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THE COMPARATIVE MORPHOLOGY, PHYLOGENY AND EVOLUTION OF THE GASTROPOD FAMILY LITTORINIDAE

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An account is given of the comparative morphology of the family Littorinidae, based on examination of 122 species, grouped into 32 subgenera. The shell, operculum and principal organ systems are described, and their phylogenetic significance assessed. A total of 53 characters, coded as 131 character states, were chosen for inclusion in a cladistic analysis of the phylogenetic relationships of the subgenera. This was performed by the program PAUP, using the principle of maximum parsimony. The outgroup for the analysis comprised representatives of the Pomatiasidae and Skeneopsidae. A consensus tree was obtained from cladograms with consistency indices of 0.408 (autapomorphies excluded).

The analysis supports the monophyly of the Littorinidae, and the family can be formally defined by the two synapomorphies of a spiral pallial oviduct and an anterior bursa copulatrix. Three principal clades are identified and given subfamilial rank. The Lacuninae and Laevilitorininae show more plesiomorphic character states, are specialized for life in temperate and polar waters, and occupy the low eulittoral zone and continental shelf. In contrast, the Littorininae occur mainly on tropical and temperate shores, and their synapomorphies of pelagic egg capsules, complex penial glands, paraspermatic nurse cells and sculptured shells can be interpreted as adaptations for their typical habitat in the high eulittoral zone and littoral fringe.

The reconstruction of character states on the cladogram provides hypotheses about the evolution of individual characters. Primitively, the male reproductive tract appears to have been an entirely closed duct, opening at the penial tip. Progressive opening of the anterior part of the tract occurred, and was correlated with the appearance of paraspermatic nurse cells to prevent premature dispersal of euspermatozoa. The littorinid capsule gland, responsible for the production of pelagic egg capsules, is believed to be a new structure, not homologous with that of related families. In three cases there is evidence, from both parsimony and protoconch morphology, of reversion from non-planktotrophic to planktotrophic development.

The cladogram is used as a basis for a new classification of the Littorinidae, in which three subfamilies and 14 monophyletic genera are recognized. This is summarized in an appendix, with diagnoses of supraspecific taxa, including descriptions of one new subfamily and four new subgenera, and a list of the 173 recognized Recent species.

The poor fossil record of the family is reviewed, and its biogeography discussed in the light of the phylogenetic hypothesis. Of particular interest is the bipolar distribution of the marine Lacuninae, the possible origin in Gondwanaland of the Indian freshwater genus *Cremnoconchus*, the presence of several relict taxa of Littorininae in the tropical and temperate Atlantic and the probable dispersal of the genus *Littorina* from the Tethys Sea to the northwestern Pacific and thence to the northern Atlantic in the late Pliocene.

Some ecological implications of the phylogenetic hypothesis are considered, with special reference to the diverse types of spawn and life-history strategies. The primitive benthic gelatinous spawn can be viewed as a phylogenetic constraint on the range of habitat and latitudinal distribution of the Lacuninae and Laevilitorininae. The pelagic egg capsules of the Littorininae may have been an important adaptation permitting their exploitation of the littoral fringe and tropical regions, but preventing radiation into terrestrial and freshwater habitats. Non-planktotrophic, non-planktonic development in benthic egg masses is found only at high latitudes, and has appeared independently in Lacuninae, Laevilitorininae and *Littorina*. The only other non-planktotrophic littorinids are two ovoviviparous tropical species of restricted distribution and probably recent origin.

1. Introduction

Members of the family Littorinidae, commonly called 'winkles' or 'periwinkles', are found on most shores of the world. They are among the most conspicuous and abundant of intertidal gastropods on hard substrates. As a result, there is probably more information available on their ecology, physiology, behaviour and biochemistry than for any other group of marine gastropods (see bibliography and reviews by Pettitt (1974), Raffaelli (1982) and Reid (1986*a*)). Much of this work, however, has been limited to the genus *Littorina* in northern temperate waters, and the many tropical members of the family are less well known. The anatomy of *Littorina* has been described in detail (Linke 1933*a*; Johansson 1939; Fretter & Graham 1962), and there are also descriptions, especially of the reproductive anatomy, of some other genera (Linke 1935*a*; Gallien & de Larambergue 1938; H. Anderson 1958; Marcus & Marcus 1963; Reid 1986*a*, *b*, 1988).

Despite this attention, the systematics and evolution of the family have been neglected. As reviewed below (see §2), the traditional classification of littorinids has relied heavily on characters of the shell, radula and operculum (see, for example, Wenz 1938; Rosewater 1970, 1972, 1981). However, phylogenetic hypotheses should be based on the widest range of available evidence. Using a range of anatomical characters, with emphasis on the reproductive tracts, Reid (1986*a*) produced a preliminary phylogeny of some of the littorinid genera, showing that the traditional classification did not accurately reflect evolutionary relationships. A classification based on phylogeny is desirable, because it provides an evolutionary framework within which to understand the otherwise confusing morphological diversity of the family. A phylogeny is also an essential prerequisite for the formulation and testing of hypotheses about biogeography and the evolution of ecological, behavioural and other characteristics. It is therefore the aim of the present study to produce a phylogenetic hypothesis for the Littorinidae.

Accordingly, original observations have been made on the morphology and anatomy of the shell, operculum and principal organ systems of representatives of the 32 valid Recent subgenera. This information has been analysed by the cladistic method, which is a widely accepted technique for phylogenetic analysis (Hennig 1966; Wiley 1981; Ax 1987). For higher taxa the resulting cladogram can be interpreted as a hypothesis of their phylogenetic relationships, but for species there is not an exact correspondence between the cladogram and a phylogenetic tree, because species can be ancestral to other taxa (Wiley 1981). To construct the cladogram the method of maximum parsimony has been used, which seeks to minimize the incidence of parallelism and reversal in the reconstruction of the evolution of characters (Felsenstein 1983). Whether this is an acceptable model of the evolutionary process is debated (Felsenstein 1982; Gauld & Underwood 1986), but it is a method that seeks to derive the most probable phylogenetic hypothesis. The choice of an outgroup for cladistic analysis requires knowledge of relationships of the ingroup with adjacent taxa. This was available in the family-level phylogeny of the superfamilies Littorinoidea (= Littorinacea), Truncatelloidea (= Rissoacea (Ponder & Warén 1988)) and Cingulopsoidea given by Ponder (1988). It must be emphasized that the resulting phylogeny is a hypothesis, to be tested as additional evidence becomes available.

As a result of the analysis, the classification of the Littorinidae has been revised, to make it consistent with the phylogeny. The distribution of character states on the cladogram is a hypothesis about the evolution of each character, and possible adaptive or functional interpretations have been considered. The phylogeny itself is a hypothesis about the history of the taxa, showing their relative recency of common ancestry. The only direct historical evidence comes from palaeontology, but the fossil record of littorinids is poor and their historical biogeography must be reconstructed largely from their phylogeny and modern distributions. An attempt has also been made to relate some aspects of the ecology of the Littorinidae to their phylogeny.

2. Historical review of supraspecific classification of the Littorinidae

The earliest use of the family name Littorinidae that has been traced was for the genera *Littorina*, *Truncatella* and *Valvata* (Anon. (1834); the author may have been J. C. Children).

Table 1. Classification of Recent littorinids after Rosewater (1970, 1972, 1981, 1982) and Ponder & Rosewater (1979), with Antarctic genera after Powell (1951) and Ponder (1976), and lacunid genera (excluding non-littorinids) after Wenz (1938)

family	subfamily	genus	subgenus	approximate number of recognized species
Lacunidae		*Lacuna*	*Lacuna*	5
			Epheria	6
			Temanella	2
		Sublacuna	—	2
		Carinolacuna	—	1
		Aquilonaria	—	1
		Mainwaringia	—	1
		Haloconcha	—	2
Littorinidae	Bembiciinae	*Bembicium*	—	3
		Risellopsis	—	1
		Peasiella	—	5
	Littorininae	*Laevilitorina*	*Laevilitorina*	13
			Corneolitorina	3
		Macquariella	—	4
		Laevilacunaria	*Laevilacunaria*	3
			Pellilacunella	1
		Rufolacuna	—	1
		Rissolittorina	—	1
		Pellilitorina	—	2
		Littorina	*Littorina*	11
			Littoraria	9
			Littorinopsis	8
			Austrolittorina	15
			Melarhaphe	3
			Fossarilittorina	2
			Algamorda	1
		Nodilittorina	*Nodilittorina*	5
			Echinolittorina	1
			Granulilittorina	8
			Liralittorina	1
	Tectariinae	*Tectarius*	*Tectarius*	5
			Cenchritis	1
	Echinininae	*Echininus*	—	2
		Tectininus	—	1
	?	*Cremnoconchus*	—	2

Gray (1840) used the name for non-nacreous shells with an entire aperture and an oval, horny operculum. This diagnosis encompassed many genera currently assigned to the Epitoniidae, Turritellidae, Cerithiidae, Melaniidae and Truncatelloidea, besides those now recognized as littorinid. Orbigny (1840) used the family in a similar sense. Subsequently Gray (1847, 1857) removed most of the cerithioidean and some truncatelloidean genera from the family, although *Modulus*, *Fossarus* and various truncatelloideans still remained. The modern concept of the family Littorinidae can be traced back to Troschel (1858), who arranged the lower mesogastropods in 'groups' on the basis of radular structure. His group Littorinae was defined by a broad lateral tooth with a basal notch, which excluded the non-littorinids mentioned above. Although following Gray (1857) quite closely, Adams & Adams (1858) narrowed the definition of the Littorinidae by removal of all but one of the truncatelloidean genera, and essentially similar schemes were adopted by Chenu (1859), Stoliczka (1868) and Nevill (1885). Some authors, however, retained a broader definition, including planaxids (Deshayes 1864) or truncatelloideans (Jeffreys 1865). Although the cerithioidean affinities of the fossarid group had been indicated by Troschel (1858), and Adams (1860) had suggested familial status, this

TABLE 2. SUMMARY OF CLASSIFICATION OF RECENT LITTORINIDAE PROPOSED HEREIN (SEE APPENDIX 1 FOR DIAGNOSES AND SPECIES LISTS)

family	subfamily	genus	subgenus	number of recognized species
Littorinidae	Lacuninae	*Pellilitorina*	—	2
		Lacuna	*Lacuna*	16
			Epheria	6
		Cremnoconchus	—	2
		Bembicium	—	5
		Risellopsis	—	1
	Laevilitorininae	*Laevilitorina*	*Pellilacunella*	1
			Macquariella	6
			Laevilitorina	15
			Rissolittorina	1
			Rufolacuna	1
	Littorininae	*Melarhaphe*	—	1
		Peasiella	—	6
		Cenchritis	—	1
		Tectarius	*Tectarius*	5
			Echininus	2
			Tectininus	1
			new subgenus	1
		Littoraria	new subgenus	1
			Palustorina	7
			Littoraria	14
			Lamellilitorina	1
			Littorinopsis	12
			new subgenus	1
		Nodilittorina	*Fossarilittorina*	3
			Echinolittorina	11
			Nodilittorina	30
		Littorina	*Liralittorina*	1
			new subgenus	1
			Littorina	6
			Neritrema	10
		Mainwaringia	—	2

was not widely accepted until later (Stoliczka 1871; Fischer 1885; Tryon 1887). Likewise the genus *Modulus* was commonly included in the Littorinidae until removed by Fischer (1884).

Several authors have supported further division, at the family level, of the Littorinidae as recognized herein. Gray (1857) distinguished the family Lacunidae from the Littorinidae on the basis of the presence of tentacles on the opercular lobe in the former and supposed differences in the structure of the mouth, but this distinction was not accepted by most other 19th-century workers. Winckworth (1932) also united the two groups, but under the name Lacunidae. The two families have, however, commonly been retained in this century (Cossmann 1915; Thiele 1929; Wenz 1938; Taylor & Sohl 1962; Golikov & Starabogatov 1975; Boss 1982). Most recently, the two families have again been merged, because of the lack of significant differences in either radular (Arnaud & Bandel 1978) or other anatomical characters (Ponder 1976; Reid 1988). Kesteven (1903) established the family Risellidae (renamed Bembiciidae by Finlay (1928)) for *Bembicium*, on the basis of the presence of an ovipositor and a closed penial duct in this genus, but this did not gain wide acceptance, and these anatomical features occur in other littorinids as well (Reid 1988). Kesteven (1903) also proposed the removal of littorinids with a multispiral operculum (*Echininus* and *Peasiella*) to the Modulidae, but anatomical evidence does not support this (Abbott 1954; Rosewater 1972; Reid 1986*a*). Rosewater (1972, 1982) continued to recognize opercular differences at the subfamilial level.

At the generic level, the majority of 19th-century authors (see, for example, Gray 1847, 1857; Adams & Adams 1858; Troschel 1858; Chenu 1859; Stoliczka 1867, 1871; Fischer 1885; Tryon 1887) accepted six genera in the Littorinidae: *Littorina*, *Bembicium*, *Tectarius*, *Echininus*, *Lacuna* and *Cremnoconchus* (using the more familiar modern names for the genera; see Appendix 1 for synonymy). A few authors continued to use the name *Littorina* in a broader sense, to include *Tectarius* and *Echininus*, and even *Bembicium* (see, for example, Philippi 1847–8; Reeve 1857; Deshayes 1864; Nevill 1885). Although earlier authors had relied mainly on shell and opercular characters for generic diagnoses, Thiele (1929) made use of the radula also, and recognized 11 genera in the family as defined herein. Wenz (1938) used only shell and radular characters, but by subdividing the genus *Lacuna* increased the number of Recent littorinid genera to 17. Powell (1951) also relied on radular characters in his diagnoses of four genera of Antarctic Littorinidae.

More recently, increased emphasis on anatomical characters has resulted in the recognition of more genera and in the refinement of generic diagnoses. For example, early authors included all large littorinids with smooth or spirally sculptured shells in the genus *Littorina*. The group now known as *Littoraria* was given generic rank by Cossmann (1915), Wenz (1938) and some Japanese authors (Azuma 1960; Higo 1973), on the basis of distinctive shell characters, but until recently most taxonomic works subdivided the genus *Littorina* at the subgeneric level (Bequaert 1943) or not at all. The significance of reproductive anatomy in the classification of the group was recognized by Rosewater (1970, 1972, 1981, 1982), who used penial anatomy and type of development, as well as traditional characters, to define subgenera of *Littorina* (table 1), but his generic definitions were still based on characters of the shell, operculum and sometimes the radula. Bandel & Kadolsky (1982) have since raised three of Rosewater's subgenera to generic rank, and their decision has been supported by the anatomical studies and preliminary phylogenetic analysis of Reid (1986*a*). The classification of the nodulose and spinose littorinids shows a similar history. Early authors used the name *Tectarius* for the groups now known as *Nodilittorina* and *Cenchritis*, besides *Tectarius* (*sensu stricto*), and in some cases included *Echininus* also (Tryon 1887; Thiele 1929; Wenz 1938). Characters of the penis, spawn and operculum were used by Abbott (1954) to define the genera *Nodilittorina* and *Echininus*, and *Cenchritis* has been given generic rank by Bandel & Kadolsky (1982) and Reid (1986*a*). Rosewater (1970, 1981) included only nodulose shells in *Nodilittorina*, but studies of radulae (Bandel & Kadolsky 1982) and reproductive anatomy (Reid 1986*a*) have shown that some spirally sculptured, non-nodulose species (previously classified in *Littorina*) should also be included.

The shells of littorinids are of generalized turbinate, trochoidal or elongate form, characterized by a lack of distinctive apertural or sculptural features. In consequence, several genera of which only shells were initially available have at times been erroneously assigned to the Littorinidae. Since the treatment of the Lacunidae and Littorinidae by Thiele (1929) and Wenz (1938) nine genera have been removed to other families (see Appendix 1).

At present the most widely used classification of littorinids (summarized in table 1) is based on the works of Rosewater (1970, 1972, 1981, 1982), Ponder & Rosewater (1979), Powell (1951) and Ponder (1976). Several additional species have since been recognized or described, and many must be reassigned in the light of the revised generic and subgeneric concepts discussed herein. The classification advocated as a result of the present study is summarized in table 2, and given in a more complete form, with generic diagnoses, synonymies and species lists, in Appendix 1.

3. Material and methods

The method of cladistic analysis involves three stages: the choice of taxa and outgroup, the choice of characters and their coding into ordered character states, and lastly the analysis of the data and construction of the cladogram.

In an initial survey of the morphological diversity of the family 122 species were examined and dissected (table 3). These included representatives of almost all the genera and subgenera of previous authors (table 1), and constituted 71% of the approximate total of 173 extant species recognized by the present author (see Appendix 1). The species examined were classified into 34 groups, of which 28 corresponded with previously named genera and subgenera, and six were single species of uncertain affinity. Where possible, the previously named taxa were represented in the cladistic analysis by their type species (table 3). In four cases, where material was unavailable or inadequate, species other than the types were taken as representative. As a result of the survey it was found necessary to revise the status of some of the currently accepted generic groups and species. Furthermore, after the analysis was completed it was necessary to change the rank of some generic groups to make the classification consistent with the phylogeny. Throughout the text generic and specific names are employed in their revised senses. To clarify these changes in the classification of the Littorinidae, generic diagnoses, synonymies and an annotated list of the valid extant species are given in Appendix 1. Four new subgenera, all monotypic, are described in Appendix 1, but are not used in the text.

Selection of suitable outgroups for a cladistic analysis requires knowledge or assumptions about the taxa related to the ingroup. Unfortunately, the phylogeny of the families making up the littorinoidean–truncatelloidean radiation of the Neotaenioglossa (*sensu* Haszprunar (1988), consisting of most of the Mesogastropoda of Thiele (1929)) is still somewhat uncertain.

TABLE 3. SPECIES AND NUMBERS OF SPECIMENS OF LITTORINIDAE EXAMINED DURING PRESENT STUDY

(Key: *, type species; †, species used in cladistic analysis; L, information available in literature as quoted in text.)

genus	subgenus	species	males	sperm	females	spawn	radulae	nervous system	histology
Pellilitorina		*pellita*	4	2	2	L	2L	—	—
		*setosa**†	2	2	4	L	1, 2L	2	1♂
Lacuna	*Lacuna*	*crassior*	2	—	1	—	1	—	—
		pallidula†	2	1	1	L	2	—	—
		*parva**	1	1	1	L	—	—	—
	Epheria	*porrecta*	2	—	1	—	—	—	—
		*vincta**†	4	2	4	2	4	1	1♂,2♀
Cremnoconchus		*syhadrensis**†	2	2	3	1	2	2	1♂,1♀
Bembicium		*auratum*	21	4	6	L	10	1	3♂,2♀
		flavescens	10	—	5	—	5	—	—
		*melanostoma**†	13	—	5	—	5	—	1♂
		nanum	13	3	8	L	5	—	1♂,1♀
		vittatum	12	—	3	L	5	—	1♂
Risellopsis		*varia**†	6	2	5	1	5	—	1♂,1♀
Laevilitorina	*Pellilacunella*	*bennetti**†	3	2	3	L	1, L	—	—
	Macquariella	*antarctica*	3	2	4	L	2, 3L	—	—
		*hamiltoni**†	2	1	2	L	1, L	—	—
	Laevilitorina	*caliginosa**†	4	2	6	L	2, 3L	1	1♂,1♀
		mariae	1	—	2	—	L	—	—
	Rissolittorina	*alta**†	2	1	2	—	1, L	—	—
	Rufolacuna	*bruniensis**†	1	1	3	—	L	—	—
Melarhaphe		*neritoides**†	6	4	6	L	2	—	1♂,1♀
Peasiella		*conoidalis*	3	—	2	—	5	—	—
		infracostata	5	—	1	L	8	—	—
		isseli	—	1	3	—	4	—	—
		roepstorffiana	11	3	4	—	7	—	3♂,2♀
		*tantilla**†	5	1	2	—	4	—	1♀
		n.sp.	10	3	7	—	3	—	1♀
Cenchritis		*muricatus**†	11	5	3	L	2, L	—	1♂,1♀
Tectarius	*Tectarius*	*grandinatus*†	2	—	2	—	2	—	—
		*pagodus**	1	—	1	—	1	—	—
	Echininus	*cumingii**†	1	—	2	—	1, L	—	—
	Tectininus	*antonii**†	7	1	2	L	2, 2L	—	1♂
	n.subgen.	*viviparus**†	2	—	1	1	1, L	—	—
Littoraria	n.subgen.	*pintado**†	7	3	3	L	4	1	2♂
	Palustorina	*articulata*	22	20	27	1	4	—	1♂,2♀
		carinifera	9	6	5	—	4	—	—
		conica	4	6	2	—	4	—	—
		*melanostoma**†	9	5	6	L	4	—	1♂,3♀
		strigata	12	8	12	L	4	—	—
		sulculosa	7	3	7	—	4	—	—
	Littoraria	*cingulifera*	4	—	3	—	1	—	—
		coccinea	5	1	2	L	1, L	—	—
		fasciata	4	3	1	—	1	—	—
		flava	2	L	1	L	1	—	—
		glabrata	9	—	2	—	2	—	—
		irrorata	3	1	2	L	1, 2L	—	1♂
		mauritiana	3	—	1	—	1, L	—	—
		nebulosa	7	3	2	L	1, L	—	—
		tessellata	1	—	1	—	L	—	—
		undulata	3	2	1	L	2, L	—	1♂
		varia	6	4	1	—	L	—	—

TABLE 3 (*cont.*)

genus	subgenus	species	males	sperm	females	spawn	radulae	nervous system	histology
Littoraria	*Littoraria*	*vespacea*	6	6	3	—	4	—	—
		*zebra**†	5	3	3	—	2	—	—
		n.sp.	5	7	1	—	L	—	—
	Lamellilitorina	*albicans**†	4	3	3	—	4	—	—
	Littorinopsis	*angulifera**†	15	6	3	3	2, L	—	—
		ardouiniana	4	3	2	—	4	—	—
		cingulata	15	13	9	—	8	—	—
		filosa	30	20	6	6	4	1	—
		intermedia	28	20	5	5	4	—	—
		lutea	7	3	3	2	4	—	—
		luteola	10	6	4	4	4	—	1 ♀
		pallescens	21	8	4	3	4	—	—
		philippiana	19	20	4	4	4	—	1 ♂
		scabra	16	20	5	5	4	—	1 ♂,4 ♀
		subvittata	10	3	3	3	4	—	—
	n.subgen.	*aberrans**†	5	2	4	4	2	—	1 ♂
Nodilittorina	*Fossarilittorina*	*meleagris**†	5	3	3	1	1, L	—	1 ♂
		mespillum	2	—	2	—	—	—	—
		modesta†	5	1	2	—	1	—	1 ♂
	Echinolittorina	*africana*	5	1	2	—	L	—	1 ♂
		angustior	14	10	1	1	L	—	—
		dilatata†	15	12	6	L	4, 2L	—	—
		granosa	1	—	1	—	—	—	—
		interrupta	3	3	1	L	2L	—	—
		miliaris	2	—	1	—	L	—	—
		peruviana	2	L	1	—	2	—	—
		punctata	1	—	1	—	L	—	—
		riisei	5	5	1	L	L	—	—
		*tuberculata**	2	—	1	L	4, 2L	—	—
		ziczac	8	8	3	L	2L	—	—
	Nodilittorina	*acutispira*	3	3	3	—	1, L	—	1 ♂
		antipodum	1	—	2	L	—	—	—
		araucana	3	L	1	L	1	—	—
		aspera	8	3	3	1	1	—	1 ♂
		australis	1	—	1	—	—	—	—
		fernandezensis	1	—	4	—	2	—	—
		galapagiensis	—	—	1	—	1	—	—
		hawaiiensis	2	2	2	L	—	—	—
		lineolata	2	—	1	L	L	—	—
		millegrana	1	—	2	—	—	—	—
		natalensis	1	—	1	—	—	—	—
		novaezelandiae	3	3	1	—	—	—	—
		porcata	4	2	2	1	—	—	—
		praetermissa	2	—	1	—	L	—	—
		*pyramidalis**†	3	3	1	—	1	—	2 ♂,1 ♀
		sundaica	1	—	2	—	L	—	—
		trochoides	4	3	6	L	1	—	—
		unifasciata	4	3	3	—	L	—	—
		vidua	3	—	1	L	—	—	—
		2 n.spp.	4	2	1	—	—	—	—
Littorina	*Liralittorina*	*striata**†	5	7	2	1	2, L	—	1 ♀
	n.subgen.	*keenae*†	4	3	6	L	3	—	1 ♂,1 ♀
	Littorina	*brevicula*	4	6	2	L	2	—	—
		*littorea**†	2	3	2	L	3	1	1 ♀
		mandshurica	4	3	3	L	2	—	—
		plena†	6	2	1	L	L	—	—
		scutulata	3	3	3	L	1	—	—
		squalida	4	2	4	L	2	—	—

TABLE 3 (*cont.*)

genus	subgenus	species	males	sperm	females	spawn	radulae	nervous system	histology
Littorina	*Neritrema*	*aleutica*	2	—	4	—	2	—	—
		arcana	6	—	2	L	—	—	—
		kurila	5	3	6	—	3	—	—
		mariae	15	16	20	L	10	—	—
		neglecta	4	1	9	1	L	—	—
		nigrolineata	1	2	1	L	2L	—	—
		*obtusata**†	27	21	25	L	6	—	1 ♂,1 ♀
		saxatilis	18	17	11	1	3	—	
		sitkana	5	2	5	L	2	—	—
	Mainwaringia	*rhizophila*†	10	4	8	1	2	—	1 ♂,1 ♀
		*leithii**	—	—	—	—	2	—	—

Ponder (1988) has reviewed the available data and has recognized three superfamilies: Truncatelloidea, Cingulopsoidea (Eatoniellidae, Cingulopsidae, Rastodentidae) and Littorinoidea. This superfamilial arrangement has been followed here. As defined by Ponder, the Littorinoidea comprise the families Littorinidae, Pomatiasidae and Skeneopsidae. In some of the alternative cladograms discussed by him these form a monophyletic group, often with Pomatiasidae as the sister-group of Littorinidae. Accordingly, Pomatiasidae and Skeneopsidae have been used as the outgroup in the present study. The Pomatiasidae were represented in the analysis by *Pomatias elegans* (Müller), with anatomical data derived from Creek (1951) and personal observations. Additional information was available for *Meganipha rhecta* Thompson (Thompson 1978), a member of the Annulariinae (= Chondropominae; often accorded familial status, but see §6*a*). The Skeneopsidae were represented by *Skeneopsis planorbis* (Fabricius), with anatomical data derived from Fretter (1948) and Ponder (1988). Throughout §4 comparisons are drawn not only with members of the outgroup but also with the more distant outgroups Truncatelloidea, Cingulopsoidea and Cerithioidea, and with the Aciculidae (a family of uncertain affinities; see §6*a*), to define the synapomorphies of the Littorinidae and discuss their relationships within the Littorinoidea.

The characters chosen for inclusion in the analysis were those known or found to be of high taxonomic value. That is, the characters were constant within species, relatively uniform within generic groups, and useful for distinguishing between such groups. Characters constant within the Littorinidae were also included if they were known or suspected to be synapomorphies defining the family. Metric characters were not used, and characters with two or more clearly defined alternative states were preferred. Characters showing functional correlation with other established characters were excluded (e.g. type of development is correlated with shape of protoconch). Useful characters were found in the shell, operculum, head–foot, pallial complex, reproductive systems, spermatozoa, spawn, radula, alimentary and nervous systems. The choice of characters and the discrimination of character states are described in detail in §4. Particular emphasis was placed on characters of the reproductive systems, spermatozoa and spawn, because these characters are often of a complex nature and not obviously correlated with habitat or ecology. They are therefore less likely to show parallel or convergent evolution, which can confuse the recognition of homology and common ancestry.

