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On the nature of the coastal lagoon winkles attributed to *Littorina tenebrosa* and *Littorina saxatilis*

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Abstract : The name *Littorina tenebrosa* (Montagu) has been used in the past for (at least) two different winkles : *sensu* Muus (1967), etc. for the "lagoon winkle", a small, fragile, low-spired form that lives permanently submerged climbing on macrophytes in non-tidal coastal lagoons and lagoon-like pools, and *sensu* Forbes & Hanley (1853) *et al.* for a large, intertidal, brackish and sheltered shore form with a high spire that also commonly occurs in lagoons, though usually only on the substratum. The Forbes & Hanley usage appears to be that of the original author and in this usage *L. tenebrosa is* generally agreed to be synonymous with the sheltered-habitat form of *Littorina saxatilis*. Authors using the name *sensu* Muus *et al.*, however, have argued that their "*L. tenebrosa*" is not synonymous with *L. saxatilis*. This conclusion is supported by behavioural, morphological and habitat differences between the lagoon winkle and both lagoonal and marine *L. saxatilis*, but not by preliminary breeding experiments. In practice, the lagoon winkle is reproductively isolated from even the sheltered-habitat form of *L. saxatilis* sharing the same lagoonal habitat (*L. tenebrosa sensu* Forbes & Hanley) and it is here given a new name, *Littorina saxatilis* var. *lagunae*. It is suggested that *L. s. lagunae* has had a paedomorphic origin. The nomenclature of the exposed- and sheltered-habitat forms of *L. saxatilis* is also discussed in relation to the nature of the rough winkles in the Venetian Lagoon type locality and in other coastal lagoons ; it is concluded that the names *L. s.* var. *saxatilis* and *L. s.* var. *rudis* both apply to the sheltered habitat form and not, respectively, to the exposed and sheltered forms as used in some recent literature.

Résumé : Le nom de *Littorina tenebrosa* (Montagu) a été utilisé dans le passé pour (au moins) deux espèces différentes : *sensu* Muus (1967) pour l'espèce lagunaire, forme petite, fragile, peu spiralée, vivant en permanence submergée accrochée à des macrophytes dans des lagunes côtières non soumises à marée et *sensu* Forbes & Hanley (1853) *et al.* pour une forme grande, intertidale, d'eau saumâtre et de côte abritée avec une large spirale, forme qui apparaît communément dans les lagunes bien qu'habituellement seulement sur le substrat. L'usage de Forbes & Hanley paraît être la forme de l'auteur d'origine et dans cet usage *Littorina tenebrosa* est généralement admis comme synonyme de la forme à l'habitat abrité de *Littorina saxatilis*. Les auteurs qui emploient le nom *sensu* Muus *et al.*, cependant, ont prétendu que leur *Littorina tenebrosa* n'est pas synonyme de *Littorina saxatilis*. Cette conclusion est confortée par les différences comportementale, morphologique et d'habitat entre l'espèce lagunaire et les deux espèces lagunaires et marines de *Littorina saxatilis*, et non par les expériences d'élevage préliminaire. En pratique, l'espèce lagunaire est isolée pour la reproduction de la forme à l'habitat abrité *Littorina saxatilis* partageant le même habitat lagunaire (*Littorina tenebrosa sensu* Forbes & Hanley) et, l'auteur donne un nouveau nom *Littorina saxatilis* var. *lagunae*. Il suggère l'origine pédomorphique de *Littorina saxatilis lagunae*. La nomenclature des formes à l'habitat exposé ou abrité de *Littorina saxatilis* est discutée ici en relation avec la nature des espèces dans les sites du type de la lagune de Venise et dans d'autres lagunes côtières ; la conclusion est que les noms de *Littorina saxatilis* var. *saxatilis* et *Littorina tenebrosa* var. *rudis* s'appliquent tous deux à la forme d'habitat abrité et non, aux formes d'habitat respectivement exposé et abrité comme le mentionne la littérature récente.

INTRODUCTION

Following the standard monographs of Forbes & Hanley (1853), Jeffreys (1865), Dautzenberg & Fischer (1912) and Fretter & Graham (1962), the rough winkle, *Littorina saxatilis* (Olivi), was until the mid 1970s regarded as being a highly variable species, of which "many trifling varieties have been named" (McMillan, 1968, p. 31), all grading "easily into one another" (Fretter & Graham, 1962, p. 538). Since then, however, it has been generally though not universally agreed that, in Britain and the northeastern Atlantic, rocky-shore populations of rough winkles are composed of four segregate, sibling and often sympatric species : *L. saxatilis s.s.*, *L. nigrolineata* Gray, *L. neglecta* Bean, and *L. arcana* Ellis (Raffaelli, 1979, 1982 ; Graham, 1988 ; Reid, 1989). Most doubt has been expressed on the validity of *L. neglecta*, e.g. by Johannesson & Johannesson (1990), which in any event appears to be the species most closely related to *L. saxatilis s.s.* (Reid 1990).

Smith (1981), amongst others, has also presented a case for subdividing *L. saxatilis s.s.* into two species ; a sheltered-habitat form with a relatively small aperture, which he identified with *L. rudis* (Maton), and a smaller, exposed-habitat, crevice-dwelling one with a relatively large aperture, which he considered to be the true *L. saxatilis*. This has attracted little support (Faller-Fritsch & Emson, 1985), mainly because these exposed and sheltered varieties are connected by intermediates (Janson, 1982), albeit that each does appear to be at a selective advantage in its own characteristic habitat type (Janson, 1983) and to have a distinct reproductive strategy (Faller-Fritsch, 1977). Graham (1988) retains the two names in the form *L. saxatilis saxatilis* and *L. saxatilis rudis* (see Appendix).

