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ELLOBIIDAE—LOST BETWEEN LAND AND SEA

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ABSTRACT The Ellobiidae are a diverse group of archaeopulmonate snails living mostly near the sea. Their shell length ranges from barely 2 mm to over 100 mm. Six structural types of reproductive system set the boundaries for the subfamilial division: Pythiinae, Ellobiinae, Carychiinae, Cassidulinae, Pedipedinae, and Melampodinae. This division is in general supported by four structural types of nervous system and by the internal morphology of the penial complex. The halophile ellobiids are commonly associated with the supratidal fringe of mangroves and salt marshes; they are also important components of the supratidal biota of the mobile rocky shore. The various species occupy different portions of the shore. In rocky habitats, in addition to horizontal zonation, the ellobiids also partition their vertical distribution. The purpose of this study is to describe the zonation patterns of the halophile ellobiids of the cobble shores of the Açores and, in less detail, of the associated malacofauna.

KEY WORDS: Ellobiidae, systematics, morphology, anatomy, ecology, cobble shores, Açores

INTRODUCTION

The Ellobiidae have long been recognized as a cohesive taxonomic unit (Lamarck 1809) and were illustrated in the most important iconographic works of the nineteenth century (Reeve 1841, Reeve 1877, Küster 1844, Kobelt 1897–1901). Classification was based exclusively or primarily on shell morphology. Pfeiffer (1856, 1876), elaborating on shell descriptions of all species known at the time and adding many of his own, provided an important monographic treatment for the group. Zilch's (1959) subfamilial arrangement was also based on shell characteristics. Radular (Odhner 1925) and anatomical features have since been included in taxonomic research and have contributed greatly to the clarification of the relationships of the various taxa (Morton 1955, Martins 1996a, Martins 1996b, Martins 1998).

Ellobiids are important members of the supratidal communities of marshes and mangroves, and their contribution to the ecological balance of those environments has been somewhat recognized in studies dealing with their general biota (Berry 1963, Brown 1971, Sasekumar 1974, Murty & Balaparameswara Rao 1977, Li & Gao 1985). More specific studies have been done on *Melampus bidentatus* and *M. coffeus* (Hausman 1932, Holle & Dineen 1957, Morrison 1958, Morrison 1959, Golley 1960, Grandy 1972, Russell-Hunter et al. 1972, Orton 1976).

The various species of halophile ellobiids occupy different portions of the shore, their distribution being loosely related to their

