Littorina naticoides, New Species, with Notes on the Other Smooth-shelled *Littorina* Species from the Northwestern Pacific

David G. Reid
Department of Zoology
The Natural History Museum
London SW7 5BD, U.K.

Alexander N. Golikov
Zoological Institute
Academy of Sciences of the U.S.S.R.
Leningrad 199034, U.S.S.R.

ABSTRACT

A new species, *Littorina* (*Neritrema*) *naticoides*, is described from the northwestern Bering Sea, Kamchatka and Kurile Islands. It is believed to be the sister species of *L. aleutica* and they can be distinguished by penial and shell characters. The two are allopatric, *L. aleutica* showing an oceanic distribution and *L. naticoides* a more continental one, but their ranges are known to approach to within 250 km of each other. Five *Littorina* species from the northwestern Pacific have smooth-shelled forms, which can be difficult to distinguish. These are *L.* (*N.*) *naticoides*, *L.* (*N.*) *aleutica*, *L.* (*N.*) *sitkana*, *L.* (*N.*) *subrotundata* and *L.* (*Littorina*) *kasatka*. The diagnostic features of their shells and reproductive anatomy are reviewed.

Key words: *Littorina*; Pacific; biogeography.

INTRODUCTION

Systematic studies of the family Littorinidae have been revolutionised by two developments over the past two decades. Firstly, anatomical features have been found to be more reliable than traditional shell characters for identification of species, and, secondly, there has been a growing appreciation of the wide range of shell variation shown by some species, and an understanding of its biological significance. The first use of anatomical characters to discriminate between sibling species (with similar or identical shells) was in the genus *Littorina*. (The generic name is here used in the strict sense, as defined by the cladistic analysis of Reid, 1989a). The most informative of these new characters have proved to be the shape of the penis, type of egg capsules and development (Sacchi & Rastelli, 1966; Heller, 1975; Hannaford Ellis, 1979; Murray, 1979) and also the form of the pallial oviduct (Reid, 1989a, 1990a). In all cases, studies of electrophoretically detectable genetic variation have supported the status of the sibling species initially recognized by anatomical differences (Ward, 1990). Although sometimes only one or other sex can be unequivocally identified by anatomical characters, there are no known cases of morphologically inseparable *Littorina* species.

Extreme intraspecific variation in coloration, sculpture and shape of the shell is a well-known feature of *Littorina*, and contributes to the difficulties of identification. Shell variation is especially marked in those species which show direct development, for here the lack of a widely-dispersed larval phase enhances the potential for adaptation to local environments. Selective factors influencing morphological and color variation between populations are believed to include predation, wave action and damage by mobile boulders (e.g., review by Raffaelli, 1982; Janson, 1982, 1983; Johannesson, 1986; Seeley, 1986). Other factors such as growth rate can also contribute to non-genetic shell variation (Kemp & Bertness, 1984).

The genus *Littorina* is restricted to the northern hemisphere, and most species occur on temperate and cold temperate shores (Reid, 1990b). So far, modern systematic revisions using anatomical details have only been done in Europe and the northeastern Pacific. *Littorina* species are also abundant in the northwestern Pacific, and the most recent review of the littoral molluscs of the Siberian region (Golikov & Kusakin, 1978) recognized six species: *L. squalida* Broderip & Sowerby, 1829; *L. brevicula* (Philippi, 1848); *L. mandshurica* Schrenck, 1861; *L. aleutica* Dall, 1872; *L. sitkana* Philippi, 1846; *L. kurila* Middendorff, 1848. The identifications were based only on characters of the shells. The first anatomical work on northwestern Pacific *Littorina* was done as part of a cladistic analysis of the 20 species then recognized in the genus (Reid, 1990a). This largely supported the classification of Golikov and Kusakin (although *L. kurila* was synonymized with *L. sitkana*), but the anatomical material used did not include any from the Soviet Union.

As part of a wider study of the systematics and distribution of *Littorina* species (Reid, in prep.), it has recently been possible to examine the extensive collection of preserved material from the Siberian coast held in the Zoological Institute, Leningrad. Preliminary results indicate that *L. squalida*, *L. brevicula* and *L. mandshurica* can each be readily identified by shell characters, as described and illustrated by Golikov and Kusakin (1978) and Reid (1990a). The remaining three of the species listed above were distinguished by Golikov and Kusakin (1978) primarily by their shell sculpture: *L. sitkana* having spiral ribs, *L. kurila* being smooth or almost so, and *L. aleutica* having rows of nodules. This division now seems to be an artificial one. Differences in reproductive

anatomy define five species in this group: *L. sitkana*, *L. aleutica*, *L. subrotundata* (Carpenter, 1864), *L. kasatka* (recently described by Reid *et al.*, 1990) and *L. naticoides*, which is described herein. The shell characters of all five species are variable, and in particular *L. sitkana*, *L. aleutica* and *L. subrotundata* can show smooth or sculptured shells. "*Littorina kurila*," as defined by Golikov and Kusakin (1978), embraced smooth or slightly sculptured forms of all five species.

The nomenclature of these species is rather complex. During the wider study of *Littorina* systematics all available type specimens (housed in Natural History Museum, London; National Museum of Natural History, Washington, D.C.; Zoological Institute, Leningrad) have been examined and all original descriptions consulted, to ascertain that the new species is indeed undescribed. The available names include 18 synonyms of *L. sitkana* and three of *L. subrotundata*. Complete synonymies and full accounts of the described species will be given elsewhere. Here it need only be noted that preserved syntypes of *L. kurila* Middendorff, 1848 in the Zoological Institute, Leningrad, have shown that this taxon is a synonym of *L. sitkana* (see note added in proof in Reid, 1990a). As discussed below, the name "*L. kurila*" was incorrectly applied by Reid (1989a, 1990a,b) to what is here considered an open-coast form of *L. subrotundata*.