The status of a sixth segregate, the lagoon winkle, normally referred to as *L. tenebrosa* (Montagu), *L. saxatilis* var. *tenebrosa* or *L. rudis* var. *tenebrosa* is still undecided. [Unfortunately, it is unlikely that use of the name *tenebrosa* is appropriate (see below and the Discussion)]. Not really at issue is that this "*L. tenebrosa*" is a distinctive winkle restricted to a characteristic habitat type. It is a small form with a very fragile, smooth, black or dark brown and often reticulated, plumply whorled shell that lives not on the substratum but climbing on permanently submerged macrophytes such as *Chaetomorpha, Chara, Ruppia* or *Potamogeton* in coastal lagoons or other nontidal lagoon-like brackish pools (Muus, 1967 ; Remane, 1971 ; Verhoeven, 1980 ; etc.). Although it occurs over a wide range in salinity - down to 6-8 ‰ (Muus, 1967 ; Remane, 1971) - it is uncommon and little studied, not least because its coastal lagoon habitat is itself rare (Barnes, 1989) but also because it only occurs in a few of the apparently suitable and available sites (Barnes, unpublished). When present, however, it may be abundant ; Muus (1967), for example, records adult densities of >30,000/m^2 and juvenile ones of >225,000/m^2.

In spite of its unique ecology and behaviour amongst rough winkles, the literature contains conflicting views as to whether it is a valid species or just an extreme form of the sheltered-habitat variety of *L. saxatilis s.s.* (Fretter & Graham, 1980 ; Graham, 1988). Thorson (1946), for example, was of the opinion that it is the "special ecological type [of *L. saxatilis*] which is capable of surviving under the poorest conditions... [including] under conditions so near its extreme limit for life that it is approaching total degeneration" (p. 171). Janson & Ward (1985) appeared to have settled the issue when they compared Scottish and Swedish individuals of "*L. tenebrosa*" and *L. saxatilis s.s.* and found them to be genetically almost identical, the shell form of one grading smoothly into that of the other along a gradient of shelter. Accordingly, they regarded them as being conspecific, and "*L. tenebrosa*" as being the lagoonal ecotype of *L. saxatilis*. Smith (1982), on the other hand, had earlier pointed out that both "*L. tenebrosa*" and *L. saxatilis s.s.* inhabit lagoons ; indeed, the type locality of *L. saxatilis s.s.* is the Venetian Lagoon, where it was discovered in fissures within the vertical canal walls - a site that it still occupies (Torelli, 1982) - although it is also recorded as occurring in the main body of the lagoon (Torelli, 1978). Further, the two winkles have been recorded as present in the same lagoon (Smith, 1982), as in Cemlyn Lagoon, Anglesey (Barnes, 1987) and The Fleet, Dorset (Seaward, 1980), U.K., for example, and when sympatric there is apparently no overlap in their microhabitats : "*L. tenebrosa*" being found on submerged weed in the lagoonal water mass, whilst *L. saxatilis s.s.* (in its sheltered-habitat form) occurs on the substratum around the margins, usually where gravel or shingle is present (e.g. Smith, 1982 ; Little *et al.*, 1989 ; and see Mill & Grahame, 1990) ; no intermediates have been recorded from such shared localities. Smith (1982) therefore suggested that the two winkles were behaving as if they were good species, and Muus (1967), on the basis of Danish material, has also argued to the effect that (p. 218) "I find it most probable that closer investigations will disclose forma *tenebrosa* as a distinct species".

Regrettably the experimental work of Janson & Ward (1985) is not conclusive, because their "*L. tenebrosa*" were not obtained from lagoons but from sediment, stones and fucoid algae, and on or amongst *Zostera*, in sheltered marine inlets. There must therefore be some question as to whether the material that they compared with their *L. saxatilis s.s.* was the same as the lagoon winkle. Moreover, a survey of the literature indicates that those authors who have argued for the synonymy of the two species have used the name *tenebrosa* for a largely intertidal brackish/marine mudflat winkle, whilst all those who have argued for the validity of a separate *L. tenebrosa* have applied the name specifically to a winkle only living permanently submerged in lagoons (see Discussion). Further studies are clearly needed to resolve the issue of these non-rocky-shore forms (Muus, 1967 ; Smith, 1982) and some such are reported in the present paper.

MATERIALS AND METHODS

Live specimens of rough winkles were obtained mainly from The Fleet lagoon, Dorset (near Langton Herring - SY606813) (lagoonal *L. saxatilis*) and from two adjacent north Norfolk sites, respectively the Salts Hole lagoon, Holkham (TF886451) ("*L. tenebrosa*"), and the West Sands intertidal sand flats, Holkham Bay (TF909469) (interdidal marine *L. saxatilis*). Specific comparison of sympatric "*L. tenebrosa*" and *L. saxatilis* was attempted on winkles from the Cemlyn lagoon, Anglesey (SH330933) and The Fleet, Dorset but in both 1990 and 1991 no "*L. tenebrosa*" could be found at either site. Additional material of *L. saxatilis s.s.* was examined from lagoons and lagoon-like habitats at Snettisham, Norfolk (TF648319), Shingle Street, Suffolk (TM372437) and Brightlingsea, Essex (TM082164), as well as from marine salt pans on Missel Marsh, Scolt Head Island, Norfolk (TF805462). All the above material of *L. saxatilis* was found on the substratum or, more rarely, on floating

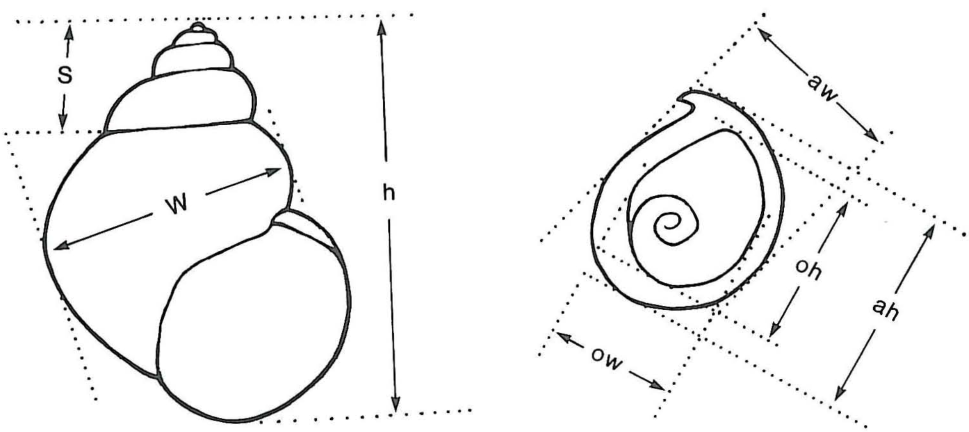

Fig. 1 : Camera lucida drawings of a *Littorina saxatilis* shell and of the operculum in the shell aperture showing the various measurements taken : *s* spire height ; *w* shell width ; *h* shell height ; *aw* aperture width ; *ah* aperture height ; *ow* operculum width ; *oh* operculum height.