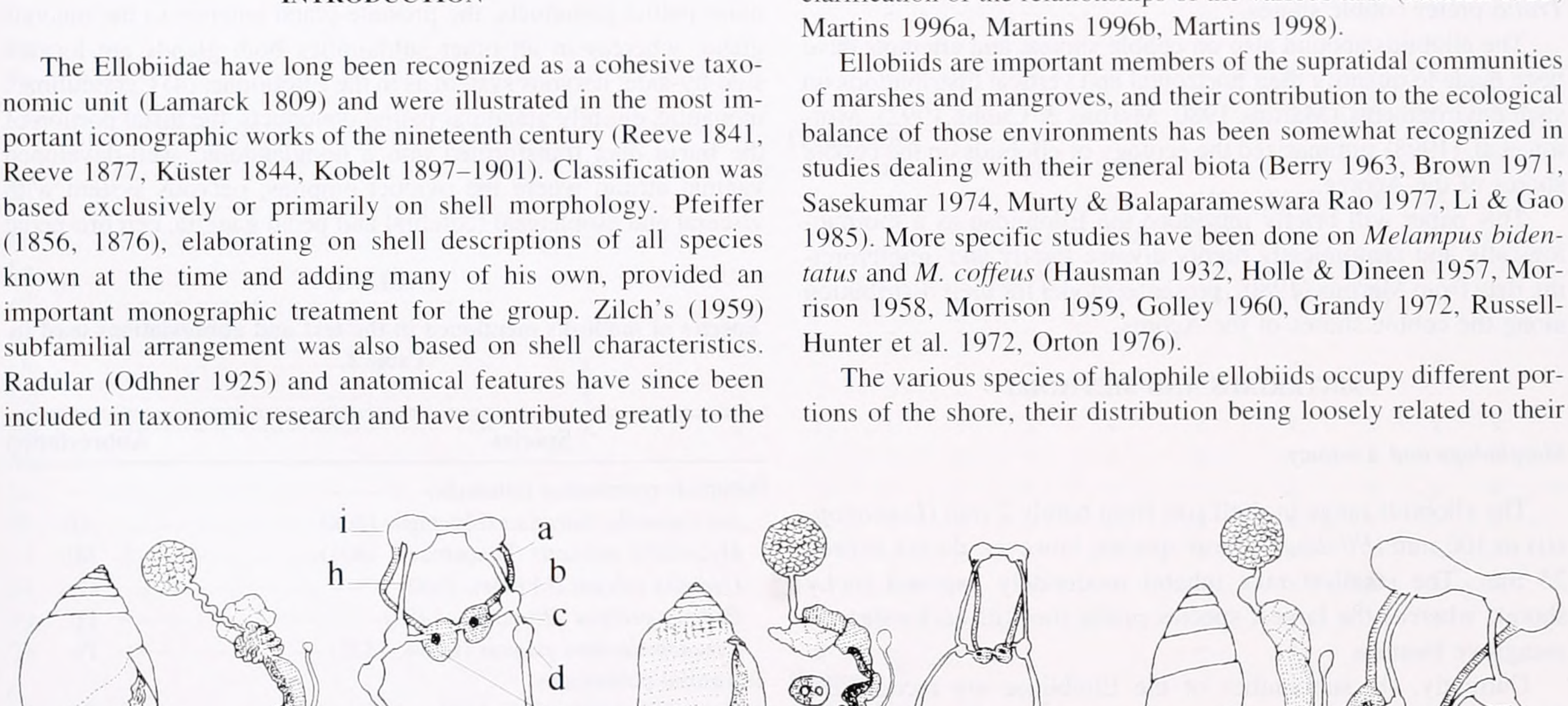

Figure 1. Shell, reproductive system, and nervous system of selected species of Ellobiidae, exemplifying the structural patterns characterizing the various subfamilies. A, Pythiinae *Pythia scarabaeus* (L., 1758); B, Ellobiinae *Ellobium aurismidae* (L., 1758); C, Carychiinae *Carychium minimum* (O.F. Müller, 1774); D, Cassidulinae *Cassidula aurisfelis* (Bruguière, 1789); E, Pedipedinae *Pedipes pedipes* (Bruguière, 1791); F, Melampodinae *Melampus coffeus* (L., 1758). a, cerebro-pedal connective; b, pleural ganglion; c, pleuro-parietal connective; d, parietal ganglion; e, pedal ganglion; f, parieto-visceral connective; g, visceral ganglion; h, cerebro-pleural connective; i, cerebral ganglion; j, ovotestis; k, hermaphroditic duct; l, posterior mucous gland; m, bursa; n, bursa duct; o, posterior vas deferens; p, vagina; q, prostate gland; r, anterior mucous gland; s, albumen gland. (Adapted from Martins 1996a.)

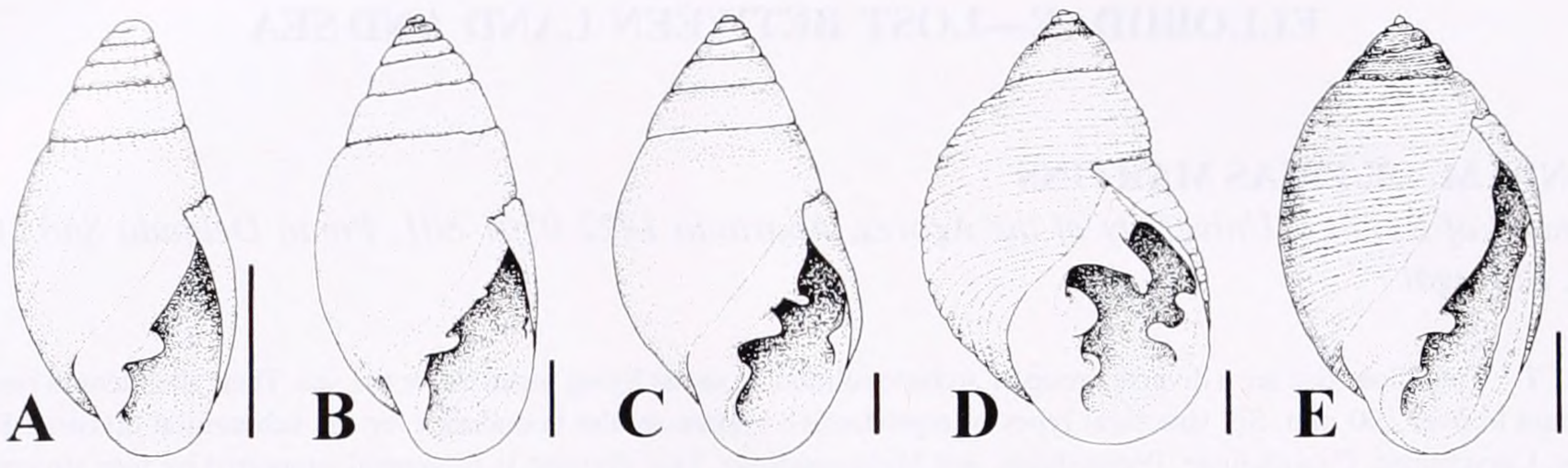

Figure 2. Ellobiids of the cobble shores of the Açores. A, *Auriculinella bidentata*; B, *Myosotella myosotis*; C, *Ovatella vulcani*; D, *Pedipes pedipes*; E, *Pseudomelampus exiguus*. Scale bars = 1 mm.

