Aldabra group endemic species. The population located on Assumption is distinctive, two forms were found; small shells 4.2–4.8mm long and larger, elongate ones 8.6–8.9mm long. The small shells appear to be juveniles although no intermediates were found. The large shells are comparable to the attenuate form from Aldabra (Patterson, 1975) but differ in having smaller, narrower apertures and an extra 0.5–1 whorl (Table 2). These differences may indicate that the Assumption population represents a distinct subspecific form or that it is derived from attenuate colonists from Aldabra and the present-day morphology shows a strong founder-effect. Spirit material is needed to resolve this question. The are no attenuate specimens from Aldabra in the collections from 1997 and 2000.

Aldabra: 1966; Picard 11/97, (back path) 12/12/2000, (islet near La Gigi) 9/12/2000; Malabar 6/89, (coral pit at Middle camp) 9–10/10/97, (Gionnet) 27/11/97, (Polymnie) 9/12/2000; Grande Terre 1907, (east) 1967, (Anse Tambalico) 1974, (Cinq Cases) 1974 & 18/2/97, (Bassin Flamant) 6/89, (Dune d'Messe) 23/6/97 & 27/9/97, (Bassin Fregate) 7/7/97, (Takamaka) 3/11/97, (Bras Deux Cedres) 10/12/2000; Esprit 16/12/2000; Orchid island 1974.

GASTROCOPTIDAE

Gastrocopta microscopica (Nevill, 1878) (Plate 3q, NMW.Z.2002.027.00022)

This species has been recorded from the western Indian Ocean: Seychelles, the Mascarenes, Chagos, Madagascar (as *Gastrocopta seignaciana* (Crosse & Fischer, 1879)) and the Comoros (as *G. tripunctata*).

Aldabra: 1907; Picard 6/89, 3/3/97, 20/4/97 & 11/97, (Anse Var) 8/12/2000, (400m east of camp) 1/11/97, (islet near La Gigi) 9/12/2000, (Bassin Lubine) 12/12/2000; Malabar 6/89, (coral pit at Middle camp) 9–10/10/97, (200m east of camp) 11/10/97, (rail trail) 10/97, (Gionnet) 27/11/97 & 11/12/2000; Grande Terre (Cinq Cases) 1973–4, 6/89, (Anse Mais) 1974 & 17/4/97, (Anse Tambalico) 1974, (Dune d'Messe) 23/6/97& 27/9/97, (Bassin Fregate) 7/7/97, (Takamaka) 3/11/97, (Dune Jean Louis) 9/10/97; Esprit 16/12/2000.

Assumption: 18/12/2000
Astove: Cocos wooldand 3/12/97
Cosmoledo: 1907; Menai 3/12/97

NESOPUPIDAE

The Seychelles species of Nesopupidae presently include only two recorded species; *Nesopupa minutalis* (Morelet, 1881) (a species from the Comores recorded from D'Arros; Verdcourt, 1986) and *N. rodriguezensis* (a Mascarene species recorded from Mahé; Gerlach, 1994). The species of this family are all very similar and earlier records may not be correct. The present collection includes two species.

Nesopupa pelei Madge, 1938 (Plate 3r, NMW.Z.2002.027.00027)

Recorded from the Mascarenes, Chagos and Seychelles.

Aldabra: Picard 3/3/97 & 11/97; Polymnie 9/12/2000; Malabar (200m east of camp) 11/10/97, (coral pit) 10/10/97; Grande Terre (Anse Mais) 17/4/97, (Takamaka) 3/11/97; Esprit 16/12/2000.

Nesopupa cf. *rodriguezensis* Conolly, 1925 (Plate 3s, NMW.Z.2002.027.00007)

Recorded from the Mascarenes and Seychelles.

Aldabra: Picard 11/97; Malabar (coral pit) 10/10/97, (Gionnet) 27/11/97; Esprit 16/12/2000.

Plate 3 **q** *Gastrocopta microscopica* **r** *Nesopupa pelei* **s** *Nesopupa* cf. *rodriguezensis* **t** *Pupisoma orcula* **u** *Subulina octona* **v** *Opeas pumilum* **w** *Bulinus bavayi* **x** *Louisia barclayi* and *L. duponti* **y** *Dupontia* sp. **z** *'Kaliella'* sp.

VALLONIDAE

Pupisoma orcula (Benson,1850) (Plate 3t, NMW.Z.2002.027.00026)

A widespread African species also recorded in Seychelles and the Mascarenes.
Aldabra: Picard 11/97; Esprit 16/12/2000.

SUBULINIDAE

Subulina octona (Bruguière, 1792) (Plate 3u, NMW.Z.2002.027.00005)

A widespread species, widely introduced. A subfossil specimen originally identified as *Stereostele nevilli* (Taylor *et al.*, 1979) was identified as *Subulina octona* by Gerlach & Bruggen (1999), this would indicate that the species has a long history on Aldabra although its current restricted distribution suggests an introduction.
Aldabra: Picard 11/97, (back path) 12/12/2000.

Opeas pumilum (Pfeiffer, 1840) (Plate 3v, NMW.Z.2002.027.00024)

A widespread species, widely introduced.
Aldabra: Picard (back path) 3/3/97, 11/97 & 12/12/2000; Grande Terre (Takamaka) 3/11/97.
Assumption: 18/12/2000

Paropeas achatinaceum (Pfeiffer, 1840)

A widespread species, recorded from Aldabra by Naggs (1994) based on 2 specimens. There are no recent specimens and this may have been a temporary introduction.

ACHATINELLIDAE

Tornatellinops sp.

A widespread Indo-Pacific genus with many very similar species, the Aldabra specimens are smaller than any of the 3 species recorded from the Mascarenes.
Aldabra: Grande Terre (Takamaka) 3/11/97.

PLANORBIDAE

Bulinus bavayi (Dautzenberg, 1894) (Plate 3w, NMW.Z.2002.027.00020)

Isidora forskalii Ehrenberg	Connolly, 1925; 265
	Barnacle 1969; 56

Widespread in Madagascar.
Aldabra: Grande Terre (Takamaka) 1907, 1967 & 3/11/97, (Bassin Fregate) 1967 & 7/7/97, (Cinq Cases) 1967, 1974, 6/89 & 18/2/97, (north-east of Croix Blanc) 1974.

HELICARIONIDAE

Louisia barclayi (Benson, 1850) (Plate 3x, NMW.Z.2002.027.00028)

Recorded from the western Indian Ocean islands: Reunion, Mauritius, Chagos (Diego Garcia), Seychelles (Mahé); Verdcourt 1992.
Aldabra: Polymnie 9/12/2000; Grande Terre (Dune Jean Louis) 9/10/97, (Takamaka 3/11/97).