mats of filamentous algae, whilst all specimens attributed to "*L. tenebrosa*" were observed climbing on *Ruppia* or on waterlogged wood ; all lagoonal specimens of *L. saxatilis* were present around the margins of the inhabited lagoons, except in The Fleet in which they also occurred in the submerged vegetation.

Various measurements of shell dimensions were taken by means of ocular micrometer as indicated in Fig. 1. The areas of the operculum and shell aperture were estimated by πr^2 in which r = 0.25 [maximum length + maximum breadth] as also shown in Fig. 1. Methods of quantifying shell thickness vary from author to author ; James (1968a), for example, estimated it by measuring the density of the shell and contained snail, whilst Hughes (1979) calculated the ratio of shell weight to external shell volume. Here it was decided directly to measure thickness, at the outer apertural lip, by means of vernier calipers.

Preliminary breeding experiments were carried out from December 1989 to May 1990 in 12 cm diameter glass dishes each containing 10 male and 10 female winkles (of "*L. tenebrosa*" and/or intertidal marine *L. saxatilis* in the four possible intra- and interspecific combinations), together with sea water and (carefully rinsed) algal coated *Ostrea* shells collected from the West Sands locality and *Chaetomorpha* from the Salts Hole. The dishes otherwise conformed to the recommendations of Warwick (1982), except that the water was maintained at a relatively high level to accommodate the life style of the "*L. tenebrosa*". The dishes were inspected for the presence of young snails at intervals over a period of 5 months, the test period regarded as sufficient by Warwick *et al.* (1990). The snails concerned were collected in October 1989 and the sexes of each species were separated and maintained for 2 months in isolation at 12 °C to maximize the chance that any young in the brood chamber could be released before the experiment started. It should be noted, however, that it is uncertain for how long *L. saxatilis* may store sperm after copulation (R.N. Hughes, pers. comm.) and hence certainty in this respect can only be achieved by raising juveniles through to maturity in isolation before conducting breeding tests : this was not attempted here.

RESULTS

In all the winkles examined, regardless of provenance and putative species, the relationship with shell height of (a) shell width (Fig. 2), (b) area of the aperture (Fig. 3) and shell thickness (Fig. 4) clearly each lie on the same line. The lagoonal "*L. tenebrosa*" therefore have thin shells, for example, simply because they are small (Fig. 4). There is a clear difference, however, indeed no overlap, between the interdidal *L. saxatilis* and the lagoonal "*L. tenebrosa*" in the proportion of the shell aperture occluded by the operculum, with the

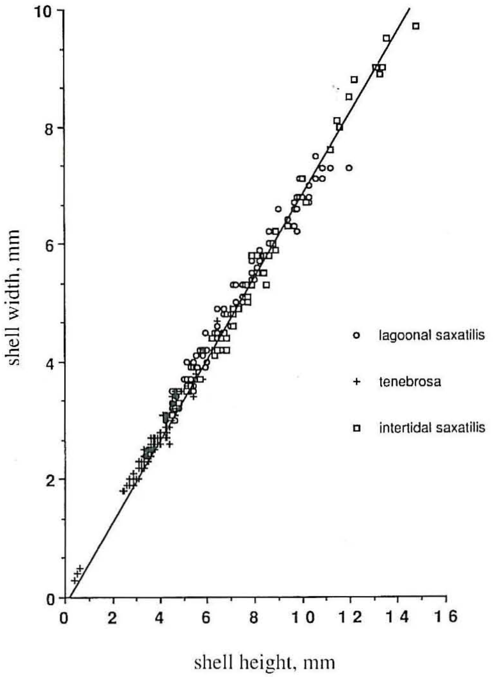

Fig. 2 : The width of the shell in relation to shell size (height) in the lagoon winkle and in both lagoonal and intertidal marine specimens of *Littorina saxatilis* (width = - 0.16 + 0.70 height ; $r^2 = 0.99$).

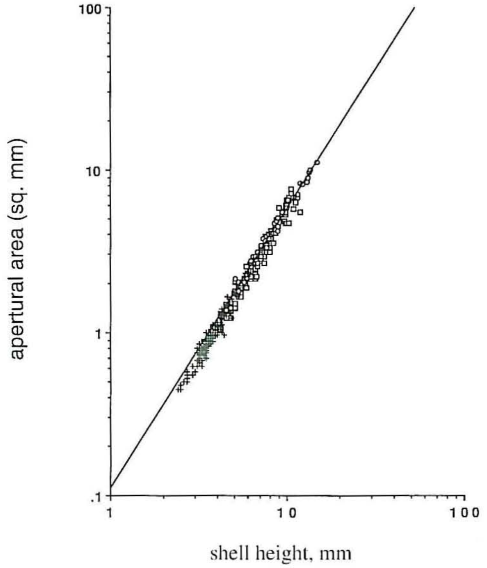

Fig. 3 : The area of the shell aperture in relation to shell size (height) in the lagoon winkle (+) and in both lagoonal (o) and intertidal marine (□) specimens of *Littorina saxatilis* (area = 0.11 height$^{1.72}$; r^2 = 0.98).