The account of the morphology of the Littorinidae (see §4) draws on information from the dissection of approximately 1400 animals, during this and previous studies of the family (Reid 1984, 1986*a*, *b*, 1988). Spermatozoa, spawn, radulae, nervous systems and histological sections were examined in fewer specimens, as listed in table 3. The whorls of the protoconch were counted as described by Reid (1988) (e.g. the protoconch in figure 3*e*† has 1.7 whorls). Shell microstructure was investigated by acetate peels of ground sections, scanning electron microscopy of etched sections, and X-ray analysis for the identification of aragonite and calcite (Taylor & Reid 1989). To search for an internal chitinous layer the entire shell was dissolved in dilute hydrochloric acid. Calcification of the operculum was detected by effervescence in dilute hydrochloric acid. Material for the majority of dissections was fixed in 10% seawater formalin and stored in 80% ethanol. Where possible, spermatozoa were removed from the seminal vesicle of living snails and fixed in a dilute solution (approximately 1% by volume) of glutaraldehyde or formalin in seawater, before examination at high power (×1000) with a light microscope. The nuclei of paraspermatic nurse cells were identified by staining of histological sections through the seminal vesicle with either Mayer's haemalum or the Feulgen reaction (specific for DNA) (Culling 1963). The structure of the pallial oviduct was investigated by cutting gross serial transverse sections, and the identification of glandular elements confirmed histologically, as described by Reid (1986*a*). Serial histological sections were prepared of penis, prostate gland and pallial oviduct, for selected species (table 3), and stained either with Masson's trichrome (MT) (Culling 1963) or by the alcian blue-periodic acid-Schiff (ABPAS) technique for the histochemical differentiation of mucins (Mowry 1956). Radulae were cleaned in hot, concentrated potassium hydroxide solution for examination with a scanning electron microscope, as described by Reid (1988), or alternatively were mounted flat under glass for examination with a light microscope and drawn by camera lucida.

Most of the material used for dissection is deposited in the British Museum (Natural History), and additional specimens were borrowed from the institutions listed in the Acknowledgements.

After identification of the discrete states of a character, the next stage in the cladistic analysis is their ordering into an evolutionary sequence and the determination of the polarity of the sequence. In this study the only criterion for the recognition of the ancestral (plesiomorphic) state was outgroup comparison (Wiley 1981). The sequence of the derived (apomorphic) states was judged from developmental or functional criteria, or from degree of complexity. In cases where the sequence was unclear, the character states were specified as unordered in the computer analysis. The sequence and polarity of the character states are re-examined in §5*c*(i), because application of the principle of maximum parsimony to the entire data set during the analysis demonstrated that some of the original decisions were probably incorrect.

A total of 53 characters, coded as 131 character states, was selected for inclusion in the cladistic analysis (table 5). This was performed using version 2.4.1 of the PAUP program for inferring phylogenies by the principle of maximum parsimony (Swofford 1985). Details of the use of the program are given, and the results discussed, in §5.

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† Figures 1–3 appear on plates 1–3.

4. SELECTION, DESCRIPTION AND CODING OF CHARACTERS

(a) *Shell and protoconch* (*characters* 1–4)

Although ecological work has demonstrated that shell shape can show considerable intraspecific variability (see, for example, Janson 1982; Kemp & Bertness 1984; Seeley 1986), some shell characters are nevertheless of probable phylogenetic significance. Shell shape in the family is usually of a turbinate or low conical form. However, the proportions of the shell, as a ratio of height to breadth (perpendicular to coiling axis) vary from 0.44 (*Risellopsis varia*) to 2.50 (*Mainwaringia leithii*) (figures 1 and 2). Only one shell shape is regarded as sufficiently distinct from the turbinate form to be used as a character in the phylogenetic analysis. This is the shape known as trochoidal (character 1), a term here applied to shells that are either pyramidal (height:breadth ratio $\leqslant 1.3$ and height:height of aperture, measured parallel to coiling axis, $\geqslant 2.1$) or depressed (height:breadth ratio $\leqslant 0.7$), and which usually have a strongly keeled periphery. *Laevilitorina* (*Rufolacuna*) and *Risellopsis* are depressed, *Tectarius* and *Cenchritis* are pyramidal, and *Bembicium* and *Peasiella* may be either depressed or pyramidal, sometimes changing from the first form to the second because of allometric growth (Reid 1988). The functional significance of a trochoidal shape is unclear, and there is no obvious association with a particular type of habitat or zonation level. In the outgroup, some of the Pomatiasidae are pyramidal, whereas others, including *Pomatias elegans*, are turbinate, and the Skeneopsidae are depressed. The turbinate-to-conical form predominates in the Cingulopsoidea and Truncatelloidea, and is probably plesiomorphic in the Littorinidae.

Another obvious feature of the shell is the umbilicus, present in *Peasiella*, *Lacuna*, *Laevilitorina* (*Macquariella*), *L.* (*Rufolacuna*), several *L.* (*Laevilitorina*) and in *Cremnoconchus syhadrensis*. In *Risellopsis*, *Cenchritis*, *Tectarius* (*Echininus*) and *Nodilittorina* (*Fossarilittorina*) (except *N. modesta*) the umbilicus is usually open, but may become closed in some adult shells. In *Bembicium* an open umbilicus is found mostly among juveniles, whereas in *Nodilittorina* (*Nodilittorina*) *porcata* the umbilicus develops in adults. All other members of the family are imperforate. The umbilicus has no obvious functional significance and is often, but not always, found in trochoidal shells. Owing to the irregular occurrence of this character it is not considered to be of phylogenetic significance.

A slight 'tooth' is developed at the base of the columella in species of *Tectarius* (*Tectarius*) (figure 1*o*). A similar swelling can be found in some species of *Littoraria* which also have a

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DESCRIPTION OF PLATE 1

FIGURE 1. Shells of Littorinidae. Heights in parentheses. All specimens in British Museum (Natural History), except (*k*) National Museum of New Zealand, (*n*) National Museum of Natural History, Smithsonian Institution. (*a*) *Laevilitorina* (*Pellilacunella*) *bennetti*, Signy I., South Orkney Is. (4.4 mm); (*b*) *Laevilitorina* (*Macquariella*) *hamiltoni*, Macquarie I. (3.0 mm); (*c*) *Laevilitorina* (*Laevilitorina*) *caliginosa*, Macquarie I. (3.6 mm); (*d*) *Laevilitorina* (*Rufolacuna*) *bruniensis*, Bramble Cove, Tasmania (1.2 mm); (*e*) *Laevilitorina* (*Rissolittorina*) *alta*, Wooley's Bay, New Zealand (2.2 mm); (*f*) *Pellilitorina setosa*, Signy I., South Orkney Is. (14.9 mm); (*g*) *Lacuna* (*Lacuna*) *pallidula*, Exmouth, England (9.0 mm); (*h*) *Lacuna* (*Epheria*) *vincta*, Milford Haven, Wales (14.3 mm); (*i*) *Cremnoconchus syhadrensis*, Western Ghats, India (9.4 mm); (*j*) *Bembicium melanostoma*, Western Port Bay, Victoria (14.1 mm); (*k*) *Risellopsis varia*, Stewart I., New Zealand (3.1 mm); (*l*) *Melarhaphe neritoides*, Rhodes, Greece (9.0 mm); (*m*) *Cenchritis muricatus*, Port Everglades, Florida (18.9 mm); (*n*) *Peasiella tantilla*, Oahu, Hawaii (3.7 mm); (*o*) *Tectarius* (*Tectarius*) *grandinatus*, Polynesia (30.9 mm); (*p*) *Tectarius* (*Echininus*) *cumingii*, Madang, Papua New Guinea (13.5 mm); (*q*) *Tectarius* (*Tectininus*) *antonii*, South Water Cay, Belize (13.2 mm); (*r*) *Tectarius viviparus*, Guam, Mariana Is. (9.3 mm); (*s*) *Littoraria pintado*, Oahu, Hawaii (14.0 mm); (*t*) *Littoraria* (*Palustorina*) *melanostoma*, Kanchanadit, Thailand (23.3 mm).

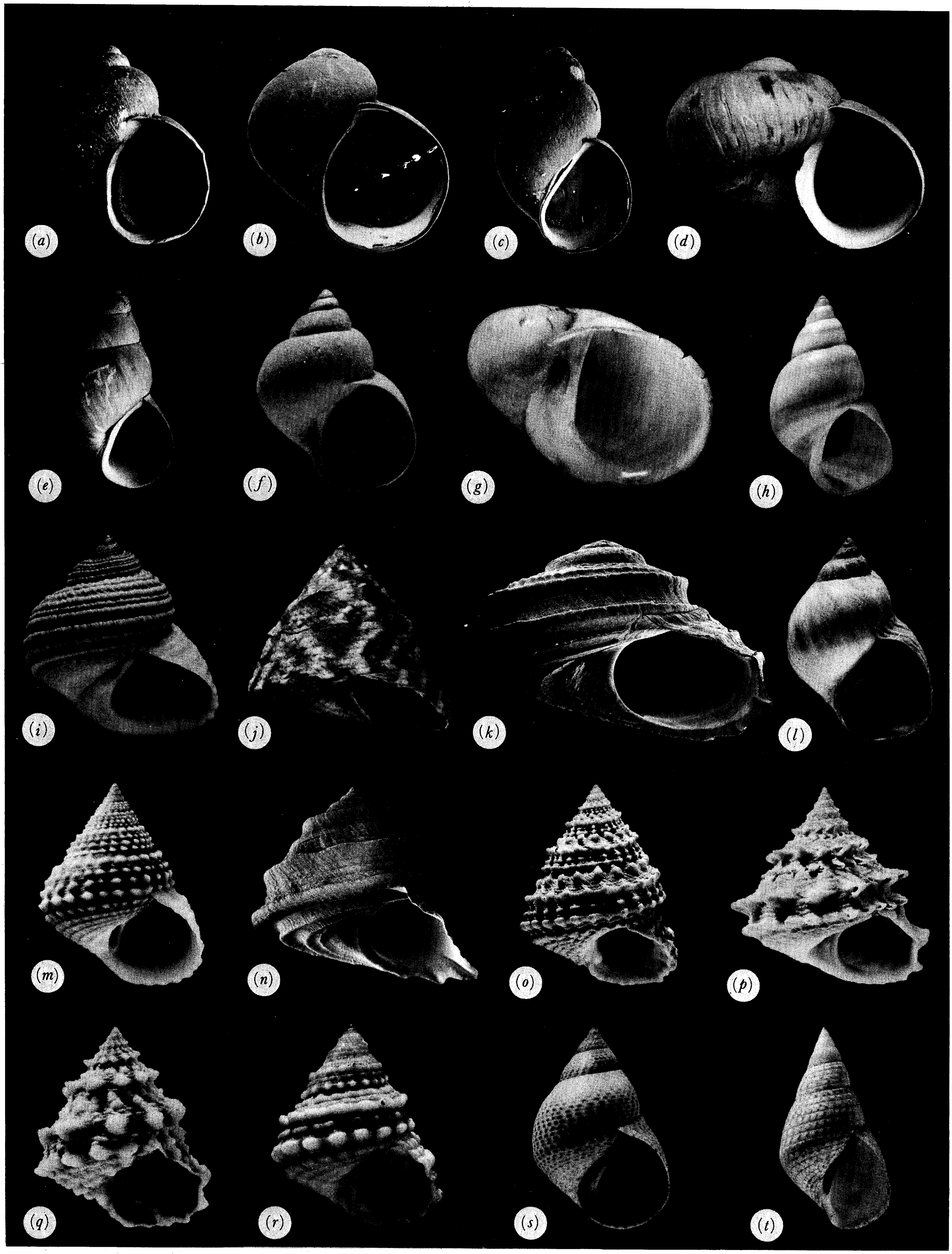

FIGURE 1. For description see opposite.

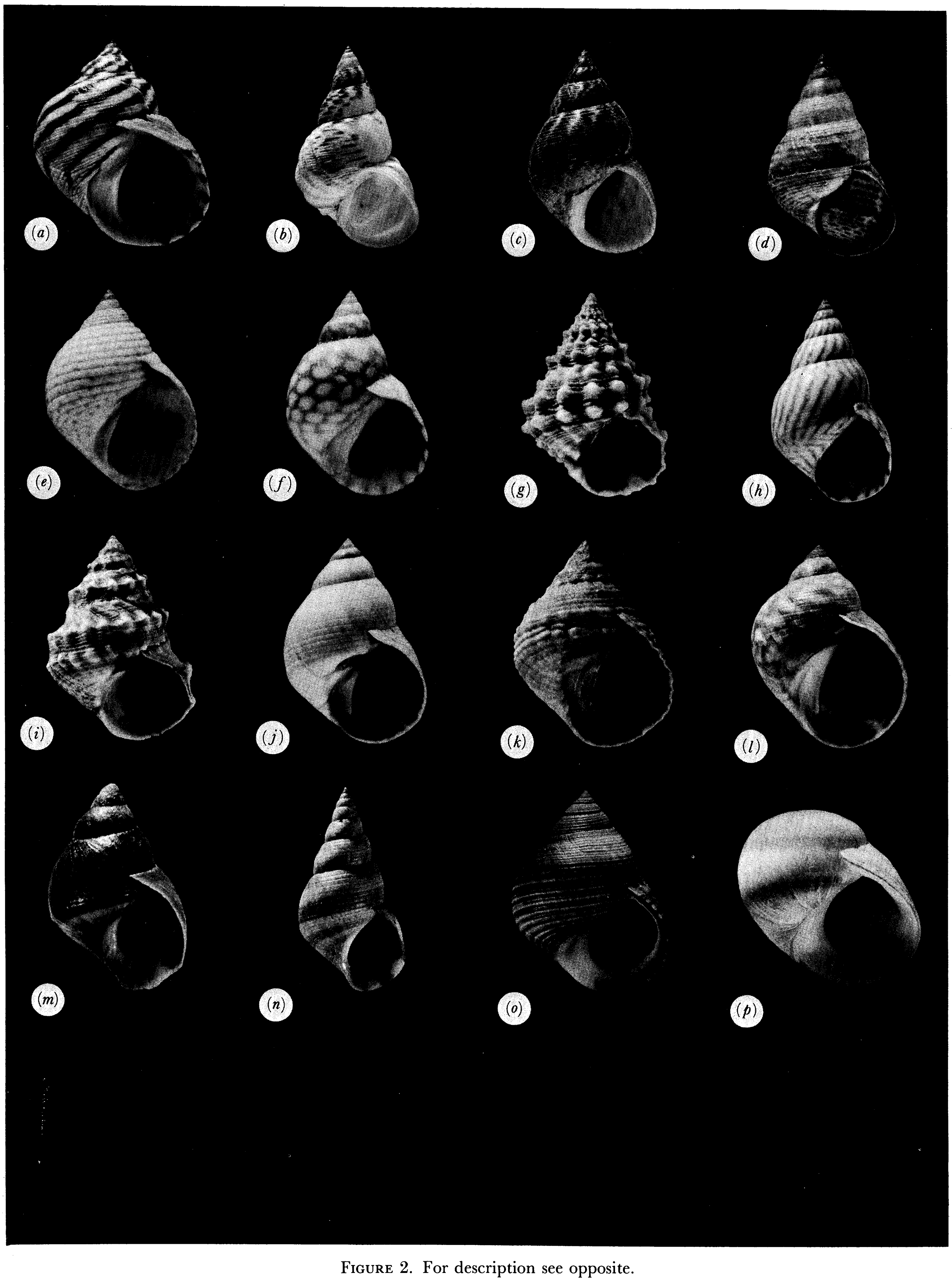

FIGURE 2. For description see opposite.

DESCRIPTION OF PLATE 2

FIGURE 2. Shells of Littorinidae (continued). Heights in parentheses. All specimens in British Museum (Natural History). (*a*) *Littoraria* (*Littoraria*) *zebra*, Panama (35.3 mm); (*b*) *Littoraria* (*Lamellilitorina*) *albicans*, Santubong, Sarawak (21.1 mm); (*c*) *Littoraria* (*Littorinopsis*) *angulifera*, east coast of Mexico (31.6 mm); (*d*) *Littoraria aberrans*, Golfo de Nicoya, Costa Rica (17.3 mm); (*e*) *Nodilittorina modesta*, Cocos I. (10.4 mm); (*f*) *Nodilittorina* (*Fossarilittorina*) *meleagris*, St Thomas (7.2 mm); (*g*) *Nodilittorina* (*Echinolittorina*) *dilatata*, Port Everglades, Florida (15.1 mm); (*h*) *Nodilittorina* (*Echinolittorina*) *ziczac*, Goff's Cay, Belize (16.4 mm); (*i*) *Nodilittorina* (*Nodilittorina*) *pyramidalis*, Karuah, New South Wales (19.6 mm); (*j*) *Nodilittorina* (*Nodilittorina*) *unifasciata*, Penguin I., Western Australia (15.4 mm); (*k*) *Littorina* (*Liralittorina*) *striata*, Madeira (9.6 mm); (*l*) *Littorina keenae*, San Diego, California (12.2 mm); (*m*) *Littorina plena*, San Luis Obispo Bay, California (5.5 mm); (*n*) *Mainwaringia rhizophila*, Santubong, Sarawak (13.7 mm); (*o*) *Littorina* (*Littorina*) *littorea*, Lyme Regis, England (27.6 mm); (*p*) *Littorina* (*Neritrema*) *obtusata*, Stromness, Orkney Is., Scotland (14.4 mm).

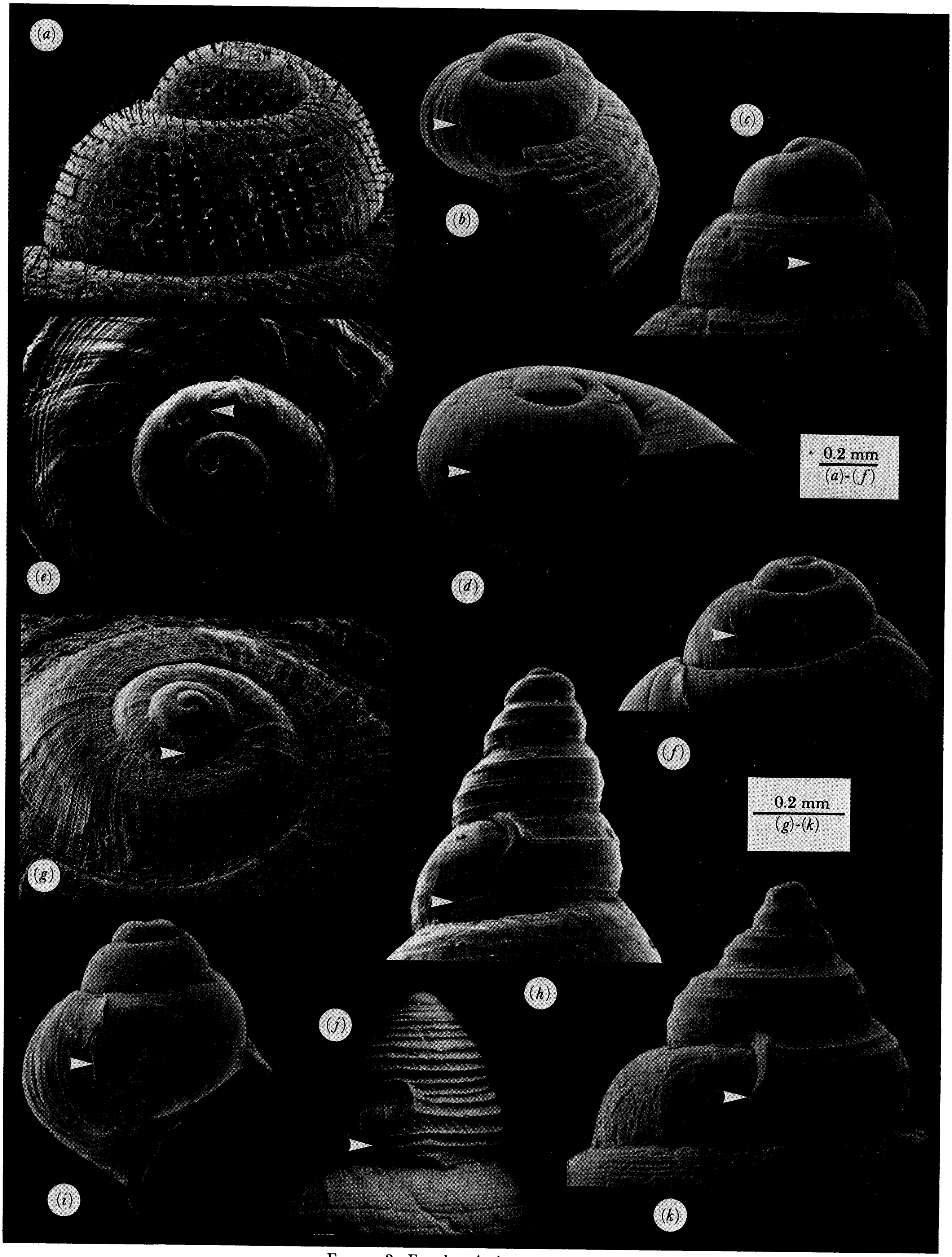

FIGURE 3. For description see opposite.

thickened columella (Reid 1986*a*) and does not indicate a close relationship. Spiral ridges within the aperture occur only in *Tectarius* (*Tectarius*).

Shell sculpture in littorinids consists of spiral striations, ridges and grooves, sometimes in combination with nodules or short spines (figures 1 and 2). Axial sculpture consists only of fine growth lines and, rarely, of major varices formed during interruptions to growth (as in some *Littoraria* (*Littorinopsis*) and in *L.* (*Lamellilitorina*) (Reid 1986*a*)). Spiral sculpture is of two kinds, fine striae and major grooves (Reid 1986*a*). Fine striae are present on all littorinid shells, although only very faint in *Pellilitorina*, *Lacuna* and *Laevilitorina*. In some cases (e.g. *Littorina* (*Neritrema*), *Mainwaringia*) the striae are periostracal, but in strongly sculptured shells (e.g. *Tectarius*, *Nodilittorina*) they are impressed in the calcareous material of the shell. Major grooves are of more restricted occurrence, being found in *Bembicium*, *Risellopsis*, *Cenchritis*, *Peasiella*, *Tectarius*, *Nodilittorina* (except *N.* (*Fossarilittorina*) *meleagris* and *N.* (*F.*) *mespillum*) and in *Cremnoconchus syhadrensis*. The number of primary major grooves is often rather constant within species, and a useful taxonomic character, although on later whorls of the shell further grooves may be intercalated, giving rise to secondary and tertiary orders of sculpture (Bandel & Kadolsky 1982; Reid 1986*a*). The presence of major spiral grooves has been included as a character in the analysis (character 2). Outgroup comparison yields equivocal evidence as to its polarity, because strong spiral sculpture occurs in Pomatiasidae, but is infrequent in Truncatelloidea and Cingulopsoidea, whereas in Skeneopsidae the shells are smooth or only finely striated (Gofas 1982*a*).

Nodulose sculpture is conspicuous in some littorinids, and this character has been employed in previous classifications. For example, Rosewater (1970) included only nodulose species in *Nodilittorina*, whereas smooth shells with almost identical anatomical and radular characters were placed in *Littorina* (*Austrolittorina*). This anomaly has been rectified by Bandel & Kadolsky (1982), who pointed out the close relationship between nodulose and non-nodulose species of *Nodilittorina*. Nodulosity is a poor guide to relationships in this genus, and can show considerable variation within some species, which range from spirally grooved alone to grooved and strongly nodulose (e.g. *N.* (*N.*) *hawaiiensis* (see Struhsaker 1968); *N.* (*N.*) *australis* and *N.* (*N.*) *nodosa*, which probably constitute a single species (see Rosewater 1970)). Similar intraspecific variability occurs in *Risellopsis varia*, *Peasiella roepstorffiana*, *Littorina* (*Littorina*) *brevicula* and *L.* (*Liralittorina*) *striata*. In the family as a whole the occurrence of nodulose sculpture is erratic, being present in *Bembicium*, *Risellopsis*, one fossil *Melarhaphe* (Kadolsky 1973), *Cenchritis*, one *Peasiella*, *Tectarius*, two *Littorina* (*Littorina*), *L.* (*Liralittorina*) and many *Nodilittorina* species. The character is evidently not of phylogenetic importance and appears to have developed independently in several lineages. Neither of the outgroup families displays

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DESCRIPTION OF PLATE 3

FIGURE 3. Protoconchs of Littorinidae. (*a*)–(*d*) Non-planktotrophic; (*e–f*) intermediate; (*g–k*) planktotrophic. Arrows indicate termination of protoconch. In (*a*) the junction of protoconch and teleoconch is unclear, but according to Picken (1979) this species hatches from the egg mass at a shell height of 1.34 mm. All specimens in British Museum (Natural History), except (*e*) Australian Museum, (*h*) National Museum of Natural History, Smithsonian Institution. (*a*) *Pellilitorina setosa*, Signy I., South Orkney Is; (*b*) *Littorina* (*Neritrema*) *saxatilis*, Tjärnö I., Sweden; (*c*) *Littoraria aberrans*, Golfo de Nicoya, Costa Rica; (*d*) *Lacuna* (*Lacuna*) *pallidula*, Dunbeath, Scotland; (*e*) *Bembicium nanum*, Iluka, New South Wales; (*f*) *Lacuna* (*Epheria*) *vincta*, Dunbeath, Scotland; (*g*) *Peasiella roepstorffiana*, Orpheus I., Queensland; (*h*) *Mainwaringia leithii*, Bombay, India; (*i*) *Melarhaphe neritoides*, County Clare, Ireland; (*j*) *Littoraria* (*Littorinopsis*) *philippiana*, Magnetic I., Queensland; (*k*) *Littoraria* (*Lamellilitorina*) *albicans*, Santubong, Sarawak.

nodulose sculpture. It is significant that the most strongly nodulose members of the family are species of *Cenchritis*, *Tectarius* and *Nodilittorina* with tropical or subtropical distributions. Although in some gastropod groups a latitudinal trend of increasing sculpture towards the tropics is interpreted as a consequence of selection for defence against crushing predators (Vermeij 1978), in these littorinids from high tidal levels shell sculpture apparently has a function in temperature regulation (Vermeij 1973).

The protoconch (the shell formed before metamorphosis (see Jablonski & Lutz (1980) for review of terminology of protoconch and development)) is variable in form, but reflects the type of larval development rather than phylogenetic relationship. Species with non-planktotrophic development and no planktonic stage have a large (0.40–1.49 mm diameter), almost smooth protoconch with few whorls (1.0–2.0), which is often not strongly demarcated from the post-larval shell or teleoconch (Thorson 1946; Smith 1973; Bandel 1975*a*; Arnaud & Bandel 1978; Picken 1979; Rosewater 1982) (figure 3*a–d*). This type occurs in *Pellilitorina*, *Lacuna* (*Lacuna*), *Cremnoconchus*, *Laevilitorina*, *Tectarius viviparus*, *Littoraria aberrans*, *Littorina* (*Neritrema*) and probably also in *Bembicium melanostoma* (see Reid (1988) for discussion of development in *Bembicium*). Pitted microsculpture has been described on the protoconch of *Pellilitorina* (Arnaud & Bandel 1978), reminiscent of that in Barleeidae, Anabathridae and some Rissoidae (Ponder 1983, 1985*a*). However, this has not been confirmed by the present study, in which the thick, bristly periostracum has been found to extend almost to the apex (figure 3*a*). Possibly the pits indicate the position of the bristles after the periostracum has been removed.