In the present paper the new species will first be described, then the four other similar species which sometimes show smooth shells will be discussed and distinguished.

MATERIALS AND METHODS

This resolution of the smooth-shelled *Littorina* species of the northwestern Pacific is based on examination of all material in the collections of the Natural History Museum, London (BMNH), the Zoological Institute, Leningrad (ZIL) and the National Museum of Natural History, Washington, D.C. (USNM). The new species is described from 21 lots in the ZIL, many of which are duplicated in the BMNH. A total of 27 males and 18 females were dissected, from 8 localities covering the known range of the species. Five radulae were extracted from specimens from three localities, and after cleaning in hot, concentrated sodium hydroxide solution were examined by scanning electron microscopy. For comparison, 32 specimens of *L. aleutica*, 82 of *L. subrotundata*, 45 of *L. sitkana* and 19 of *L. kasatka* were dissected, all from a wide range of localities.

SYSTEMATIC DESCRIPTION

Littorina (*Neritrema*) *naticoides* new species
(figures 1–12, 15–23, 28–35, 37)

Types: holotype BMNH 1990053, Milne Bay, Simushir I., Kurile Is, USSR (figures 1, 16); 2 dry paratypes BMNH 1990054; 6 paratypes in alcohol BMNH 1990055; 2 paratypes in alcohol ZIL.

Etymology: *Natica*-like, a reference to shell shape.

Shell (figures 1–12): *Dimensions:* Adult size range 6.2–15.9 mm shell height.

Shape: Teleoconch approximately 4 whorls, moderately solid. Turbinate, often rather patulous, whorls smoothly rounded, sutures distinct. Columella relatively wide, slightly excavated, pillar concave.

Sculpture: Protoconch 0.73–0.75 mm diameter, 1.8 whorls. Teleoconch: indistinct axial growth lines only, no spiral grooves; faint spiral striae sometimes visible at high magnification, but no strong striations.

Color: Orange brown to dark purple brown, usually 5–12 dark brown or black spiral lines; sometimes a pale spiral band on base. Aperture orange brown to purple brown. Columella white, sometimes tinged purple brown.

Animal: *Head-foot (figures 28–30):* Head grey to black, paler at tips of tentacles and snout; unpigmented patch over eye and usually another at inside of tenacle base. Sides of foot usually pale grey speckles or unpigmented, sometimes blackish.

Operculum: normal, paucispiral littorinid (type A of Bandel & Kadolsky, 1982).

Penis (figures 15–20): Wrinkled base with 4–15 mamilliform penial glands in single row on anterior edge (one specimen with a single gland); filament short, less than half length of base, broadly triangular, with simple subepithelial glandular region (more opaque in preserved specimens); sperm groove open to tip.

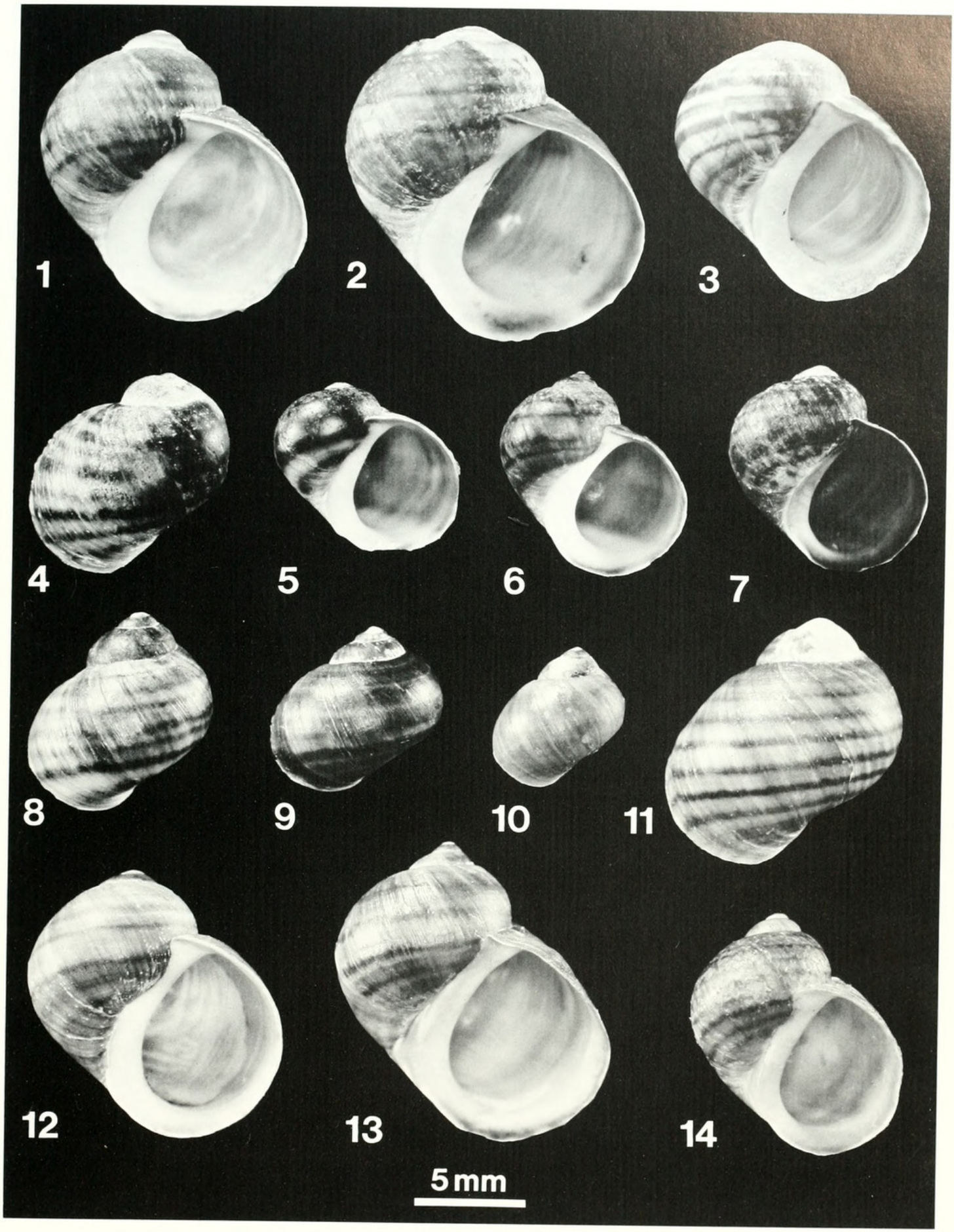
Pallial oviduct (figures 21–23, 37): Complex spiral of 3 loops, first of albumen gland, second and third of capsule gland; final straight section a large, swollen, septate jelly gland. Bursa copulatrix in anterior position.