taxonomic affiliation. The Pythiinae (*Pythia* and, to a lesser extent, *Myosotella*) venture farther inland and may live in an almost terrestrial environment, whereas the Pedipedinae prefer the upper intertidal. Within the Melampodinae, some species of *Melampus* are found usually in mangroves and marshes, whereas others and *Tralia* prefer cobble shores.

The ellobiids abound also on cobble shores, and attempts have been made to quantify their horizontal and vertical distributions on such environments (Martins 1980, Martins & Cunha 1992). Morton et al. (1998) summarized the ecology of ellobiids on the cobble shores of the Açores.

This paper will briefly introduce the Ellobiidae as a morphologically and anatomically highly diverse family and, reinterpreting data from Martins (1980), present a model for their distribution along the cobble shores of the Açores.

MATERIALS AND METHODS

Morphology and Anatomy

The ellobiids range in shell size from barely 2 mm (*Leuconopsis*) to 100 mm (*Ellobium*); most species, however, do not exceed 25 mm. The smallest taxa inhabit moderately exposed rocky shores, whereas the largest species prefer the still backwaters of mangrove swamps.

Currently, six subfamilies of the Ellobiidae are recognized: Pythiinae, Ellobiinae, Carychiinae, Cassidulinae, Pedipedinae, and Melampodinae. Although shell morphology and internal anatomy have been considered in delimiting the subfamilies, these are based primarily on characteristics of the reproductive and nervous systems (Morton 1955, Martins 1996a, Martins 1996b, Martins 1998).

The dentate appearance of the shell aperture establishes a generalized ellobiid profile. However, the elaboration of the apertural teeth is far from uniform and, although relatively constant at the genus level, shows variability within and similarities across the subfamilies, which is not consistent with the corresponding internal anatomy. For example, a tridentate inner lip with the middle tooth strongest is seen in *Myosotella* (Pythiinae), *Ellobium* (Ellobiinae), and *Tralia* (Melampodinae); a narrow, elongated aperture, typical of *Melampus*, is also found in *Microtralia* (Cassidulinae) and *Pseudomelampus* (Pedipedinae); a double columellar tooth, typical of *Pedipes*, is also found in some *Auriculastra* (Ellobiinae) as well as in *Creedonia* (Cassidulinae).

The anatomy of the reproductive and nervous systems shows a series of patterns that lead to more consistent assemblages (Fig. 1) (see also Martins 1996a, Martins 1998). The subfamilies can then be characterized as follows: (1) Pythiinae: monaulic, entirely glandular pallial gonoducts and long visceral nerve ring (pleural, parietal and visceral ganglia and respective connectives) with both parieto-visceral connectives of about the same length; (2) Ellobiinae: diaulic, entirely glandular pallial gonoducts and long visceral nerve ring with the right parieto-visceral connective much shorter than its left counterpart; (3) Carychiinae: monaulic, entirely glandular pallial gonoducts, the prostate gland anterior to the mucous gland, whereas in all other subfamilies both glands are located side-by-side; nervous system as in the Ellobiinae; (4) Cassidulinae: monaulic, entirely glandular pallial gonoducts, the distal portion of the bursa duct transformed into a nonglandular, well-developed vaginal atrium where the oviduct empties; nervous system with visceral and esophageal (cerebral and pedal ganglia, cerebro-pedal

TABLE 1.

Species of mollusks mentioned in the text and abbreviations used in Table 2.