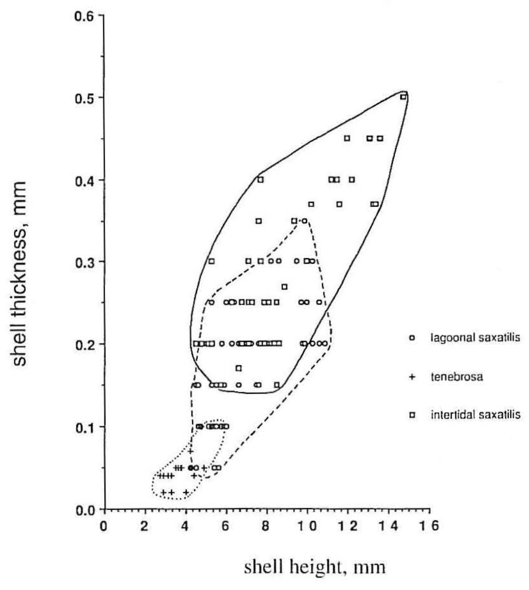

Fig. 4 : The thickness of the shell in relation to shell size (height) in the lagoon winkle and in both lagoonal and intertidal marine specimens of *Littorina saxatilis*.

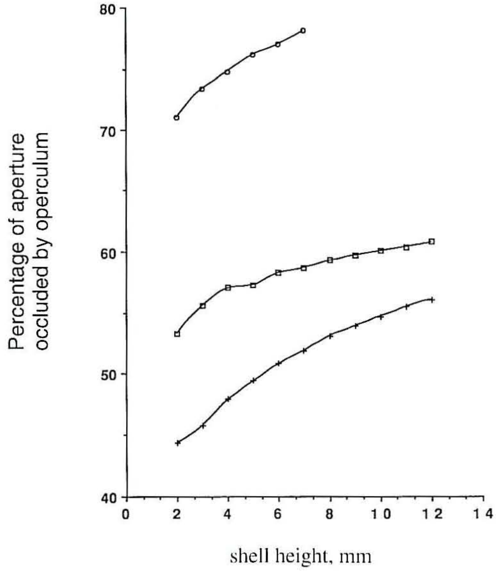

Fig. 5 : The percentage of the shell aperture occluded by the operculum in the lagoon winkle (upper line) in comparison with intertidal marine (lower-line) and lagoonal (middle line) *Littorina saxatilis* in relation to shell size (height). The data on opercular and apertural areas were derived for the various shell heights from the best-fit regression equations of the curves in Figs. 6, 7 & 8.

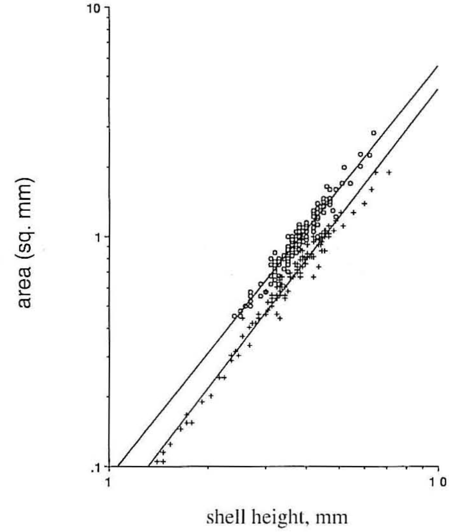

Fig. 6 : The relationship between area of the shell aperture (circles) and of the operculum (crosses) to shell size (height) in the lagoon winkle (aperture = 0.089 height$^{1.79}$; r^2 = 0.98. operculum = 0.060 height$^{1.87}$; r^2 = 0.98).

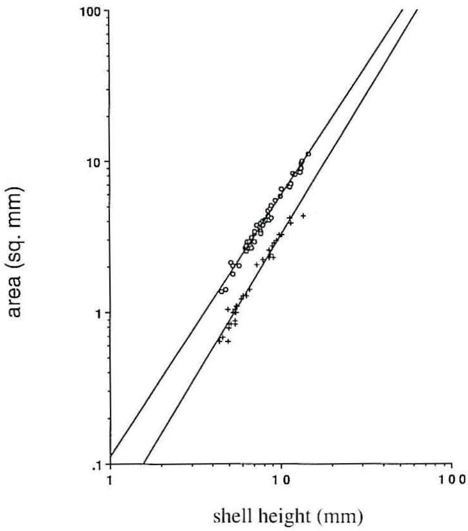

Fig. 7 : The relationship between area of the shell aperture (circles) and of the operculum (crosses) to shell size (height) in intertidal marine *Littorina saxatilis* (aperture = 0.11 height$^{1.72}$; r^2 = 0.98. operculum = 0.043 height$^{1.86}$; r^2 = 0.97)

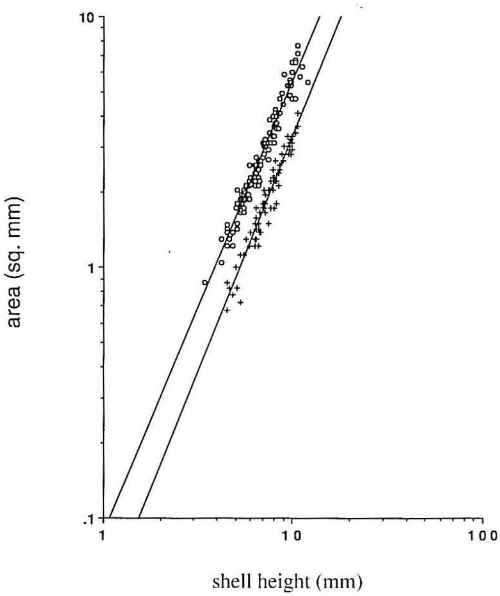

Fig. 8 : The relationship between area of the shell aperture (circles) and of the operculum (crosses) to shell size (height) in lagoonal *Littorina saxatilis* (aperture = 0.087 height$^{1-80}$; r^2 = 0.96. operculum = 0.045 height$^{1.86}$; r^2 = 0.93).