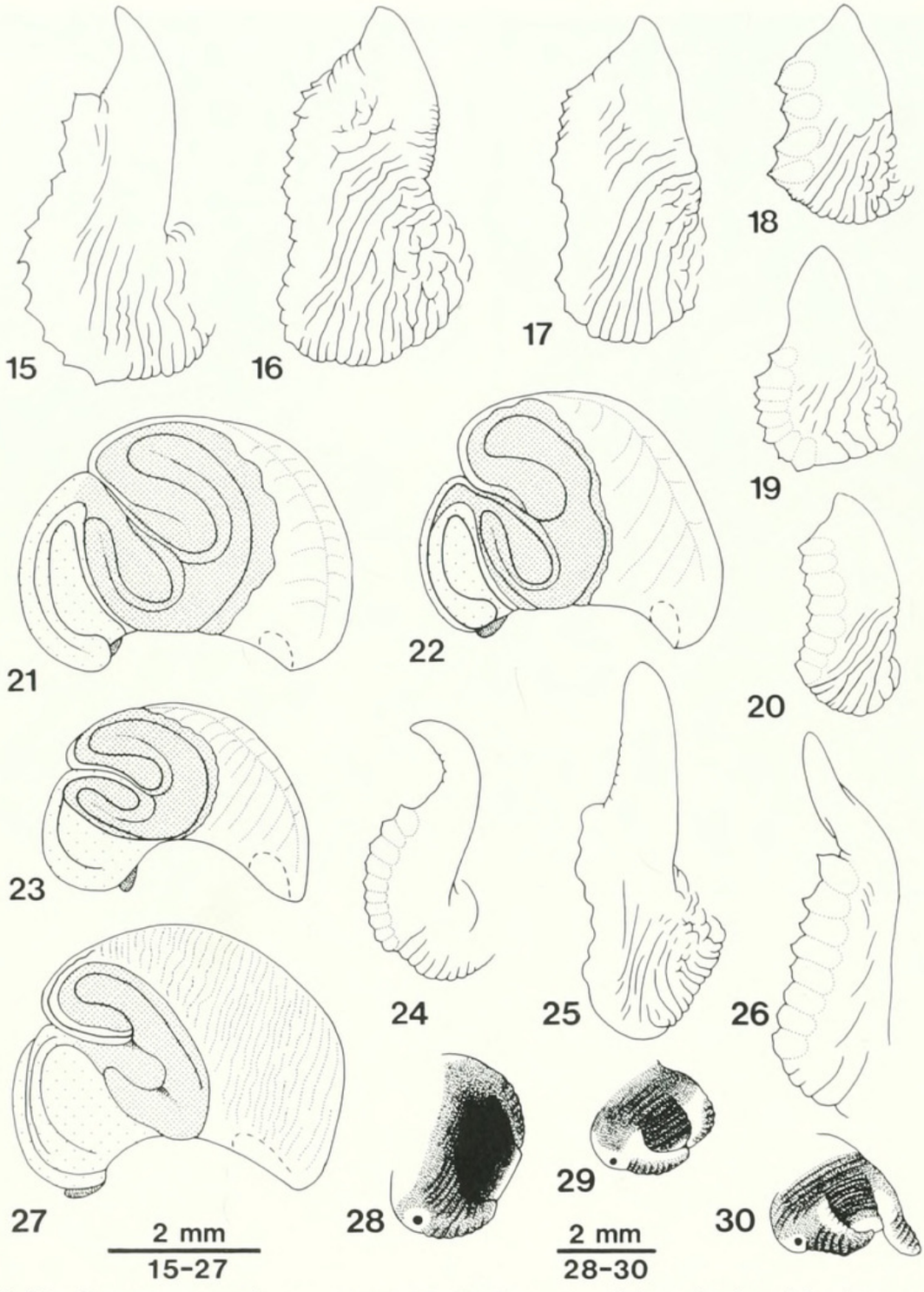
Spawn: Benthic, gelatinous egg mass up to 6 mm in diameter, containing spherical capsules 0.7–0.8 mm in diameter, each with single egg surrounded by albumen layer 0.5–0.6 mm in diameter.

Radula (figures 31–34): All cusps bluntly rounded. Rachidian with 3 large, 2 small cusps; outline of tooth (viewed flat from above) varies from square to oblong (ratio of length of tooth: width at mid-point 0.77–2.0). Lateral and inner marginal teeth each 4 large cusps. Outer marginal 5–7 cusps.