The great majority of littorinids are planktotrophic, including all those with pelagic egg capsules, as well as those brooding the embryos to the early veliger stage. In these cases the protoconch is smaller (0.21–0.44 mm diameter, but 0.52 mm in *Littoraria* (*Lamellilitorina*) *albicans*), sculptured, consists of more whorls (2.0–4.0) and is terminated by a strong sinusigera rib (Thorson 1946; Struhsaker & Costlow 1968; Pilkington 1971; Thiriot-Quiévreux & Babio 1975; Fish & Fish 1977; Fretter & Manly 1977; Thiriot-Quiévreux 1980; Rosewater 1981; Bandel & Kadolsky 1982; Reid 1986*a*, *b*) (figure 3*g–k*). The apertural edge of the shell of free-swimming veligers is usually produced into a beak between the velar lobes, and this remains as the sinusigera rib after metamorphosis, when the margin of the post-larval shell becomes straight. In planktotrophic species the protoconch is demarcated into a smooth or minutely granulose apical region (protoconch I) and a distal region that bears the spiral sculpture (protoconch II). Because these parts are formed respectively before and after hatching from the egg membrane, they are sometimes known as the embryonic and larval shells (Bandel 1975*a*, *b*), and consequently the entire protoconch may be termed an embryonic shell in species lacking a planktonic stage. The sculpture of the protoconch II varies from scattered granules roughly arranged in spiral rows (*Melarhaphe neritoides* (figure 3*i*), *Littorina* (*Littorina*) *littorea*, *Littoraria* (*Littoraria*) *irrorata*), to 6–10 rows of elongated tubercles, which may fuse to form undulating or straight spiral ridges (*Peasiella* (figure 3*g*), *Littoraria* (figure 3*j*), *Nodilittorina*, *Mainwaringia* (figure 3*h*)). There may be intraspecific variation in the development of sculpture, as reported in *Nodilittorina* (*Nodilittorina*) *hawaiiensis* (Struhsaker 1968) and *N.* (*N.*) *millegrana* (Bandel & Kadolsky 1982). Only in *Littoraria* (*Lamellilitorina*) *albicans* is the form of the protoconch II diagnostic, being unusually large and trochoidal (Reid 1986*a*) (figure 3*k*). In other cases neither the shape nor the sculpture of the protoconch II appears to be of systematic value at the generic level.

An intermediate type of development, in which planktotrophic veligers hatch from benthic egg masses, is shown by a few littorinids (*Lacuna* (*Epheria*) *vincta*, *Risellopsis varia*, *Bembicium auratum*, *B. nanum*). In these cases the protoconch is more like that of non-planktotrophic species, being unsculptured, of 1.25–2.5 whorls, with a slight or absent sinusigera rib, but of the size of planktotrophic species (0.35–0.47 mm diameter; figure 3*e*–*f*). They do, however, appear to be genuinely planktotrophic, because considerable growth occurs between hatching and settlement (Thorson 1946; Pilkington 1976; Reid 1988).

The form of the protoconch and type of larval development has been included in the analysis as a single character (character 3). Four character states have been defined: non-planktotrophic, intermediate, planktotrophic, and planktotrophic with a large protoconch (as in *Littoraria* (*Lamellilitorina*)). In the outgroup both families show non-planktotrophic development, as is bound to be the case in the Pomatiasidae, which are terrestrial. However, among neotaenioglossans as a whole the hatching of planktotrophic veligers with sculptured shells from benthic eggs is certainly plesiomorphic, as for example in most Cerithioidea and some Truncatelloidea. Accordingly, it could be argued that the intermediate type of protoconch and development is primitive in the Littorinidae. Nevertheless, the lack of a typically sculptured, planktotrophic protoconch in littorinids with intermediate development suggests that this type may in fact have been derived from non-planktotrophic ancestors. Planktotrophic development with a normal planktotrophic protoconch is here considered to be plesiomorphic in the Littorinidae, even though, as discussed later (see §4*g*), the production of pelagic egg capsules, from which these veligers hatch, is apomorphic. The four character states have been coded as unordered for the analysis, because of the uncertain derivation of the intermediate type. The type of spawn and method of brooding of embryos are also important characters, which are reviewed in §4*g*.

In most littorinids the shell surface is covered by a closely adherent periostracum which is so thin as to be inconspicuous, but in members of the genera *Pellilitorina*, *Lacuna* and *Laevilitorina* the periostracum is of moderate thickness. The periostracum is relatively thin in the members of the outgroup, so a thick layer could be regarded as a synapomorphy. However, all three genera share an Antarctic or largely sub-Arctic distribution and, in common with many cold-water molluscs, have thin shells, perhaps as a result of physiological limitations on calcification at low temperatures (Graus 1974; Vermeij 1978). It is possible that a thick periostracum may simply be a parallel adaptation to strengthen or protect the thin shell. A thick periostracum is also found in *Cremnoconchus*, the only freshwater genus of the family. As in many freshwater molluscs, the periostracum protects the shell from erosion. Bristles are found on the periostracum in only seven species of littorinids (*Pellilitorina setosa* (figure 3*a*), *P. pellita*, *Risellopsis varia*, *Peasiella isselli*, *Littoraria* (*Littoraria*) *vespacea*, *Mainwaringia leithii*, *M. rhizophila*), and there is no obvious phylogenetic or functional explanation for this erratic occurrence.

When the shells of members of the Skeneopsidae, Cingulopsoidea and some primitive Truncatelloidea are dissolved in dilute hydrochloric acid, two organic layers remain. In addition to the periostracum there is an inner, transparent, iridescent layer which has been termed the 'inner chitinous layer' (Ponder 1983, 1988). This layer has not been found in any members of the Littorinidae, nor in the Pomatiasidae or Aciculidae, and has not been reported in any of the Cerithioidea.

There is considerable variation in the mineralogy and microstructure of the shell in the Littorinidae (Taylor & Reid 1989) (character 4). As in most caenogastropods, the shell usually consists of two or three aragonitic layers of crossed-lamellar structure. However, calcitic layers occur in three genera. In *Pellilitorina* the entire shell is made of calcite, in a crossed-foliated structure. In *Risellopsis* and *Littorina* (excluding *L. striata* and *L. keenae*) the shell is partly of aragonite, but with an outer calcitic layer of irregular-prismatic structure. In Pomatiasidae the shell is entirely of aragonite, so that the presence of a calcitic layer is regarded as apomorphic. The different microstructure of the two types of calcitic layer suggests that they are of separate origin, and they have been coded separately in the analysis. It is interesting that the calcitic layers are always external, and are present only in genera from high latitudes (*Pellilitorina* in the Antarctic, *Risellopsis* in New Zealand, *Littorina* in the northern Pacific and northern Atlantic). Taylor & Reid (1989) have suggested that this is an adaptation to resist shell dissolution in cold water, because calcium carbonate is more soluble in cold than warm water, and calcite is less soluble than aragonite.

The microstructure of the aragonitic layers also shows some variation (Taylor & Reid 1989). The outermost layer in the shell of *Lacuna* and *Laevilitorina* has a spherulitic-prismatic structure, as is also found in Pomatiasidae. Most species of *Nodilittorina* and two of *Littorina* (*L. striata* and *L. keenae*) show an outermost layer of very fine crossed-lamellar structure, with conspicuous growth increments. Because of the difficulties in establishing the homologies of the shell layers, the five types of shell mineralogy and microstructure have been coded as unordered states of a single character.

The colour and pattern of the shell of littorinids shows considerable intraspecific variation, especially in the truly polymorphic species (see, for example, Heller 1975; Reid 1986*a*, 1987). It is nevertheless possible to make some generalizations about the occurrence of pattern types in littorinid genera. Two pattern types can be distinguished: spiral bands of dark pigment and axial or oblique flames of pigment. The spiral pattern does not necessarily bear any relation to the sculpture of the shell, for colour bands occur in species with and without spiral grooves, and in those with grooves the pigment may be concentrated in the grooves (e.g. *Littorina nigrolineata*), on the ribs (e.g. *Tectarius coronatus*) or spread over the width of several ribs and grooves (e.g. *Mainwaringia rhizophila*, figure 2*n*). Axial flames are sometimes uninterrupted (e.g. *Nodilittorina ziczac*, figure 2*h*), but often pigment does not appear in the grooves, so that the pattern appears to be of short dashes on the ribs, aligned into axial series (e.g. *Littoraria angulifera*, figure 2*c*). In extreme cases the pigment may be reduced to a scattering of dots on the ribs alone (e.g. *Nodilittorina modesta*, figure 2*e*). Of the members of the outgroup, the Skeneopsidae are sometimes spotted (Gofas 1982*a*), and species of the Pomatiasidae, if coloured, show spiral bands. The two pattern types are not mutually exclusive in littorinids. In *Risellopsis varia* both spiral lines and axial blotches appear on the same shells; in tesselated colour morphs of *Littorina obtusata* and *L. mariae* spiral lines may change during the course of growth to oblique or zigzag lines, or form tesselated patterns; and in *Peasiella infracostata* and *Littoraria zebra* initially oblique lines may become almost or entirely spiral in some large individuals. Because of these difficulties, and also the absence of pattern in some groups (e.g. *Pellilitorina*), the character has not been employed in the cladistic analysis. It is nevertheless of interest that only spiral bands occur in *Lacuna*, *Cremnoconchus*, *Melarhaphe* and *Tectarius*, and predominate in *Laevilitorina* (*L. mariae* is an exception) and *Littorina* (exceptions are *L. keenae*, *L. brevicula* and *L. scutulata* with pale flecks on a dark ground). Oblique or axial patterns occur in *Cenchritis*, *Peasiella*, *Littoraria* and *Nodilittorina*. In *Nodilittorina* conspicuous colour patterns occur only in species lacking nodulose sculpture (Bandel & Kadolsky 1982), and in species of *Cenchritis* and *Tectarius*, all of which are nodulose, colour patterns are inconspicuous or absent.

A spiral white stripe within the aperture, near the anterior end, is a conspicuous feature of the coloration of some littorinids, especially in the genera *Melarhaphe* and *Nodilittorina*. In other genera, particularly if the shell is thin, pigmentation pale, or the aperture lined by a whitish callus, this stripe is not clearly visible. Its position corresponds with the base of the gill filaments when the animal is extended.

(*b*) *Operculum* (*characters* 5–7)

Some authors have emphasized the form of the littorinoidean operculum as an important character at familial and subfamilial levels. Kesteven (1903) advocated inclusion of *Echininus* and *Peasiella* in the Modulidae on the basis of the multispiral operculum. Rosewater (1972) created the subfamilies Tectariinae and Echinininae largely on the basis of their mesospiral and multispiral opercula, respectively. In contrast, Bandel & Kadolsky (1982) suggested that the operculum was of little value as an indicator of relationships, tightly coiled forms having evolved repeatedly from the ancestral paucispiral type. These authors classified littorinid opercula into four types: paucispiral type A (width of last whorl, measured on long axis of operculum, more than half total length), paucispiral type B (more circular, width of last whorl less than half total length), mesospiral type C (nearly circular, width of last whorl about one fifth total length), multispiral type D (circular, last whorl very narrow). They pointed out that both types A and B occurred within the genus *Nodilittorina*, and this is also the case in *Cremnoconchus*, *Laevilitorina*, *Littoraria* and *Littorina*. Type B alone is found in *Risellopsis* and *Cenchritis*; type C occurs only in *Tectarius* (*Tectarius*), *T.* (*Tectininus*) and *T. viviparus*; type D is present in *T.* (*Echininus*) and *Peasiella*; all other littorinid genera have opercula of type A (figure 4). The difference between types C and D is slight, the width of the last whorl being one sixth to one seventh of the total length in *Tectarius* (*Echininus*) and *Peasiella*.

If a different, coarser classification of opercular types is used, grouping A and B as paucispiral, and defining as mesospiral opercula in which the width of the last whorl is less than

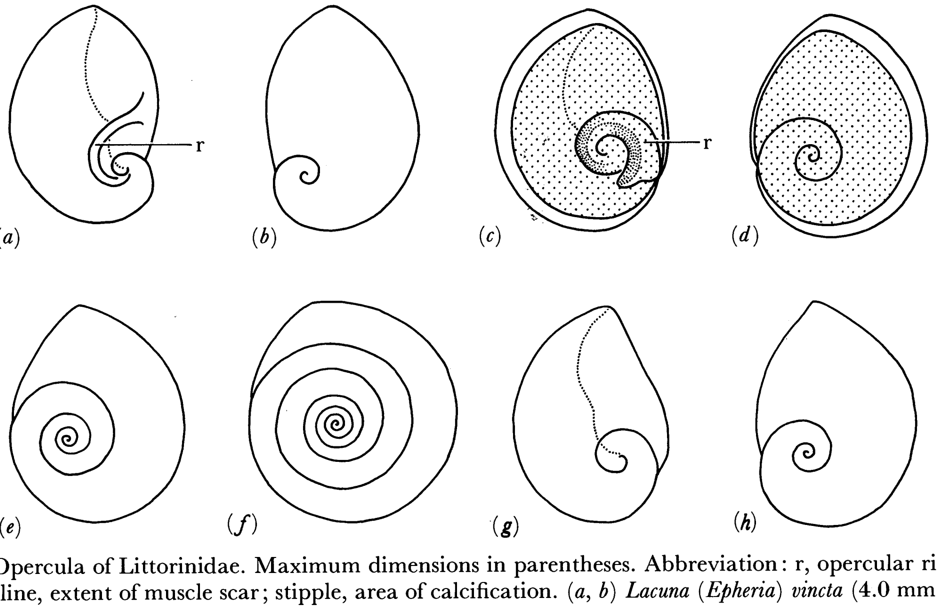

FIGURE 4. Opercula of Littorinidae. Maximum dimensions in parentheses. Abbreviation: r, opercular ridge. Key: dotted line, extent of muscle scar; stipple, area of calcification. (*a*, *b*) *Lacuna* (*Epheria*) *vincta* (4.0 mm), internal and external views; (*c*, *d*) *Cremnoconchus syhadrensis* (3.7 mm), internal and external views; (*e*) *Cenchritis muricatus* (6.4 mm), external view; (*f*) *Tectarius* (*Echininus*) *cumingii* (4.7 mm), external view; (*g*) and (*h*) *Littorina* (*Neritrema*) *obtusata* (5.4 mm), internal and external views.

or equal to one quarter of the total length, it becomes clear that the character is a significant one (character 5). The mesospiral type occurs only in *Peasiella* and *Tectarius*. This type is probably derived, despite its occurrence in the Skeneopsidae (Fretter 1948), because the paucispiral type is found in many Pomatiasidae (including *Pomatias elegans*) and predominates in Aciculidae, Cingulopsoidea and Truncatelloidea.

The functional significance of tight coiling of the operculum is twofold: it thickens the operculum by increasing the number of revolutions (thereby reducing evaporation) and produces a more nearly circular outline (to fit a more circular aperture) (Bandel & Kadolsky 1982). Littorinids occupying the littoral fringe on tropical rocky shores often have smaller and more circular apertures to reduce water loss (Vermeij 1973), so for both reasons mesospiral opercula would be predicted in *Tectarius* species, which occupy this habitat and have pyramidal shells with rather round apertures. The correlation is not perfect, however, because *Cenchritis* occupies a tropical supralittoral habitat and has a rounded aperture, but a paucispiral operculum, whereas *Peasiella* has a pyramidal shell, round aperture and mesospiral operculum, yet occupies the high eulittoral zone. The occurrence of the mesospiral operculum therefore cannot be explained entirely as a necessary consequence of shell shape, nor as a parallel adaptation to the tropical supralittoral habitat, and the hypothesis of common ancestry is likely.

A conspicuous peg is present on the adaxial side of the opercula of the Cingulopsoidea and some Truncatelloidea (Ponder & Yoo 1978; Ponder 1988). Although this is not seen in any littorinids, members of *Pellilitorina*, *Lacuna*, *Cremnoconchus*, *Bembicium* and *Mainwaringia* do show a thickened spiral ridge on the inner side of the operculum in the corresponding position, where the opercular muscle attachment is partly divided into two (figure 4*a*, *c*). It could be suggested that this ridge is a remnant of the opercular peg, which has been lost in other littorinids. However, the absence of either peg or ridge in the outgroup makes it possible that the ridge is an apomorphic character (character 6).

The operculum of littorinids is composed of brown, horny, proteinaceous material, as in the Skeneopsidae, Cingulopsoidea and most Truncatelloidea. Only in *Cremnoconchus* is the operculum calcified. This operculum is similar to that found in the terrestrial Pomatiasidae, although in *Cremnoconchus* there are proteinaceous layers on both external and internal surfaces, whereas in Pomatiasidae there is horny material on the internal surface only. For this reason the calcified opercula have probably been derived independently in the two groups, as reflected in the coding of the character states (character 7). Bandel & Kadolsky (1982) reported a calcified operculum in *Tectarius* (*Echininus*), but in both species of the subgenus the operculum appears black and horny and does not effervesce in dilute hydrochloric acid.

(*c*) *Head-foot and pallial complex* (*characters* 8–14)

As in other neotaenioglossans, three regions may be distinguished in the foot of littorinids; the small anterior region is the propodium, usually separated from the mesopodium by a deep transverse groove almost at the anterior edge of the sole, whereas the metapodium is the posterior region bearing the operculum. In addition to the sub-epithelial sole glands scattered over the foot, there is in most littorinids a large anterior pedal gland, which opens into the transverse groove (Shirbhate & Cook 1987). *Cremnoconchus* is an exception, lacking a transverse propodial groove and showing a much reduced anterior pedal gland. In the Pomatiasidae also there is no transverse groove, nor a discernible propodium, and the anterior pedal gland (here known as the suprapedal gland (Shirbhate & Cook 1987)) opens by a pore at the front end of the longitudinal groove in the sole. Nevertheless, the presence of the transverse groove is believed to be plesiomorphic, because it occurs in Skeneopsidae (Fretter 1948) and in many other neotaenioglossans (Fretter & Graham 1962) (character 8).

A second gland, the posterior pedal gland, is found beneath the sole in the centre of the foot in some groups. This is present in the Eatoniellidae (Ponder 1965), Rastodentidae (Ponder 1966*a* and personal communication), Anabathridae, Barleeidae (both Ponder 1983) and Cingulopsidae (Fretter & Graham 1962, p. 116), in all of which the gland opens to a longitudinal slit which reaches back to the posterior edge of the foot. A similar gland is present in the Skeneopsidae (Fretter 1948), but here the slit does not reach the posterior edge of the foot. The posterior mucous gland is absent in all members of the Littorinidae, and also in the Pomatiasidae (Shirbhate & Cook 1987) and Aciculidae (Delahaye 1974; D.G.R., personal observation). The tubulous gland of the Pomatiasidae, consisting of a mass of tubules in the haemocoele and opening by a pore halfway along the longitudinal groove dividing the sole, is not a mucous gland, but is concerned with osmoregulation (Delahaye 1974), and is therefore not homologous with the posterior pedal gland.

In most species of Littorinidae the sole of the foot is divided longitudinally by a deep groove extending from the posterior edge almost to the anterior transverse groove (character 9). This is a sign of the functional division of the foot into two halves, responsible for the retrograde ditaxic style of locomotion (Miller 1974). This division is usually clear in preserved, as well as crawling, animals. However, in *Pellilitorina*, *Lacuna*, *Cremnoconchus*, *Laevilitorina*, *Melarhaphe*, *Peasiella* and *Mainwaringia* no such division can be seen, although locomotory waves are probably still retrograde and ditaxic (as in *Lacuna* (Miller 1974; D.G.R., personal observation) and *Melarhaphe* (D.G.R., personal observation)). The foot is not divided in the Skeneopsidae, Aciculidae, Eatoniellidae or Truncatelloidea, and in *Skeneopsis* and the few truncatelloideans for which information is available, locomotion is by ciliary action or direct monotaxic waves (Miller 1974). The terrestrial Pomatiasidae do have a longitudinal division of the sole, but here the ditaxic waves are direct (Miller 1974). Although in prosobranchs as a whole retrograde ditaxic locomotion is the most common type, in neotaenioglossans it is uncommon (Miller 1974) and Ponder (1988) has suggested that ditaxic locomotion may be a synapomorphy of the Pomatiasidae and Littorinidae. Nevertheless, the morphological (as opposed to functional) division of the foot is tentatively regarded as apomorphic within the Littorinidae, because the different direction of the waves and terrestrial habit of the Pomatiasidae suggest that parallel evolution could have occurred in this family, whereas in other outgroups division is absent. Ditaxic waves are believed to facilitate turning and adhesion during locomotion (Miller 1974). These functions are likely to be especially significant in snails of high intertidal habitats, and might be improved by morphological division of the foot, but observations of living animals are needed to substantiate this. *Mainwaringia rhizophila* is unusual in that locomotion is not ditaxic, and proceeds almost entirely by ciliary gliding. This type is effective on loose substrates (Miller 1974) and the mangrove bark on which the species lives is often muddy.

The head-foot of littorinids lacks the neck lobes that have been reported in the Cingulopsoidea and some primitive Truncatelloidea (Ponder 1966*a*, 1983, 1988).

Accessory tentacles (pallial and metapodial) are present on the head-foot in some Truncatelloidea (Ponder 1968, 1983, 1988), but are absent in the Littorinoidea. The foot of *Mainwaringia* is tapered posteriorly, but there is no metapodial tentacle. In the Eatoniellidae there may be one or two tentacles on the opercular lobe, or these may be absent (Ponder 1965).

In the Littorinidae two short opercular tentacles are found in *Lacuna*, and eight are present in *Laevilitorina* (*Pellilacunella*) (character 10). Ponder (1988) regarded opercular tentacles as a plesiomorphic character of the littorinoidean–truncatelloidean radiation. Although this may be so in the Eatoniellidae, their absence in other families more closely related to the Littorinidae suggests that in this family the tentacles are apomorphic.

Another pedal structure of littorinids is the ovipositor. If present, this is visible as an unpigmented, raised area with a median groove, on the right side of the head, in the same position as the penis of males. In the present study a distinct ovipositor has been found only in *Cremnoconchus*, *Bembicium*, *Melarhaphe*, *Tectarius* (*Tectininus*), *Nodilittorina* (*Fossarilittorina*) and *Littorina*. Its function is unclear, but may in some cases be concerned with moulding or hardening the egg capsule (Linke 1933*a*; Fretter & Graham 1962, p. 47). It is not known whether the ovipositor becomes less conspicuous outside the spawning season. For this reason, and because of its sporadic occurrence in littorinids, it has not been used as a character in the analysis.

The genus *Pellilitorina* is unique among the Littorinoidea in possessing a flange leading from the edge of the foot up towards the right side of the head in females (character 11). Although this structure is unlike a true ovipositor in position and appearance, it is probably concerned with deposition of the egg mass.

The head of littorinids ends in a fairly short snout, which is not distinctly bilobed. The pair of cephalic tentacles are long, tapering and mobile, and do not show the conspicuous cilia which are evident in many of the Truncatelloidea, including some Cingulopsidae and Rastodentidae (Ponder 1988). The cephalic tentacles of the Eatoniellidae are of the same primitive, unmodified type seen in the Littorinidae (Ponder 1988). The eyes are borne at the outer bases of the cephalic tentacles, on slight swellings. Only in *Pellilitorina* are the eyes borne on short peduncles, a derived condition unlike that seen in the outgroup (character 12).

The pattern of pigmentation on the head has sometimes been employed as a taxonomic character in littorinids. However, it is rarely species specific, and particularly in cases of polymorphic or variably patterned shells shows considerable intraspecific variation, often correlated with the degree of pigmentation of the shell (James 1968*a*, *b*; Smith 1976; Reid 1986*a*). At higher taxonomic levels some generalizations can be made. The majority of littorinids show black or grey pigmentation on the snout, and often on the cephalic tentacles and sides of the foot also, although in some small *Laevilitorina* species and morphs of *Littoraria* and *Littorina* with pale shells the animal may be unpigmented. In *Pellilitorina*, *Lacuna* (figure 5*b*), *Cremnoconchus*, *Bembicium*, *Laevilitorina* (figure 5*a*) and *Mainwaringia* the head is dark, sometimes paler at the tip of the snout, pale around the eyes and with pale or dark tentacles. *Laevilitorina* (*Rissolittorina*) *alta* is unusual in showing a single longitudinal black stripe on each tentacle (Ponder 1966*b*). A dark head and pale patch around or behind the eye also occur in *Risellopsis*, *Cenchritis* (figure 5*d*), *Tectarius*, *Littorina* (figure 5*k*) and *Nodilittorina africana*, but in these cases the tentacles show diffuse transverse bands and sometimes also an indistinct longitudinal stripe. In *Littoraria* (figure 5*f*) the pattern is similar, but there is usually a pale patch on the inside of the tentacle base as well as behind the eye. The pigmentation of the remaining *Nodilittorina* species is distinctive; again the head is dark and the area around and sometimes behind the eye is pale, but the tentacles are marked by two or three longitudinal black stripes. The stripes may not extend for more than half the length of the tentacles, and rarely may be fused to form a transverse black band in front of the eye (e.g. *N. quadricincta*,

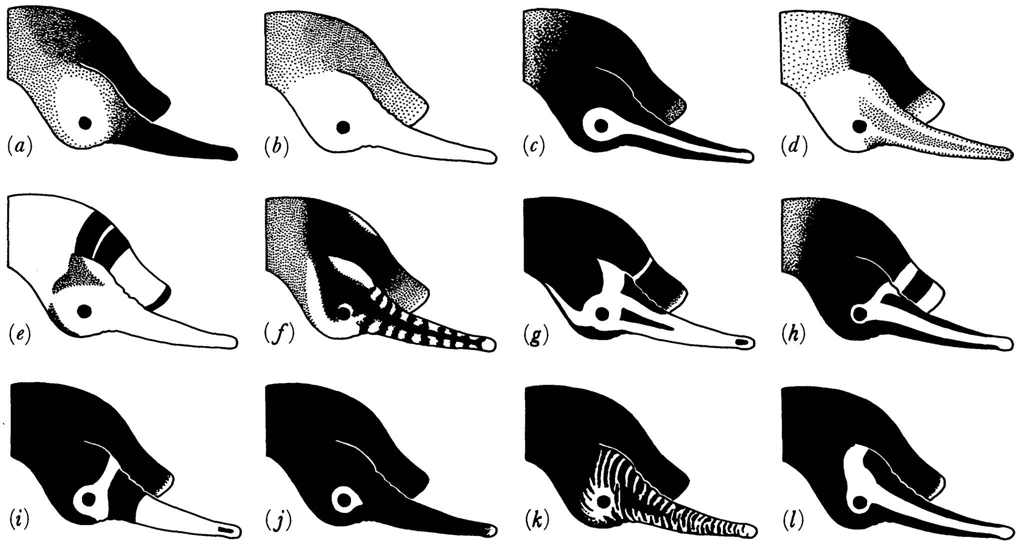

FIGURE 5. Pigmentation patterns on heads of Littorinidae. (*a*) *Laevilitorina* (*Pellilacunella*) *bennetti*; (*b*) *Lacuna* (*Epheria*) *vincta*; (*c*) *Melarhaphe neritoides*; (*d*) *Cenchritis muricatus*; (*e*) *Peasiella tantilla*; (*f*) *Littoraria* (*Littorinopsis*) *scabra*; (*g*) *Nodilittorina* (*Echinolittorina*) *dilatata*; (*h*) *Nodilittorina* (*Nodilittorina*) *porcata*; (*i*) *Nodilittorina* (*Nodilittorina*) *novaezelandiae*; (*j*) *Nodilittorina* (*Echinolittorina*) *peruviana*; (*k*) *Littorina* (*Littorina*) *littorea*; (*l*) *Littorina* (*Neritrema*) *saxatilis*.