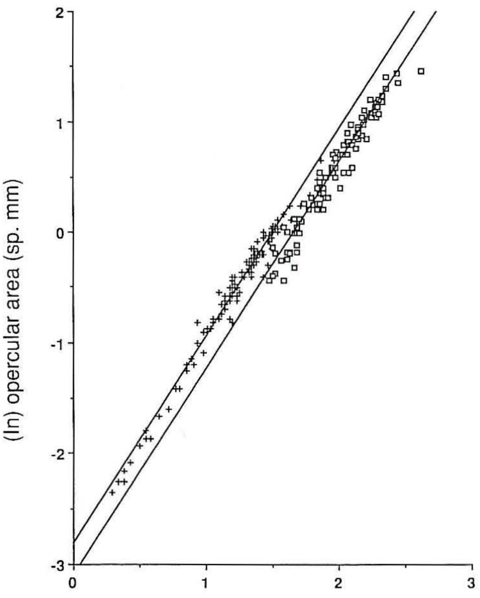

Fig. 9 : Comparison between the relationships of operculum area to shell size (height) in *Littorina tenebrosa* (crosses) and *L. saxatilis* (lagoonal and intertidal marine material combined) (open squares). Data transformed to natural logarithms. (*L. tenebrosa* : ln aperture = - 2.82 + 1.87 ln height ; r^2 = 0.98. *L. saxatilis* : ln aperture = - 3.11 + 1.86 ln height ; r^2 = 0.93.) Note the identical slopes of the two relationships. (ANCOVA ; F_{slope} = 0.02 ; 1223 d.f. ; p = 0.9).

lagoonal *L. saxatilis* being intermediate in this respect (Fig. 5). The operculum of "*L. tenebrosa*" is only slightly smaller than the aperture (Fig. 6) whereas that of *L. saxatilis* is much smaller (Figs 7 & 8). This difference between the two winkles is a result not of interspecific or intervarietal variation in growth of the aperture (Fig. 3) but in that of the operculum (Fig. 9) (ANCOVA ; $F_{elevation}$ = 230 ; 1224 d.f. ; $p < 0.1 \times 10^{-33}$).

The proportion of the shell height taken up by the spire is also significantly less in "*L. tenebrosa*" than in either intertidal *L. saxatilis* (Student's t = 7.1 ; 196 d.f. ; p < 0.0001) or those in lagoons (t = 19.4 ; 275 d.f. ; p < 0.0001). The relative height of the spire is also larger in lagoonal than in intertidal *L. saxatilis* (t = 7.7 ; 173 d.f. ; p < 0.0001) (Fig. 10). The effect of these differences on general shell shape is illustrated in Fig. 11 by camera lucida drawings of "*L. tenebrosa*" and of both lagoonal and sheltered intertidal marine individuals of *L. saxatilis* ; Fig. 11 also includes traced reproductions of drawings of material attributed to *L. tenebrosa* in the early literature for comparison. The use of the name *tenebrosa* for winkles of two radically different shell morphologies, as exemplified by the lagoon winkle and lagoonal *L. saxatilis*, is evident in the latter.

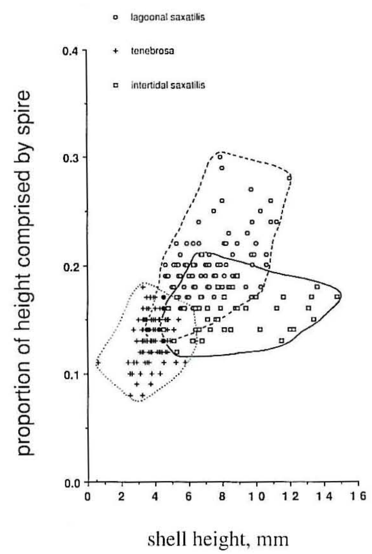

Fig. 10 : The proportion of the shell height comprised by the spire in relation to shell size (height) in the lagoon winkle and both lagoonal and intertidal marine specimens of *Littorina saxatilis*.

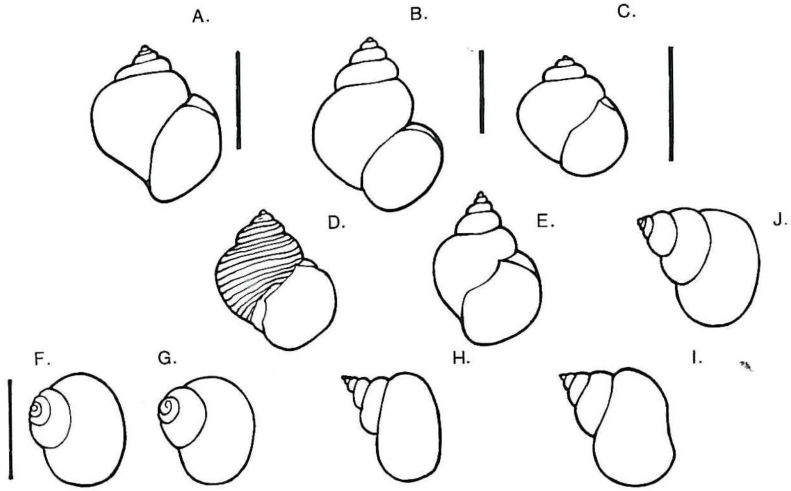

Fig. 11 : Camera lucida and traced drawings of various *Littorina* : A-E in apertural view ; F-J with the shell resting on its aperture. A, sheltered, intertidal marine *L. saxatilis* (West Sands) ; B, lagoonal *L. saxatilis* (The Fleet) ; C, lagoonal *L. tenebrosa* (Holkham Salts Hole) ; D, *L. saxatilis* from the Venetian Lagoon (Torelli, 1982, Fig. 41) with the shell ridges indicated ; E, the *L. tenebrosa* of Forbes & Hanley (1853, Plate 84, Fig. 12) ; F, lagoonal *L. tenebrosa* (Holkham Salts Hole) ; G, the lagoonal *L. tenebrosa* of Muus (1967, Fig. 64) ; H, the *L. tenebrosa* of Montagu (1808, Plate 20, Fig. 4) ; I, the *L. tenebrosa* of Forbes & Hanley (1853, Plate 84, Fig. 11) ; and J, the same specimen of *L. saxatilis* from The Fleet illustrated in "B". Note the similarity of "J" to "H" and "I", and the marked difference between "H"-"J" and "F" and "G". Scale lines 5 mm.