Louisia duponti Godwin-Austen, 1908 (Plate 3x, NMW.Z.2002.027.00018)

Recorded from the Indo-Pacific islands, in the Indian Ocean it is recorded from Mauritius. Fragments of '*Kaliella*' sp. A. collected on Coetivy in 1905 are identifiable as a *Louisia* species (Gerlach, 1998) and the remaining fragments of these specimens appear to be referable to *L. duponti*.
Aldabra: Malabar (Gionnet) 27/11/97; Esprit 16/12/2000

This species was suggested to be a Pacific *Liardetia*, possibly *Liardetia (L.) samoensis* (Mousson, 1865) or *L. (Belopygmaeus) dolium* (Pfeiffer, 1846),(Verdcourt, 1992). *L. duponti* lacks the spiral striae and keeled periphery of *L. doliolum* and the elongate caudal tail (further anatomical details of *L. doliolum* are not known). *L. samoensis* also has a keeled periphery and it therefore seems unlikely that *L. duponti* is synonymous with either *L. samoensis* or *L. doliolum*, although it may prove to be conspecific with another supposedly Pacific *Liardetia* when the anatomy of that genus is better known. It is possible that the three species previously referred to *Louisia* (*L. duponti, L. barclayi* and *Liardetia sculpta*) originated in the western Indian Ocean. The latter species has been recorded from the Caroline islands, Macau, Guam, the Mascarenes (since 1907) and granitic Seychelles islands (since 1974 - J.G. pers. obs.).

Dupontia sp. (Plate 3y, NMW.Z.2002.027.00002)

An undescribed species, probably an Aldabra endemic.

Aldabra: Grande Terre (Takamaka) 3/11/97; Esprit 16/12/2000. A specimen in the Aldabra Research Station is labelled 'Sp. A', station data record cards list 'Mollusca sp. A' from Grande Terre (Tambalico and Cinq Cases) and Ile Esprit.

This species resembles *D. poweri, D. virginica* and *D. levensoniae* in the presence of spiral striae. These are restricted to the sutures and not on the underside in *D. virginica*, thus the Aldabra species may be referred to either *D. poweri* or *D. levensoniae*; these species differ in shell colour but the Aldabra shells are all bleached white and the fresh colour cannot be determined.

CHRONIDAE

'*Kaliella*' sp. (Plate 3z, NMW.Z.2002.027.00019)

Kaliella sp. B.	Barnacle, 1968
	Lionnet, 1984
	Gerlach, 1987

An Aldabra endemic species, presently undescribed. Sprit material is required before the true generic position of this species can be determined.

Aldabra: 1966; Picard 1907; Polymnie 9/12/2000; Esprit 16/12/2000.

ACKNOWLEDGEMENTS

We are grateful to K. Beaver and R. Chapman for collecting material and to the warden of Aldabra and the Seychelles Islands Foundation for facilitating the collection in December 2000.

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HERAULTIELLA NEW NAME FOR *HERAULTIA* BODON, MANGANELLI & GIUSTI, 2001 (GASTROPODA: HYDROBIIDAE)

After the publication of our paper on the European valvatiform hydrobiids (Bodon *et al*, 2001[1]), we discovered that *Heraultia* Bodon, Manganelli & Giusti, 2001, is prepoccupied by *Heraultia* Villeneuve, 1920 (Insecta, Diptera) and *Heraultia* Cobbold, 1935 (Mollusca, Rostroconchia).

We therefore propose *Heraultiella* as new name for *Heraultia* Bodon, Manganelli & Giusti, 2001.

[1] BODON M. *ET AL*. 2001 *Malacologia* **43**: 103-215.

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VERTIGO ANGUSTIOR JEFFREYS, 1830 AND *VERTIGO MOULINSIANA* (DUPUY, 1849), NEW TO GREECE, ON THE AEGEAN ISLAND OF THÁSOS

The molluscan fauna of the Aegean islands has a long history of study and the rich assemblages of endemic species on islands such as Crete are well-documented. In fact most of the islands have been surveyed to some degree, enabling Welter-Schultes & Williams (1999)[1] to undertake a biogeographical analysis of species composition in relation to land area, isolation, and habitat. Thásos was not included in this analysis, which is surprising as there has been a tradition of molluscan survey on the island since Boettger (1907)[2], whilst Reischütz (1983)[3] published a checklist of the fauna consisting of 46 taxa. Subsequent investigations have increased the number of non-marine mollusc species known from Thásos to sixty-six (see http://thasos.users.btopenworld.com/mollusca.htm) and it is clear that the fauna is influenced by its proximity to mainland Greece (6 kms) and Turkey, with a strong eastern Balkan element apparent. There are also several endemics or near-endemics present on the island, such as *Vitrea thasia* Riedel & Reischütz, 1983, *Balcanodiscus carinatus* Reischütz, 1988, *B. difficilis* Riedel, 1988, and *Zebrina (Rhabdoena) mirifica* Bank & Menkhorst, 1992.

On 29 September 2001 I collected a small sample of molluscs from sedge litter in a narrow calcareous valley fen on the outskirts of Thassos Town (also known as *Limenas*). Subsequently the specimens were identified as numerous *Vertigo angustior* Jeffreys, a single *V. pygmaea* (Draparnaud, 1801) and a single *V. moulinsiana* (Dupuy). Prior to this the only *Vertigo* species reported from Greece were *V. antivertigo* (Draparnaud, 1801) and *V. pygmaea*. However, P.L. Reischütz (pers. comm.) informs me that in August 1982 he collected *V. angustior* shells of uncertain age, though probably recent, from a small spring-fed wetland on the north-eastern slopes of the Pangaion mountains besides the road from Nikissiani to Palaiochori, some 30 kms west of Kavala. *V. moulinsiana* has not previously been found in Greece, although it is known from Bulgaria and its European range extends to north-western Turkey (Killeen 1996)[4].

Thásos has very few surviving wetland habitats and the occurrence of *V. angustior* and *V. moulinsiana*, both of which are included on Annex II of the EU Habitats & Species Directive, in this small fen is remarkable. On present knowledge it is doubted that any other suitable localities for these species occur on the island. The area, which also supports stands of great horsetail *Equisetum telmateia* in its only island location, consists of a mosaic of tall sedge fen *Carex* spp. and poplar *Populus* spp. scrub with small unimproved damp pastures. Unfortunately, tipping of marble spoil from the local quarries affects the southern end of the valley and, in addition to the direct destruction of habitat, threatens to alter the hydrological conditions which sustain this wetland.

I am grateful to Lance Chilton for drawing my attention to this interesting wetland and to Ian Killeen and Peter Reischütz for identification of specimens. My thanks also to Peter Reischütz for permission to refer to his record of *Vertigo angustior* on mainland Greece and for much valuable assistance with the mollusc fauna of Thásos. Specimens of both *angustior* and *moulinsiana* have been deposited in the collections of the National Museums and Galleries of Wales, Cardiff.