Species	Abbreviation
Halophile pulmonates (ellobiids)	
Auriculinella bidentata (Montagu, 1808)	Ab
Myosotella myosotis (Draparnaud, 1801)	Mn
Ovatella vulcani (Morelet, 1860)	Ov
Pedipes pedipes (Bruguière, 1789)	Pp
Pseudomelampus exiguus (Lowe, 1832)	Pe
Terrestrial pulmonates	
Euconulus fulvus (O. F. Müller, 1774)	Ef
Lauria anconostoma (Lowe, 1831)	La
Leiostyla fuscidula (Morelet, 1860)	Lf
Oestophora barbula (Rossmässler, 1838)	Ob
Oxychilus draparnaudi (Beck, 1837)	Od
Punctum azoricum (de Winter, 1988)	Pa
Systellomatophoran	
Onchidella celtica (Cuvier, 1817)	Oc
Prosobranchs	
Alvania mediolittoralis Gofas, 1989	Am
Assiminea eliae Paladilhe, 1875	Ae
Cingula trifasciata (Adams, 1798)	Ct
Fossarus ambiguus (Linnaeus, 1758)	Fa
Littorina striata King & Broderip, 1832	Ls
Manzonia unifasciata (Dautzenberg, 1889)	Mu
Melaraphe neritoides (Linnaeus, 1758)	Mn
Paludinella littorina (delle Chiage, 1828)	Pl
Patella gomesii Drouët, 1858	Pg
Peringiella ovummuscae (Gofas, 1990)	Po
Thais haemastoma (Linnaeus, 1767)	Ts
Bivalves	
Cardita calyculata Linnaeus, 1758	Cc
Lasaea adansoni (Gmelin, 1791)	Lr
Mysella bidentata (Montagu, 1803)	Mb

TABLE 2.

Number of specimens of ellobiids and presence (x) of associated malacofauna per m^2 along transects on five cobble shores of the Açores.

Species	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	−1	−2	−3	−4
Transect A																					
Mn	6	8	2	12	4	6	9	2	–	–	3	–	8	–	–	–	–	–	–	–	
Ov	–	–	–	–	–	–	–	–	–	–	3	4	22	23	–	105	105	60	40	1	
Pe	–	–	–	–	–	–	–	–	–	–	3	1	75	290	10	190	600	250	50	2	
Pp	–	–	–	–	–	–	–	–	–	–	1	–	16	50	–	170	600	55	75	13	
Ab	–	–	–	–	–	–	–	–	–	–	–	–	3	2	–	15	63	23	7	2	
Pa	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
Ef	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
Lf	x	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
La	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
Ae	–	–	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
Mn	–	–	–	–	–	–	–	–	x	–	–	–	x	x	x	x	x	x	x	x	
Ls	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	x	x	x	
Ts	–	–	–	–	–	–	–	–	x	–	–	x	x	–	–	–	x	–	–	–	
Pl	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	x	–	–	
Ct	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	x	x	
Fa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	x	x	–	
Po	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	x	x	x	
Pg	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	x	
Transect B																					
Mn	– – – – – – – – – – – – – – – – – – – –							17	10	70	70	80	90	130	20	–	–	–	–	–	
Ov	– – – – – – – – – – – – – – – – – – – –							3	–	–	1	10	13	140	1,200	4,850	2,680	590	65	1	
Pe	– – – – – – – – – – – – – – – – – – – –							–	–	–	2	2	1	30	430	470	–	–	–	–	
Pp	– – – – – – – – – – – – – – – – – – – –							–	–	–	–	1	2	10	270	950	1,100	320	35	1	
Ab	– – – – – – – – – – – – – – – – – – – –							–	–	–	–	–	–	5	75	50	60	70	12	1	
La	– – – – – – – – – – – – – – – – – – – –							x	–	–	–	–	–	–	–	–	–	–	–	–	
Ob	– – – – – – – – – – – – – – – – – – – –							x	–	–	–	–	–	–	–	–	–	–	–	–	
Od	– – – – – – – – – – – – – – – – – – – –							x	–	–	–	–	–	–	–	–	–	–	–	–	
Ae	– – – – – – – – – – – – – – – – – – – –							x	x	x	x	x	x	x	x	x	x	x	x	x	
Mn	– – – – – – – – – – – – – – – – – – – –							–	–	–	–	–	x	x	x	x	x	x	x	x	
Ls	– – – – – – – – – – – – – – – – – – – –							–	–	–	–	–	–	–	–	–	x	x	x	x	
Pl	– – – – – – – – – – – – – – – – – – – –							–	–	–	–	–	–	–	–	x	x	x	x	x	
Ct	– – – – – – – – – – – – – – – – – – – –							–	–	–	–	–	–	–	–	x	x	x	x	x	
Fa	– – – – – – – – – – – – – – – – – – – –							–	–	–	–	–	–	–	–	–	x	x	x	x	
Pg	– – – – – – – – – – – – – – – – – – – –							–	–	–	–	–	–	–	–	–	–	x	x	x	
Th	– – – – – – – – – – – – – – – – – – – –							–	–	–	–	–	–	–	–	–	–	–	x	–	
Transect C																					
Mm	– – – – – – – – – – – – – – – – – – – –							270	550	440	110	170	23	5	–	–	–	–	–	–	–
Ov	– – – – – – – – – – – – – – – – – – – –							1	5	6	12	5	10	5	1	15	2	–	1	–	–
Pe	– – – – – – – – – – – – – – – – – – – –							–	120	1,140	120	700	720	210	15	20	2	2	2	3	1
Pp	– – – – – – – – – – – – – – – – – – – –							–	–	–	–	25	85	75	3	20	6	–	1	2	–
Mn	– – – – – – – – – – – – – – – – – – – –							–	–	–	–	–	–	–	–	x	x	x	x	–	–
Ls	– – – – – – – – – – – – – – – – – – – –							–	–	–	–	x	x	x	x	x	–	–	–	–	–
Ct	– – – – – – – – – – – – – – – – – – – –							–	–	–	–	–	–	–	–	–	–	x	x	x	–
Fa	– – – – – – – – – – – – – – – – – – – –							–	–	–	–	–	–	–	–	–	x	–	x	x	–
Po	– – – – – – – – – – – – – – – – – – – –							–	–	–	–	–	–	–	–	–	x	x	–	x	–
Pg	– – – – – – – – – – – – – – – – – – – –							–	–	–	–	–	–	–	–	–	–	–	–	x	–
Oc	– – – – – – – – – – – – – – – – – – – –							–	–	–	–	–	–	–	–	–	–	–	x	x	–
Transect D																					
Mm	– – – –	15	10	15	25	15	57	30	45	75	41	42	45	7	11	2	–	–	–	–	–
Ov	– – – –	–	–	–	–	–	–	–	–	1	–	3	26	80	140	95	3	–	–	–	–
Pe	– – – –	–	–	–	–	–	15	33	5	5	21	25	100	65	50	20	25	–	–	–	–
Pp	– – – –	–	–	–	–	–	–	1	–	–	–	7	31	106	105	85	80	1	5	–	2
Mn	– – – –	–	–	–	–	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	–
Ls	– – – –	–	–	–	–	–	–	–	x	–	–	x	x	x	x	x	x	x	x	x	–
Pl	– – – –	–	–	–	–	–	–	–	–	–	–	–	x	x	x	x	x	x	–	–	–
Fa	– – – –	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	x	x	x	x	–
Pg	– – – –	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–