The results of attempts to interbreed "*L. tenebrosa*" and intertidal marine *L. saxatilis* are given in Table 1. Clearly, in the laboratory, at least, when confined in close proximity to each other the two appear to be interfertile in both potential crosses, although possibly less so than "intraspecifically" within either of the two winkle types (however, see "Methods"). It was notable that mortality of the otherwise intertidal *L. saxatilis*, though not that of "*L. tenebrosa*", was high under the permanently submerged conditions that had to be adopted.

TABLE I

Numbers of offspring produced after 5 months in the laboratory in the various possible potential matings between and within intertidal marine *L. saxatilis* and lagoonal *L. tenebrosa*.

tenebrosa : males x females	*tenebrosa* males x *saxatilis* females	*saxatilis* males x *tenebrosa* females	*saxatilis* : males x females
185	56	116	150

DISCUSSION

The genus *Littorina* is believed to be in the process of rapid differentiation (Fretter, 1980 ; Ward & Warwick, 1980) and this is especially true of the *L. saxatilis* aggregate that, unusually amongst winkles (Reid, 1989), contains ovoviviparous species. Microgeographic morphological differentiation of directly-developing winkles is well known (Behrens Yamada, 1989), and even adjacent populations of *L. saxatilis* may vary in shell characteristics quite markedly (van Marion, 1981 ; Janson, 1982 ; Grahame & Mill, 1989), as a consequence of local adaptation and of their poor dispersability (Ward & Warwick, 1980 ; Janson & Ward, 1984 ; Faller-Fritsch & Emson, 1985). Janson (1983), for example, records individuals of this species as moving no more than 4 m in 3 months. Under these circumstances, it would be relatively easy for speciation to occur when barriers to dispersal are present, and in winkles this can apparently take place without the necessity of much genetic divergence (Janson, 1985). Moreover, even in the absence of such geographical barriers, the lagoon winkle and lagoonal *L. saxatilis s.s.* appear still to be reproductively isolated even though they may be potentially capable of interbreeding. They do not overlap in microhabitats exploited when sympatric (Smith, 1982 ; and pers. obs.), and no other winkle varieties span the habitat divide. A combination of ovoviviparity and internal fertilization via copulation provides no opportunity to exchange genes via mobile or dispersive propagules even when both forms occur within one small lagoon. Such is presumably sufficient in itself to account for the lack of recorded intermediates under these circumstances.

Of its distinguishing features, the permanently submerged life of "*L. tenebrosa*" would appear to be the most remarkable in that Berry (1961) and Faller-Fritsch (1975) record

L. saxatilis s.s. (in its sheltered-habitat variety - Raffaelli, 1977) becoming inactive when submerged and then neither feeding nor copulating ; its high mortality in the breeding experiments tends to confirm these observations although copulation under these circumstances may have occurred. It should also be noted, however, that lagoonal *L. saxatilis* although living around the margins must nevertheless also spend considerable periods submerged and, in The Fleet at least, they also occur in a fully submerged state. The changes in behaviour patterns required have been evolved by other gastropods ; lagoonal *Hydrobia ulvae* (Pennant), for example, have lost the tendency of intertidal marine individuals to climb above the water level when submerged, even though populations may only have been isolated within a lagoon for some 250 years (Barnes, 1988a). All other rough winkles, including lagoonal *L. saxatilis*, are also closely associated with the substratum (Mill & Grahame, 1990), whereas the lagoon winkle has very rarely been recorded other than crawling on macrophytes. Barnes (1990), for example, sampled at least twelve 0.01 m^2 quadrats every 4 weeks for nearly 2 years in the Holkham Salts Hole, along a transect immediately adjacent to dense *Ruppia* containing several thousand lagoon winkles per m^2, without finding more than the occasional one on the sediment surface - and that probably accidentally dislodged or stranded by seasonal die-back of the weed (Barnes, unpublished).

Populations of *L. saxatilis s.s.* in lagoons do not appear visibly to have diverged much from the shell form and behaviour of their conspecifics in other highly sheltered coastal habitats, e.g. on salt marshes or intertidal mudflats (Fig. 11), although the spire is significantly larger and higher. Those of "*L. tenebrosa*", however, have evolved a number of features characteristic of other lagoonal molluscs but not otherwise of members of the *L. saxatilis* aggregate ; their ventricosely whorled shells, for example, are parallelled by the lagoonal form of *Rissostomia membranacea* (Adams) [c.f. the marine form of the same species (if they are conspecific ; Munksgaard, 1990)] and by the lagoonal *Hydrobia* [c.f. intertidal marine *H. ulvae*] (Graham, 1988 ; Barnes, 1988a), and their weed-dwelling habits are shared by numerous other lagoonal species (Verhoeven, 1980).

Other typical features are not diagnostic. The shell form of rough winkles is known to be an important genetically-determined component of fitness (Janson, 1983 ; Janson & Warwick in Janson & Ward, 1985) and several workers have commented on the apparent relationship between, on the one hand, shell size, thickness, and relative area of the aperture and, on the other, the degree of exposure of the inhabited shore (e.g. Newkirk & Doyle, 1975 ; Heller, 1976 ; Raffaelli, 1978, 1979 ; Hughes, 1979 ; Smith, 1981 ; Atkinson & Newbury, 1984 ; Janson & Ward, 1984 ; Johannesson, 1986). Shells on exposed shores are smaller, thinner, more globose and have a relatively large aperture as presumed adaptations to inhabiting crevices and to possessing an enlarged foot (Heller, 1976 ; Atkinson & Newbury, 1984), whereas sheltered-habitat individuals have large, thick shells with relatively small apertures to minimize crab predation (Johannesson, 1986), desiccation (Newkirk & Doyle, 1975 ; Grahame *et al.*, 1990) and/or being crushed by mobile pebbles (Raffaelli, 1978). Paradoxically, in being small, thin and rounded the shell morphology of the lagoon winkle is then that typical of the most exposed-habitat rough winkles and not that of, for example, most sheltered populations of *L. saxatilis s.s.*, notwithstanding that it has no need to fit into crevices. Further, the common shore crab, *Carcinus*, may be present (Muus, 1967) or absent (as in the Salts Hole in this study) from lagoons inhabited by the lagoon winkle without any consequent variation in shell morphology. It is notable, however, that all the features jointly characteristic of exposed-habitat *L. saxatilis s.s.* and of the lagoon winkle are precisely those of juvenile rough winkles and therefore it is likely that these shared features indicate a paedomorphic origin, as was suggested for *L. neglecta* by Raffaelli (1979), and that small size, the underlying and determining variable, is a preadaptation both to life in crevices (and empty barnacle shells) and to the weed-dwelling habit. The small number of penial glands and low fecundity considered by Muus (1967) to be distinguishing features of the lagoon winkle are also probably but direct reflections of the animal's small size (Raffaelli, 1979 ; Hughes, 1986).