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CORRIGENDA

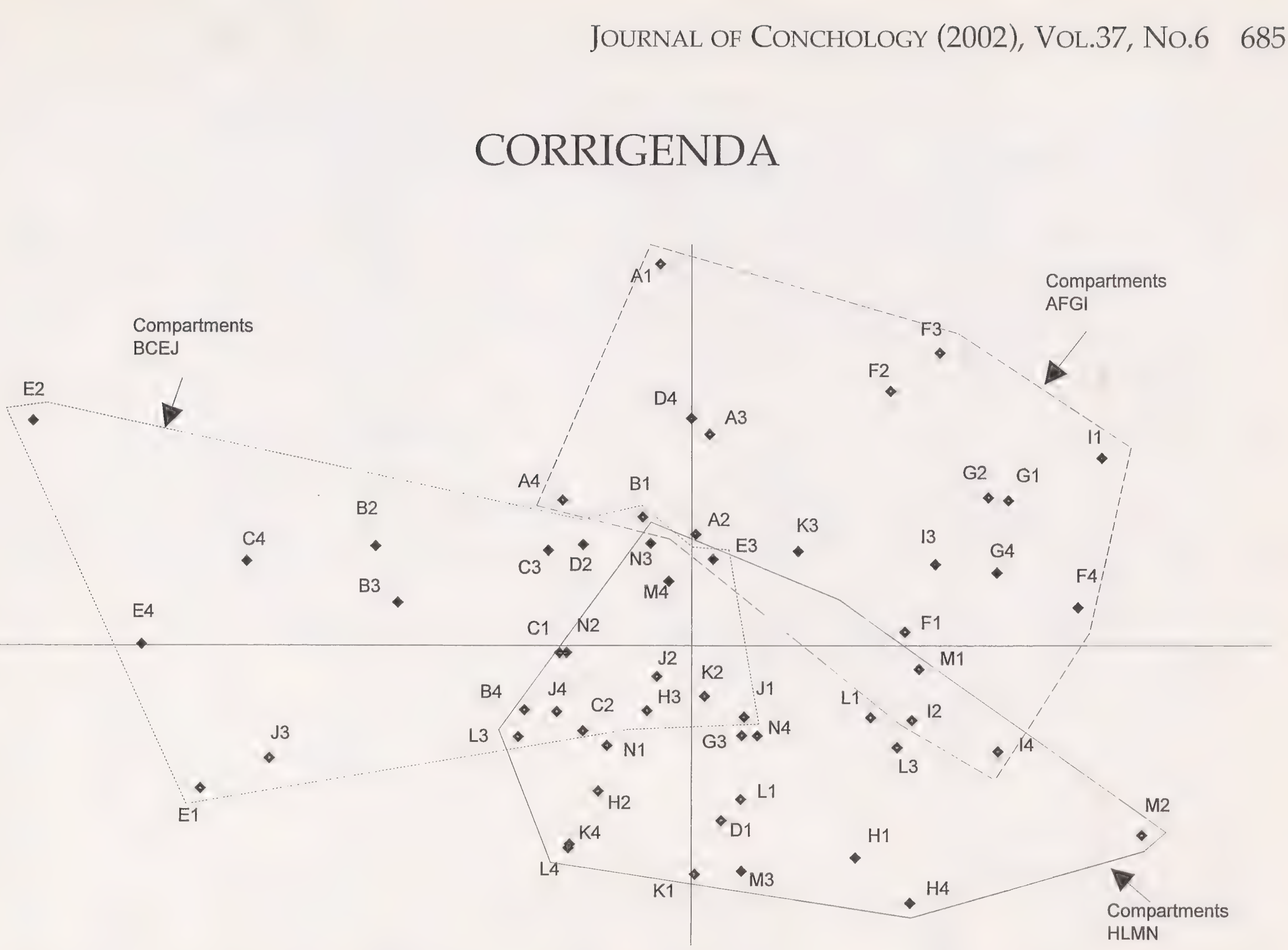

Figure 1 Principal Component Analysis: Ordination of compartments (quadrats) based on soil fractions.

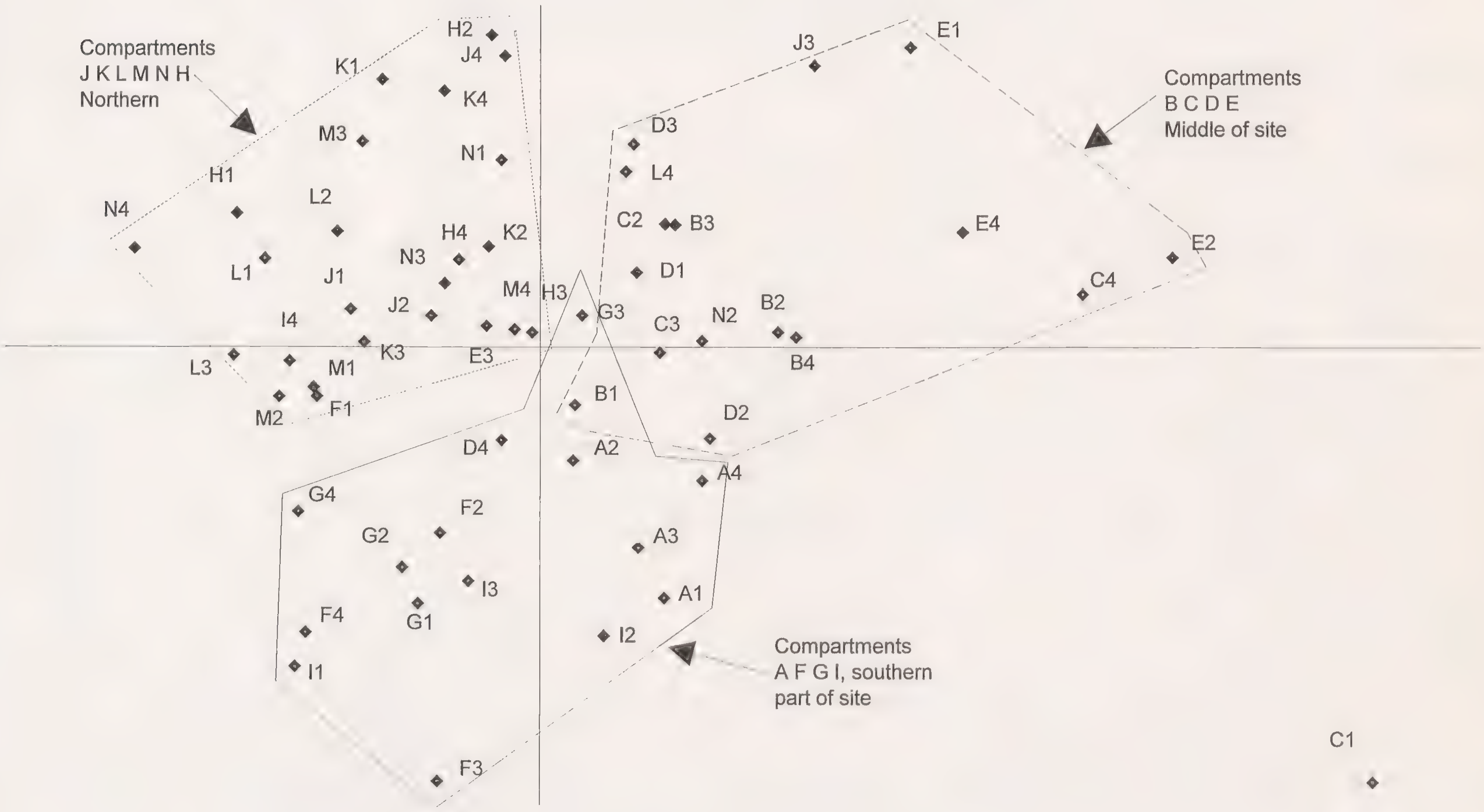

Figure 2 Principal Component Analysis: Ordination of compartments (quadrats) based on soil and other environmental characteristics.