Continued

TABLE 2.

continued

Species	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	−1	−2	−3	−4
										Transect E											
Mn	–	–	–	–	20	40	15	30	70	85	40	72	15	–	–	–	–	–	–	–	
Ov	–	–	–	–	–	–	–	–	–	2	5	23	400	255	515	500	15	–	–	–	
Pe	–	–	–	–	–	–	–	–	2	47	80	700	1,730	1,860	1,440	200	1	–	–	–	
Pp	–	–	–	–	–	–	–	–	–	–	–	60	485	1,250	1,760	1,080	1,000	60	4	1	
Ab	–	–	–	–	–	–	–	–	–	–	–	–	–	2	5	2	–	–	–	–	
Ob	–	–	–	–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
Mn	–	–	–	–	–	–	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
Ls	–	–	–	–	–	–	x	–	–	–	x	x	x	x	x	x	x	x	x	x	
Pl	–	–	–	–	–	–	–	–	–	x	x	x	x	x	x	x	x	x	x	x	
Ct	–	–	–	–	–	–	–	–	–	–	–	x	x	x	x	x	x	x	x	x	
Mu	–	–	–	–	–	–	–	–	–	–	–	x	x	–	–	–	–	–	–	–	
Fa	–	–	–	–	–	–	–	–	–	–	–	–	x	x	x	x	x	x	x	x	
Am	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	x	x	x	x	x	
Lr	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	x	x	x	x	x	
Mb	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	–	–	–	–	
Cc	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	x	x	–	–	–	
Pg	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	x	x	x	x	

High tide level at 0; remaining numbers are meters away from 0, with negative numbers being seaward. See text for transect identification and Table 1 for species abbreviations (data from Martins 1980).

connectives and pedal commissure) rings moderately wide, approximately of equal size; (5) Pedipedinae: monaulic to incipient semidiaulic, pallial gonoducts with glandular coverage only on the proximal (posterior) half; visceral nerve ring extremely concentrated, right connectives of the esophageal nerve ring shorter than their left counterparts; and (6) Melampodinae: advanced semidiaulic pallial gonoducts, the residual glandular portion concentrated proximally (posteriorly); visceral nerve ring extremely concentrated, connectives of the esophageal nerve ring of approximately equal length.

Additional diagnostic features have been sought in the internal morphology of the penis, which have in many cases corroborated the assemblages just presented (Martins 1996a, Martins 1998).