The formal status of the lagoon winkle still remains open to question. In the laboratory it may interbreed with intertidal marine *L. saxatilis* when the two forms are maintained in close proximity (although see Warwick *et al.*, 1990), yet in nature "*L. tenebrosa*" and *L. saxatilis* appear to occur in different habitats within any shared lagoon. Except in The Fleet, this habitat difference persists in the absence of the other member of the pair ; e.g. in the Shingle Street and Snettisham lagoons where only *L. saxatilis* occurs, notwithstanding that suitable habitat for "*L. tenebrosa*" appears to be present, and in the Holkham Salts Hole from which *L. saxatilis* is absent. They appear to behave as if they are good species and clearly differ in both behaviour and shell morphology. Muus (1967) has drawn attention to the occurrence of pairs of species of which one member is relatively specialist and largely restricted to coastal lagoons, whereas the other is generalist and widely distributed through the coastal zone, being found, for instance, in the sea and in estuaries as well as in some lagoons. The "*L. tenebrosa*" /*L. saxatilis s.s.* pair may provide an example of this phenomenon, although like other gastropods that have been investigated recently - *Hydrobia ulvae* (Barnes, 1988a), *Akera bullata* (Thompson & Seaward, 1989) - the lagoonal and coastal marine populations, although phenotypically distinct and (micro)geographically separate, have not (*Hydrobia*) or probably have not (*Akera*) achieved reproductive isolation in the biological sense. Since in practice it is reproductively isolated the lagoon winkle at least deserves the status of a distinct variety, the more so since Warwick *et al.* (1990) point out that successful crosses within *Littorina* of the type reported here do not necessarily demonstrate conspecificity.

Just what name should be applied to it, however, is far from obvious. The use of Montagu's *tenebrosa* thus far in this paper is *sensu* Muus (1967), Remane (1971), Verhoeven (1980), etc., but other interpretations are possible as noted above. Montagu's original (1803) habitat description : "This littoral species, is found on the mud, and on rocks near high-water mark, and even in ditches subject to the daily flux of the tide." (p. 303) clearly covers winkles other than *L. tenebrosa sensu* Muus (1967), etc., and, it could be argued, does not cover the lagoon winkle at all. His description would include any small, dark brown form. Most early authors, though not Sykes (1892), used the name *tenebrosa* for a winkle living on intertidal mud flats, salt-marshes and in sheltered estuaries or marine inlets (e.g. Alder, quoted by Johnston, 1841 ; Forbes & Hanley, 1853 ; Jeffreys, 1865), including the same habitats in Devon, U.K., as those from which *L. rudis* had earlier been described, although Dautzenberg & Fischer (1912) and more recently James (1968a, b) have used the name *tenebrosa* in connection with rocky-shore winkles, including for some that today are known as *nigrolineata*. The nomenclature of the *L. saxatilis* aggregate is notoriously complicated and confused (Dautzenberg & Fischer, 1912 ; Heller, 1975). Jeffreys (1865), for example, was seemingly unaware of Olivi's (1792) description of *Turbo saxatilis*, and in company with Forbes & Hanley (1853), used that specific name for a winkle then known from the North Sea coast of southern Scotland and northern England and independently described as *Littorina saxatilis* by Johnston (1841). This species is now known as *L. neglecta*. All material that today would be termed *L. saxatilis* was known to Montagu (1803), Johnston (1841), Forbes & Hanley (1853) and Jeffreys (1865) as *L. rudis*. Forbes & Hanley (1853) were aware of Olivi's species but they considered it to be a synonym of *L. neritoides* (Linn.) (which can also be found in the Venetian Lagoon ; Torelli, 1982). In the light of this confusion and because the lagoon winkle was then apparently unknown, it is hardly surprising that all these early authors were using the name *tenebrosa* for a winkle that would today be termed the most sheltered-habitat form of *L. saxatilis*, including the benthic non-paedomorphic winkles in lagoons. It then appears that later authors working in the coastal lagoon habitat uncritically applied Montagu's name to their form too. This confused position has not been aided by uncertainty as to which variety of *L. saxatilis s.s.* occurs in the Venetian lagoon type locality (see Appendix).

It is not then contentious that the *L. tenebrosa* of Montagu (1803), Forbes & Hanley (1853) and other authors, the rocky shore material described as *L. saxatilis tenebrosa* by Dautzenberg & Fischer (1912), the Swedish material given that name by Janson & Ward (1985), the British material here compared with the lagoon winkle and referred to in the Appendix as *L. saxatilis* var. *saxatilis*, and more generally the sheltered habitat and often estuarine form associated by Graham (1988) with the name *rudis* (including *L. rudis* (Maton) itself), and most of the Venetian lagoon material (see Appendix) are conspecific. This conclusion has already been reached by Janson (e.g. 1982, 1985 ; Janson & Ward, 1984, 1985) after her various comparisons. It therefore follows, however, that if Montagu's *tenebrosa* is but the most sheltered-habitat variety of the "estuarine winkle", or *L. saxatilis* var. *saxatilis*, which even in the Venetian lagoon is intertidal in habitat (Torelli, 1982), then the specialist submerged, nontidal-lagoon winkle, or *L. tenebrosa sensu* Muus (1967), cannot bear Montagu's name.