Distribution: *Habitat:* A range of intertidal habitats are reported: on dead shells in sheltered inlets; *Mytilus*

Figures 1–12. *Littorina naticoides* new species. **1.** Holotype (BMNH 1990053), Milne Bay, Simushir I., Kurile Is. **2, 3.** Ozernovskiy, Kamchatka. **4, 5.** 10 km east of Cape Kamchatskiy, Kamchatka. **6.** Avacha Bay, Kamchatka. **7.** Kronotskiy Gulf, Kamchatka. **8–10.** Egvekinot Inlet, Anadyrskiy Gulf. **11, 12.** Ozerniy River estuary, Kamchatka. **Figure 13.** *Littorina aleutica*, Provideniya. **Figure 14.** *Littorina subrotundata*, Milne Bay, Simushir I., Kurile Is. (All specimens in BMNH).


1
2
3
4
5
6
7
8
9
10
11
12
13
14
5 mm

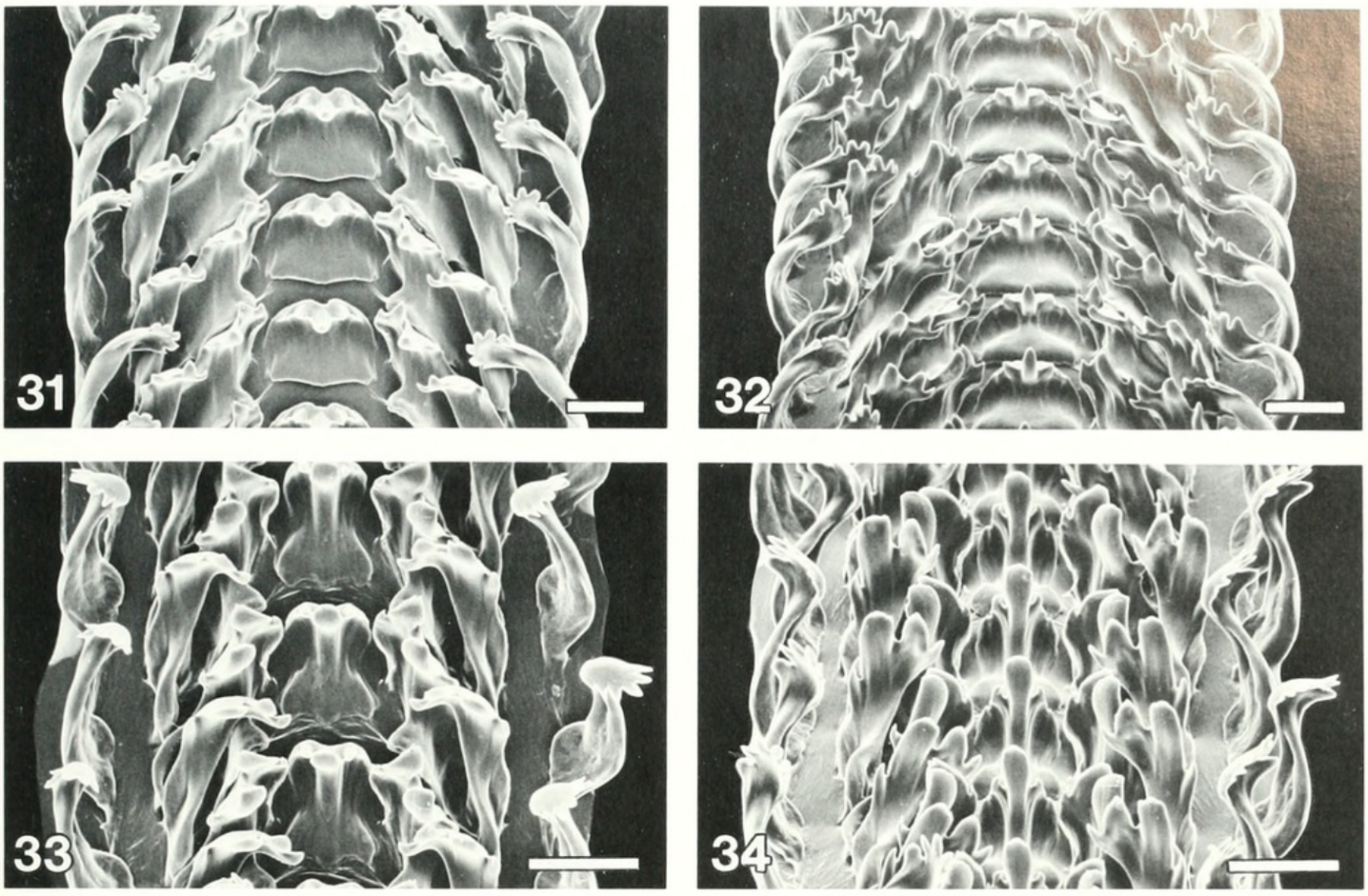


Figures 15–23, 28–30. *Littorina naticoides* new species. **15–20.** Penes: mamilliform glands on left edge, sometimes visible by transparency. **21–23.** Pallial oviducts. **28–30.** Heads. **15, 17, 18.** Ozernovskiy, Kamchatka. **16.** Penis of holotype, Milne Bay, Simushir I., Kurile Is. **18, 19, 23, 30.** Krista Gulf, Anadyrskiy Gulf. **20.** Egvekinot Inlet, Anadyrskiy Gulf. **21, 29.** Kronotskiy Bay, Kamchatka. **22.** 10 km east of Cape Kamchatskiy, Kamchatka. **Figures 24–27.** *Littorina aleutica*. **24–26.** Penes. **24, 26.** Lihacheva, Provideniya. **25.** Adak I., Aleutian Is. **27.** Pallial oviduct, Nizki I., Aleutian Is. Key to figures 21–23, 27: sparse stipple, albumen gland; dense stipple, capsule gland; dotted lines, septa of jelly gland (visible by transparency); dashed lines, bursa copulatrix (visible only by dissection).

zone on exposed shores; on *Halosaccion* (red alga); in *Alaria* (brown alga) belt.