Ellobiids on Cobble Shores

The ellobiids are common inhabitants of the supratidal of certain rocky habitats. Cobble beaches are a common feature of the Açorean rocky shore (Morton et al. 1998) and are the habitat of five species of halophile ellobiids (Fig. 2). The distribution of these species along the cobble shores has previously been recorded (Martins 1980). Following is an elaboration on those data to present a model for their distribution. The distribution of the associated malacofauna will also be presented (Table 1).

Five of the original 11 transects of 1-m^2 quadrats (Martins 1980) were selected on the basis of their relatively similar length to provide a more or less homogeneous set of data (Table 2). The locations of the transects and the sampling dates are as follows:

Transect A: West of Ponta do Alcaide, Silveira, Terceira, Açores. February, 1976.

Transect B: Calhau da Pata, Caminho de Baixo, São Mateus, Terceira, Açores. March, 1976.

Transect C: Pópulo, São Miguel, Açores. January, 1976.

Transect D: Ponta de São Pedro, Vila Franca do Campo, São Miguel, Açores. February, 1976.

Transect E: Atalhada, Lagoa, São Miguel, Açores. March, 1976.

Cobble shores are, in principle, exposed to at least moderate wave action. All but transect C have moderate to high exposure to wave action, with transect C being more protected.

Kite diagrams were constructed to illustrate the distributions of the species. For ellobiids, data (as percentages) from the five transects were combined, and the percentages present at each height above or below high tide level were used to construct the kite diagrams. For other species, presence/absence was simply totaled for all five quadrats at a particular height, for a maximum of five.

RESULTS

The distribution of the ellobiids and associated malacofauna along the cobble shores of the Açores is summarized in Figure 3.

DISCUSSION

The five species of ellobiids exhibit a definite pattern of distribution along the cobble shore. *Myosotella myosotis* lives highest up, almost assuming a terrestrial habitat, indicated by the presence of terrestrial pulmonates at these levels. It is followed by *Ovatella vulcani* and *Pseudomelampus exiguus*, which closely overlap. Additional information (Martins 1980) showed that, although overlapping along the transect, both species are somewhat separated vertically in the cobble accumulation. The former prefers the upper levels, whereas the latter is more abundant toward the bottom, frequently found under half-buried porous rocks. *Pedipes pedipes*, although overlapping with the latter two species, aggregates closer to a level just above the high tide level, a distribution more narrowly exhibited by *Auriculinella bidentata*. Here, too, there appears to exist vertical zonation, with *P. pedipes* preferring the upper levels, whereas *A. bidentata* lives underneath the rocks (Martins 1980). The single specimen of *P. pedipes* recorded from D9 (quadrat 9 of transect D) could be interpreted as accidental presence because the next closest recording is another single specimen in A6. However, transect D is in a highly exposed area, and