N. novaezelandiae (figure 5*i*), *N. hawaiiensis*, *N. trochoides*), sometimes with a black spot at the tentacle tip. In the most heavily pigmented *Nodilittorina* species the pattern is obscured, the tentacles being entirely black with a white patch over the eye (e.g. *N. peruviana* (figure 5*j*), *N. araucana*). A typical *Nodilittorina*-like pattern of two longitudinal black stripes on the tentacles is found in *Melarhaphe* (figure 5*c*). *Peasiella* is difficult to characterize; most commonly the tentacles are unpigmented (figure 5*e*) or bear a single longitudinal black stripe, but occasionally two black stripes occur. The only other occurrence of the *Nodilittorina*-like pattern in littorinids is in the *Littorina* (*Neritrema*) *saxatilis* group (*L. saxatilis* (figure 5*l*), *L. arcana*, *L. neglecta*, *L. nigrolineata*). The *Nodilittorina*-like pattern has been included as an apomorphic character in the analysis (character 13). Members of the outgroup do not show distinctive pigmentation.

Variation in the structure of the pallial complex appears to be correlated with habitat. In species of *Tectarius* and *Nodilittorina* living at supratidal levels of rocky shores, and of *Littoraria* in mangrove trees, the gill leaflets are relatively reduced in size, forming mere wrinkles on the surface of the mantle for much of their length (Reid 1986*a*). In addition, the hypobranchial gland is relatively narrower in these species. The osphradium consists of a long, narrow ridge, bordered by a strip of ciliated epithelium on either side. Haszprunar (1985) noted an asymmetry of the lateral zones of two species, and correlated this with a supratidal habitat. In *Pomatias* the lateral ciliated zone is present on the right side only, but in the Truncatelloidea the organization of the osphradium is similar to that of *Littorina* species (Haszprunar 1985). A character of apparent systematic importance is a terminal flexure in the long axis of the osphradium, so that the distal end is turned back on itself to about one third of the length of the organ. This is seen only in the genus *Lacuna*, and because it is unknown in related families is evidently apomorphic (character 14).

(*d*) *Male reproductive system* (*characters* 15–25)

The sexes are separate in all littorinids with the exception of *Mainwaringia rhizophila*, which is a protandrous hermaphrodite (Reid 1986*b*). Because no other cases of hermaphroditism have been reported in the Littorinoidea or Cingulopsoidea, and only one in the Truncatelloidea (Bieler & Mikkelsen 1988), this is a derived condition (character 15). Current theories of the selective advantages of hermaphroditism fail to explain adequately this unique occurrence in the Littorinidae (Reid 1986*b*). It is noteworthy that in the intersexual stage both pallial oviduct and pallial prostate are present simultaneously. This suggests either that these structures are not homologous (despite their similar ontogenies (Guyomarc'h-Cousin 1976)), or that the prostate of *M. rhizophila* is a new structure. This true hermaphroditism should not be confused with cases of abnormal development that occur in some littorinids when females develop penes (review by Reid (1986*b*)).

The male reproductive tract of littorinids follows the typical caenogastropod plan, with a testis of tubules that ramify in the digestive gland, and from which spermatozoa are collected in the visceral section of the vas deferens, which is expanded and coiled against the columella of the shell to form a seminal vesicle for sperm storage. The visceral vas deferens leads to the pallial section, which forms a large prostate gland. From the prostate sperm pass over the side of the head, in the anterior vas deferens, to reach the penis, which is situated below and behind the right cephalic tentacle. There is no gonopericardial duct, nor any duct leading from the distal end of the visceral vas deferens to the back of the mantle cavity (as for example in *Skeneopsis* (Fretter 1948) and as reported in *Lacuna vincta* by Fretter & Graham (1962, p. 345), but not confirmed by the present study). The pallial and cephalic sections of the sperm pathway may be open grooves or closed ducts. These differences, combined with the form of the penis and its glandular elements, are of great importance in the classification and phylogenetic reconstruction of the Littorinidae.

Among most genera the prostate is an open groove, communicating with the mantle cavity all along its length (character 16). The exceptions, with a closed, tubular prostate, are *Pellilitorina*, *Lacuna*, *Cremnoconchus*, *Laevilitorina* and *Littoraria*. Because the pallial genital ducts are believed to be primitively open in neotaenioglossans (Fretter & Graham 1962, p. 345; Ponder 1988), the open prostate might be thought to be the primitive condition. However, a parsimony argument suggests that this is not the case, for in both members of the outgroup the prostate is closed (Fretter 1948; Creek 1951; Thompson 1978). This condition is also found in the Aciculidae (see Creek 1953; Jackiewicz 1967), Rastodentidae (Ponder 1966*a*), Cingulopsidae (see Fretter & Patil 1958; Ponder & Yoo 1980) and in almost all the families of the Truncatelloidea (Ponder 1988). An open prostate occurs in the Eatoniellidae (Ponder 1965, 1968), but even here some closure has occurred, as in *Eatoniella kerguelenensis regularis* (Smith) in which the prostate is only open for the anterior one third of its length (D. G. R., personal observation). The open condition may be primitive in the Eatoniellidae, as in the Cerithioidea (Ponder 1988). However, within the Littorinoidea it is possible that the plesiomorphic condition is a closed prostate. If so, the prostate has become secondarily opened in many littorinids. No functional explanation for this can be offered; it is not obviously connected with a narrow mantle cavity in an elongate shell as suggested by Fretter & Graham (1962, p. 359) in some other families. Nevertheless, as discussed below, both the anterior vas deferens and the penial vas deferens appear to show the same evolutionary trend, so the opening of the pallial gonoduct is apparently of functional significance. One possibility is that it is quicker to transport sperm, by a combination of ciliary and muscular action, along an open groove than through a narrow tube. This could be of importance in the intertidal environment, where animals are more susceptible to desiccation and dislodgement while copulating. Observations of intertidal littorinids show that copulation lasts for less than 45 min, is inhibited by wave splash and desiccation, and seldom takes place under water (Berry 1961; Gibson 1964; Struhsaker 1966; Jordan & Ramorino 1975).

The histology of the littorinid prostate provides another character for the analysis (character 17). In those species that have been sectioned, the glandular lining is epithelial and the granular secretion usually stains red in MT and magenta with ABPAS. Differentiation of the staining reactions along the length of the prostate has been observed only in *Laevilitorina antarctica*, *Nodilittorina pyramidalis* and *Littorina obtusata*, and has also been reported in the *Littorina saxatilis* group (Hannaford Ellis 1979) and in Pomatiasidae (Creek 1951). The structure of the glandular epithelium of the prostate has been described in *Littorina* (Linke 1933*a*), *Bembicium* (Bedford 1965) and in the outgroup (see Fretter 1948; Creek 1951). A more elaborate, apomorphic condition occurs in *Cremnoconchus*, with subepithelial glandular follicles (Linke 1935*a*; D.G.R., personal observation). Alone in the Littorinidae, glandular cells are absent in the prostate of *Lacuna* (*Epheria*) *vincta*, and this is also likely to be a derived condition.

The anterior vas deferens is a ciliated channel that conducts sperm from the distal end of the prostate over the side of the head to the base of the penis. Like the prostate, this channel may be open or closed in littorinids (character 18). Because the condition of the two structures is not always correlated, they have been included as two separate characters in the cladistic analysis. The groups in which the anterior vas deferens is closed are *Pellilitorina*, *Lacuna*, *Cremnoconchus*, *Bembicium*, *Laevilitorina*, *Melarhaphe*, *Cenchritis* and a few species of *Littoraria* (Reid 1986*a*). The same condition occurs in Pomatiasidae (Creek 1951; Thompson 1978; D.G.R., personal observation) and in Skeneopsidae (Fretter 1948), suggesting that a closed anterior vas deferens could be plesiomorphic for the Littorinidae. The anterior vas deferens is open in Aciculidae (Creek 1953).

In all littorinid species a penis occurs in the same position, below and a little behind the right cephalic tentacle. Ponder (1988) has pointed out the importance of penial innervation to the consideration of the homology of the littorinid penis. The penial nerve originates from the right pedal ganglion in littorinids, as is also found in the Skeneopsidae (Ponder 1988). It has been stated that although the penis of the Pomatiasidae is of pedal origin, that of the Annulariidae is innervated from the left pleural ganglion via the suboesophageal nerve, and is therefore of pallial origin (Thompson 1978). This has been cited as the main reason for separation of the two families. However, in *Pomatias elegans* the base of the penis receives nerves from both the right pedal ganglion and the suboesophageal ganglion, raising the possibility that the penis may be homologous and of pedal origin in the two groups. The innervation of the penis in the Aciculidae is not known. A penis of pedal origin also occurs in all truncatelloidean families, with the exceptions of the Anabathridae and Emblandidae, in which penial innervation is from the cerebral ganglion (Ponder 1988). The Cingulopsoidea are aphallate, probably a retention of the plesiomorphic condition found in Cerithioidea, although there is a possibility that a penis may have been lost, because some Eatoniellidae have a ‘rudimentary penis’ (Ponder 1968, 1988). Ponder (1988) has argued that because of the non-homology of the penis in Anabathridae and Emblandidae (considered by him to be the most primitive of the

Truncatelloidea) with that of other Truncatelloidea, the pedal penis has probably arisen independently from an aphallate condition in the Truncatelloidea and Littorinoidea. Ponder also cites as evidence small differences in the origin of the penial nerve in the two groups, from the anterior part of the pedal ganglion in *Littorina* (and in most of the other genera examined in the present study), and from the base of the pleuropedal connective (or further up this connective) in the Truncatelloidea. Because the penial nerve of *Cremnoconchus* (Linke 1935*a*; D. G. R., personal observation) and of *Pomatias* arises at the base of the pleuropedal connective (as does the nerve to the 'rudimentary penis' of Eatoniellidae), this difference may be less clear cut than previously thought. In conclusion, it appears that the pedal penis of the Littorinoidea is a synapomorphy of the superfamily, derived independently from that of the Truncatelloidea. It may be mentioned that the penis of the Pomatiasidae arises close to the anus, much further back on the head-foot than in the Littorinidae.

It has long been recognized that the shape of the penis is the single most important taxonomic character of the Littorinidae, at both specific and generic levels (review by Reid 1986*a*) (figures 6 and 7). There are two likely explanations for the wide diversity of penial form. The genera of littorinids can often be defined by the possession of characteristic types of conspicuous mucous glands, which represent different solutions to the problem of securing the penis in position during copulation. At the specific level, penial shape (especially proportions of filament and base, and numbers of glands) is so often diagnostic, that it is believed to be a species-recognition device, selected for by female choice.

The littorinid penis is usually differentiated into a wrinkled basal region and a more slender, terminal filament, which enters the bursa copulatrix of the female to deposit sperm during copulation. Sperm are transmitted along the ciliated penial vas deferens, which may be an open groove, as in *Risellopsis*, *Tectarius*, *Littorina*, *Nodilittorina* (except *N.* (*Fossarilittorina*) *meleagris* and *N.* (*F.*) *mespillum*) and *Littoraria* (except *L.* (*L.*) *flava*, *L.* (*L.*) *tessellata*, *L.* (*Littorinopsis*) *intermedia*, *L.* (*Littorinopsis*) *philippiana*, *L.* (*Littorinopsis*) *subvittata*) or in all other genera a closed duct (character 19). In littorinids with a closed penial vas deferens, histological sections reveal two character states. In most cases closure is superficial, the duct being connected to the penial epidermis by a line of epithelial cells, presumably reflecting its origin by infolding of the surface epithelium. Only in *Pellilitorina*, *Lacuna*, *Cremnoconchus* and *Bembicium* is the duct separated from the epidermis and completely surrounded by muscle tissue (deep closure). In the outgroup the duct is deeply closed in both the Skeneopsidae (Fretter 1948) and Pomatiasidae. The penial duct is open in Aciculidae (Creek 1953). As in the case of the anterior vas deferens and prostate, a parsimony argument suggests that the closed condition is plesiomorphic in the Littorinidae. Deep closure is probably primitive, but because the sequence of the two remaining character states is uncertain, the character has been specified as unordered in the analysis.

In most littorinids the opening of the penial vas deferens is terminal, as in the outgroup (character 20). The subterminal opening of *Bembicium*, *Risellopsis*, *Tectarius* (except *T.* (*Tectarius*)), *Nodilittorina acutispira*, *N. riisei*, *N. unifasciata* and *Littorina scutulata* is regarded as apomorphic.

Penial shape is difficult to code for analysis, but it is notable that the base is bifurcate in some groups (*Risellopsis*, *Laevilitorina* (*Rissolittorina*), *L.* (*Rufolacuna*), *Nodilittorina* (except *N.* (*Fossarilittorina*) and *N. modesta*) and *Littoraria* (except *L. pintado*, *L.* (*L.*) *fasciata*, *L.* (*L.*) *flava*, *L.* (*L.*) *irrorata*, *L.* (*L.*) *vespacea* and *L.* (*Palustorina*)) (character 21; figures 6 and 7). This is in contrast to the simple form of the penis in the outgroup (Fretter 1948; Creek 1951;

Thompson 1978), and is therefore considered apomorphic. The basal appendage usually bears complex glandular elements (*Risellopsis* is an exception), although not all littorinids with such glands show a bifurcate base. For this reason this character has been coded as unknown in *Nodilittorina modesta*, *N.* (*Fossarilittorina*) and *Littorina* (*Liralittorina*), in which penial glands are believed to have been secondarily lost, with possible concomitant simplification of the penis. *Cremnoconchus* shows a unique condition, in which the filament is retracted into the base when the penis is at rest (Linke 1935*a*; D.G.R., personal observation) (character 22; figure 6*i*).

Two classes of penial mucous gland can be distinguished in littorinids, on the basis of their staining reactions. The ABPAS technique differentiates acidic mucins (blue) and neutral mucins (magenta) (Mowry 1956). Cells containing acidic secretions occur as scattered goblet cells in the columnar, unciliated epithelium, and are often concentrated on the penial filament. Cells with the same staining reaction as goblet cells occur singly or in groups in the subepithelial muscle layers of the penial filament. Where these subepithelial cells are abundant the penis appears opaque white or cream in living animals, as, for example, in the distal swellings of *Bembicium*. Because of the concentration of cells with an acidic mucous secretion on the penial filament, it appears that the secretion serves as a lubricant during copulation. Glands of these acidic types have been found in most of the littorinids examined.

The second class of mucous gland is characterized by a neutral, granular secretion, which stains magenta with ABPAS and blue or reddish in MT. These glands can be further classified into simple glands and mamilliform glands, according to their organization into more complex, compound structures. At the simplest level the glandular cells are scattered singly or in groups in the subepithelial tissues of the penial base or filament, and discharge by individual cytoplasmic extensions between the columnar epithelial cells (character 23). Glands of this type occur in the majority of littorinids, but are absent in *Pellilitorina*, *Bembicium*, *Risellopsis*, *Laevilitorina* (*Macquariella*), *Melarhaphe*, *Cenchritis* and *Nodilittorina* (*Fossarilittorina*) *meleagris*. Their presence is often difficult to detect without histological examination, and it is not known whether they occur in *Laevilitorina* (*Pellilacunella*), *Tectarius* (*Tectarius*) or *T. viviparus*. In *Lacuna* (*Epheria*) *vincta* the gland cells lie in the penial tip, and mostly discharge together over a small area, which appears as a slight papilla. Simple, neutral mucous glands of this type are absent in the Skeneopsidae (Fretter 1948) and Pomatiasidae, and are therefore probably apomorphic in the Littorinidae. Penial glands are also found in some of the Truncatelloidea, but, as discussed above, the penis is probably not homologous in the two groups. In all members of the genus *Littoraria* (except *L. pintado*) and in most species of *Nodilittorina* (exceptions are *N. modesta*, *N. africana* and *N.* (*Fossarilittorina*)) these glandular cells are concentrated in a small area, forming a lobe or disc-shaped structure referred to as the penial glandular disc (Reid 1986*a*) (figure 7). The glandular disc is conspicuous in fresh material, being more opaque than the surrounding tissue. Discharge of the secretion still occurs through the epithelium over the surface of the disc. The glandular disc is believed to be a more apomorphic state of the simple mucous glands. A still more derived condition of the glandular disc occurs in *Littoraria aberrans*, as described below. A peculiar condition is found in *Nodilittorina africana*, in which no subepithelial glands occur in the position expected of a glandular disc; instead the area is covered by a very tall, glandular epithelium, having the staining reactions of the neutral mucous glands. Apparently the mucous cells have become superficial in this species.

The mamilliform penial glands (called simply 'penial glands' by Reid (1986*a*)) are of a more elaborate structure (character 24). These are usually found only on the penial base, and

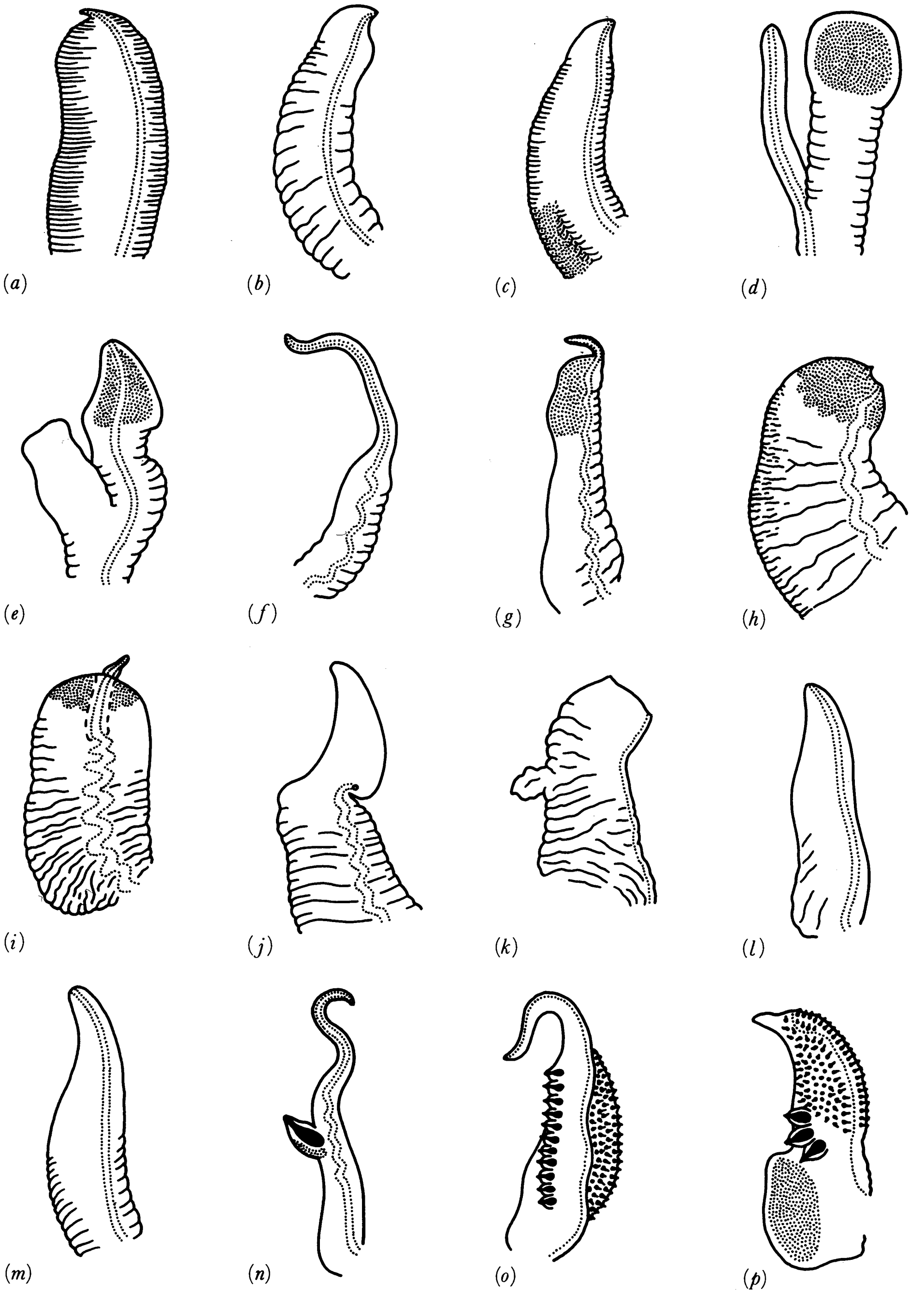

FIGURE 6. Penes of Littorinidae. Not to scale. Key: stipple, simple penial glands; black, mamilliform penial glands; double dotted line, closed penial sperm duct; single dotted line, open penial sperm groove. (*a*) *Laevilitorina* (*Pellilacunella*) *bennetti*; (*b*) *Laevilitorina* (*Macquariella*) *hamiltoni*; (*c*) *Laevilitorina* (*Laevilitorina*) *caliginosa*; (*d*) *Laevilitorina* (*Rissolittorina*) *alta*; (*e*) *Laevilitorina* (*Rufolacuna*) *bruniensis*; (*f*) *Pellilitorina setosa*; (*g*) *Lacuna* (*Lacuna*) *pallidula*; (*h*) *Lacuna* (*Epheria*) *vincta*; (*i*) *Cremnoconchus syhadrensis*; (*j*) *Bembicium melanostoma*; (*k*) *Risellopsis varia*; (*l*) *Melarhaphe neritoides*; (*m*) *Cenchritis muricatus*; (*n*) *Peasiella tantilla*; (*o*) *Tectarius* (*Tectarius*) *grandinatus*; (*p*) *Tectarius* (*Echininus*) *cumingii*.

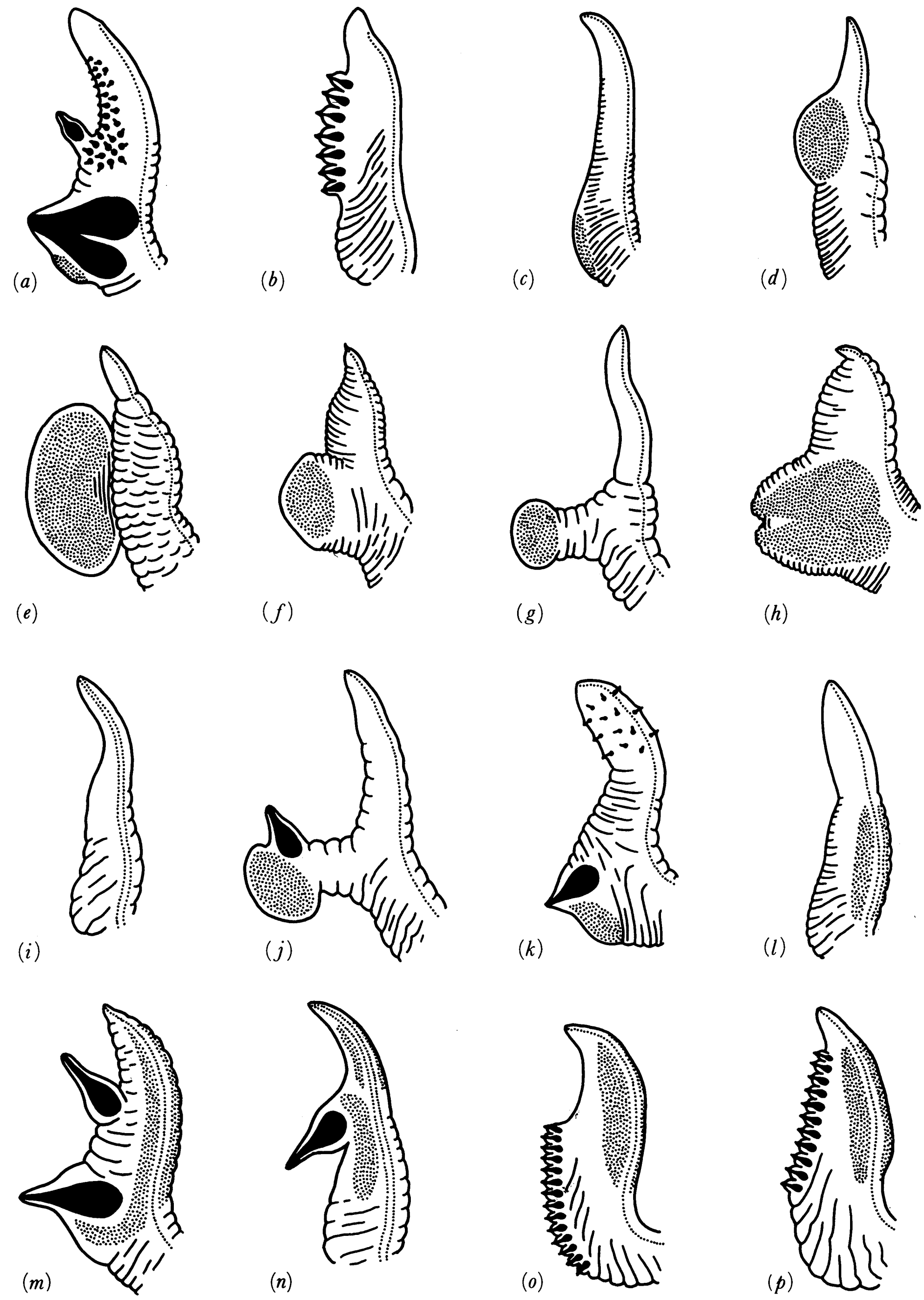

FIGURE 7. Penes of Littorinidae (continued). Not to scale. Key: as in figure 6. (*a*) *Tectarius* (*Tectininus*) *antonii*; (*b*) *Tectarius viviparus*; (*c*) *Littoraria pintado*; (*d*) *Littoraria* (*Palustorina*) *melanostoma*; (*e*) *Littoraria* (*Littoraria*) *zebra*; (*f*) *Littoraria* (*Lamellilitorina*) *albicans*; (*g*) *Littoraria* (*Littorinopsis*) *angulifera*; (*h*) *Littoraria aberrans*; (*i*) *Nodilittorina* (*Fossarilittorina*) *meleagris*; (*j*) *Nodilittorina* (*Echinolittorina*) *dilatata*; (*k*) *Nodilittorina* (*Nodilittorina*) *pyramidalis*; (*l*) *Littorina* (*Liralittorina*) *striata*; (*m*) *Littorina keenae*; (*n*) *Mainwaringia rhizophila*; (*o*) *Littorina* (*Littorina*) *littorea*; (*p*) *Littorina* (*Neritrema*) *obtusata*.

each is visible externally as a conspicuous raised papilla with a hyaline core. Each mamilliform gland comprises several clusters of subepithelial cells, which discharge through individual cellular extensions into a single large reservoir (the 'accessory flagellum' described by Rosewater (1970)), lined by a tall and sometimes much-folded epithelium and encased in a muscular coat, and which in turn empties at the tip of a raised papilla. The structure of mamilliform glands has been described by Linke (1933*a*) and Marcus & Marcus (1963). Glands of this type occur only in *Peasiella*, *Tectarius*, *Nodilittorina* (except *N. modesta* and *N.* (*Fossarilittorina*)), *Littorina* (except *L.* (*Liralittorina*) and *L.* (*Littorina*) *scutulata*) and *Mainwaringia*. Because they are absent in the outgroup, they are considered to be apomorphic. Mamilliform glands were probably derived by infolding of the surface epithelium overlying clusters of simple neutral mucous glands. However, where both types now occur on the penis together some differentiation of the glandular cell types is evident, for the simple mucous cells stain bright magenta with ABPAS, in contrast to the pale magenta of the cells of the mamilliform glands. For this reason the simple and mamilliform glands are classified as two distinct characters. The neutral secretion from both types of cells is viscous, and serves to secure the penis in position in the mantle cavity of the female during copulation (Linke 1933*a*; Bingham 1972; Reid 1986*a*). There is no obvious correlation between the habitats of species and the presence or absence of these types of penial glands.