That being so, as far as this author is aware the lagoon winkle is currently without a valid name, none of the many names applied to rough winkles (Dautzenberg & Fischer, 1912 ; Fischer-Piette & Gaillard, 1971) having been based on this form although some English records of *L. palliata* (Say) (Forbes & Hanley, 1853 ; Sowerby, 1859) - though not the *Turbo palliatus* of Say (1821) itself - may be of this species. Accordingly, the name *Littorina saxatilis* var. *lagunae* nov. (the varietal name being from the romance languages derivative of *lacuna*, Latin for a natural hollow filled with water, especially a pool or lagoon) is here applied to that member of the *Littorina saxatilis* aggregate species that, characteristically, lives permanently submerged amongst vegetation in coastal lagoons and lagoon-like pools in northwestern Europe. Morphologically, it has an almost black shell when juvenile but adults frequently possess on the last whorl a dark brown reticular pattern of the type illustrated by Muus (1967 ; fig. 64), the many other colour varieties known in *L. saxatilis s.s.* do not occur ; the shell is small (usually < 6 mm height), smooth (i.e. without spiral ridges), globose, fragile by virtue of being extremely thin walled (*c.* 0.1 mm thick), and with a low, rounded spire and an aperture almost completely filled by the operculum ; maturity is reached at *c.* 3 mm shell height when some 4 months old and maximum life span is of the order of 2-3 years (Muus, 1967) ; the soft-part anatomy is as in *L. saxatilis s.s.* (Fretter & Graham, 1980).

L. s. var. *lagunae* and *L. saxatilis s.s.*, although differing quite markedly in behaviour and habitat, can nevertheless be similar in shell thickness and tenebrous colour (Smith, 1982) ; the lagoon winkle being particularly difficult to distinguish in these respects from the form of *L. saxatilis* originally described by Montagu (1803) as *Turbo tenebrosus* - the cause of much of the confusion recorded above. As pointed out by Forbes & Hanley (1853), Jeffreys (1865) and more recently by Newkirk & Doyle (1975) and Hughes (1979), however, and confirmed by examination of some of Montagu's original material, the shell of the mudflat winkle occurring in highly sheltered localities (including in lagoons) has a prominent and acute spire (Fig. 11), as clearly shown by Montagu himself (1808, Plate 20, Fig. 4) and Dautzenberg & Fischer (1912, e.g. Plate 10, Figs 4, 9 & 10) whereas that of the lagoon winkle is depressed and rounded (this paper, Figs. 10 & 11). Seen from above, *L. s. lagunae* also lacks the prominent and projecting columellar lip of sheltered-shore populations of the rough winkle (Fig. 11). These two features will therefore serve to identify material if precise habitat data are not available.

APPENDIX : *LITTORINA SAXATILIS* IN THE VENETIAN LAGOON

Smith (1981) compared individuals of *L. saxatilis* from Scivolo Macello in the city of Venice to British rocky shore material and considered them to lie well within the range of his restricted meaning of *L. saxatilis* (the exposed-cliff habitat, crevice-dwelling form) on the basis of their large aperture. Thus Graham (1988) termed the exposed-shore variety *L. saxatilis saxatilis*. Janson (1985), however, found that specimens from the Chioggia region of the Venetian lagoon, although occurring at high tide level on the vertical walls of a road bridge (i.e. an appropriate exposed-habitat *L. saxatilis* location) had the shell morphology of Swedish "*L. tenebrosa*". This Chioggia material was of the tesselated shell form described by Torelli (1978) as being the dominant type within the city of Venice, which as illustrated by that same author (Torelli, 1982) is clearly the small-apertured, sheltered-habitat type of *L. saxatilis*, termed by Graham (1988) *L. saxatilis rudis*. The same tesselated shell pattern is displayed amongst the lagoonal *L. saxatilis* in The Fleet (pers. obs.). The dominant form within the Venetian lagoon itself (Dautzenberg & Fischer, 1912 ; Torelli, 1982) is characteristically salmon pink to pale fawn in colour (Dautzenberg & Fischer's, 1912, "var. ex col. *fulva* Monterosato"), a colouration unknown in *L. s. lagunae* which is diagnostically the tenebrous var. *fusca* that gave rise to the specific name of *tenebrosa*.

For this and other reasons there would appear to be two different winkles referred to as *L. saxatilis* in the Venetian lagoon (S.M. Smith and A. Torelli *in litt.*). Thus the material from there described and figured by James (1968a, b) is of a small, thin-shelled, apparently paedomorphic form not unlike *L. neglecta, L. s. lagunae*, etc., whereas that described and illustrated by Torelli (1978 ; 1982) is, in contrast, the larger, non-paedomorphic species with spiral ridges around its shell, as indicated above. To which of the two Olivi (1792) originally gave the name *saxatilis* is unknown ; his description could include either or both, and his illustrations are inconclusive although tending towards Torelli's material. This would also seem to be the most widespread type on the canal walls, the type habitat (Torelli, 1978 ; 1982). If this is so, then, not surprisingly considering the sheltered nature of coastal lagoons, Olivi's *saxatilis* and Maton's (estuarine) *rudis* are not only synonymous (Janson, 1985 ; Warwick *et al.*, 1990) but both are of the sheltered-habitat variety. It is then this form that must be the nominate *L. saxatilis* var. *saxatilis*. Further complicating the matter is the opinion of Smith (1982) that some or all of the Venetian *L. saxatilis s.s.* may be an accidental introduction from elsewhere, *L. saxatilis* being otherwise virtually unknown in the Mediterranean, i.e. except for two other possible sites of introduction, including the nearby Grado-Marano Lagoon (Smith, 1982 ; Torelli, 1982).

The nature of the apparently paedomorphic form in the Venetian lagoon is as yet unknown. The fact that its shell is described as being pale grey or grey and white (James, 1968a) does not argue in favour of its being *L. s. lagunae*, neither does the stated habitat of Smith's (1981) material - the walls of the canals. Perhaps paedomorphic populations of *L. saxatilis* are commonly and independently established in suitable habitat types and can then spread to adjacent lagoons that lack *L. saxatilis* via floating macrophyte debris during coastal flooding (Barnes, 1988b).

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