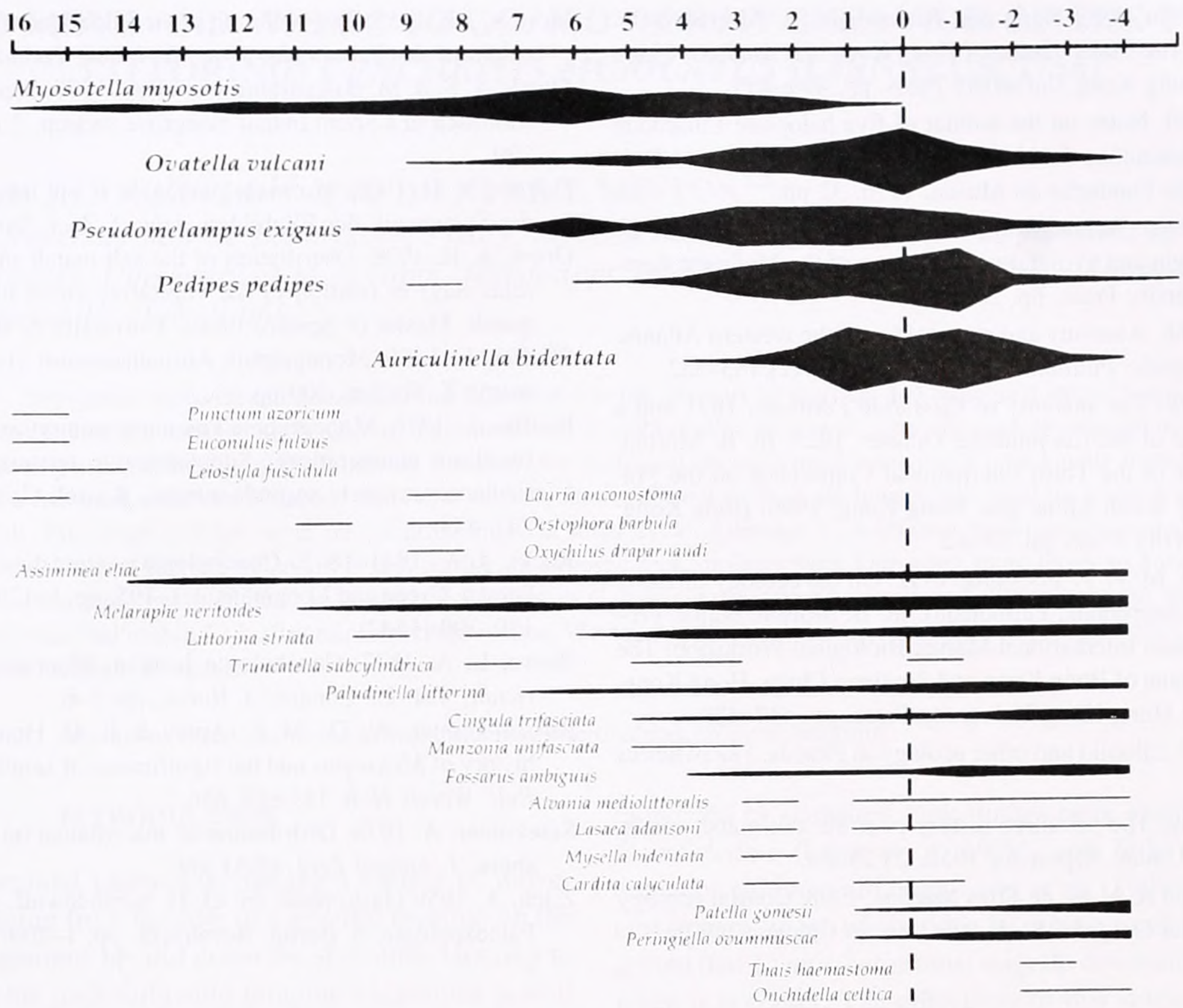

Figure 3. Distribution of ellobiids and associated malacofauna along the cobble shores in the Açores. Combined percentage (ellobiids) and cumulative presence (associated malacofauna) on five transects of different lengths. Dotted line (0) marks the high tide limit, located at the landward end of quadrat 0. Associated malacofauna not recorded in quadrat −4. (Adapted from Martins 1980.)

strong hydrodynamism could explain this apparently unusual presence, an interpretation supported by the equally more landward distribution of *Pseudomelampus exiguus* in transect D.

The ellobiids of a boulder shore of Hong Kong, although a different species assemblage, exhibited similar distribution patterns (Martins & Cunha 1992). Their horizontal distribution was more clearly understood when their vertical distribution in each quadrat along the transect was examined: In general, the horizontally widely distributed species maintained some preference for an upper vertical level as they approached the sea. The data for the Açores, presented here, lack transect profiles and vertical quantification, not allowing for inferences of this kind. However, as already referred to by Martins (1980), in many instances similar behavior occurs in the Açorean species.

Worth mentioning, within the associated malacofauna, is the wide horizontal range of *Assiminea eliae*, restricted to Terceira Island, contrasting with the more marine preference of another assimineid, *Paludinella littorina*, which is present on both islands.

The two littorinids present in the studied areas exhibit their commonly observed relative distribution pattern, with *Melaraphe neritoides* extending farther inland than *Littorina striata* (Morton et al. 1998).

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LITERATURE CITED

Berry, A. J. 1963. Faunal zonation in mangrove swamps. *Bull. Nat. Mus. Singapore* 32:90–98.

Brown, D. S. 1971. Ecology of Gastropoda in a South African mangrove swamp. *Proc. Malac. Soc. London* 39:263–279.

Golley, F. B. 1960. Ecologic notes on Puerto Rican Mollusca. *The Nautilus* 73:152–155.

Grandy, J. W., Iv. 1972. Winter distribution of *Melampus bidentatus* Say on a Cape Cod salt marsh. *The Nautilus* 85:106–109.

Hausman, S. A. 1932. A contribution to the ecology of the salt marsh snail *Melampus bidentatus* Say. *Am. Naturalist* 64:541–545.

Holle, P. A. & C. F. Dineen. 1957. Life history of the salt-marsh snail *Melampus bidentatus* Say. *The Nautilus* 70:90–95.

Kobelt, W. 1897–1901. Die Familie Auriculacea, 1(16):1–76, pls. 10, 11, 13 [1897]; 77–228, pls. 12, 14–30 [1898]; 229–268, pls. 31, 32 [1900]; 269–316, pl. 33 [1901]. In: F. H. W. Martini & J. H. Chemnitz. Systematisches Conchylien-Cabinet. Nürnberg: Verlag von Bauer & Raspe (Emil Küster).