*Range (figure 35):*Kurile Islands, south and west Kamchatka, Anadyrskiy Gulf.

Records: Kurile Is: Urup I.; Milne Bay, Simushir I.; Spaseniya, Simushir I.; Diani Bay, Ketoi I., Paramushir I.; Kamchatka: Ozerniy River estuary, Okhotsk Sea; Ozernovskiy; Avachinskaya Bay, near Cape Vilkova; Avacha Bay, near Petropavlovsk; Kronotskiy Gulf; 10 km east of Cape Kamchatskiy; Anadyrskiy Gulf: Egvekinot Inlet, Krista Gulf (all ZIL and BMNH).



Figures 31–34. Radulae of *Littorina naticoides* new species. Scale bars = 50 μm. **31, 32.** 10 km east of Cape Kamchatskiy, Kamchatka. **33, 34.** Egvekinot Inlet, Anadyrskiy Gulf. **31, 33.** Viewed flat. **32, 34.** Same radulae as figures 31, 33, but viewed from an angle of 45° to show cusp shape.

Similar species: As mentioned above, *L. kurila* Middendorff, 1848 is a junior synonym of *L. sitkana* Philippi, 1846, but the name has been widely used in the literature for any of the five *Littorina* species (including *L. naticoides*) in the northwestern Pacific that frequently have smooth shells. The other four members of the group will be considered in turn, and the characters of all five species are summarized in table 1. Radular characters have not proved useful in discriminating between them.

L. (Neritrema) sitkana (figure 39): The typical form of this species has a strongly carinate shell with spiral stri-

Table 1. Summary of characters of five *Littorina* species from the northwestern Pacific.

		aleutica	*kasatka*	*naticoides*	*sitkana*	*subrotundata*
Shell:	adult size (mm)	6–14	6–11	6–16	6–23	4–14
	patulous shape	+	–	+	–	(+)
	nodulose sculpture	(+)	–	–	–	–
	spiral ribs	(+)	–	–	(+)	(+)
	spiral microstriae	+	–	–	(+)	–
	pattern of dark spiral lines	(+)	–	+	(+)	+
	pattern of pale flecks	–	+	–	–	–
Penis:	mamilliform glands	7–12	0	1–15	5–14	5–17
	filament ≥ ½ length of base	+	–	–	–	–
Pallial oviduct:	spiral pattern	fig. 38	fig. 36	fig. 37	fig. 39	fig. 40
	swollen, septate jelly gland	+	–	+	+	+
Spawn:	benthic egg mass	+	–	+	+	+
	pelagic capsules	–	+	–	–	–

+ = Present; (+) = sometimes present; – = absent.

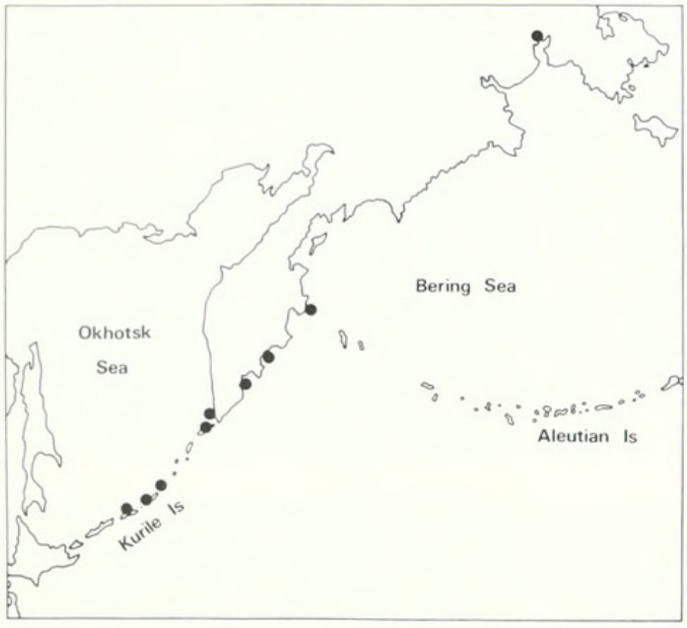


Figure 35. Distribution of *Littorina naticoides* new species.