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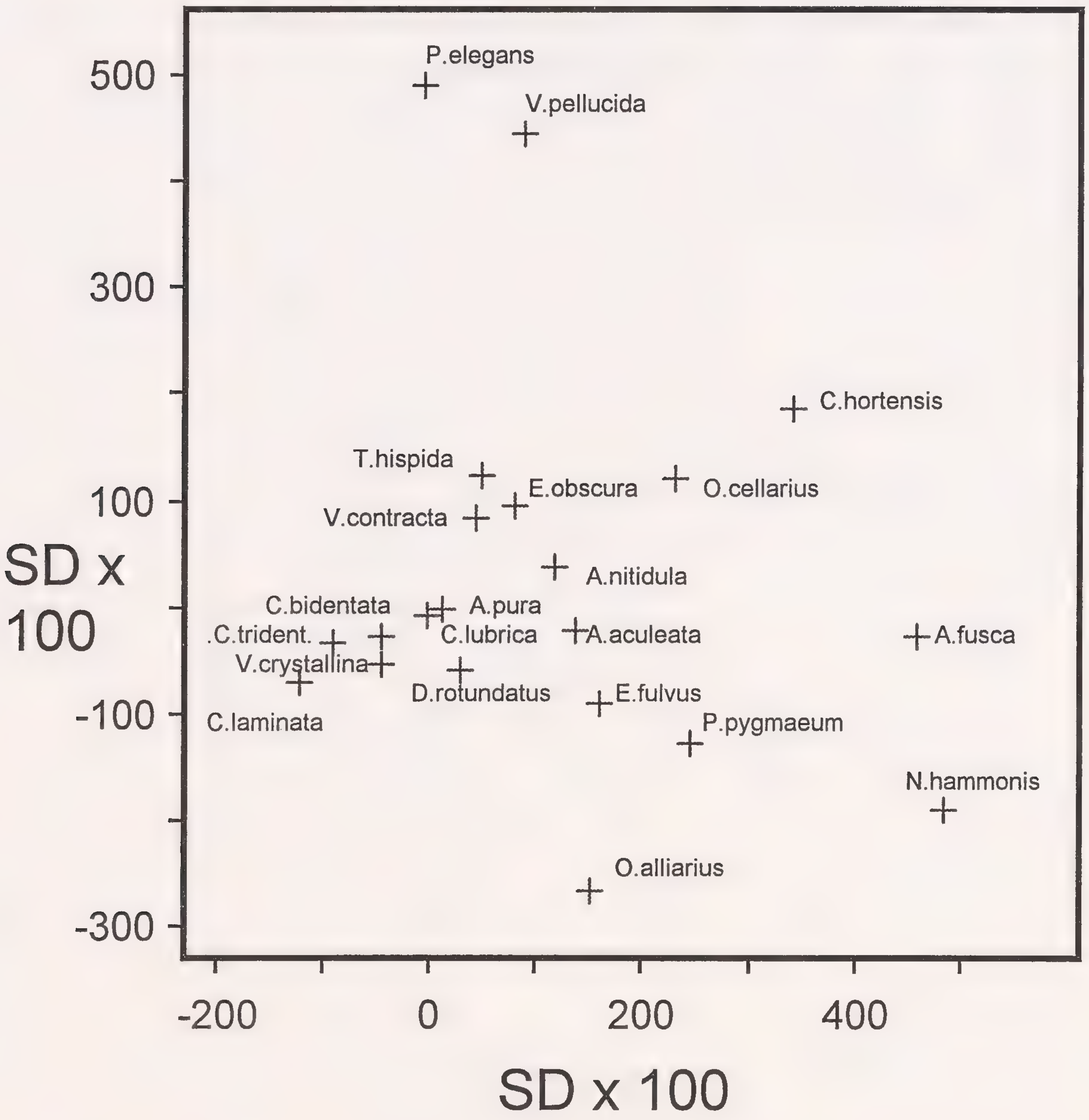

Figure 4 Detrended Correspondence Analysis. Species ordination. (Axes are Standard Deviation x 100)

TABLE 1

The occurrence of land mollusc species by site and habitat on North Ronaldsay. Asterisks indicate presence in the habitat indicated, GR indicates the non-machair grassland of site 2 (see text).

SPECIES	**GARDENS**					**ROADSIDES**				**MACHAIR/DUNE**						**WETLAND**					**GR**	**TOT**
SITES	1	3	9	10		5	15	16		4	7	8	12	14		6	11	13	17		2	
Carychium minimum																X		X		*		2
Oxyloma pfeifferi																X		X	X	*		3
Cochlicopa lubrica																X		X		*		2
Cochlicopa lubricella		X		X	*	X			*	X	X	X	X	X	*							8
Lauria cylindracea	X	X	X	X	*	X	X	X	*	X	X	X	X	X	*	X	X	X	X	*	X	17
Vallonia sp.																X				*		1
Punctum pygmaeum																X		X		*		2
Arion ater agg.	X				*			X	*	X					*							3
Arion subfuscus		X			*																	1
Arion silvaticus	X				*																	1
Arion fasciatus	X	X	X	X	*																	4
Arion distinctus	X	X	X	X	*																	4
Arion intermedius	X	X	X	X	*		X	X	*		X	X	X	X	*	X		X	X	*	X	14
Vitrina pellucida		X			*	X	X	X	*	X	X	X	X	X	*							9
Vitrea contracta			X		*	X	X	X	*					X	*	X	X	X		*		8
Aegopinella nitidula	X	X	X	X	*									X	*							5
Oxychilus draparnaudi		X		X	*																	2
Oxychilus cellarius		X	X	X	*								X		*	X	X			*		6
Oxychilus alliarius	X	X	X	X	*	X	X	X	*	X	X	X	X	X	*	X	X	X		*		15
Milax gagates	X	X	X	X	*	X			*				X		*							6
Lehmannia marginata	X	X			*																X	3
Deroceras reticulatum	X	X	X	X	*	X	X	X	*	X	X	X	X	X	*	X		X	X	*	X	16
Deroceras panormitanum		X			*																	1
TOTAL	11	15	10	11	**18**	7	6	7	**9**	6	6	6	8	8	**11**	11	4	9	4	**11**	4	**23**
SLUGS	8	8	5	5	**10**	2	2	3	**4**	2	2	2	3	2	**4**	2	0	2	2	**3**	3	**10**

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CONCHOLOGICAL SOCIETY OF GREAT BRITAIN & IRELAND

REPORT OF THE COUNCIL 2001–2002

The Society announces with regret the deaths of four members, Mr Eric Badcock, member since 1957, Dr Lloyd Evans, member since 1965, Dr Nigel Nicholson, member since 1993 and Mr G W Pitchford, member since 1948.