The suggestion that infolding of the surface epithelium can occur to produce papillose glands is supported by observations on *Littoraria aberrans*. Whereas all other members of this genus (except *L. pintado*) possess a glandular disc on the penial base, in *L. aberrans* two large papillae are found (figure 7*h*). Their tips are wide and puckered, unlike the sharp points of true mamilliform glands. Histologically their structure is similar, however. Two important points of difference are that the glandular secretion stains bright magenta with ABPAS, and that the epithelial lining of the reservoir contains abundant goblet cells, which secrete acidic mucins. Goblet cells do not occur deep within the reservoir of mamilliform glands, but are commonly found on the surface of the penial glandular disc. It is therefore proposed that the glands of *L. aberrans* have been formed by infolding of a glandular disc, and they have been coded as the most derived state of character 23.

The penial glandular disc is always borne singly. Mamilliform glands have become either lost or multiplied in various lines. This is suggested by the variations in numbers of these glands within genera and species. Examples include *Littorina* (0 in *L.* (*Liralittorina*) *striata*, 2 or rarely 1 in *L. keenae*, 0 in *L. scutulata*, 1 in *L. plena*, 1–4 in *L.* (*L.*) *brevicula*, 16–30 in *L.* (*L.*) *littorea*, 13–54 in *L.* (*Neritrema*) *obtusata*), *Nodilittorina* (1 in all members of subgenera *Nodilittorina* and *Echinolittorina* except 0 or 2 in some abnormal animals, and many in *N.* (*N.*) *pyramidalis*; 0 in *Fossarilittorina* and *N. modesta*) and *Peasiella* (1 in all species except 0 or 1 in *P. roepstorffiana*). Within species with many penial glands there is a correlation between shell size and gland number (Raffaelli 1979; Janson 1982). There is also variation in the size of individual mamilliform glands (figure 7). Usually they are all of similar size on the penis. However, in *Nodilittorina pyramidalis* there is one large mamilliform gland on the base and many minute ones ('papillae' of Reid 1986*a*) on the filament. Minute and very numerous penial glands are also found on the filament of *Tectarius* (*Tectarius*), *T.* (*Echininus*) and *T.* (*Tectininus*), but here there are respectively 25–100, 2–12 and 3–4 larger penial glands on the base. The situation is, in fact, even more complex in *T.* (*Tectininus*) *antonii*, with penial glands of three sizes, and the two largest glands open via a common duct. There are 5–8 glands, all of which are large, in

Tectarius viviparus. Four apomorphic, but unordered, states of mamilliform glands have been defined in the cladistic analysis: glands few (1–2); glands many (4 or more) and uniform; few large glands and many small ones; many glands, of two or more sizes.

Numerous rounded papillae are present on the adaxial side of the penial base in *Lacuna* species (character 25). These resemble miniature mamilliform glands, but histological sections show that there is no glandular material associated with these structures. Instead, they are points at which the normally columnar epithelium becomes squamous, and the underlying muscle fibres approach closely to the surface. A single muscular papilla of this type is found at the apex of the penis in *Risellopsis*. The presence of these papillae is considered to be apomorphic, because they have not been described in other genera or in related families. Their function is unknown.

(*e*) *Spermatozoa* (*characters* 26, 27)

As in many other prosobranchs, the spermatozoa of littorinids are sometimes dimorphic, consisting of euspermatozoa (the so-called 'typical' sperm responsible for fertilization) and paraspermatic cells ('atypical' sperm, see Healy & Jamieson (1981) and Healy (1983) for discussion of terminology).

The euspermatozoa of littorinids are filiform, and structural details are only clearly visible by electron microscopy. The ultrastructure of euspermatozoa has been described only in *Littorina scutulata* (Buckland-Nicks 1973), *Bembicium auratum* and *Littoraria articulata* (as '*Littorina scabra*', both Healy (1984)). The only structural difference noted in these three species is the extent of the basal invagination of the nucleus, deep in *Littorina* and *Littoraria*, but shallow in *Bembicium*. Although in neotaenioglossans as a whole the latter condition may be primitive, the nuclei in Eatoniellidae, Cingulopsidae and primitive Truncatelloidea (Barleeidae, Rissoidae) show a long invagination (Healy 1984). This suggests that a deep invagination could be ancestral in the Littorinidae, but investigation of additional species is required. The euspermatozoa show considerable variation in length in the family: 220–250 μm in *Bembicium* (Reid 1988), 61–64 μm in *Melarhaphe*, 174–205 μm in *Cenchritis*, 96 μm in *Tectarius* (*Tectininus*), 39–50 μm in *Peasiella*, 100–350 μm in *Littoraria* (Reid 1986*a*), 55–100 μm in *Nodilittorina* and 38–91 μm in *Littorina*. These differences suggest that the character may be of phylogenetic importance, but information is lacking for other genera.

The paraspermatic cells of littorinids have been considered distinct from those of other prosobranchs, because they are usually rounded and aflagellate. They have been variously called 'nurse cells' (review by Reid (1986*a*)) or 'free cells' (Nishiwaki 1964) or 'homologues of paraspermatozoa' (Healy & Jamieson 1981). It is now known that these cells are sometimes elongate and flagellate (Reid 1986*a*) and that they are derived from the germinal epithelium in the testis (Buckland-Nicks & Chia 1977), so the nurse cells can be considered as a type of paraspermatic cell.

Dimorphic sperm occur only in the genera *Melarhaphe*, *Cenchritis*, *Peasiella*, *Tectarius*, *Littoraria*, *Nodilittorina*, *Littorina* and *Mainwaringia* (character 26). In these genera paraspermatic nurse cells are readily observed in the seminal vesicle by light microscopy in fresh and fixed specimens. In *Pellilitorina*, *Lacuna*, *Cremnoconchus*, *Bembicium*, *Risellopsis* and *Laevilitorina* the seminal vesicle contains only euspermatozoa, and nurse cells of the type seen in other littorinids are absent. It is possible that examination of spermatogenesis in these genera may reveal nutritive cells similar to, or even homologous with, nurse cells; for example, so-called 'nurse cells' have been described in the development of euspermatozoa in the tubules of the testis of

Bembicium nanum by Bedford (1965). The nurse cells are rounded or oval in shape (figure 8) and measure about 12–55 μm in length. They are packed with more or less distinct, rounded vesicles, variously reported as mitochondria, yolk granules, polysaccharide or ribonucleic material, but now thought to be proteinaceous (Giusti & Selmi 1982). A nucleus persists in the mature nurse cells of some species (*Littorina brevicula*, *Nodilittorina radiata* (both Tochimoto (1967), the latter as '*Tectarius granularis*'), *Melarhaphe neritoides* (Giusti & Selmi 1982), *Peasiella*, *Littorina striata*, *L. kurila*, *L. obtusata* and *Nodilittorina ziczac*), but degenerates at maturity in others (*Littorina sitkana* (Buckland-Nicks & Chia 1977), *Littoraria irrorata* (Woodard 1942*a*), *Littoraria scabra*). The nucleus is seldom visible in fresh, unstained material, although *Littorina striata* (figure 8*c*) and *Peasiella* species are exceptions, in which it appears as a refractile body with minutely granular contents. In histological sections of the seminal vesicle the nuclei can be stained with Mayer's haemalum or by the Feulgen reaction.

In addition, the nurse cells may contain one or several rod-shaped or lozenge-shaped,

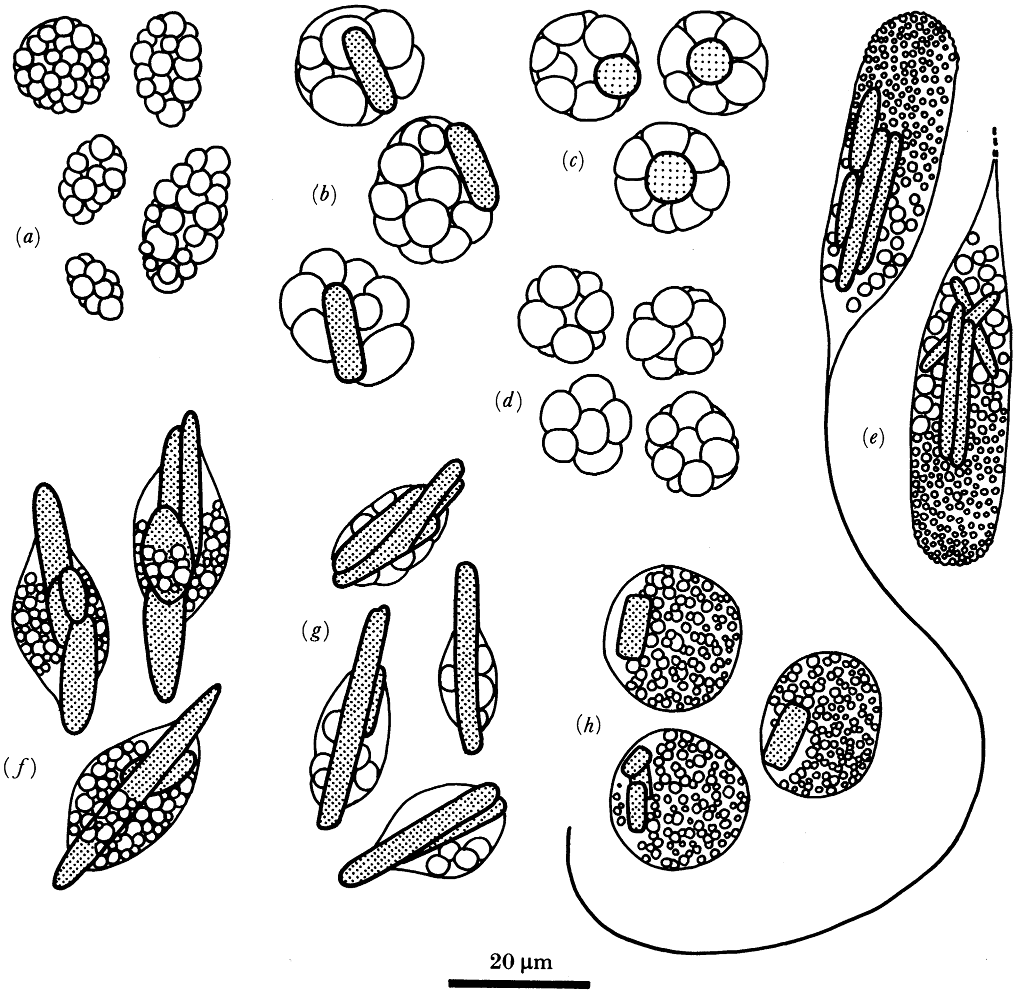

FIGURE 8. Paraspermatic nurse cells of Littorinidae. Unstained material from seminal vesicles of living snails, viewed by light microscopy. Key: light stipple, nucleus; heavy stipple, rod pieces. (*a*) *Melarhaphe neritoides*; (*b*) *Cenchritis muricatus*; (*c*) *Littorina* (*Liralittorina*) *striata*; (*d*) *Littorina* (*Neritrema*) *obtusata*; (*e*) *Littoraria* (*Palustorina*) *melanostoma*; (*f*) *Littoraria* (*Littorinopsis*) *scabra*; (*g*) *Nodilittorina* (*Echinolittorina*) *dilatata*; (*h*) *Littoraria* (*Littoraria*) *zebra*.

refractile inclusions, which sometimes project conspicuously from the outline of the cell (figure 8*b*, *e–h*). The rods are apparently hard, for they remain discrete when the cells are squashed or dried, and may be crystalline, as suggested by their rather regular shape and sometimes hexagonal cross section. The origin of these inclusions is uncertain, but according to Woodard (1942*a*) they are formed from euspermatozoan heads that enter the cell. Rods occur in the genera *Cenchritis*, *Tectarius*, *Littoraria* and *Nodilittorina*. In a few species of *Littoraria* they are absent and may have been lost (*L.* (*Littoraria*) *nebulosa*, *L.* (*Littorinopsis*) *philippiana*, *L.* (*Littorinopsis*) *subvittata*, *Littoraria aberrans*). Rods are also absent in the nurse cells of *Melarhaphe*, *Peasiella*, *Littorina* and *Mainwaringia*. In the first two the cells are often somewhat variable in shape (figure 8*a*), in contrast to the more uniform, rounded cells of *Littorina* and *Mainwaringia*. The distinction has not, however, been made in the analysis, for few specimens of *Peasiella* and *Mainwaringia* have yet been examined.

The occurrence of paraspermatic cells is widespread in caenogastropods, including the basal group Cerithioidea (Nishiwaki 1964; Haszprunar 1988), so that their presence might be supposed to be plesiomorphic. However, no marked structural dimorphism of sperm has been observed in the Pomatiasidae (Creek 1951; D.G.R., personal observation), or in any of the more primitive Truncatelloidea (Healy 1984). Paraspermatic cells have not been found in the Eatoniellidae (Healy 1984), despite the open genital ducts (often associated with paraspermatic cells in other groups, as discussed below). Among the Truncatelloidea, paraspermatic cells have been recorded only in *Bithynia*, but here they resemble euspermatozoa (Ankel 1924). The presence of nurse cells is therefore likely to be apomorphic within the Littorinidae, and consequently they may not be homologous with the paraspermatic cells of other prosobranchs. The sequence of the two character states (presence and absence of rods) is not known, so this character has been specified as unordered in the analysis.

Uniquely in the Littorinidae, the nurse cells of *Littoraria* (*Palustorina*) bear a long, probably compound, flagellum (figure 8*e*), strengthening the analogy with the paraspermatic cells of other prosobranchs (Reid 1986*a*) (character 27).

The function of paraspermatic cells has been the subject of debate, but as suggested by the name 'nurse cell' a role in the nutrition of euspermatozoa has generally been considered likely (see, for example, Healy & Jamieson 1981; Healy 1984). In littorinids the nurse cells are said to degenerate in the bursa of the female, perhaps releasing nutrients (Fretter & Graham 1962, p. 342). However, Woodard (1942*b*) reported that nurse cells ingest excess sperm and are then extruded. Within the seminal vesicle the euspermatozoa are attached in bunches to the nurse cells by their acrosomal tips, forming composite structures known as spermatozeugmata. This suggests an additional, or alternative, function of the nurse cells, as mechanical carriers for the euspermatozoa. Except in the case of *Littoraria* (*Palustorina*) species, the nurse cells are not themselves motile, but the tails of the attached euspermatozoa beat in unison, and the unit may thereby be propelled more effectively. The proteinaceous composition of the vesicles in the paraspermatic cells has been taken as evidence of a mechanical, rather than nutritive, role (Giusti & Selmi 1982). Spermatozeugmata are found elsewhere in Epitonoidea, Triphoroidea and Cerithiopsoidea (Healy 1984), and because these groups are all aphallate it has been suggested that spermatozeugmata may fulfil the role of sperm transfer to the female (Fretter & Graham 1962, p. 340). However, these spermatozeugmata are not always motile, and furthermore spermatozeugmata are also present in the cymatiid *Fusitriton oregonensis* with a well-developed penis (Buckland-Nicks *et al.* 1982). A more likely function for spermatozeugmata is therefore prevention of premature dispersal of euspermatozoa in these groups, which have open genital ducts (Buckland-Nicks *et al.* 1982; Giusti & Selmi 1982; Healy 1984). The pallial genital ducts are also open in the Cerithioidea, but here spermatophores are formed, preventing sperm dispersal (Healy 1984). The Littorinidae are an interesting case, containing genera with open and closed pallial genital ducts in the male, with and without spermatozeugmata. In fact, there is a close correlation between the two, although it is not exact. In *Pellilitorina*, *Lacuna*, *Cremnoconchus* and *Laevilitorina* with entirely closed ducts, nurse cells are indeed absent, but they are also absent in *Bembicium* and *Risellopsis*, with partly and entirely open ducts, respectively. Of the littorinids with nurse cells, all (except a few species of *Littoraria*) have partly or completely open pallial gonoducts in the male. This is strongly suggestive of a mechanical role for the paraspermatic nurse cells of littorinids.

It is interesting that in the genera *Littoraria* and *Nodilittorina* there are striking differences between sympatric, congeneric species in the form of the nurse cells, especially in the shape of the rod-like inclusions and size of the vesicles (Reid 1986*a*). This is not the case in *Littorina*, in which nurse cells are of rather uniform appearance. A possible role for the paraspermatic nurse cells in preventing interspecific sperm transfer might therefore be investigated.

(*f*) *Female reproductive system* (*characters* 28–37)

As in other prosobranchs, the female reproductive tract of littorinids comprises a narrow proximal oviduct of ovarian origin, a short renal section, and a large distal part formed from the mantle wall (Fretter & Graham 1962, p. 45). A gonopericardial duct, arising from the junction of the ovarian and renal sections, has been reported in some species of *Littoraria*, *Nodilittorina* and *Littorina* (see Fretter & Graham 1962, p. 45; Marcus & Marcus 1963; Berry & Chew 1973) and *Bembicium* (Reid 1988), but is always difficult to trace and sometimes is apparently absent (e.g. *Littoraria* (Reid 1986*a*)). The pallial and renal parts of the oviduct have a rather complex structure, concerned with their functions of reception, transport and storage of sperm, production of albumen and other material coating the egg, and sometimes also with brooding of embryos.

During ontogeny the pallial oviduct of littorinids develops as an open groove, which closes to form a laterally compressed tube (Guyomarc'h-Cousin 1976). The dorsal (egg) groove of the lumen conducts eggs in an anterior direction for oviposition, whereas the ventral (sperm) groove transports sperm in a posterior direction for storage and fertilization. The primitive condition of an open pallial oviduct is found in the Cerithioidea (Ponder 1988). Among the Littorinoidea, Cingulopsoidea, Truncatelloidea and Aciculidae, the open condition (of the region anterior to the albumen gland) occurs only in the Eatoniellidae (Ponder 1968), some Rissoidae, Iravadiidae and Tornidae (Ponder 1988) and Pomatiasidae (Creek 1951; Thompson 1978). In the Eatoniellidae the open oviduct is probably plesiomorphic, and in the Truncatelloidea closure of the oviduct has apparently occurred independently in several clades (Ponder 1988). However, in the Pomatiasidae it has been suggested that the long opening of the oviduct has been secondarily acquired, in connection with the production of the larger eggs necessary for terrestrial development (Creek 1951). An opening from the posterior end of the pallial oviduct to the posterior part of the mantle cavity is found in some groups (some Cingulopsidae (Fretter & Patil 1958), but see Ponder (1968), Aciculidae (Creek 1953), some Truncatelloidea (Ponder 1988)), but does not occur in the Littorinidae.

In most littorinids there are two sperm sacs associated with the pallial oviduct (figures 9 and 10). During copulation spermatozoa are deposited in the bursa copulatrix, an elongate sac usually situated at the anterior end of the oviduct. Although sperm may be temporarily attached to the lining of the bursa, they are soon transferred along the ventral sperm groove within the closed oviduct to the posterior seminal receptacle, which is usually small and bulb-shaped, with a short duct. Sperm are stored for long periods in the receptacle, oriented with their heads attached to the epithelial lining. In *Bembicium* and *Risellopsis* the seminal receptacle is reached by a long duct, separated from the lumen of the pallial oviduct almost to the anterior opening of the latter (character 28; figure 9*j*, *k*). The condition of this character is unknown in those littorinids that lack a seminal receptacle (*Pellilitorina*, *Lacuna*, *Cremnoconchus*). The condition in *Bembicium* and *Risellopsis* is a synapomorphy, not seen in other groups, and probably arose by anterior migration and lengthening of the originally short duct joining the receptacle to the sperm groove, rather than by closure of the sperm groove to form a duct (because a sperm groove persists in *Risellopsis* (Reid 1988)). Partial closure of the sperm groove, for a segment midway along its length, has, however, occurred in *Mainwaringia* (Reid 1986*b*) (character 29). This is the only example of a diaulic oviduct in the Littorinidae, although the condition is common in some truncatelloidean groups (Ponder 1988).

Within the Littorinidae the two sperm sacs, bursa and receptacle, are both functionally and anatomically distinct. Histological differences have also been reported, the bursa being lined by a ciliated, columnar epithelium, and the receptacle lined mainly by a cuboidal, unciliated layer (Linke 1933*a*; Bedford 1965; D.G.R., personal observation). However, the possible homologies of these sperm sacs with similar structures in related families are uncertain, and the terminology is confused.

Whether the genital ducts are open or closed, or a penis present or absent, sperm storage is a necessary function of the pallial oviduct. A sperm storage sac, generally called a seminal receptacle, is common to many of the families of the littorinoidean–truncatelloidean radiation, occurring at the back of the pallial oviduct and probably formed from an outgrowth of the renal oviduct (Linke 1933*a*; Ponder 1988). The occurrence of a seminal receptacle is probably a symplesiomorphy of the Littorinoidea, Cingulopsoidea and Truncatelloidea. In the Cerithioidea the seminal receptacle occurs in combination with an open pallial oviduct, whereas a separate sac, the spermatophore bursa, functions for the initial reception of sperm (Houbrick 1980, 1984, 1985, 1987*a*). The Eatoniellidae are likewise aphallate, with open genital ducts, but are not known to produce spermatophores. In this family the posterior sperm sac has been called a bursa (Ponder 1988), although it stores sperm and has unciliated walls (Ponder 1968) and so functions as a seminal receptacle. A true seminal receptacle apparently occurs in some members of this family (Ponder 1988 and personal communication). Among the Truncatelloidea the closure of the pallial oviduct in several clades has been accompanied by formation of a bursa from the sperm groove, which, although generally towards the posterior of the pallial oviduct, is quite variable in position and not strictly homologous in all groups (Ponder 1988). Presence of a bursa is not always associated with that of a penis; the Cingulopsidae are aphallate, yet there is a posterior bursa (said to be unciliated (Ponder 1968)) in addition to a seminal receptacle, both arising from the posterior end of the closed pallial oviduct (Fretter & Patil 1958; Ponder 1968). The possibility of secondary loss of the penis in Cingulopsoidea has, however, been noted (see §4*d*). Both a seminal receptacle and a posterior bursa may be present in the Skeneopsidae (see Fretter (1948), in which the possible homologue of the seminal receptacle is referred to as a 'fertilization chamber', and the bursa as a 'seminal receptacle'), although the unique opening of the bursa to the exterior of the mantle suggests

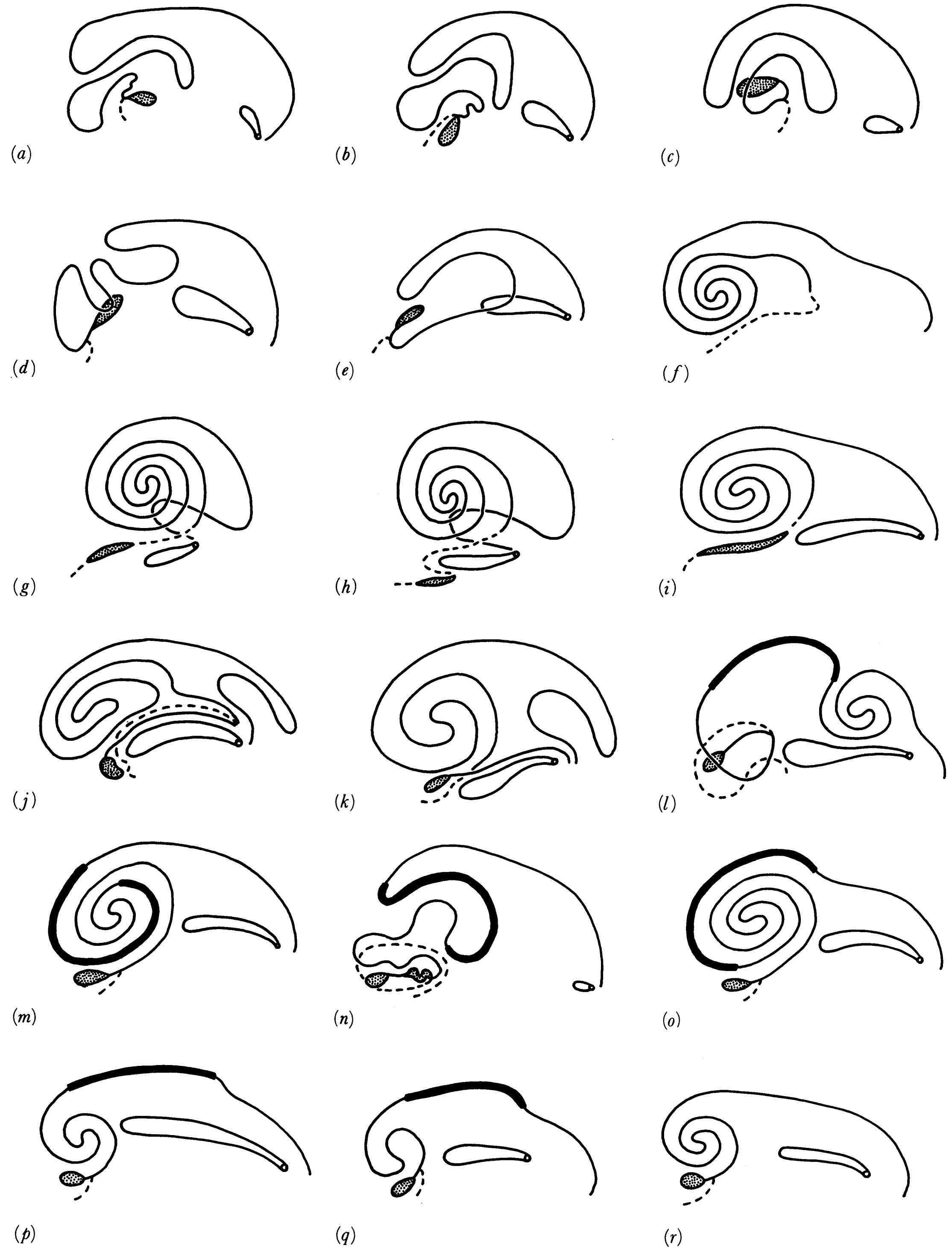

FIGURE 9. Diagrams of pallial oviducts of Littorinidae. Key: continuous line, spiral route of egg groove from renal oviduct (at left) to opening into mantle cavity (at right); thickened part of line, opaque capsule gland; dashed line, renal oviduct; stipple, region of sperm storage (usually seminal receptacle, except (*g*), (*h*), (*i*), where sperm storage area is in renal oviduct); unshaded sac, bursa copulatrix. Coding of states of character 36: state 1 (one spiralled loop) in all except state 2 (two spiralled loops) in (*a–e*), (*l*), (*n*). (*a*) *Laevilitorina* (*Pellilacunella*) *bennetti*; (*b*) *Laevilitorina* (*Macquariella*) *hamiltoni*; (*c*) *Laevilitorina* (*Laevilitorina*) *caliginosa*; (*d*) *Laevilitorina* (*Rissolittorina*) *alta*; (*e*) *Laevilitorina* (*Rufolacuna*) *bruniensis*; (*f*) *Pellilitorina setosa*; (*g*) *Lacuna* (*Lacuna*) *pallidula*; (*h*) *Lacuna* (*Epheria*) *vincta*; (*i*) *Cremnoconchus syhadrensis*; (*j*) *Bembicium melanostoma*; (*k*) *Risellopsis varia*; (*l*) *Melarhaphe neritoides*; (*m*) *Cenchritis muricatus*; (*n*) *Peasiella tantilla*; (*o*) *Tectarius* (*Tectarius*) *grandinatus*; (*p*) *Tectarius* (*Echininus*) *cumingii*; (*q*) *Tectarius* (*Tectininus*) *antonii*; (*r*) *Tectarius viviparus*.