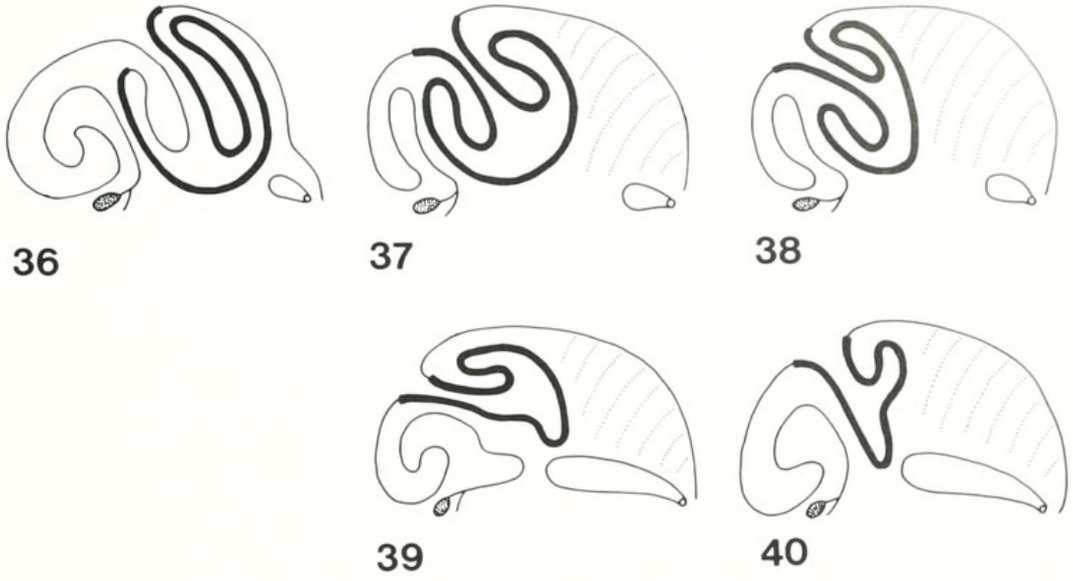
ations between the carinae (e.g., Reid, 1990a: fig. 11) and is most frequent in the north and northeastern Pacific from Oregon to the Aleutian Islands, while in northern Japan it is usually only the base that bears strong grooves. In either case the shell is thereby distinguished from all others in the group except rare forms of *L. subrotundata*. Problems arise with the smooth forms of this species (Reid *et al.*, 1990: figs 5–7), which predominate in the Kurile Islands and Kamchatka, and also occur in other parts of the range. These shells may be quite large (up to 23 mm), are less patulous than *L. naticoides* and *L. aleutica* and are often uniformly black or brown (except in the Okhotsk Sea, *L. sitkana* commonly lacks the pattern of narrow black lines seen in *L. naticoides* and *L. subrotundata*). Synonyms based on smooth forms of this species include *L. kurila* Middendorff, 1848, *L. subtenebrosa* Middendorff, 1848 and *L. sitkana* var. *atkana* (Dall, 1886). Females of *L. sitkana* can be immediately recognized by the unique spiral pattern of the pallial oviduct (figure 39; Reid *et al.*, 1990: fig. 21) with its long backward loop of capsule gland, but the penis is similar to that of both *L. naticoides* and *L. subrotundata*.

L. (Neritrema) subrotundata (figures 14, 40): There has been confusion about the identity of this species, and the name is here used in a wider sense than by previous authors. As interpreted here, the species has a wide distribution around the northern Pacific, from northern California through the Aleutian Islands to the southern Kurile Islands.

The name has previously been applied only to the thin-shelled, tall-spired form (Reid, 1990a: fig. 1n) initially described by Carpenter (1864) as a doubtful member of the genus *Assiminea*. Synonyms are ?*Paludinella castanea* Carpenter, 1865, and *Paludinella newcombiana* Hemphill, 1877, and the species has sometimes been placed in the genus *Algamorda* Dall, 1918 (a synonym of *Neritrema* Récluz, 1869, regarded as a subgenus of *Littorina*, see Reid, 1989a). The species was poorly known and believed to be restricted to brackish-water salt marshes from northern California to Washington (MacDonald, 1969; Reid, 1990b). The form from this habitat is analogous to the form "*tenebrosa*" of the Atlantic *L. saxatilis* (Olivi, 1792), which is also small, thin-shelled and tall-spired (Muus, 1967; Janson & Ward, 1985), probably as a result of similar selection pressures or ecophenotypic effects in the brackish lagoons in which it occurs. This form of *L. saxatilis* contrasts with the lower-spired and more patulous form on exposed coasts (e.g., Raffaelli, 1979; Janson, 1982).

As a result of the dissection of additional material, it is now believed that, like *L. saxatilis*, *L. subrotundata* also occurs in habitats covering a wide range of wave exposures, and has a similarly wide range of variation in shell morphology. The forms from exposed rocky coasts, here assigned to *L. subrotundata* for the first time, have (like *L. saxatilis* from similar habitats) a lower spire and larger aperture than the salt-marsh form, and were previously incorrectly identified as *L. kurila* (Reid, 1990a, b). A shell of this type from the Aleutian Islands was illustrated by Reid (1990a: fig. 1m), and figure 14 shows a slightly more patulous form. A population from the exposed shores of Tatoosh Island, Washington, has recently been studied by Boulding (1990), who concluded that it was an undescribed subspecies of *L. kurila*. However, examination of specimens from this locality has revealed no significant anatomical differences from either typical *L. subrotundata* collected in salt marshes in Washington, or from specimens of this species from the Aleutian Islands. Furthermore, no diagnostic allelic differences between samples from these three areas have been found by enzyme electrophoresis (E. G. Boulding, personal communication). The available evidence therefore suggests that they are conspecific, but further study would be desirable. Neither the known geographical distribution of *L. subrotundata*, nor its considerable variation in shell morphology throughout its range, support its division into subspecies.

One reason why the name *L. subrotundata* has not previously been used for the exposed-coast form is that, at least in Washington, it appears to be completely ecologically segregated from the typical form in salt marshes, because the species is not known to occur in intermediate habitats. This locally disjunct distribution need not, however, imply genetic isolation of the two forms. It could be maintained, for example, by the action of crab or other predators. It is known that the exposed-coast form is susceptible to attack by crabs because of its thin shell, and that crabs are more abundant in protected rocky habitats than on exposed coasts (Boulding, 1990). It is possible that both exposed coasts and salt marshes are refuges for this species from crab predators. Further north in its range, in Alaska (personal observation), *L. subrotundata* does occur on both exposed and sheltered rocky shores and there is continuous variation in shell shape between the two extremes of habitat. In-



Figures 36–40. Diagrammatic representation of pallial oviducts of *Littorina* species from the northwestern Pacific. **36.** *Littorina (Littorina) kasatka*. **37.** *L. (Neritrema) naticoides*. **38.** *L. (N.) aleutica*. **39.** *L. (N.) sitkana*. **40.** *L. (N.) subrotundata*. Key: continuous line with spiral loops represents path of egg groove through pallial oviduct; thick section, capsule gland; dense stipple, seminal receptacle at posterior end; anterior sac, bursa copulatrix; dotted lines, septa of jelly gland. Shape of loops of capsule gland and its relative size are most important features. Oviducts of *L. aleutica* and *L. naticoides* sometimes indistinguishable; c.f. figures 21–23, 27.

terestingly, there is again a parallel with *L. saxatilis*, which shows a comparable segregation of low-spired and high-spired forms on exposed coasts and in salt marshes respectively, at the southern limit of its European range (Gofas, 1975; personal observation), whereas at more northerly latitudes it occupies the entire spectrum of habitats and morphological intermediates are common (Janson & Ward, 1985; personal observation).