Council Positions

Dr Rundle began his second year as President of the Society. Dr Chatfield was elected as Hon. Non-marine Recorder, while a presentation was to be made to Dr Kerney in appreciation of his forty years as Hon. Non-marine Recorder. New Ordinary members of Council were Miss Fogan, Mr Dansey and Mr Killeen.

Dr Alexander, Ms McIvor and Mr Carr began their second year, while Mr Palmer and Dr Honnor began their third year with Mr Wimbleton co-opted.

Publications

Two issues of the *Journal of Conchology* (Volume **37**: 3-4) and four issues of the *Conchologists' Newsletter* (Volume 10, Part 1, Numbers 157-160) were published. The Society also published the Annual Programme Card and a revised Members' Guide.

Dr Honnor publicised a scheme offering members some of a large stock of Past Publications on advantageous terms.

Other Council Matters

Seven Council meetings were held and in addition there were two meetings of the Publications Committee.

A major concern has been retention of members and ways of encouraging more active involvement in Society activities. Related to this have been proposals to produce a new-style Newsletter and development of the Society's Website.

Amongst other issues raised by Council were Society Finances and Investments, issue of Revised Guidelines for Grant Requests and arrangements for publication of future issues of the *Journal of Conchology*.

The Society gratefully acknowledges the legacy of Francis de Bartolomé's Conchological books, which were auctioned to members on 17 February 2001, and which realised £18,175.50 after auctioneer's fees and expenses. Books donated by Mr Tony Swann of Wheldon and Wesley were also auctioned to members at the same time. £859. 50 was realised from this generous donation, for which the Society is very grateful.

I would like to thank all members of Council for their contributions during the year.

Colin Gillard
Hon. Secretary

PROGRAMME SECRETARY'S REPORT - MARCH 2002

The programme for 2001 consisted of seven indoor meetings held at the Natural History Museum in London, six field meetings and one workshop.

Lectures at indoor meetings were given by Robert Cameron (Changes in the land mollusc fauna of the British Isles over the 20th Century), David Aldridge (The conservation and eradication of freshwater mussels), Adrian Rundle (Presidential address: Love darts), Michael Weideli (The National Biodiversity Network - a new challenge for molluscan recording), June Chatfield (Local non-marine recording schemes)/Michael Weideli (Small scale variation in molluscan distribution), Michael Barker (Colour preservation in fossil shells) and Graham Oliver (Marine bivalves of the Mascarene Islands).

Field meetings were held at the following venues: Barton on Sea, Hampshire (fossil meeting, Leader: Bill Pocock), Morden Hall Park, London (Leader: June Chatfield), Sydenham Hill Wood and Dulwich Wood, London (Leaders: Ron Boyce and June Chatfield), Kimmeridge, Dorset (marine meeting, Leader: Rosemary Hill), Purton timber ponds and Walmore Common, Gloucestershire (Leader: David Long), and Fife, Scotland (marine/land meeting, Leader: William Penrice).

The Foot and Mouth epidemic resulted in postponement of our planned meeting to Ightham Mote and its replacement by a further site in the London area. The marine meeting in Fife was enlivened by two successful dredging sessions in the Firth of Forth.

The Society's fifteenth Molluscan Workshop was on the subjects of small marine bivalves and Barton Beds fossil molluscs, held at Judith Nelson's home in Woking, Surrey, and tutored by Adrian Rundle and Bill Pocock.

The Society is grateful to all those people who contributed to the above programme, as speakers, field meeting leaders, and meeting and workshop organisers and tutors.

Ron Boyce
Hon. Programme Secretary

ACCOUNTS FOR THE YEAR ENDED 31 DECEMBER 2001

STATEMENT OF FINANCIAL ACTIVITIES

Note		**2001**	**2000**
Incoming resources			
Fees and subscriptions		**£10,360**	£11,202
Investment income	4	**£5,137**	£3,311
Income from charitable trading		**£413**	£668
Other incoming resources		**£16**	£99
Donations and legacies		**£19,177**	£1,025
Total incoming resources		**£35,102**	£16,305
Expenditure			
Publications costs		**£11,125**	£9,460
Stationery and postage		**£1,094**	£1,456
Meetings costs		**£1,620**	£1,808
Sundry expenses and fees		**£805**	£287
Grants	1	**£3,691**	£800
Depreciation		**£600**	£600
Total expenditure		**£18,934**	£14,411
Net incoming/(outgoing) resources		**£16,168**	£1,894
Realised gains/(losses) on investment assets			
Unrealised gains/(losses) on investment assets		**-£4,220**	£14,220
Unrealised gains/(losses) on tangible fixed assets			
Net movement in funds		**£11,948**	£16,114
Fund balances brought forward		**£104,402**	£88,288
Fund balances carried forward		**£116,350**	£104,402

BALANCE SHEET AT 31 DECEMBER 2001

	Note	**2001**	**2000**
Fixed Assets			
Intangible assets		**£0**	£0
Tangible assets	5	**£1,200**	£1,800
Investments	3	**£84,521**	£88,740
Total fixed assets		**£85,721**	£90,540
Current Assets			
Debtors	6	**£1,072**	£36
Short term investments and deposits		**£28,136**	
Cash at bank and in hand		**£11,467**	£21,879
Total current assets		**£40,675**	£21,915
Short term creditors	7	**£5,948**	£3,600
Net current assets/(liabilities)		**£34,727**	£18,315
Total assets less current liabilities		**£120,448**	£108,855
Provisions for liabilities	2	**£4,098**	£4,453
Net assets		**£116,350**	£104,402
Unrestricted income funds		**£116,350**	£104,402
Total funds		**£116,350**	£104,402

NOTES TO THE FINANCIAL STATEMENTS

ACCOUNTING POLICIES

General

- These statements have been prepared in accordance with Financial Reporting Standard for Smaller Entities (FRSSE) and the Charities SORP.
- Investments are valued at market value on 31st December.
- No trustee has received any remuneration during the current or previous year. Expenses incurred on behalf of the Society have been reimbursed.

Funds

- All Society funds are unrestricted funds.
- The accounts include transactions, assets and liabilities for which the Charity can be held liable.

Note 1. Grants awarded:

Rodrigues Project	£2,155
Attendance at World Congress of Malacology by four students	£1,536
	£3,691

Note 2. Provision for liabilities:	**2001**	**2000**
Subscriptions in advance	£937	£1,412
Life membership fund	£2,875	£2,760
Marine fieldwork fund	£286	£281
Total	£4,098	£4,453

Note 3. Investments:	**2001**	**2000**
Market value at beginning of year	£88,740	£74,520
Net gain/(loss) on revaluation	(£4,219)	£14,220
Market value at end of year	£84,521	£88,740
Historic cost at end of year	£29,920	£29,920

Note 4. Investment income from:	**2001**	**2000**
Stock listed on recognised stock exchange	£4,610	£2,729
National Savings Income Bond	£527	£582
Total	£5,137	£3,311

Note 5. Tangible fixed assets:

Cost of computer	£3,000
Depreciation on straight line basis over 5 years	
Accumulated depreciation brought forward	£1,200
Charge for the year	£600
Balance of depreciation carried forward	£1,800
Net book value carried forward	£1,200

Note 6. Analysis of debtors:	**2001**	**2000**
Tax debtors	£940	£0
Other debtors	£132	£36
Total	£1,072	£36

Note 7. Analysis of creditors and accruals:	**2001**	**2000**
Publications accruals	£4,348	£3,600
Meetings costs	£1,600	£0
Total	£5,948	£3,600

RECORDER'S REPORT: NON-MARINE MOLLUSCA

The recording year 2001 started with access to most of the British countryside closed as a result of the foot and mouth epidemic which broke out in February. Although footpaths and access to some low risk areas reopened during the summer, restrictions on access to some farmland continued until the epidemic was declared over in the autumn. This put most non-marine mollusc fieldwork and commissioned survey work on hold and brought a focus on urban areas, churchyards and gardens.