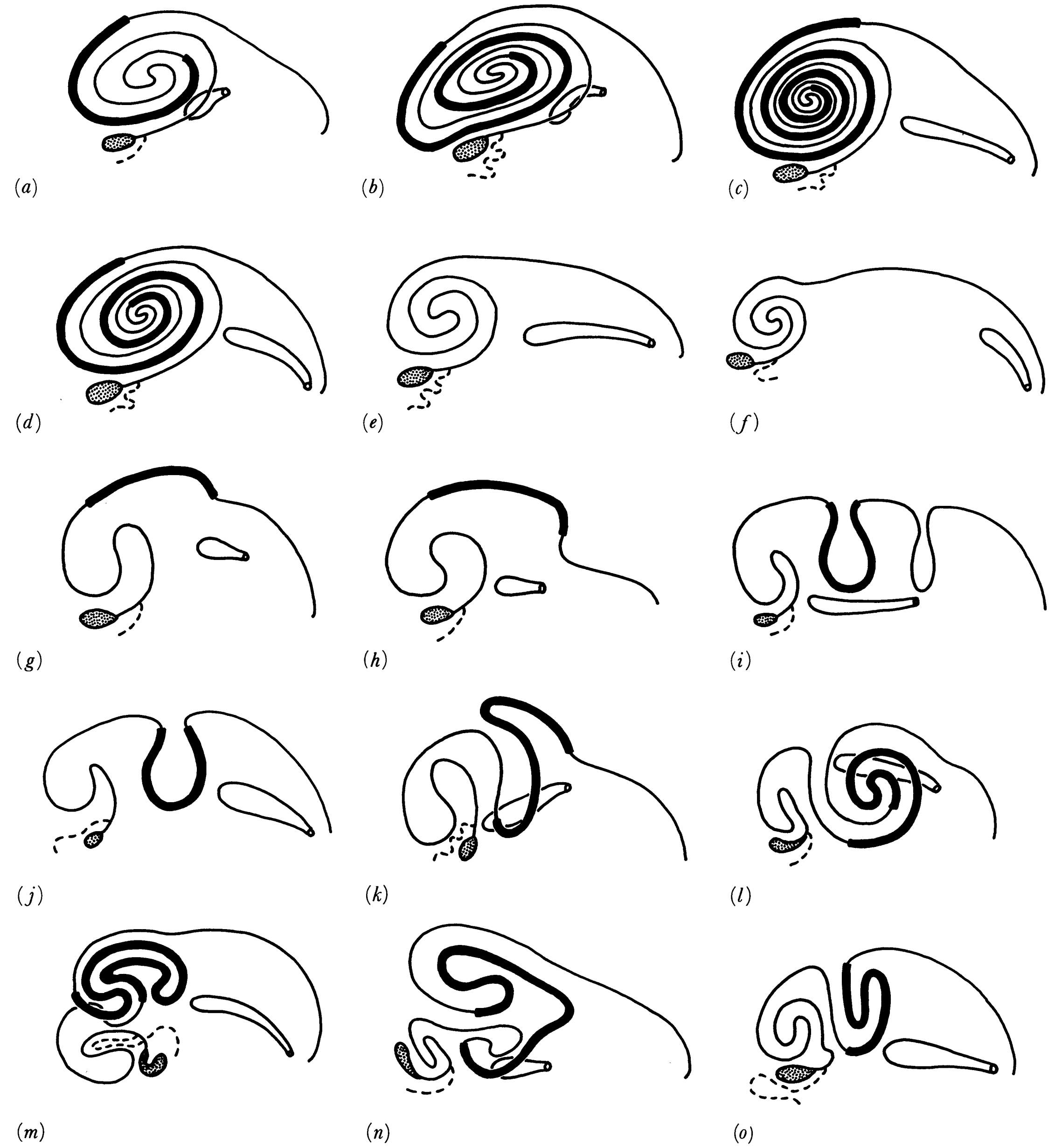

FIGURE 10. Diagrams of pallial oviducts of Littorinidae (continued). Key: as in figure 9. Coding of states of character 36: state 2 (two spiralled loops) in (*k*), (*l*), (*o*); state 3 (three spiralled loops) in (*m*), (*n*); state 1 (one spiralled loop) in others. (*a*) *Littoraria pintado*; (*b*) *Littoraria* (*Palustorina*) *melanostoma*; (*c*) *Littoraria* (*Littoraria*) *zebra*; (*d*) *Littoraria* (*Lamellilitorina*) *albicans*; (*e*) *Littoraria* (*Littorinopsis*) *angulifera*; (*f*) *Littoraria aberrans*; (*g*) *Nodilittorina* (*Fossarilittorina*) *meleagris*; (*h*) *Nodilittorina* (*Echinolittorina*) *dilatata*; (*i*) *Nodilittorina* (*?Echinolittorina*) *africana*; (*j*) *Nodilittorina* (*Nodilittorina*) *pyramidalis*; (*k*) *Littorina* (*Liralittorina*) *striata*; (*l*) *Littorina keenae*; (*m*) *Mainwaringia rhizophila*; (*n*) *Littorina* (*Littorina*) *littorea*; (*o*) *Littorina* (*Neritrema*) *obtusata*.

that it is a new structure, not homologous with other bursae. In contrast, in each of the two terrestrial families, Pomatiasidae and Aciculidae, there is only a single sperm sac, in a posterior position, which has been referred to as a 'bursa' (Creek 1951, 1953; Thompson 1978; Ponder 1988). In the Aciculidae this sac is an unciliated outgrowth of the renal oviduct, which is used for sperm storage (Creek 1953), and is therefore considered to be a seminal receptacle. The nature of the 'bursa of the Pomatiasidae is unclear, for although unciliated it does not store sperm (this function being fulfilled by the renal oviduct itself), and its position suggests a possible pallial origin. Reid (1988) suggested a possible homology with the seminal receptacle, but this was disputed by Ponder (1988), who considered it a bursa, although not homologous with those of other families. The latter view is accepted here; as discussed later, a seminal receptacle may have been lost in the Pomatiasidae.

In summary, all the families under discussion, except the Pomatiasidae, are believed to possess a seminal receptacle, possibly homologous throughout, although not always used for sperm storage (Skeneopsidae). The posterior bursae of various truncatelloidean families, Cingulopsidae, Skeneopsidae and Pomatiasidae are not homologous. Further work is necessary on the ontogeny, structure and function of sperm sacs in these groups.

Returning to the Littorinidae, in those genera possessing a bursa (all except *Pellilitorina* and some *Peasiella*), it is in a relatively anterior position (although in a few cases moved somewhat posteriorly along the oviduct, as discussed below).. Strict outgroup comparison suggests that absence of the bursa is plesiomorphic (character 30). The evolution of an anterior bursa may have been related to speed and efficiency of copulation, or to the increasing separation of the sperm-conducting and egg-transporting functions of the pallial oviduct.

The bursa is usually separated from the lumen of the pallial oviduct near its opening into the mantle cavity, and is thus clearly in an anterior position (figures 9 and 10). However, in several groups the bursa is situated further back, only becoming completely separated from the lumen of the oviduct halfway or even further along the straight section of the oviduct (measured from the anterior end of the oviduct to the anterior end of the opaque capsule gland). These groups are *Tectarius* (*Tectininus*), *Nodilittorina* (except *N.* (*Nodilittorina*)), *Littorina* (except *L.* (*Neritrema*)), *Littoraria* (*Palustorina*) and all *Littoraria* (*Littoraria*) species except *fasciata*, *irrorata*, *varia*, *vespacea* and *zebra*. Anterior to the point of separation the bursa is represented by a deep groove in the lumen, ventral to the sperm groove. Owing to the absence of an anterior bursa in the outgroup, the three states of this character (absent, anterior, further back) have been specified as unordered in the cladistic analysis.

In most littorinids the bursa lies ventrally or laterally in relation to the pallial oviduct, but in *Littorina* (*Littorina*), *L. keenae* and *Mainwaringia* it lies medially. Uniquely in the family, the bursa of *Nodilittorina* (*Nodilittorina*) *trochoides* bifurcates posteriorly.

In three genera (*Pellilitorina*, *Lacuna*, *Cremnoconchus*) the seminal receptacle is absent (character 31). If, as suggested above, the receptacle is homologous throughout the littorinoidean–truncatelloidean radiation, outgroup comparison dictates that this absence is an apomorphic loss. In *Lacuna* (Gallien & de Larambergue 1938; D.G.R., personal observation) and in *Cremnoconchus* (Linke 1935*a*) sperm are now stored in the renal oviduct. A similar condition, which may also be a consequence of loss of a seminal receptacle, occurs in the Pomatiasidae (Creek 1951; Thompson 1978). The site of sperm storage in *Pellilitorina* is not known. Sperm storage in the renal oviduct is probably a minor modification, for in various littorinids with a fully developed seminal receptacle some sperm have been found attached to the walls of the duct of the seminal receptacle or to the renal oviduct itself, close to the receptacle (e.g. *Laevilitorina* (*Laevilitorina*), *L.* (*Macquariella*), *Peasiella*, *Mainwaringia*). The junction of renal and pallial oviducts with the seminal receptacle is a complex region of folds, diverticula, coiled ducts and ciliated tracts, and always difficult to interpret in serial sections.

Eggs enter the pallial oviduct from the renal section of the duct, and fertilization presumably occurs at the junction of the two, before the eggs pass into the albumen gland. This junction is almost always posterior in littorinids, as in other Littorinoidea, but in *Bembicium* the renal oviduct (or an extension from the pallial section) runs forward almost to the opening of the pallial oviduct into the mantle cavity (Reid 1988) (character 32; figure 9*j*). It may be noted that a superficially similar condition, with the opening into the mantle cavity close to the junction of the renal oviduct and albumen gland, is found in *Lacuna*, but in this case it is achieved by a shortening and looping of the jelly gland, as described below, and not by lengthening of the renal oviduct as in *Bembicium*. In most cases the renal oviduct is lined with a tall, glandular, ciliated epithelium (staining blue in MT, blue and purple with ABPAS), and in dissection appears thick-walled and often coiled in the region behind the seminal receptacle. Of the species examined histologically, the renal oviduct is not glandular in *Lacuna* (*Epheria*) *vincta* or *Laevilitorina* (*Macquariella*) *antarctica*, nor is it glandular in the Pomatiasidae (Creek 1951). The upper oviducal gland of the Rissoidae is a glandular renal oviduct, and as in the Littorinidae its staining reactions resemble those of the albumen gland (Ponder 1985*a*). Dissection of *Pellilitorina* suggests that as in *Lacuna* the renal oviduct may not be glandular. However, more species must be examined histologically before this character can be employed in the analysis.

The proximal glandular region of the pallial oviduct of the Littorinoidea and Truncatelloidea has been named the albumen gland, and the distal region the capsule gland, reflecting their supposed contributions to the layers that successively cover the egg during its passage along the egg groove. In littorinids the situation is more complex, because the histology of the oviduct has been examined in more detail, and because of the diversity of types of development within the family. Knowledge of the secretions of the pallial oviduct is nevertheless fragmentary, because of lack of uniformity of techniques of fixation and staining, because of possible changes in secretory activity with the spawning cycle, and because of a lack of detailed studies relating the glandular secretions to the structure of the egg mass or capsule (only Linke 1933*a*). The greatest differentiation of the pallial oviduct occurs in those genera producing pelagic egg capsules, in which three glandular types can be distinguished (see Reid (1986*a*) for a review of earlier studies and a discussion of nomenclature).

At the proximal end of the pathway of the eggs through the egg groove lies the albumen gland, present in all littorinids. This is usually differentiated into an initial opaque albumen gland (opaque white or cream in fresh or preserved material; blue in MT; blue or sometimes magenta with ABPAS) and a more extensive translucent albumen gland (translucent fawn or cream unstained; colourless in MT; magenta to purple with ABPAS). However, in *Lacuna* (*Epheria*) *vincta* the opaque albumen gland stained strongly red in MT, and was tentatively identified as such only because of its position. Some reddish staining was evident in *Laevilitorina* (*Macquariella*) *antarctica* and *Mainwaringia rhizophila* also. The albumen gland produces the innermost egg covering, which may have both nutritive and osmoregulatory functions (Hertling 1928; Linke 1933*a*).

The following section of the egg groove is surrounded by the capsule gland. Again this is differentiated into two parts, an initial opaque capsule gland (opaque pink or cream unstained; red in MT; pale purple to magenta with ABPAS) and a distal translucent capsule gland (translucent red-brown unstained; blue in MT; dark purple with ABPAS). Capsule glands occur only in *Melarhaphe*, *Cenchritis*, *Peasiella*, *Tectarius* (except *T. viviparus*), *Littoraria* (except *L.* (*Littorinopsis*) and *L. aberrans*), *Nodilittorina*, *Littorina* and *Mainwaringia* (character 33).

A well-developed translucent capsule gland is present only in littorinids that produce pelagic egg capsules (it is small in *Littorina* (*Neritrema*) *obtusata* and absent in viviparous littorinids), leading to the suggestion that it secretes the capsular material (Reid 1986*a*). The region between the albumen coat and the egg capsule is filled with a viscous fluid, which is therefore probably produced by the opaque capsule gland (Linke 1933*a*; Reid 1986*a*).

The third and final gland of the pallial oviduct has been named the jelly gland. This region is especially large, with internal septa, in those littorinids producing a benthic gelatinous spawn (*Pellilitorina*, *Lacuna*, *Cremnoconchus*, *Bembicium*, *Risellopsis*, *Laevilitorina*, some *Littorina* (*Neritrema*)) (character 34). It produces the gelatinous matrix in which the albumen-coated eggs are embedded, and presumably also the outer rind of the spawn mass. In those species that release pelagic capsules it is reduced to a small lobe of tissue around the egg grove, and probably produces the mucous strings or ephemeral gelatinous matrix in which capsules are initially shed (Reid 1986*a*). Although producing pelagic capsules, *Littorina keenae* has a large jelly gland, because the capsules are initially shed in gelatinous masses (Schmitt 1979). In those littorinids that brood larvae in the mantle cavity the jelly gland is also reduced, whereas in those brooding larvae in the pallial oviduct it functions as a brood chamber and its walls are no longer thick and glandular (Hannaford Ellis 1979). The staining reactions of the jelly gland vary; in most cases it is pale blue or colourless in MT, and magenta and blue with ABPAS, but in *Laevilitorina* it is red in MT. In some littorinids different regions of the jelly gland can be distinguished by their staining reactions (especially striking in *Lacuna*). Pending further investigation, the jelly gland is identified by its position in the terminal straight portion of the oviduct, and by its conspicuous septation in species in which it is well developed.

The evolution of these glandular components requires careful consideration. In the outgroup (Creek 1951; Fretter 1948), two principal glandular types are recognized, a posterior albumen gland and an anterior 'capsule' gland, although there are also mucus-secreting regions within the latter. Albumen and 'capsule' glands are also distinguished in the Cingulopsoidea and Truncatelloidea (Ponder 1968, 1988). The albumen glands are presumed to be homologous in all members of the Littorinoidea, Cingulopsoidea and Truncatelloidea. However, the homologies of the capsule gland are unclear. It is proposed that the jelly gland of littorinids is the homologue of the 'capsule' gland of the other families, and that the littorinid capsule gland is a new and apomorphic structure. This is justified by the similarity of the benthic spawn of littorinids lacking a capsule gland to that of the Skeneopsidae and marine truncatelloideans (see §4*g*). There are no reports of pelagic capsules in the Truncatelloidea, and the capsules of some Littorinidae, like the gland that produces them, are considered to be apomorphic. Further histological, histochemical and ultrastructural studies of the pallial oviducts of neotaenioglossans are required to test this hypothesis.

Secondary reduction and loss of the capsule gland has occurred in some littorinid genera. For example, within the genus *Littorina* the size of the capsule gland is correlated with the type of spawn and development. In those species producing egg capsules it is large, in those with unencapsulated eggs in gelatinous masses it is reduced, and very small in ovoviviparous species that brood embryos in the oviduct. In the remaining ovoviviparous littorinids, all of which brood embryos in the mantle cavity (*Tectarius viviparus*, *Littoraria* (*Littorinopsis*), *L. aberrans*), the capsule gland is entirely lost. The types of development in the Littorinidae are discussed in detail in §4*g*.

If the homology of the jelly gland with the large 'capsule' gland in members of the outgroup is accepted, then an enlarged jelly gland must be regarded as plesiomorphic, and a reduced jelly gland as apomorphic (character 34). The three characters: presence of capsule gland, reduction of jelly gland and production of egg capsules are correlated, but not completely so, and in this study have been coded separately to demonstrate their differing patterns of reversal in the several ovoviviparous and non-planktotrophic littorinids.

Within the Littorinidae the glands of the pallial oviduct are not of uniform histological structure (character 35). In *Pellilitorina*, *Lacuna*, *Bembicium*, *Risellopsis* and *Laevilitorina* the albumen gland is composed of tall, glandular, epithelial cells alternating with ciliated supporting cells (see Bedford (1965) for *Bembicium*). This is also the case both for albumen and capsule glands of *Melarhaphe*. However, in all other littorinid genera (including *Cremnoconchus* (Linke 1935*a*; D.G.R., personal observation)) the secretory cells of the albumen and capsule glands are subepithelial, lying in closely packed, indistinct lobules beneath the basement membrane of the cells of a ciliated epithelium, between which the secretions are discharged (Linke 1933*a*, figures 57, 62). In the Pomatiasidae (Creek 1951), and Skeneopsidae (Fretter 1948), as well as in the Eatoniellidae (Ponder 1968), Cingulopsidae (Fretter & Patil 1958) and Aciculidae (Creek 1953), only epithelial glandular cells occur in the pallial oviduct, so this is believed to be the plesiomorphic condition. Interestingly, infolding of the glandular cells to form vase-like structures has also occurred independently in the Truncatelloidea (Ponder 1988).

In the case of the jelly gland the situation is more complex. In *Pellilitorina*, *Lacuna*, *Bembicium*, *Risellopsis*, *Laevilitorina*, *Melarhaphe*, *Littorina* (*Littorina*) and *L.* (*Neritrema*) the gland is epithelial. However, in the posterior part of the straight section of the oviduct of *Peasiella*, *Tectarius* (*Tectininus*), *Littoraria*, *Nodilittorina*, *Littorina* (*Liralittorina*), *L. keenae* and *Mainwaringia* there is in addition some subepithelial tissue with the staining reactions of the jelly gland. The jelly gland is also subepithelial in *Cremnoconchus* (Linke 1935*a*; D.G.R., personal observation). This structure is probably apomorphic, but further histological work is required to confirm the occurrence and homology of the subepithelial jelly gland.

The sequential passage of eggs through the glands of the pallial oviduct has been described above. However, in all littorinids the path of the egg groove is not straight, but is thrown into a more or less complex spiral (figures 9 and 10) (see Reid (1986*a*), figure 6, for a diagrammatic representation). This spiral coiling presumably serves to lengthen the path of the eggs through the oviducal glands, enabling egg production to proceed at a greater rate. The spiral structure was first accurately described by Berry & Chew (1973), for *Littoraria* (*Palustorina*) *melanostoma*, and has since been shown to be an important taxonomic character, the shape of the spiral being diagnostic of most littorinid genera (Reid 1986*a*, *b*, 1988). In all other Littorinoidea, Cingulopsoidea and Truncatelloidea the pallial oviduct is basically a straight tube, occasionally with glandular pouches, so the spiral form found in Littorinidae is apomorphic. The form of the egg groove has been coded as a single character (character 36) with three apomorphic states, arranged in a sequence of increasing complexity (figures 9 and 10). In most littorinids there is a single loop, twisted back on itself into an anticlockwise spiral (*Pellilitorina*, *Lacuna*, *Cremnoconchus*, *Bembicium*, *Risellopsis*, *Cenchritis*, *Tectarius*, *Littoraria*, *Nodilittorina*). Two anticlockwise spirals are present in *Laevilitorina*, *Melarhaphe*, *Peasiella*, *Littorina* (*Liralittorina*), *Littorina keenae* and most *L.* (*Neritrema*). Three spirals occur only in *Littorina* (*Littorina*) (including *L. plena* and *L. scutulata*), *L.* (*Neritrema*) *aleutica* and *Mainwaringia*. The exact form of the spiral pattern of the egg groove, involving not only the number of successive spirals, but also the degree of coiling of each, is conservative within littorinid genera. It is therefore useful for the phenetic grouping of subgeneric taxa, and sometimes provides additional support for the recognition of phyletic clades that are otherwise poorly defined (see §5*c*(ii)). However, degree of coiling is difficult to code for phylogenetic analysis of the family as a whole, because of uncertainties about the homologies of the successive spirals, and has therefore not been used as a character. All members of *Nodilittorina* have been classed as having a single spiral, although in a few species small additional loops are present, approaching the double spiral shown by *Littorina* (*Liralittorina*) (figure 10).

In most littorinids the jelly gland occupies only the distal, straight section of the pallial oviduct. In *Lacuna*, *Bembicium* and *Risellopsis* the path of the egg groove through the jelly gland makes a backward loop (character 37; figure 9*g*, *h*, *j*, *k*), and in transverse section the jelly gland therefore appears to be partly divided into two chambers (Reid 1988). Because of this loop of the jelly gland, the opening into the mantle cavity is no longer at the anterior extremity of the pallial oviduct. The opening is only pushed back a short way in *Bembicium* and *Risellopsis*. However, in *Lacuna* there is such foreshortening that the opening is pushed back against the spiral portion of the pallial oviduct, almost to the point where the renal oviduct enters the albumen gland. Comparison with the straight course of the 'capsule' gland in the Pomatiasidae and Skeneopsidae suggests that the loop in the jelly gland is apomorphic. Presumably this modification serves to increase the size of the gland without lengthening the pallial oviduct as a whole.

(*g*) *Spawn and larval development* (*characters* 38–40)

It is well known that the Littorinidae show a wide range of types of larval development, including benthic egg masses with planktotrophy or non-planktotrophy, pelagic egg capsules with planktotrophy, partial brooding of embryos followed by planktotrophy, and complete ovoviviparity (table 4). In the following discussion the types of spawn will be described first, then the method of development, and lastly the attainment of ovoviviparity.

Within the Littorinidae the primitive type of spawn is a gelatinous mass containing embedded eggs, which is enclosed within a firm rind and attached to the substrate. This type occurs in the Skeneopsidae, although with only one or two eggs in each mass (Linke 1933*b*). Comparison with the Pomatiasidae is not meaningful, because the family is modified for terrestrial life. Turning to more distant outgroups, spawn of the primitive type is found in the Cingulopsidae and many Truncatelloidea (see Thorson 1946; Fretter & Graham 1962, 1978). Egg masses of this type have been described in *Pellilitorina* (Picken 1979), *Lacuna* (Thorson 1946; Fretter & Graham 1980; Golikov & Kusakin 1978), *Bembicium* (H. Anderson 1958; D. T. Anderson 1961, 1962), *Risellopsis* (Pilkington 1974; Reid 1988) and *Laevilitorina* (including subgenera *Laevilitorina*, *Macquariella* and *Pellilacunella* (Picken 1979; Simpson & Harrington 1985)). In these genera the spawn mass is usually oval or hemispherical, containing from 7 to 1200 eggs, but in *Lacuna* (*Epheria*) the egg mass is ring-shaped. The spawn of *Cremnoconchus* is unknown, but is likely to be of the primitive type also. In dissected specimens the large jelly gland contains 4 or 5 large eggs with a thick albuminous coating, and these are probably attached to the substrate singly or together in a gelatinous matrix. Elsewhere in the family a benthic egg mass is also found in a few species of *Littorina* (*Neritrema*), including *L. obtusata* and *L. mariae* (Linke 1933*a*; Goodwin & Fish 1977), *L. nigrolineata* and *L. arcana* (Hannaford Ellis 1979). The special case of *L. sitkana* is discussed later. In these *Littorina* species the spawn appears superficially similar to the primitive type, but there is no firm outer rind

Table 4. Summary of spawn and larval development in Littorinidae

(Only species for which spawn (or ovoviviparity) has been described are listed; type of spawn and development can be deduced for other species from protoconch and oviduct, as described in text. References are not exhaustive. Nomenclature follows classification given in Appendix 1, rather than original citation.)

genus	species	spawn	development	references
Pellilitorina	*pellita*, *setosa*	benthic gelatinous, ova unencapsulated	non-planktotrophic	Picken (1979)
Lacuna (*Lacuna*)	*pallidula*, *parva* *reflexa*	benthic gelatinous, ova unencapsulated	non-planktotrophic	Thorson (1946); Golikov & Kusakin (1978); Goodwin (1979); Fretter & Graham (1980)
Lacuna (*Epheria*)	*porcata*, *turrita*, *vincta*	benthic gelatinous, ova unencapsulated	planktotrophic	Thorson (1946); Golikov & Kusakin (1978)
Cremnoconchus	*syhadrensis*	benthic gelatinous, ova unencapsulated	non-planktotrophic	Linke (1935*a*)
Bembicium	*auratum*, *nanum*	benthic gelatinous, ova unencapsulated	planktotrophic	H. Anderson (1958); D. T. Anderson (1961, 1962)
	vittatum	benthic gelatinous, ova unencapsulated	non-planktotrophic	H. Anderson (1958); Reid (1988)
Risellopsis	*varia*	benthic gelatinous, ova unencapsulated	planktotrophic	Pilkington (1974, 1976); Reid (1988)
Laevilitorina (*Pellilacunella*)	*bennetti*	benthic gelatinous, ova unencapsulated	non-planktotrophic	Picken (1979)
Laevilitorina (*Macquariella*)	*antarctica*, *hamiltoni*	benthic gelatinous, ova unencapsulated	non-planktotrophic	Picken (1979); Simpson & Harrington (1985)
Laevilitorina (*Laevilitorina*)	*caliginosa*, *coriacea*	benthic gelatinous, ova unencapsulated	non-planktotrophic	Picken (1979); Simpson & Harrington (1985)
Melarhaphe	*neritoides*	pelagic pill-box capsules, single ova	planktotrophic	Linke (1935*b*); Lebour (1935)
Peasiella	*infracostata*	pelagic cupola capsules, single ova	planktotrophic	Tokioka (1950); Habe (1956)
Cenchritis	*muricatus*	pelagic pill-box capsules, single ova, ?facultative brooding in mantle cavity	planktotrophic	Lebour (1945); Lewis (1960); Borkowski (1971); Bandel (1974)
Tectarius (*Tectininus*)	*antonii*	pelagic cupola capsules, single ova	planktotrophic	Borkowski (1971)
Tectarius	*viviparus*	ovoviviparous, brooding in mantle cavity	non-planktotrophic	Rosewater (1982); D.G.R., personal observation

Table 4 (*cont.*)

genus	species	spawn	development	references
Littoraria	*pintado*	pelagic cupola capsules, single ova	planktotrophic	Struhsaker (1966)
Littoraria (*Palustorina*)	*articulata*, *melanostoma*, *strigata*	pelagic biconvex disc capsules, single ova	planktotrophic	Kojima (1958*e*); Berry & Chew (1973); Berry (1986); Reid (1986*a*)
Littoraria (*Littoraria*)	*coccinea*, *flava*, *irrorata*, *nebulosa*, *undulata*	pelagic biconvex disc capsules, single ova	planktotrophic	Marcus & Marcus (1963); Rosewater (1970); Bingham (1972); Bandel (1974)
Littoraria (*Littorinopsis*)	*angulifera*, *filosa*, *intermedia*, *lutea*, *luteola*, *pallescens*, *philippiana*, *scabra*, *subvittata*	ovoviviparous, brooding in mantle cavity	planktotrophic	Reid (1986*a*)
Littoraria	*aberrans*	ovoviviparous, brooding in mantle cavity	non-planktotrophic	D. G. R., personal observation
Nodilittorina (*Fossarilittorina*)	*meleagris*	pelagic cupola capsules, single ova	planktotrophic	Borkowski (1971); Bandel (1974)
Nodilittorina (*Echinolittorina*)	*angustior*, *dilatata*, *peruviana*, *riisei*, *tuberculata*, *ziczac*	pelagic cupola capsules, single ova	planktotrophic	Abbott (1954); Borkowski & Borkowski (1969); Borkowski (1971); Bandel (1974); Jordan & Ramorino (1975); Bandel & Kadolsky (1982); D. G. R., personal observation
Nodilittorina (*Nodilittorina*)	*antipodum*, *araucana*, *aspera*, *cincta*, *hawaiiensis*, *lineolata*, *millegrana*, *porcata*, *radiata*, *subnodosa*, *trochoides*, *vidua*	pelagic cupola capsules, single ova	planktotrophic	Tokioka & Habe (1953); Kojima (1958*b*, 1960); Yamamoto & Habe (1962); Marcus & Marcus (1963); Struhsaker (1966); Pilkington (1971); Jordan & Ramorino (1975); Berry (1986); Hulings (1986); D. G. R., personal observation

Littorina (*Liralittorina*)	*striata*	pelagic cupola capsules, single ova	planktotrophic	Reid (1989*a*)
Littorina	*keenae*	pelagic biconvex disc capsules in ephemeral jelly, single ova	planktotrophic	Schmitt (1979); Murray (1979)
Littorina (*Littorina*)	*brevicula*	pelagic biconvex disc capsules, usually single ova	planktotrophic	Kojima (1957, 1958*a*); Yamaguchi (1967)
	littorea, *mandshurica*, *plena*, *scutulata*, *squalida*	pelagic biconvex disc capsules, several ova	planktotrophic	Linke (1933*a*); Thorson (1946); Kojima (1958*b*, *d*, *e*); Buckland-Nicks *et al.* (1973); Murray (1979); Mastro *et al.* (1982)
Littorina (*Neritrema*)	*sitkana*	benthic gelatinous, containing biconvex disc capsules, single ova	non-planktotrophic	Kojima (1958*a*, *c*); Buckland-Nicks *et al.* (1973)
	arcana, *mariae*, *nigrolineata*, *obtusata*	benthic gelatinous, ova unencapsulated	non-planktotrophic	Linke (1933*a*); Thorson (1946); Goodwin & Fish (1977); Goodwin (1979); Hannaford Ellis (1979)
	neglecta, *saxatilis*	ovoviviparous, brooding in oviduct	non-planktotrophic	Linke (1933*a*); Thorson (1946); Heller (1975); Hannaford Ellis (1979)
Mainwaringia	*rhizophila*	pelagic biconvex disc capsules, single ova	planktotrophic	Reid (1989*a*)

(Goodwin 1979). In §4*f* it was shown that there are no capsule glands in the littorinids producing the primitive type of egg mass, whereas these are present in the genus *Littorina*. This might be reflected in the occurrence of an extra covering layer around the egg albumen in the gelatinous egg mass of *Littorina* (*Neritrema*) species, although this was not described in the only histochemical comparison of egg masses so far done (Goodwin 1979).