The shell of *L. subrotundata* is often extremely similar to that of *L. naticoides* in size, coloration and shape, although it does not attain such extreme patulous forms as the latter (e.g., figures 3–5). Like *L. naticoides*, it is usually entirely smooth, but occasional forms have spiral ribs; in such cases the lack of strong spiral striations in the grooves distinguishes it from *L. sitkana*. Once again, anatomical characters are more helpful; the form of the pallial oviduct is diagnostic (figure 40) with a relatively smaller capsule gland than that of either *L. sitkana* or *L. naticoides*, but the penis is similar to those of both these species.

L. (Neritrema) aleutica (figures 13, 24–27, 38): Shells of *L. aleutica* from the Aleutian Islands are usually sculptured by four nodulose cords with strong spiral striations in the intervening grooves (Reid, 1990a: fig. 1k). However, in the northwestern Bering Sea the shells are not nodulose; slight spiral ribs may remain, as do the striations (visible at the periphery in figure 13), which help to distinguish the shell from the very similarly shaped, but entirely smooth, *L. naticoides*. In this case it is the male anatomy that is diagnostic, the penis showing a narrower filament at least half as long as the wrinkled base, whereas that of *L. naticoides* is shorter (figures 24–26, c.f. figures 15–20). The pallial oviduct is similar only to that of *L. naticoides*, but the jelly gland is usually relatively larger and the capsule gland a little smaller (figures 22, 38, c.f. figures 21–23, 37).

L. (Littorina) kasatka: This newly-described species (Reid *et al.*, 1990) is the smallest of the five smooth-shelled *Littorina* species (6–11 mm) and has the most restricted distribution, being recorded only from the Kurile Islands and Gulf of Shelikov. The shell is closest to small, smooth specimens of *L. sitkana*, although its shape is subtly different, with a relatively narrower columella and smaller aperture. Coloration also differs, the shell of *L. kasatka* being brown, often with indistinct white flecks or tessellation, unique among the five species discussed here. Despite the superficial similarity of the shell, this species is probably not closely related to the others in the group, since its reproductive anatomy is markedly different. Mamilliform penial glands are absent in the male, while the pallial oviduct lacks a swollen, septate jelly gland and shows a unique spiral pattern of albumen and capsule glands. These characteristics of the oviduct indicate that the spawn consists of pelagic egg capsules, probably with planktotrophic development, and for this reason it is classified in the subgenus *Littorina* (Reid *et al.*, 1990). In contrast, the four other species have a large jelly gland, benthic egg masses and direct development, and are therefore members of the subgenus *Neritrema* (Reid, 1989a, 1990a).

DISCUSSION

An earlier review of living *Littorina* species with a cladistic analysis of their relationships (Reid, 1990a) must be revised in the light of the new information on material

from the Siberian coast. At least three changes are necessary. Firstly, "*L. kurila*" (*non* Middendorff, 1848) of the earlier publication is now believed to be the same as *L. subrotundata* (no differentiating characters were found in the earlier analysis). Secondly, *L. kasatka* must be added to the cladogram (Reid 1990a: fig. 5), in a position between nodes 9 and 12 (as yet unclear because of lack of information about egg capsules, but between 9 and 10 most likely, Reid *et al.*, 1990). Thirdly, *L. naticoides* must be added; this is clearly the sister species of *L. aleutica*, since with the exception of shell sculpture, all characters used in the cladistic analysis are the same in both species.

This sister-group relationship is supported by the similar oviducts, egg masses, penial glands and patulous shells. Consistent differences in the relative length of the penial filament and in shell sculpture, and small differences in relative sizes of oviducal glands, are, however, sufficient to separate *L. naticoides* as a new species. So far, the two species have not been found sympatrically. *Littorina aleutica* is recorded from the Aleutian, Komandor and Pribiloff Islands, and from St Lawrence Island and Provideniya in the northern Bering Sea. *Littorina naticoides* occurs from Anadyrskiy Gulf to the Kurile Islands, approaching within 350 km from the closest record of *L. aleutica* in the northern Bering Sea, and within 250 km in eastern Kamchatka. In part this apparent allopatry could be explained by lack of collections from the remote northwestern shores of the Bering Sea. However, the separate distributions in the Aleutian, Komandor and Kurile Islands and in Kamchatka are probably real, because there are extensive collections of *Littorina* from all these areas. Furthermore, the two distributions suggest a possible ecological separation. *Littorina aleutica* has the more "oceanic" distribution, occurring only on islands and at the tip of the Chukotskiy Peninsula, whereas *L. naticoides* is more "continental," occurring on mainland coasts, even in inlets and estuaries, as well as in the Kurile Islands. There are similar examples elsewhere in the Littorinidae of closely related congeners with contrasting "oceanic" and "continental" distributions (*Littoraria*, Reid, 1986; *Peasiella*, Reid, 1989b), but hitherto the phenomenon has been demonstrated only in the tropics.

The biogeography of *Littorina* has been analysed by Reid (1990b). These modifications to the cladogram and distributional data on new species do not alter the earlier conclusion that in general in the northeastern Pacific more apomorphic species occur at higher latitudes, perhaps as a result of climatic cooling which induced speciation. Indeed, recognition of "*L. kurila*" (*sensu* main text of Reid, 1990a and Reid, 1990b) as conspecific with *L. subrotundata* removes the anomaly of the latter's northeastern Pacific distribution. However, *L. naticoides* and *L. aleutica* are the only known example in the genus of sister species that occur in the same ocean and show allopatric distributions; in other cases distributions show broad overlap. This could indicate that a different speciation mechanism has been involved here.