A number of new Vice-county records were made during 2001, including a few records related to fieldwork in 2000. There was also a new species to the British Isles, *Cernuella aginnica*.

Cornwall West (1): *Paralaoma caputspinulae*, old cemetery, east of Swan Pool, Falmouth (10/803314), Geraldine Holyoak, 24.3.2001; *Sphaerium corneum*, Argal Reservoir, south-west of Penthyn (10/730327), Geraldine Holyoak, 6.11.2001.

Somerset South (5): *Ferissia wautieri*, West Sedgemoor (31/365261), M J Willing, 8.2001.

Wilts North (7): *Pisidium tenuilineatum*, River Churn, Cricklade (41/098945), I J Killeen, 11.7.2001.

Sussex West (13): *Ena montana*, Old Ditcham Wood (41/763195), M J Willing, 9.2000.

Kent West (16): *Cernuella aginnica*, roadside by M20, Sandling near Maidstone (51/763582), R Carr, 3/11/2000. This is also a new country record and was checked by dissection by E Gittenberger; *Pseudanodonta complanata*, River Medway, Tonbridge (51/597465), R Carr, 25.1.2002 (recently dead shells).

Herts (20): *Pisidium tenuilineatum*, Rivers Mimran and Lee, Hertford (52/316121, 52/318121, 52/319123, 52/320120, 52/319122), I J Killeen, 6.2001.

Oxford (23): *Ferissia wautieri*, River Thame, Shabbington (42/668064), I J Killeen, 9.7.2001.

Suffolk East (25): *Zonitoides excavatus*, Benacre, Easton Wood, Hogs Pen Belt and Craft Plantation (62/517802, 62/518813, 62/522829), T Abrehart, det. I J Killeen, 2001.

Bedford (30): *Hygromia cinctella*, Hedge to car park, Luton (52/096215), D Guntrip, 17.12.2000.

Monmouth (35): *Hygromia cinctella*, Quarry and garden, Cwmynyscoy Quarry, Pontypool (31/281996 and 31/281997), Leyton Williams-Davies, 9.2001.

Anglesey (52): *Planorbis carinatus*, Llyn Pen-y-parc Nature Reserve (23/584750), J H Bratton, 26.8.2001.

York South-east (61): *Columella aspera*, Eddlethorpe (44/77-66-), A Norris, 9.6.2001; *Boettgerilla pallens*, Eddlethorpe (44/77-66-), D Lindley, 9.6.2001, checked A Norris.

York South-west (63): *Hygromia cinctella*, gardens on west side of Sheffield (43/316856 and 43/332879), R M Smith 5.9.2000 and 14.10.2000, det. R A D Cameron.

Roscommon (H25): *Vertigo geyeri*, calcareous fen, Annaghmore Lough(M903840), Geraldine Holyoak, 23.8.2001.

Cavan (H30): *Theodoxus fluviatilis*, stones at edge, Lough Sheelin, north-east of Ross (N472836), Geraldine Holyoak, 8.8.2001; *Viviparus viviparus*, edge of Lough Oughter (H345066), Geraldine Holyoak, 8.8.2001; *Myxas glutinosa*, stones in shallow water, Lough Sheelin (N472836), Geraldine Holyoak, 13.8.2001; *Vallonia pulchella*, in reeds, Lough Oughter, west of Inish Connell (H357070), Geraldine Holyoak, 14.8.2001; *Boettgerilla pallens*, town park on edge of lough, Killashandra (H311077), Geraldine Holyoak, 26.8.2001; *Limax cinereoniger*, fallen branch in conifer plantation, Giant's Leap, south of Blacklion (H079352), Geraldine Holyoak, 19.8.2001; *Helicella itala*, limestone grassland, north of Manragh (H082344), Geraldine Holyoak, 19.8.2001.

Fermanagh (H33): *Pisidium pulchellum*, Lough Formal, Geraldine Holyoak, 2000.

Introduced species from other countries and continents continue to arrive and expand their range and it is important that these are monitored. Many of the introductions thrive in disturbed areas, like gardens, which offer many opportunities. Features of the incoming records this year were new localities and vice-county records for the Girdled

Snail, *Hygromia cinctella*. Last year's Non-marine Recorder's Report (Kerney, 2002) showed Norfolk as the northern-most county but it has now reached Sheffield in Yorkshire. *Hygromia cinctella* is a distinctive snail with a white line on the peripheral keel and likely to be noticed by beginners as well as by more experienced recorders. Another introduction already included in the *Atlas* (Kerney, 1999) is *Paralaoma caputspinulae*, an Australian species that has now been found in Cornwall (west). This looks like a large *Punctum pygmaeum* with a more loosely coiled umbilicus and very thin, widely spaced rib-like spines. In the slugs, the introduced *Boettgerilla pallens* has extended into two more Vice-counties.

Cernuella aginnica is new for Britain, as well as for the Vice-county. This was found near Maidstone, Kent and the identification confirmed by dissection. The shell is rather like that of *C. virgata* but with a wider umbilicus. It occurs in the Mediterranean area of France.

Parts of the country which are under-recorded, like Ireland, continue to reward the field worker with new Vice-county records. Some species that have been overlooked will reveal themselves when suitable habitats are recognised and worked by a recorder who has their eye in for that species. Commissioned surveys likewise tend to target a particular, usually rare, species as part of the BAP process (Biodiversity Action Plans) in conservation. *Pisidium tenuilineatum* has been surveyed in many rivers with the result of a great increase in records of occurrence.

Various environmental, and particularly climatic, factors affect the abundance of non-marine mollusc populations. Where a species is at a very low level of abundance it is unlikely to be found, but may reveal itself should other factors lead to an increase in density. Well established species may also change their abundance and range.

In taking over the work of Non-marine Recorder, it is a pleasure to acknowledge the work of Dr M P Kerney from 1961-2001. He pioneered the 10km grid recording through initial scepticism and achieved a good general coverage of recording that led to the first *Atlas* in 1976 (Kerney 1976) and continued, filling gaps and picking up changes in distribution and introductions, which provided material for the second *Atlas* in 1999 (Kerney 1999). A comparison of the two *Atlases* shows the dynamic nature of mollusc distribution. Over the years Dr Kerney has helped many recorders with feedback and giving much patient assistance in identification. I would also like to thank all the individual recorders who sent in records this year, both those named in the new Vice-county records and others whose recording cards start off the new century with new base-line 10km recording cards.