Küster, C. H. 1844. Die Ohrschnecken (Auriculacea), 1(16):1–77, 9 pls. In: F. H. W. Martini & J. H. Chemnitz. Systematisches Conchylien-Cabinet. Nürnberg: Verlag von Bauer & Raspe (Julius Merz).

Lamarck, J. B. P. A. 1809. Philosophie zoologique; ou exposition des considérations relatives à l'histoire naturelle des animaux. Duminil Lesueur, Paris, 2 vols.

Li, F.-X. & S.-H. Gao. 1985. The ground-dwelling molluscan faunas of

mangrove swamps in Hong Kong and Xiamen. In: B. Morton & D. Dudgeon, editors. The Malacofauna of Hong Kong and southern China II. Hong Kong: Hong Kong University Press. pp. 449–455.

Martins, A. M. F. 1980. Notes on the habitat of five halophile Ellobiidae in the Azores. Publicações do Museu "Carlos Machado." Ponta Delgada: Centenário da Fundação do Museu. 1976. 32 pp.

Martins, A. M. F. 1996a. Relationships within the Ellobiidae. In: J. D. Taylor, editor. Origin and evolutionary radiation of the Mollusca. London: Oxford University Press. pp. 285–294.

Martins, A. M. F. 1996b. Anatomy and systematics of the western Atlantic Ellobiidae (Gastropoda: Pulmonata). *Malacologia* 37(2):163–332.

Martins, A. M. F. 1998. The anatomy of *Cassidula* Férussac, 1821 and a case for the revival of the Cassidulinae Odhner, 1925. In: B. Morton, editor. Proceedings of the Third International Conference on the Marine Biology of the South China Sea, Hong Kong, 1996. Hong Kong: Hong Kong University Press. pp. 25–42.

Martins, A. M. F. & R. M. P. T. T. Cunha. 1992. On the ecology of Hong Kong Ellobiidae (Gastropoda, Pulmonata). In: B. Morton, editor. Proceedings of the Fourth International Marine Biological Workshop: The marine flora and fauna of Hong Kong and Southern China, Hong Kong, 1989. Hong Kong: Hong Kong University Press. pp. 417–429.

Morrison, J. P. E. 1958. Ellobiid and other ecology in Florida. *The Nautilus* 71:118–124.

Morrison, J. P. E. 1959. The primitive history of some salt-marsh snails. Bull. Am. Malac. Union, Report for 1958, 25:25–26.

Morton, B., J. C. Britton & A. M. de Frias Martins. 1998. Coastal ecology of the Açores. Ponta Delgada: Sociedade Afonso Chaves. 249 pp.

Morton, J. E. 1955. The evolution of the Ellobiidae with a discussion on the origin of the Pulmonata. *Proc. Zool. Soc. London* 125:127–168.

Murty, A. S. & M. Balaparameswara Rao. 1977. Studies on the ecology of Mollusca in a South Indian mangrove swamp. *J. Moll. Studies* 43:223–229.

Odhner, N. H. 1925. *Marinula juanensis*, n. sp. nebst Bemerkungen über der Systematik der Ellobiiden. *Arkiv f. Zool. Stockholm* 17A:1–15.

Orton, A. K. 1976. Distribution of the salt marsh snail (*Melampus bidentatus* Say) in relation to the vegetative cover of a Rhode Island salt marsh. Master of Science thesis, University of Rhode Island. 57 pp.

Pfeiffer, L. 1856. Monographia Auriculaceorum viventium. Kassel, Germany: T. Fischer. 209 pp.

Pfeiffer, L. 1876. Monographia Pneumonopomorum viventium, accedente fossilium enumeratione. Supplementum tertium, Monographiae Auriculaceorum parte secunda auctum. Kassel, Germany: T. Fischer. pp. 241–479.

Reeve, L.A. 1841–1842. Conchologia systematica. London: Longman, Brown, Green and Longmans. 1:1–195, pp. 1–129 [1841]; 2:1–337, pls. 130–300 [1842].

Reeve, L. A. 1877. Conchologia Iconica. Monograph of the genus *Auricula*. Vol. 20. London: J. Reeve. pp. 1–6.

Russell-Hunter, W. D., M. L. Apley & R. D. Hunter. 1972. Early life-history of *Melampus* and the significance of semilunar synchrony. *Biol. Bull. Woods Hole* 143:623–656.

Sasekumar, A. 1974. Distribution of macrofauna on a malayan mangrove shore. *J. Animal Ecol.* 43:51–69.

Zilch, A. 1959 Gastropoda. In: O. H. Schindewolf, editor. Handbuch der Paläozoologie, 6. Berlin: Bornträger. pp. 1–200.