ACKNOWLEDGMENTS

The visit of DGR to the Zoological Institute, Leningrad, was supported by the exchange program of the Royal Society of London and the Academy of Sciences of the USSR. DGR would like to thank the Director of the Institute, Prof. O. A. Scarlato, for the opportunity to work there. Photography of shells was by P. R. Crabb (BMNH).

LITERATURE CITED

Bandel, K. and D. Kadolsky. 1982. Western Atlantic species of *Nodilittorina* (Gastropoda: Prosobranchia): comparative morphology and its functional, ecological, phylogenetic and taxonomic implications. Veliger 25:1–42.

Boulding, E. G. 1990. Are the opposing selection pressures on exposed and protected shores sufficient to maintain genetic differentiation between gastropod populations with high intermigration rates? Hydrobiologia 193:41–52.

Carpenter, P. P. 1864. Supplementary report on the present state of our knowledge with regard to the Mollusca of the west coast of North America. Report of the British Association for the Advancement of Science 1863:517–684.

Gofas, S. 1975. Sur l'extension de *Littorina saxatilis* (Olivi) (Moll. Gaster.) dans le Détroit de Gibraltar. Bulletin de la Société des Sciences Naturelles et Physiqes du Maroc 55: 95–99.

Golikov, A. N. and O. G. Kusakin. 1978. Recent molluscs of the littoral zone of the U.S.S.R. Nauka, Leningrad, 256 p.

Hannaford Ellis, C. J. 1979. Morphology of the oviparous rough winkle *Littorina arcana* Hannaford Ellis, 1978, with notes on the taxonomy of the *L. saxatilis* species-complex (Prosobranchia: Littorinidae). Journal of Conchology 30: 43–56.

Heller, J. 1975. The taxonomy of some British *Littorina* species with notes in their reproduction (Mollusca: Prosobranchia). Zoological Journal of the Linnean Society 56: 131–151.

Janson, K. 1982. Phenotypic differentiation in *Littorina saxatilis* Olivi (Mollusca, Prosobranchia) in a small area on the Swedish west coast. Journal of Molluscan Studies 48: 167–173.

Janson, K. 1983. Selection and migration in two distinct phenotypes of *Littorina saxatilis* in Sweden. Oecologia, Berlin 59:58–61.

Janson, K. and R. D. Ward. 1985. The taxonomic status of *Littorina tenebrosa* Montagu as assessed by morphological and genetic analyses. Journal of Conchology 32:9–15.

Johannesson, B. 1986. Shell morphology of *Littorina saxatilis* Olivi: the relative importance of physical factors and predation. Journal of Experimental Marine Biology and Ecology 102:183–195.

Kemp, P. and M. Bertness. 1984. Snail shape and growth rates: evidence for plastic shell allometry in *Littorina littorea*. Proceedings of the National Academy of Sciences of the USA 81:811–813.

MacDonald, K. B. 1969. Molluscan faunas of Pacific coast salt marshes and tidal creeks. Veliger 11:399–405.

Murray, T. 1979. Evidence for an additional *Littorina* species and a summary of the reproductive biology of *Littorina* from California. Veliger 21:469–474.

Muus, B. J. 1967. The fauna of Danish estuaries and lagoons. Meddelelser fra Danmarks Fiskeri-og Havundersøgelser, N.S. 5:1–316.

Raffaelli, D. G. 1979. The taxonomy of the *Littorina saxatilis* species-complex, with particular reference to the systematic status of *Littorina patula* Jeffreys. Zoological Journal of the Linnean Society 65:219–232.

Raffaelli, D. G. 1982. Recent ecological research on some European species of *Littorina*. Journal of Molluscan Studies 48:342–354.

Reid, D. G. 1986. The littorinid molluscs of mangrove forests in the Indo-Pacific region: the genus *Littoraria*. British Museum (Natural History), London, 228 p.

Reid, D. G. 1989a. The comparative morphology, phylogeny and evolution of the gastropod family Littorinidae. Philosophical Transactions of the Royal Society of London, Series B 324:1–110.

Reid, D. G. 1989b. Systematic revision of the Recent species of *Peasiella* Nevill, 1885 (Gastropoda: Littorinidae), with notes on the fossil species. Nautilus 103:43–69.

Reid, D. G. 1990a. A cladistic phylogeny of the genus *Littorina* (Gastropoda): implications for evolution of reproductive strategies and for classification. Hydrobiologia 193: 1–19.

Reid, D. G. 1990b. Trans-Arctic migration and speciation induced by climatic change: the biogeography of *Littorina* (Mollusca: Gastropoda). Bulletin of Marine Science 47:35–49.

Reid, D. G., N. I. Zaslavskaya, and S. O. Sergievsky. 1991. *Littorina kasatka*, a new species from the Kurile Islands and Okhotsk Sea. Nautilus 105(1):1–6.

Sacchi, C. F. and M. Rastelli. 1966. *Littorina mariae*, nov. sp.: les différences morphologiques et écologiques, entre 'nains' et 'normaux' chez l'"espèce" *L. obtusata* (L.) (Gastr. Prosobr.) et leur signification adaptive et évolutive. Atti della Societa Italiana di Scienze Naturali e del Museo Civico di Storia Naturale, Milano 105:351–370.

Seeley, R. H. 1986. Intense natural selection caused a rapid morphological transition in a living marine snail. Proceedings of the National Academy of Sciences of the USA 83:6897–6901.

Ward, R. D. 1990. Biochemical genetic variation in the genus *Littorina* (Prosobranchia: Mollusca). Hydrobiologia 193: 53–69.