KERNEY M.P. 1976 *Atlas of the Non-marine Mollusca of the British Isles* Institute of Terrestrial Ecology, Cambridge.

KERNEY M.P. 1999 *Atlas of the Land and Freshwater Molluscs of Britain and Ireland* Harley Books, Colchester, Essex.

KERNEY M.P. 2002 Recorder's Report: Non-marine Mollusca *Journal of Conchology* **37**: 417-420.

MARINE RECORDER'S REPORT 2001

Compared to 2000, last year was less eventful on the marine recording front. The outbreak of foot and mouth disease undoubtedly took its toll on field activities, both organised Society meetings and individual recording endeavours. The Kimmeridge meeting in June and the Fife meeting in September were moderately well attended but full species lists have not yet been compiled.

New records have been sparse, but Julia Nunn reports 3 new species to Sea Area 35 (Mayo), namely the two sacoglossan species *Alderia modesta* and *Limapontia depressa* and *Hydrobia neglecta* (confirmed by dissection of the animal). The Irish Atlas, which has been in gestation since 1992, is on the brink of publication. Data have been incorporated into a computer database, which will generate the distribution maps. Currently there are 96,400+ records of Mollusca for the island of Ireland stored on the database representing 19,600+ visits to sites. Of these, 39,000+ records were obtained from 1700+ site visits by fieldwork specifically for this project. A bibliography of 1350+ references for marine Mollusca in Ireland has been compiled. From this dataset, a provisional checklist has been compiled of 889 taxa (live/dead, all dates), with an additional 53 species of uncertain status. Many records new to Ireland or to Sea Areas have been observed.

There is further news concerning two species which featured in my reports of 1999 and 2000. In the former, I reported the erroneous recording of *Haliotis tuberculata* from the Devon coast. A pilot study into the feasibility of introducing this species to Cornish waters has been launched at Padstow, Penzance, Falmouth and the Isles of Scilly. MAFF studies have concluded that the water temperatures in the southwest will suit the ormer and if the indications are good, hatchery work and ormer culture supported by local fishermen will get under way. In the latter report I highlighted the fact that *Sepia orbigniana* bones had been present in large strandings of cuttles in Cornwall in May and June 2000. Re-examination of Cornish material in pre-existing collections confirmed the suspicion that the species had hitherto been overlooked. Terry Wimbleton now reports that a *Sepia* bone collected from Gosport in Hampshire in March 1997 is *S. orbiginiana* and Peter Topley found a bone of the species washed up near Minehead, Somerset in April 2001.

Knowledge on the status and distribution of *Thyasira gouldi* in British waters has been increased considerably through the work of Killeen & Oliver (*Journal of Conchology* **37**: 391-402). This is one of only two marine bivalves protected on Schedule 5 of the Wildlife and Countryside Act 1981, the other being *Atrina fragilis*, and is also a priority species on the UK Biodiversity Action Plan (BAP). *T. gouldi* was believed to occur only in upper Loch Etive on the west coast of Scotland and was also considered to be in decline at that locality. The authors have recognised *T. gouldi* in samples ranging from Loch Sween north to Shetland (from where there were previous but unconfirmed records) on the west coast of Scotland and in the Firth of Forth on the east coast. The conservation status has been reviewed in light of this wider distribution and suggestions made for revising and reviewing the BAP Species Action Plan. Killeen & Oliver have also recognised an additional *Thyasira* species as part of the British fauna, namely, *T. polygona*, a Jeffreys species which had been regarded as a variety of *T. flexuosa* (*Journal of Conchology* **37**: 383-9). Their extensive taxonomic review of *Thyasira* species in North Sea oilfields (in press) has provided a substantial number of distributional records for nine *Thyasira* species over a latitudinal range from 56 to 62°N.

Although marine recording in our region of the North East Atlantic is well established, and continues to yield new species distribution information, it is worth remembering that there are large gaps in our knowledge worldwide. As part of the Society's policy to revive the Research Grant Award Scheme, support was given to an application for funding to enable participation by two members of the Society in the Shoals

Rodrigues (formerly Shoals of Capricorn) Project. The aim of this project is to study and improve knowledge on the marine fauna of the small Mascarene island, Rodrigues, 600 km east of Mauritius. The marine mollusc fauna of Rodrigues is much less well known than for other Mascarene islands such as Mauritius, Reunion and the Seychelles. The three principal objectives were to conduct general recording to augment the marine mollusc species inventory started in 2000, to elucidate the fauna, particularly microgastropods, of algal turf and other specific habitats in the lower littoral/shallow sublittoral, and the eulimid gastropod fauna and its holothurian host relationships.

It is hoped that 2002 will be a more fruitful year for marine mollusc records in the northeast Atlantic region. A training workshop to take place in Cornwall is planned for October 2002 and is designed to draw new recruits, as well as to re-invigorate old hands.

Jan Light

REPORT OF THE HON. CONSERVATION OFFICER 2001-2002

Selected key items from the 2001-02 year are summarised below.

Advice and help

Has been given to many individuals and organisations and some examples include:

- Telford and Wrekin Council were given advice on the options available in dealing with a population of the R.D.B. species *Lymnaea glabra* present on a development site. The council undertook measures to translocate the habitat and snail population to a site close by (assessment of success is to be undertaken in 2002).
- Cambridge County Council were advised on the presence and management of *Helicella itala* populations.
- English Nature were given advice on SSSI extensions in the Arun valley, West Sussex.
- Identification of specimens of possible conservation importance was undertaken for various organisations such as the Worcestershire and Sussex Biological Record Centres; The Northmoor Trust, Oxon and The National Trust.
- Advice and contacts were given to a Environment Agency scientist working on the effects of endocrine disrupting chemicals on aquatic Mollusca.
- Help and advice has been given to a wide range of undergraduate students undertaking molluscan based projects.

British Wildlife

The production of a biannual molluscan wildlife report for this journal has continued. The Conservation Officer has used this column to publicise selected aspects of work undertaken by the Society. The June 2001 report was able to give a summary of some of the most interesting items appearing in the annual Recorders' reports. Later in the year publicity was given to the Society's newly launched research grant scheme as well as a variety of other conservation work undertaken by Society members.

Invertebrate Link (formerly J.C.C.B.I.) and The Invertebrate Conservation Trust

Membership of the Committee continues providing valuable contacts with other organisations. The Conservation Officer has attended all meetings and he is also a member of the Executive. The Conchological Society gave its official support to the newly formed Invertebrate Conservation Trust (or ICT, also to be known under the popular name 'Buglife') and more recently it became a corporate member of the ICT. It is hoped that the ICT will work to successfully co-ordinate and integrate the many branches of invertebrate conservation that in the past have often worked in relative isolation.