The remaining oviparous littorinids spawn pelagic egg capsules (character 38). The shapes of the egg capsules are rather diverse (figure 11) (see reviews by Bandel (1974), Reid (1986*a*)), and have been used as taxonomic characters at the specific level (Murray 1979; Bandel & Kadolsky 1982). Trends in capsule shape at the generic level were pointed out by Reid (1986*a*). Three principal shapes can be distinguished: 'pill-box', 'biconvex disc' and 'cupola' (modified from Bandel (1974)), and have been used as discrete character states in the analysis.

The pill-box type is exemplified by *Melarhaphe neritoides* (Linke 1935*b*; Lebour 1935) (figure 11*a*), with an almost symmetrical, flat, cylindrical shape. A similar capsule is produced by *Cenchritis muricatus* (figure 11*b*), although here a slight circumferential flange is sometimes visible (Lebour 1945; Lewis 1960; Borkowski 1971).

The biconvex disc type is best exemplified by *Littoraria* (*Palustorina*) *melanostoma* (Berry & Chew 1973) (figure 11*h*), in which the lens-shaped capsule is produced into a wide circumferential flange. A basically similar type is found in most oviparous *Littoraria* species, including *L.* (*L.*) *flava* (Marcus & Marcus 1963), *L.* (*L.*) *irrorata* (Bingham 1972) and *L.* (*L.*) *nebulosa* (Bandel 1974). In *L.* (*L.*) *coccinea* and *L.* (*L.*) *undulata* (figure 11*f*) the peripheral flange is downturned to form a 'skirt' (Rosewater 1970), whereas in *L.* (*Palustorina*) *articulata* it is sometimes thickened so that the capsule approaches the pill-box shape (Kojima 1958*e*; Reid 1986*a*) (figure 11*g*). Biconvex disc capsules occur also in *Mainwaringia* and *Littorina*, including *L.* (*L.*) *squalida* (Kojima 1958*b*, *d*) (figure 11*s*), *L.* (*L.*) *mandshurica* (Kojima 1958*e*) and *L.* (*L.*) *littorea* (Linke 1933*a*) (figure 11*q*), although in the last two species the convexity is pronounced on one side only. The asymmetry is more marked in *L. scutulata* (figure 11*u*) and *L. plena* (Buckland-Nicks *et al.* 1973; Murray 1979, 1982; Mastro *et al.* 1982), with a pronounced rim on the more convex side. In *L.* (*L.*) *brevicula* (Kojima 1957, 1958*a*) (figure 11*t*) and *L.* (*Neritrema*) *sitkana* (Buckland-Nicks *et al.* 1973) the peripheral flange is less well developed, whereas in *L. keenae* (Schmitt 1979; Murray 1979) (figure 11*r*) and in *Mainwaringia rhizophila* (Reid 1989*a*) it is thickened.

The cupola type of capsule is asymmetrically convex, with the more domed upper side sculptured with 1–10 concentric rings and an overhanging skirt below. Capsules of this type occur in *Peasiella* (Tokioka 1950; Habe 1956) (figure 11*c*), *Tectarius* (*Tectininus*) *antonii* (Borkowski 1971) (figure 11*d*), *Littorina* (*Liralittorina*) *striata* (figure 11*p*) and in all the numerous species of *Nodilittorina* (see Yamamoto & Habe 1962; Struhsaker 1966; Borkowski 1971; Pilkington 1971; Bandel 1974; Jordan & Ramorino 1975; Bandel & Kadolsky 1982; Berry 1986) (figure 11*i*–*o*). The egg capsules of other *Tectarius* species have not been described, but it is expected that they will be of this type also. In some cases the peripheral skirt bears obliquely radial striations or ridges, as in *Nodilittorina riisei* (Borkowski (1971) as '*Littorina lineolata*') (figure 11*j*), the *N. millegrana* complex (see Tokioka & Habe 1953; Berry 1986) (figure 11*n*) and *Tectarius antonii*. The capsule of *Littoraria pintado* has a cupola sculptured with a single ring (Struhsaker 1966) (figure 11*e*), as does that of *Nodilittorina aspera* (figure 11*k*). The formation of the sculpture on the egg capsule is not understood, but it may be noted that in *Nodilittorina angustior* the concentric rings may be either separated or connected to form a

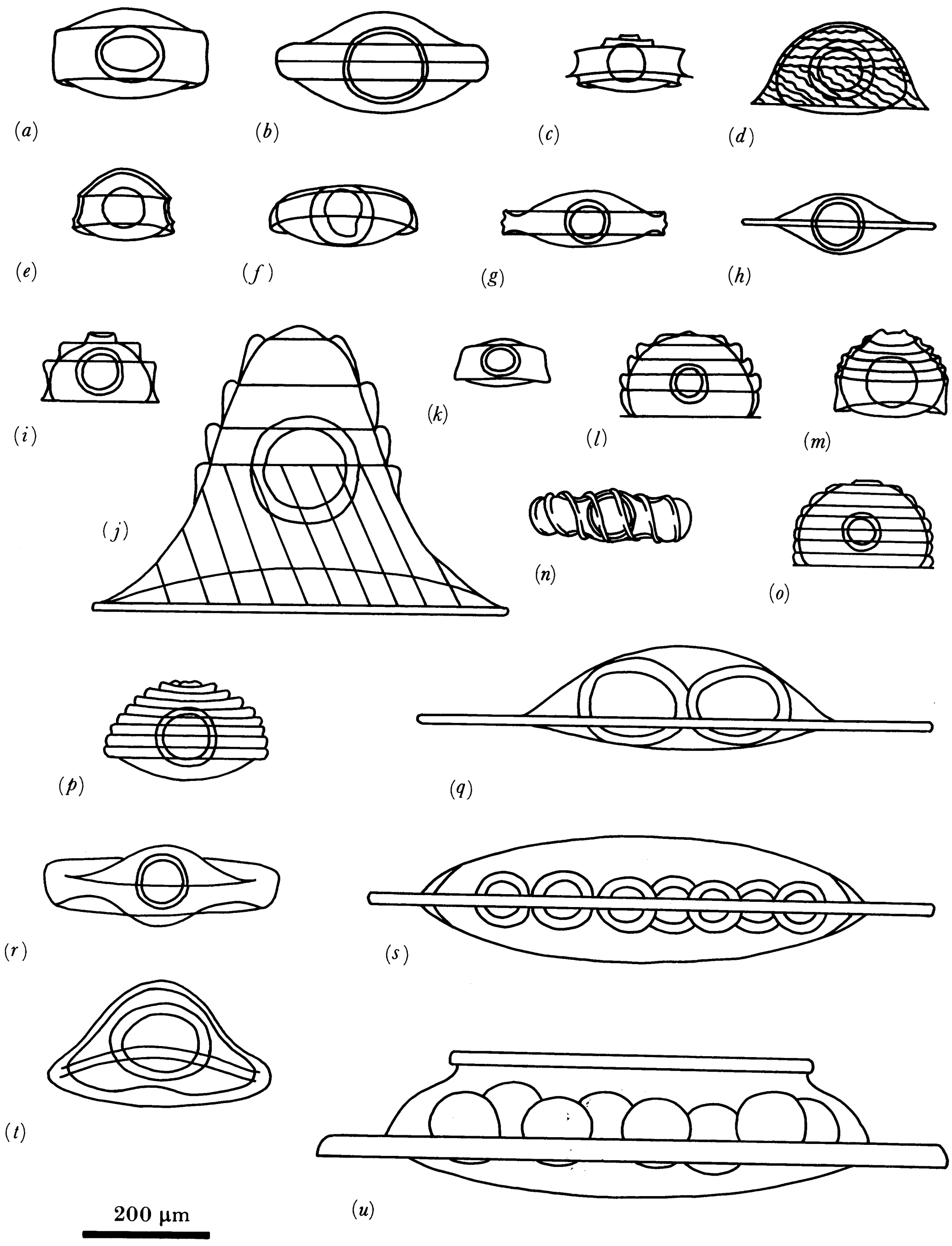

FIGURE 11. Pelagic egg capsules of Littorinidae. (*a*) *Melarhaphe neritoides* (after Linke 1935*b*); (*b*) *Cenchritis muricatus* (after Lewis 1960); (*c*) *Peasiella infracostata* (after Tokioka 1950); (*d*) *Tectarius* (*Tectininus*) *antonii* (after Borkowski 1971); (*e*) *Littoraria pintado* (after Struhsaker 1966); (*f*) *Littoraria* (*Littoraria*) *undulata* (after Rosewater 1970); (*g*) *Littoraria* (*Palustorina*) *articulata* (after Reid 1986*a*); (*h*) *Littoraria* (*Palustorina*) *melanostoma* (after Berry & Chew 1973); (*i*) *Nodilittorina* (*Fossarilittorina*) *meleagris* (after Borkowski 1971); (*j*) *Nodilittorina* (*Echinolittorina*) *riisei* (after Borkowski 1971); (*k*) *Nodilittorina* (*Nodilittorina*) *aspera* (original); (*l*) *Nodilittorina* (*Echinolittorina*) *dilatata* (after Borkowski 1971); (*m*) *Nodilittorina* (*Nodilittorina*) *hawaiiensis* (after Struhsaker 1966); (*n*) *Nodilittorina* (*Nodilittorina*) *vidua* (after Berry 1986); (*o*) *Nodilittorina* (*Echinolittorina*) *angustior* (after Borkowski 1971); (*p*) *Littorina* (*Liralittorina*) *striata* (original); (*q*) *Littorina* (*Littorina*) *littorea* (after Linke 1933*a*); (*r*) *Littorina keenae* (after Schmitt 1979); (*s*) *Littorina* (*Littorina*) *squalida* (after Kojima 1958*d*); (*t*) *Littorina* (*Littorina*) *brevicula* (after Kojima (1957); (*u*) *Littorina* (*Littorina*) *scutulata* (after Buckland-Nicks *et al.* 1973; Murray 1979; Mastro *et al.* 1982).

continuous spiral flange. Linke (1933*a*) suggested that the ovipositor is concerned with shaping the capsule, but Fretter & Graham (1962, p. 387) found fully formed capsules within the oviduct of *Melarhaphe neritoides*.

Reid (1986*a*) suggested that the biconvex and cupola shapes could have been derived from the simple pill-box type of egg capsule, because of the existence of somewhat intermediate capsule shapes (e.g. *Littoraria pintado*, *Nodilittorina aspera*, *Littorina keenae*), which all show a resemblance to the pill-box type. However, this scheme was speculative and the character states have been entered as unordered in the cladistic analysis.

In the great majority of littorinids producing pelagic eggs the capsules typically contain single ova. Within the genus *Littorina* some species produce capsules which enclose several ova (*L. littorea* 1–9; *L. mandshurica* 9–12; *L. squalida* 14–15; *L. scutulata* 1–14; *L. plena* 4–41; references given above) and are larger than all other pelagic capsules except that of *Nodilittorina riisei* (figure 11). In other *Littorina* species with egg capsules the ova are usually encapsulated singly. If the genus *Littorina* is assumed to be monophyletic, outgroup comparison with any other littorinid that produces capsules indicates that the production of capsules containing several ova is apomorphic (character 39).

There has been some debate in the literature about the evolution of types of spawn in the Littorinidae. Fretter (1980) suggested that the production of fixed gelatinous spawn, as in *Lacuna* and some *Littorina* species, was the primitive method, whereas liberation of pelagic capsules, primitively containing several ova, was the derived condition. In contrast, Reid (1986*a*), considering only the littorinids with capsule glands, proposed that the simple pelagic capsule containing a single ovum was primitive, and that from this either capsules with several ova, or benthic gelatinous spawn, could be derived. In fact these two schemes are complementary (Reid 1986*a*). Outgroup comparison indicates that a benthic gelatinous egg mass is primitive in the Littorinidae. Production of pelagic capsules depended upon the appearance of a new type of gland in the pallial oviduct, the capsule gland, and this method of development is primitive for all littorinids with this gland.

The genus *Littorina* is particularly interesting, showing a wide range of spawn and developmental types. In *L.* (*Liralittorina*) *striata* the capsules, containing single ova, are shed singly; in *L. keenae* they are released in a large, unattached, gelatinous mass, which soon disintegrates to liberate the pelagic capsules (Schmitt 1979); in *L.* (*Neritrema*) *sitkana* the ova are also encapsulated singly and deposited in a gelatinous mass attached to the substrate (Buckland-Nicks *et al.* 1973); in *L.* (*N.*) *arcana*, *L.* (*N.*) *mariae*, *L.* (*N.*) *nigrolineata* and *L.* (*N.*) *obtusata* the eggs within the benthic spawn are not encapsulated (Goodwin & Fish 1977; Hannaford Ellis 1979); in *L.* (*N.*) *neglecta* and *L.* (*N.*) *saxatilis* development is ovoviviparous (Heller 1975; Hannaford Ellis 1979). A species-level cladogram (Reid 1989*a*) confirms that this is an evolutionary sequence, reasons for which are explored in §6*d*. There is no justification for regarding benthic egg masses as primitive in *Littorina*, nor for the derivation of singly encapsulated pelagic ova from benthic egg masses via an intermediate condition with several ova in each capsule (as implied by Fretter (1980)).

All littorinids with pelagic egg capsules undergo planktotrophic development, with developmental times from spawning to settlement of several weeks (*Nodilittorina hawaiiensis* 21 days (Struhsaker & Costlow 1968), *Littorina scutulata* approximately 30 days (Buckland-Nicks *et al.* 1973), *Littorina littorea* approximately 35 days, extended by 6 weeks under unfavourable conditions (Thorson 1946)). These long developmental times permit wide dispersal (see §6*c* for discussion of biogeography). Because developmental type is correlated with the form of the protoconch, the two have been included in the analysis as a single character (character 3). Planktotrophy is believed to be the primitive type of development in the Littorinidae, and non-planktotrophy the derived one (see §4*a*).

Ovoviviparity is a more fundamental modification of development, involving both change in the glands of the pallial oviduct and elaboration of a brood pouch (character 40). Ovoviviparity occurs in *Littorina* (*Neritrema*) *saxatilis* (see, for example, Thorson 1946; Hannaford Ellis 1979), *L.* (*N.*) *neglecta* (Heller 1975), *Tectarius viviparus* (Rosewater 1982), at least nine species of *Littoraria* (*Littorinopsis*) (Reid 1986*a*) and *Littoraria aberrans*. Two independently derived types can be recognized.

In the ovoviviparous *Littorina* species the capsule gland is much reduced. Embryos are retained in a septate brood pouch formed from the distal, straight section of the pallial oviduct, homologous with the jelly gland, which now has thin, non-glandular walls. Juveniles are released at the crawling stage. This type of ovoviviparity has probably evolved from an ancestral state in which gelatinous egg masses with unencapsulated ova were retained in the enlarged jelly gland. This character state does not appear in the cladistic analysis because the species showing it belong to the subgenus *Neritrema*, of which the type species, *L. obtusata*, is oviparous. Modification of the jelly gland to form a brood pouch is a minor change, and oviparous and ovoviviparous species are clearly closely related (Hannaford Ellis 1979).

The other confirmed cases of ovoviviparity involve a quite different modification. Here the capsule glands are entirely lost. Larvae are retained not in the oviduct (as stated for *Tectarius viviparus* by Rosewater (1982)), but between the lamellae of the gill in the mantle cavity. They are spawned as planktotrophic veligers in all *Littoraria* (*Littorinopsis*) species, but in *Littoraria aberrans* and *Tectarius viviparus* a more apomorphic condition is achieved and juveniles are released at the crawling stage. These ovoviviparous species have evolved from ancestors that produced pelagic egg capsules, as do other members of their respective genera.

There is an unconfirmed report of ovoviviparity in *Cenchritis muricatus* (Bandel 1974), a species that other authors have described as oviparous (Lebour 1945; Lewis 1960; Borkowski 1971). Examination of Bandel's specimens has revealed the presence of opaque and translucent capsule glands and a normal, small, jelly gland. It is possible that brooding of encapsulated embryos in the mantle cavity could be facultative in this species.

The evolution and adaptive significance of littorinid reproductive strategies are considered in §6*d*.

Altogether, the spawn of about 77 species of Littorinidae have been described (table 4). The type of spawn and development can be predicted confidently for most of the remaining species, when information is available on the pallial oviduct and protoconch. A benthic gelatinous spawn is indicated by an enlarged jelly gland, and encapsulated ova by the presence of a translucent capsule gland and a large opaque capsule gland. The type of development, whether planktotrophic or non-planktotrophic, can be inferred from the protoconch (see §4*a*).

(*h*) *Radula* (*characters* 41–49)

The littorinid radula is of the taenioglossate type (figure 12). The radulae of numerous species have been figured in recent systematic accounts, and show a wide diversity of form (see, for example, Powell 1951; Rosewater 1970, 1972, 1980, 1981, 1982; Bandel 1974; Ponder 1976; Arnaud & Bandel 1978; Ponder & Rosewater 1979; Bandel & Kadolsky 1982; Reid

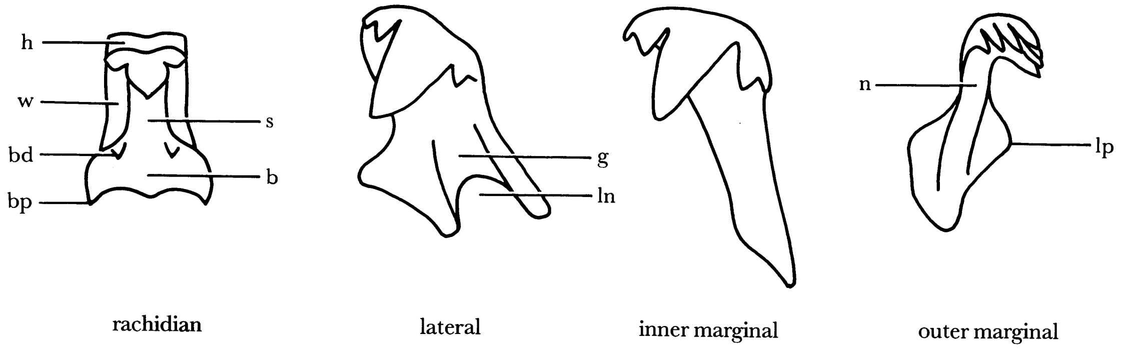

Figure 12. Terminology of radular teeth of Littorinidae. Radula mounted flat, with outer marginal folded outwards, as seen by light microscopy, viewed from above. Abbreviations: b, base; bd, basal denticle; bp, basal projection; g, groove for inner marginal; h, hood; ln, littorinid notch; lp, lateral projection; n, neck; s, shaft; w, wing.

1986*a*, *b*, 1988, 1989*a*) (figures 13 and 14). In an attempt to classify littorinid radulae, Rosewater (1980) defined five types, largely on the basis of the shape of the rachidian. These he related to diet and habitat, rather than to taxonomic groups. Other authors have distinguished generic groupings, and some have discussed possible evolutionary trends in the form and function of the radula (Bandel 1974; Bandel & Kadolsky 1982; Reid 1986*a*). At the specific level some taxonomists have defined species on the basis of differences in radular morphology (Bandel & Kadolsky 1982). However, from the few studies that have addressed the problem there is evidence of considerable intraspecific variation in radular morphology (Borkowski 1975; Goodwin & Fish 1977; Reid 1988). Used with care, radular characters do provide support for generic and subgeneric groupings based on other characters, but because tooth morphology must be related to diet and substrate, considerable homoplasy is to be expected.

In all littorinids the radula is relatively long, the radular sac lying coiled in several loops over the mid-oesophagus. Variation in relative length within the family can be correlated with the hardness of the substrate which the teeth abrade; in species of *Littoraria* living on mangroves the radula ranges from 0.58 to 1.35 times the height of the shell (Reid 1986*a*), but in species of *Nodilittorina* grazing on rocks the figure is much higher, up to 8.7 (*N. tuberculata*). In most littorinids the radula is at least as long as the greatest dimension of the shell, and is composed of at least 100 rows of teeth in even the smallest species. In related families the radula is often somewhat shorter, being less than one quarter of the greatest dimension of the shell and made up of less than 80 tooth rows in the Skeneopsidae, Eatoniellidae, Cingulopsidae, Rissoidae and Aciculidae. In *Pomatias* the radula is about one half of the length of the shell and composed of 120 tooth rows. In Cerithioidea the radula is also relatively short, from 0.09 to 0.5 of the shell length and composed of 40–98 tooth rows (Houbrick 1981*a*, 1985, 1987*a*, *b*). Coiled and short radular sacs have been distinguished by Ponder (1988), in his analysis of truncatelloidean relationships, but the distinction is of doubtful value when considering affinities within the Littorinoidea.

Another feature common to all littorinids is a well-developed lateral tooth with a trapezoid base, at the outer posterior corner of which is a deep groove with a marginal notch (the 'littorinid embayment' described by Rosewater (1970, 1980)) (figure 12), in which the inner marginal tooth lies when the radula is at rest (character 41). This was first pointed out by Troschel (1858), and used as evidence for the union of the families Littorinidae and Lacunidae by Arnaud & Bandel (1978). Nevertheless, this is not a character unique to the family. A similar groove with a more or less developed notch occurs in the Eatoniellidae (see Ponder & Yoo 1978), some Cingulopsidae (see Ponder & Yoo 1980) and some Truncatelloidea (see Ponder 1983). In the Cerithioidea a lateral tooth of similar form occurs in some families (Houbrick 1985, 1987*b*). The littorinid notch is not seen in the Pomatiasidae (Thompson 1978), Skeneopsidae (Fretter 1948) or Aciculidae (Jackiewicz 1967). The rather widespread occurrence of this character suggests that it may be plesiomorphic within the Littorinoidea. However, this is uncertain, and because it has been used to define the Littorinidae by earlier authors it has been included in the analysis for the sake of completeness.

The form of the rachidian tooth shows considerable variation within the Littorinidae (figures 13 and 14). An index of its shape is defined as the total length (when the radula is mounted flat and viewed from above) divided by the width at the mid-point (character 42). Four states are defined: square (shape index $\leqslant 1.00$), normal (1.01–2.99), narrow (3.00–9.99) and vestigial ($\geqslant 10.0$). Square teeth occur in all the species of *Pellilitorina* (figure 13*g*), *Lacuna* (figure 13*h*, *i*) and *Mainwaringia* (figure 14*p*), in most species of *Littorina* (*Littorina*) (figure 14*q*; exceptions are *L.* (*L.*) *scutulata* and *L.* (*L.*) *plena* (Mastro *et al.* 1982)) and in two of *L.* (*Neritrema*) (*L.* (*N.*) *sitkana* and *L.* (*N.*) *kurila*, but not other species, see Raffaelli (1979), Reid (1989*a*)). The great majority of littorinids show rachidian teeth of the normal shape. The narrow type occurs only in *Tectarius* (*Tectarius*), *T.* (*Echininus*), *T. viviparus* (figures 13*p*–*r* and 14*b*) and in a few *Nodilittorina* (*Echinolittorina*) species (Bandel & Kadolsky 1982) (figure 14*j*, *k*), whereas a vestigial rachidian is known only in *Tectarius* (*Tectininus*) *antonii* (figure 14*a*). It has been suggested that the square rachidian is the ancestral type (Reid 1986*a*), as could be argued from the widespread occurrence of this form in the Eatoniellidae (see Ponder 1965; Ponder & Yoo 1978), Rastodentidae (Ponder 1966*a*), Cingulopsidae (Ponder & Yoo 1980) and the Truncatelloidea (Ponder 1983, 1985*a*). However, in the outgroup, consisting of Pomatiasidae (Thompson 1978; Bandel 1984; D.G.R., personal observation) and Skeneopsidae (Fretter 1948), as in Aciculidae (Jackiewicz 1967), the shape of the rachidian falls in the normal category, and it is believed that this is the plesiomorphic type in Littorinidae.