The Fourth Quinquennial Review of Schedules 5 and 8 of the Wildlife and Countryside Act, 1981

The Conchological Society were invited by the J.N.C.C. to review the Mollusca currently protected by Schedule 5 of the Act. A team of Society members including Dr. K. Alexander, Dr. J. Chatfield, Mr. B. Eversham, Dr. D.T. Holyoak, Dr. M.P. Kerney, Mr. I. J. Killeen, Mrs. J. Light and Dr. M. J. Willing considered a range of options and agreed on a set of proposals. This resulted in the Society recommending the addition of two species, *Helix pomatia* and *Sphaerium solidum* to Schedule 5 of the Act and also the removal of two others, *Paludinella litorina* and *Thyasira gouldi*. Detailed draft recommendations for these species were sent to the J.N.C.C. and are currently being considered before final changes to Schedule 5 are settled.

Biodiversity Matters

Four Molluscan Conservation Group members continue involvement on UK BAP

Steering Groups for a number of the Biodiversity Steering Group's Priority Species. Mollusca include (1) the terrestrial species: *Vertigo geyeri, V. genesii, V. angustior, V. moulinsiana* and *Catinella arenaria* and (2) the freshwater species *Pseudanodonta complanata, Pisidium tenuilineatum, Segmentina nitida, Anisus vorticulus* and *Myxas glutinosa.*

Several Society members have been involved on a professional basis with survey and monitoring work on Biodiversity Steering Group Priority Species including *Pisidium tenuilineatum, Vertigo moulinsiana, V. geyeri, V. genesii, Myxas glutinosa,* and *Margaritifera margaritifera.* Work has also involved Biodiversity Steering Group Species of Conservation Concern such as *Valvata macrostoma* and RDB species including *Paludinella littorina.*

Associations with other organisations

The Society has for many years worked closely with the National Trust. A recent major review of National Trust business management included proposals that might lead to the loss of the National Biological Survey Team, together with its two invertebrate specialists (as well as some lowering of nature conservations centre status within the Trust). In seeking clarification of these issues, the Society has stressed the importance of maintaining a strong national invertebrate expertise within any new National Trust structures. It is believed that only in this way will the National Trust be able to integrate invertebrate information into conservation plans and policies.

The Conservation Officer attended English Nature's Species Recovery Programmes Tenth Anniversary Conference.

Conservation work undertaken throughout the Society

Many other conservation activities have been undertaken throughout the year by Society members, often in a professional capacity. These are too numerous to mention individually, but range from continued work with the DOMMIC (English Channel) marine molluscan mapping project, to molluscan surveys of freshwaters and wetlands throughout the country.

M.J. Willing

REPORT ON THE CONCHOLOGICAL SOCIETY DISPLAY MATERIAL/BOARDS

(SUBMITTED BY MR. P.T. WIMBLETON, EXHIBITS CO-ORDINATOR)

The Display Boards were in use at Cumberland House, Natural History Museum, Southsea, Hants at the time of the last AGM report. This was in conjunction with a Shell Exhibition by local member Terry Wimbleton. The exhibition ran from 17th February to 31st July 2001. A Shell Roadshow was held on 7th April 2001, when Dr June Chatfield and Terry Wimbleton were on hand to identify shells brought in by the public.

From 1st September until 6th October 2001, the display material was again in use, as an integral part of an exhibition entitled 'COME OUT OF YOUR SHELL', held at Haslemere Educational Museum, Surrey. The exhibition represented conchology in its broadest context. It featured exhibits on shell photography by Heather Angel, pencil drawings of shells by artist John Davies, shell embroidery by the Haslemere Young Embroiderers' Group, together with some beautifully made shell jewellery by the Surrey Guild of Craftsmen.

The Waveley Room contained an extensive shell exhibition by Terry Wimbleton, featuring British and Foreign marine and British and Foreign non-marine shells. Together with special exhibits on cold water whelks, alien (introduced) species, local rare shells, molluscan predation, the common garden snail, and many small cases showing various aspects of molluscan life. Young contributors, Abi (11 years) and Tim (13 years) Lender of Whitley, exhibited two live giant African land snails. Dr June Chatfield set up an aquarium of locally resident pond snails. The usual Shell Roadshow was held on 22nd September 2001, with Dr Chatfield and Terry Wimbleton available to identify shells brought in by the public. A pleasant and welcome surprise at this event was the informal attendance of Society members Judith Nelson and John Llewellyn-Jones who joined in the proceedings.

During the preparation of this exhibition, museum staff and Dr Chatfield kindly agreed to update the Society's Display material, which is now some ten years old. This was achieved with our grateful thanks and at no cost to the Society.

On 6th February 2002 the Display material was again in use, this time at an exhibition in the Leeds Central Library, Yorkshire entitled - SLIME: SLUGS AND SNAILS IN HISTORY AND MYTHOLOGY. This exhibition was conceived and put together by local member and Senior Museum Curator Adrian Norris. The centrepiece of the exhibition is an impressive thirty-two feet long model of a Giant Squid *Architeuthis* sp. Displays are devoted to various shell themes, on different aspects of shells, shapes of shells, shells as food, fossil shells, precious shells/material, shell art and craft and the founding of the Conchological Society of GB & I, with the Illuminated Address by J W Taylor.

A separate bay is devoted to the Conchological Society of GB & I. Also on display are specimens of the Giant Clam, *Tridacna gigas*, and a large fossil Ammonite from Dorset. There are very large wall mounted prints of Unionids of the USA and various posters and prints, one by the late A E Ellis. A lecture in support of the event was given by S Peter Dance: SIDE-LIGHTS ON ILLUSTRATED SHELL BOOKS, at the Rupert Becket Lecture Theatre, University of Leeds. Two large pull-up stands, one with a snail slime trail advertising the exhibition and giving acknowledgement to contributors, the other with a large emblem of the Society, are positioned at the entrance to the Exhibition. This exhibition was supported with a financial grant from the Society. The exhibition has been designed and constructed with mobility in mind. It will close on Saturday 27th April 2002 and will then move to the Yorkshire Museum at York for the summer of 2002.

Colin Gillard
Hon. General Secretary

MEMBERSHIP SECRETARY'S REPORT FOR 2001

Membership of the Society at the end of 2001 was 323. This includes Life Members, Honorary Members, Ordinary Members, Family Members, Student Members and Institutions. There have been 15 new members in the year, but 23 members have resigned or lapsed through non-payment, giving a net loss of 8 members for the year.

During the year there were 78 subscribers to the *Journal of Conchology* which is the same as in 2001.

Mike Weideli
Hon. Membership Secretary

INSTRUCTIONS TO AUTHORS

Manuscripts should be sent to:

THE HON. EDITOR, DR P.G. OLIVER,
NATIONAL MUSEUMS & GALLERIES OF WALES, CATHAYS PARK, CARDIFF CF10 3NP.
GRAHAM.OLIVER@NMGW.AC.UK

PAPERS Two copies of text and illustrations should be submitted; one set of illustrations must be good quality originals. Authors should refer to *Instructions to Authors* in Volume 37, Part 1 as a guide to format. Authors are reminded of the high cost of printing and therefore are expected to write concisely and to make maximum use of page size when designing artwork and tables.

COMMUNICATIONS These are intended to be short notes of an original nature which do not merit the treatment of a full paper. *Communications* do not normally contain any figures, tables or plates and should conform in style to that of recent issues of the *Journal.*

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