Typically, the littorinid rachidian comprises an anterior row of cusps, a thickened shaft with thinner lateral expansions (or 'wings') and an expanded, posterior base (figures 12–14). The outline is commonly rectangular, or narrowed at the mid-point, but in *Laevilitorina* (*Pellilacunella*) (figure 13*a*) and *Lacuna* (figure 13*h*, *i*) the lateral wings are expanded to give the rachidian a hexagonal outline (character 43). This is not the case in the outgroup, and is therefore considered apomorphic. The rachidian of the Skeneopsidae is, however, somewhat similar (Fretter 1948).

The number of cusps at the cutting edge is five (rarely seven or nine) in many littorinid genera (character 44). The outer pair of the five cusps is very reduced in some *Littorina* (*Littorina*) species. In *Bembicium*, *Laevilitorina* (*Rufolacuna*), *Melarhaphe*, *Cenchritis*, *Peasiella*, *Tectarius*, *Nodilittorina*, *Littorina* (*Liralittorina*), *Littorina keenae*, *L. scutulata*, *L. plena*, *Littoraria pintado* and four *Littoraria* (*Littoraria*) species (*L.* (*L.*) *coccinea*, *L.* (*L.*) *glabrata*, *L.* (*L.*) *mauritiana*, *L.* (*L.*) *undulata*) there are only three cusps (figures 13 and 14). There is only a single cusp in *Tectarius* (*Tectarius*) *pagodus* (figure 13*p*), *T.* (*Tectininus*) *antonii* (figure 14*a*) and *Laevilitorina* (*Macquariella*) *aucklandica* (Powell 1951). Because five or more cusps occur in some of the

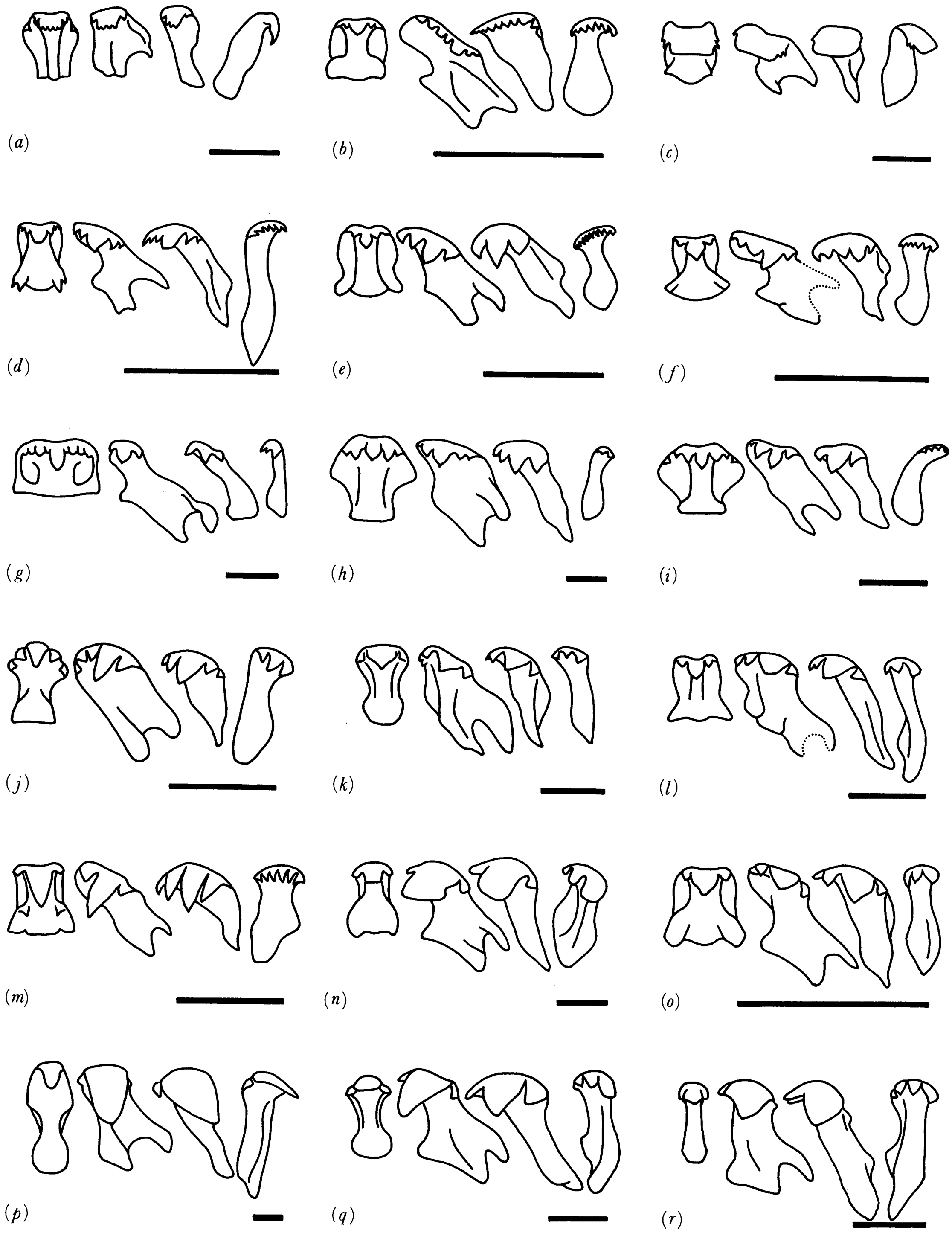

FIGURE 13. Radulae of Littorinidae. Radulae mounted flat, with outer marginal folded outwards, viewed from above; drawn by camera lucida or traced from scanning electron micrographs. Original, except as noted. Scale bars = 50 μm, except in (*e*) and (*f*) where bars = 25 μm. (*a*) *Laevilitorina* (*Pellilacunella*) *bennetti*; (*b*) *Laevilitorina* (*Macquariella*) *hamiltoni*; (*c*) *Laevilitorina* (*Macquariella*) *antarctica*; (*d*) *Laevilitorina* (*Laevilitorina*) *caliginosa*; (*e*) *Laevilitorina* (*Rissolittorina*) *alta*; (*f*) *Laevilitorina* (*Rufolacuna*) *bruniensis* (after Ponder 1976); (*g*) *Pellilitorina setosa*; (*h*) *Lacuna* (*Lacuna*) *pallidula*; (*i*) *Lacuna* (*Epheria*) *vincta*; (*j*) *Cremnoconchus syhadrensis*; (*k*) *Bembicium melanostoma*; (*l*) *Risellopsis varia*; (*m*) *Melarhaphe neritoides*; (*n*) *Cenchritis muricatus*; (*o*) *Peasiella tantilla*; (*p*) *Tectarius* (*Tectarius*) *pagodus*; (*q*) *Tectarius* (*Tectarius*) *grandinatus*; (*r*) *Tectarius* (*Echininus*) *cumingii* (after Rosewater 1982).

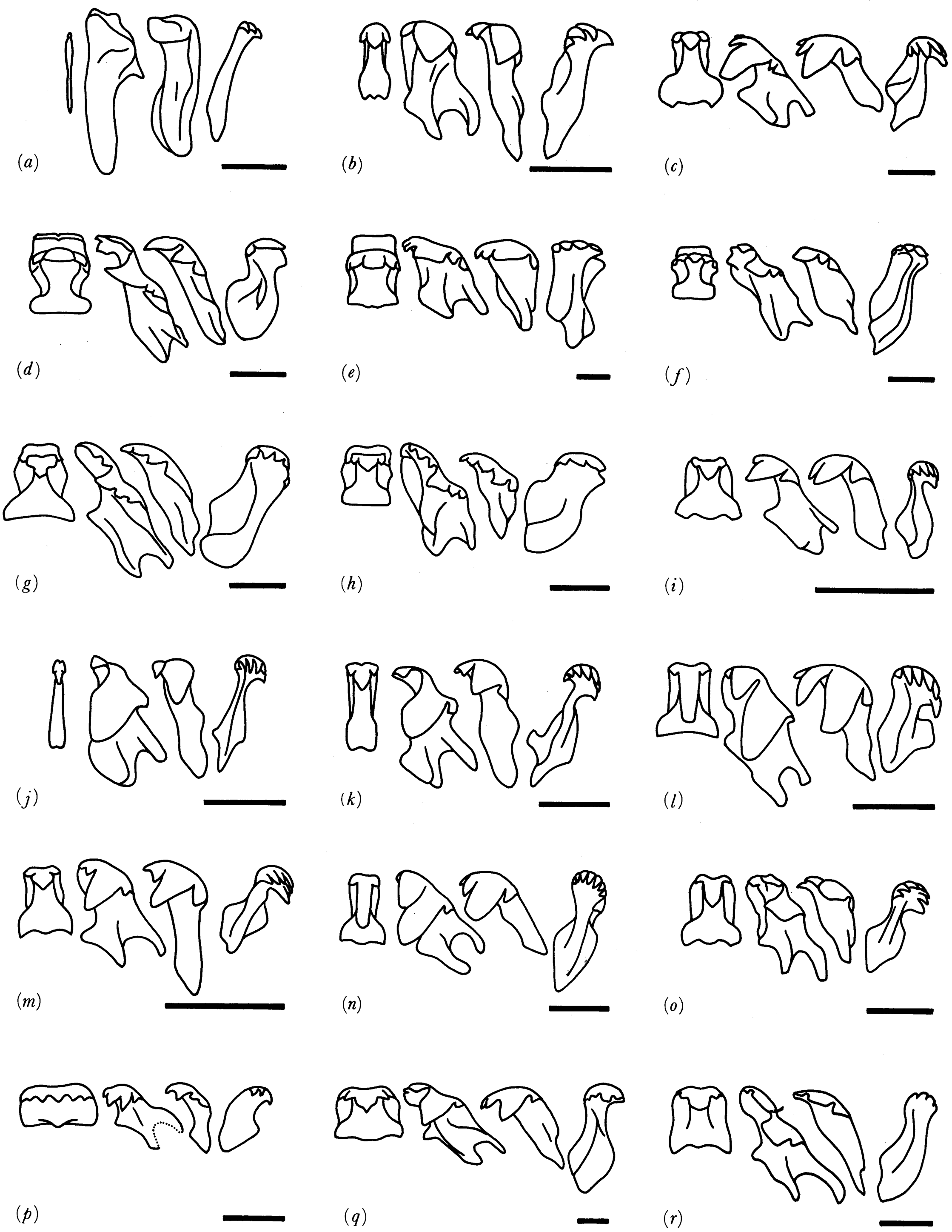

FIGURE 14. Radulae of Littorinidae (continued). Radulae mounted and drawn as in figure 10. Original, except as noted. Scale bars = 50 μm. (*a*) *Tectarius* (*Tectininus*) *antonii*; (*b*) *Tectarius viviparus* (after Rosewater 1982); (*c*) *Littoraria pintado*; (*d*) *Littoraria* (*Palustorina*) *melanostoma*; (*e*) *Littoraria* (*Littoraria*) *zebra*; (*f*) *Littoraria* (*Lamellilitorina*) *albicans*; (*g*) *Littoraria* (*Littorinopsis*) *angulifera*; (*h*) *Littoraria aberrans*; (*i*) *Nodilittorina* (*Fossarilittorina*) *meleagris*; (*j*) *Nodilittorina* (*Echinolittorina*) *tuberculata*; (*k*) *Nodilittorina* (*Echinolittorina*) *dilatata*; (*l*) *Nodilittorina* (*Nodilittorina*) *pyramidalis*; (*m*) *Nodilittorina* (*Nodilittorina*) *acutispira*; (*n*) *Littorina* (*Liralittorina*) *striata*; (*o*) *Littorina keenae*; (*p*) *Mainwaringia rhizophila*; (*q*) *Littorina* (*Littorina*) *littorea*; (*r*) *Littorina* (*Neritrema*) *obtusata*.

Pomatiasidae, in the Skeneopsidae and in other related families (references above), this is the plesiomorphic condition.

A highly distinctive rachidian tooth occurs in most species of the genus *Littoraria*, in which the anterior extremity (when the relaxed radula is viewed flat) is produced into a sharp flange, referred to as a 'hooded' rachidian (Rosewater 1980) (figures 12 and 14*d–h*; character 45). This occurs in all *Littoraria* species, with the exception of *L. pintado* (figure 14*c*), *L.* (*L.*) *coccinea*, *L.* (*L.*) *glabrata* and *L.* (*L.*) *mauritiana* (Rosewater 1970). Because it is not found in the outgroup, the hooded condition is regarded as apomorphic.

The rachidian of *Melarhaphe neritoides* is unique among littorinids in showing a pair of denticles on the base, near the junction with the shaft (Bandel 1974) (figures 12 and 13*m*; character 46). This is believed to be an autapomorphy, not to be confused with the basal projections, which are more or less well developed in most littorinids, and in many of the related families, especially Eatoniellidae (Ponder 1965; Ponder & Yoo 1978).

The range of form shown by the paired teeth is less striking. The lateral commonly bears three or more subequal cusps, as in the outgroup (character 47). In *Cenchritis* (figure 13*n*), Tectarius (figures 13*p–r* and 14*b*) and *Laevilitorina* (*Macquariella*) *antarctica* (figure 13*c*) there is only one major cusp, flanked by small denticles, whereas in *Tectarius* (*Tectininus*) (figure 14*a*) the cusps are further reduced, leaving only one.

Like the lateral tooth, the inner marginal commonly bears three or more cusps (character 48). This is also the case in the outgroup. Reduction to one or two has occurred in *Laevilitorina* (*Macquariella*) *antarctica* (figure 13*c*), *Tectarius* (*Tectarius*) *pagodus* (figure 13*p*), *T.* (*Tectininus*) *antonii* (figure 14*a*) and *Nodilittorina* (*Echinolittorina*) *tuberculata* (figure 14*j*).

The outer marginal teeth of littorinids are always rectangular or elongate, as also found in most of the related families. The Pomatiasidae (Thompson 1978; Bandel 1984; D.G.R., personal observation) are an exception, with greatly widened outer marginal teeth (character 49). Widened outer marginal teeth have also been recorded in the advanced truncatelloidean family Assimineidae (Abbott 1958; Ponder 1988) and in the Aciculidae (Jackiewicz 1967). In the Littorinidae the outer marginals are of a distinctive shape in *Nodilittorina*, with a strongly narrowed neck below the cusp-bearing head, and a lateral projection on the outer side of the base (clearly visible when outer marginals are folded outwards; figures 12 and 14*i–m*). This form occurs elsewhere only in *Littorina* (*Liralittorina*), *L. keenae*, *L. plena* and *L. scutulata* (Reid 1989*a*) (figure 14*n*, *o*). The number of cusps on the outer marginals ranges from 1 to 10; as in the other radular teeth there has probably been a trend towards a reduction in the number of cusps in several lines, but the distribution of the character in relation to others suggests that too much homoplasy has occurred for its inclusion in the cladistic analysis.

Too little is known about the functioning of the littorinid radula to understand the adaptive significance of tooth morphology, but some correlations with substrate can be pointed out. Members of the genera *Pellilitorina*, *Lacuna*, *Laevilitorina*, and also some *Littorina* species (e.g. *L.* (*Neritrema*) *obtusata*) live on the fronds of macroalgae (see §6*d*). These share a normal or square rachidian with five to seven cusps, relatively numerous and uniform cusps on the lateral and inner marginal teeth, and outer marginals with few, sometimes blunt or rounded, cusps or numerous small sharp ones. As discussed above, some of these features are plesiomorphic. Species of *Cremnoconchus*, *Bembicium*, *Risellopsis*, *Melarhaphe*, *Cenchritis*, *Peasiella*, *Tectarius*, *Nodilittorina* and some of *Littorina* occur mainly on rocky substrates. In these the rachidian is normal or narrowed, usually with three cusps; the cusps on the lateral and inner marginals are commonly reduced in number, and one or two on each tooth are massive and elongate (*Tectarius* (*Tectininus*) *antonii* being the most extreme example of these trends), whereas the outer marginals usually bear rather long and pointed cusps. Some littorinids are found mainly on mangroves, driftwood and marsh plants; these include *Mainwaringia* and most *Littoraria* species (exceptions are *L. pintado*, *L.* (*L.*) *coccinea*, *L.* (*L.*) *glabrata*, *L.* (*L.*) *mauritiana*, *L.* (*L.*) *tessellata*, *L.* (*L.*) *undulata*). The radula of *Mainwaringia* closely resembles that of the group living on macroalgae. In the genus *Littoraria* as a whole, the wood-dwelling habit shows a close, although not exact, correlation with a hooded rachidian having five cusps, and with broad and blunt cusps on all the paired teeth (Reid 1986*a*).

(*i*) *Alimentary system* (*characters* 50–52)

In addition to the radula, some prosobranchs possess a pair of cuticularized jaws flanking the buccal cavity, which are composed of rod-shaped elements. These are present in the Skeneopsidae (Fretter 1948), Eatoniellidae (Ponder 1968), Rastodentidae (Ponder 1966*a*), some Anabathridae and Barleeidae (Ponder 1983), Rissoidae (Ponder 1985*a*) and Aciculidae (Jackiewicz 1967). Jaws are absent in the Cingulopsidae (see Fretter & Patil 1958; Ponder & Yoo 1980) and Pomatiasidae. In the Littorinidae jaws occur only in *Pellilitorina* (character 50). Because jaws are present in only one of the two families constituting the outgroup, more distant outgroups must be consulted to assess the status of the character in the Littorinidae. The widespread occurrence of jaws among prosobranchs (Fretter & Graham 1962) suggests that their presence is plesiomorphic.

In common with most neotaenioglossans, a single pair of salivary glands opens into the buccal cavity of littorinids. These comprise separate narrow ducts running anteriorly from the enlarged glandular part, which is lobulate or tubular. In most littorinids the glands are posterior, with the glandular parts lying alongside or beneath the mid-oesophagus, entirely posterior to the cerebral commissure, and only the ducts pass through the nerve ring around the oesophagus to reach the buccal mass (Fretter & Graham 1962, figure 14; Ponder 1983). However, in a few genera the glands are in an anterior position, lying above and anterior to the nerve ring, and their ducts do not pass through it. This condition is found in *Cremnoconchus*, *Bembicium*, *Risellopsis*, *Laevilitorina* (*Macquariella*) (except *L.* (*M.*) *kingensis* (Ponder 1983)), *L.* (*Rufolacuna*) and *L.* (*Pellilacunella*) (character 51). An apparently intermediate condition occurs in some other genera, in which the nerve ring appears to constrict each glandular part into two, with glandular material both anterior and posterior to the cerebral commissure, joined by a thin connecting strand that passes through the nerve ring (Reid 1986*a*, figure 13*b*). This group includes *Pellilitorina*, *Lacuna*, *Laevilitorina* (*Laevilitorina*), *L.* (*Rissolittorina*), *Peasiella*, *Littoraria* and *Mainwaringia*. In the outgroup the salivary glands are anterior in the Skeneopsidae (Fretter 1948), but posterior in Pomatiasidae. Although the posterior condition is believed to be primitive in neotaenioglossans as a whole (Ponder 1988), there is some diversity among the other families of the littorinoidean–truncatelloidean radiation, with posterior glands in Cingulopsidae (Fretter & Patil 1958; Ponder 1983), constricted glands in Eatoniellidae (D. G. R., personal observation), anterior glands in the Truncatelloidea (Ponder 1983, 1985*a*, 1988) and posterior glands in Aciculidae (Jackiewicz 1967). In the cerithioidean families there is usually glandular material on both sides of the nerve ring, sometimes without an obvious constriction into two parts (Houbrick 1980, 1981*a*, *b*, 1984, 1985, 1987*a*, *b*).

Although usually of relatively small size, in *Littorina* species (except *L. striata* and *L. keenae*) the salivary glands are greatly enlarged, each of the pair being comparable in length and width to the mid-oesophagus, which is itself partly or completely concealed by them. This enlargement is not seen in the outgroup, and is therefore considered to be apomorphic (character 52).

Glandular material is also present in the walls of the mid-oesophagus (the oesophageal gland) and in the pair of oesophageal pouches, which lie anterior to the nerve ring of littorinids. Ponder (1983) suggested that the pouches represent an anterior extension of the oesophageal gland, separated from it by the constriction imposed by the nerve ring, and so these structures are considered together. A glandular mid-oesophagus is a plesiomorphic feature of neotaenioglossans (Ponder 1988), and both pouches and the oesophageal gland occur in the Eatoniellidae and some Cingulopsidae (Fretter & Patil 1958; Ponder 1983), as in the Littorinidae. An oesophageal gland alone is present in the Rastodentidae (Ponder 1966*a*) and probably Aciculidae (Creek 1953), and a pair of pouches in some Barleeidae (Ponder 1983). These structures are absent in the majority of truncatelloidean families (Ponder 1983, 1988), Skeneopsidae (Fretter 1948) and Pomatiasidae.

In littorinids the dorsal folds of the anterior oesophagus are long, extending back into the mid-oesophagus (see, for example, Reid 1986*a*, figure 13*c*), where they occupy a ventral position as a consequence of torsion. This is also the case in the Eatoniellidae (Ponder 1968) and perhaps in Cingulopsidae (Fretter & Patil 1958). In contrast, the dorsal folds are short, not extending into the mid-oesophagus, in the Skeneopsidae (Fretter 1948), Aciculidae (Jackiewicz 1967) and Pomatiasidae. In truncatelloideans the condition is variable (Ponder 1988). The extent of the folds is also variable in cerithioidean families (Houbrick 1980, 1981*a*, *b*, 1984).

The stomach is of rather uniform structure in the Littorinidae (Johansson 1939; Fretter & Graham 1962, p. 30; Reid 1986*a*). The crystalline style found in cerithioidean and many truncatelloidean families (Ponder 1983, 1985*a*, 1988) and in the Pomatiasidae (Fretter & Graham 1962, p. 220) is absent in the Littorinidae. A crystalline style is also absent in the Skeneopsidae, Cingulopsoidea and Aciculidae.

(*j*) *Nervous system* (*character* 53)

The nervous system of the Littorinidae is of the type known as epiathroid (in which pleural and cerebral ganglia are adjacent (Fretter & Graham 1962, p. 310)), with concentrated pedal ganglia connected by a commissure, and has been illustrated by Bouvier (1887), Johansson (1938), Fretter & Graham (1962) and Reid (1988). This type is also found in all other members of the littorinoidean–truncatelloidean radiation. Ponder (1988) has suggested that the nervous system of the Aciculidae (Jackiewicz 1967) approaches the hypoathroid type, and on this basis has placed the family in the Architaenioglossa. However, the pleural ganglia are situated midway between the cerebral and pedal ganglia, and pedal cords of the type found in the Aciculidae do occur in a few other neotaenioglossans (Haszprunar 1988).

The six circumoesophageal ganglia do not show a high degree of concentration in littorinids; the cerebral commissure is from one to two times the length of a cerebral ganglion, the cerebropedal and pleuropedal connectives are from two to five times the length of a cerebral ganglion (but equal to the length of a ganglion in *Lacuna* and *Cremnoconchus*), and the two pedal ganglia abut each other. A similar arrangement occurs in the Skeneopsidae (Fretter 1948), Pomatiasidae and Eatoniellidae (D.G.R., personal observation). This may be contrasted with the more concentrated system, in which connectives and commissures are so short that ganglia are adjacent or almost so, as found in the Cingulopsidae (see Fretter & Patil 1958), many truncatelloideans (see Johansson 1938; Ponder 1983, 1985*a*, 1988) and probably the Rastodentidae (Ponder 1966*a*). The concentrated condition is derived (Fretter & Graham 1962).

Another trend towards the concentration of ganglia around the oesophagus involves the reduction in length of the pleuro-supraoesophageal and pleuro-suboesophageal connectives, so that the supraoesophageal and suboesophageal ganglia come to lie close to the pleural and cerebral ganglia (Fretter & Graham 1962, p. 310). In most of the littorinids examined these connectives are long, about five to ten times the length of an oesophageal ganglion in each case. Exceptions include *Bembicium* (Reid 1988) and *Cremnoconchus*, with a short pleuro-suboesophageal connective only 1–1.5 times the length of the suboesophageal ganglion (character 53). In the outgroup, both connectives are long in the Pomatiasidae (D.G.R., personal observation), but both are short (i.e. less than or equal to the ganglion length) in Skeneopsidae (Fretter & Graham 1962, p. 313; Ponder 1988). Among related families, in the Eatoniellidae only the pleuro-suboesophageal connective is short (D.G.R., personal observation); in Aciculidae only the pleuro-supraoesophageal connective is short (Jackiewicz 1967); both connectives are short in many Truncatelloidea (Fretter & Graham 1962, p. 312; Ponder 1983, 1985*a*, 1988) and in Cingulopsidae (Fretter & Patil 1958). Among cerithioidean families the pleuro-supraoesophageal connective is long, and the pleuro-suboesophageal connective short (Houbrick 1981*a*, 1984, 1987*a*, *b*). Although long connectives have been regarded as plesiomorphic in the littorinoidean–truncatelloidean radiation (Ponder 1988), outgroup comparison shows that it is more parsimonious to regard a short pleuro-suboesophageal connective as plesiomorphic in the Littorinoidea.

The innervation of the penis has been discussed in §4*d*.

(*k*) *Chromosome numbers*

Karyotypes have been described for only eight species of Littorinidae (review by Vitturi *et al.* (1986)), and further studies are required before karyological evidence can be used in phylogenetic reconstruction. A haploid number of 17 has been reported in three species of *Littorina* (Nishikawa 1962; Janson 1983), 16 or 17 in *Melarhaphe* (Thiriot-Quiévreux & Ayraud 1982; Vitturi & Catalano 1984) and 17 in *Littoraria articulata* (Nishikawa 1962, as '*L. strigata*'). In the genus *Nodilittorina* numbers may be more variable; Nishikawa (1962) gave 15 for *N. vidua* and 18 for *N. radiata* (as '*N. picta*' and '*N. granularis*', respectively). Three species of the Pomatiasidae have been examined, with haploid numbers of 13 and 14 (Rainer 1967; Vitturi *et al.* 1986).

5. PHYLOGENETIC ANALYSIS

(*a*) *Methods*

As described in the preceding sections, 53 characters were chosen for use in the analysis, and coded as 131 character states (table 5). The complete matrix of character states for the 34 taxa of the ingroup and 2 taxa of the outgroup (*Skeneopsis* and *Pomatias*) is given in table 6. This table includes autapomorphic characters (in which the apomorphic state is unique to a single taxon). The data were analysed by using version 2.4.1 of the PAUP program (Swofford 1985).

TABLE 5. LIST OF CHARACTERS AND CHARACTER STATES USED IN CLADISTIC ANALYSIS OF SUBGENERA OF LITTORINIDAE

(All character states are ordered except those marked 'U' in column 3. Asterisks indicate terminal autapomorphic character states. The plesiomorphic states listed are those that are plesiomorphic within the family (see §5*c*(i)).)

			character states					
no.	character	un-ordered	0	1	2	3	4	plesio-morphic state
1	shell shape	—	turbinate or globular	trochoidal	—	—	—	0
2	shell sculpture	—	smooth	major spiral grooves	—	—	—	0
3	protoconch and larval development	U	planktotrophic, > 0.5 mm diam.*	planktotrophic, < 0.5 mm diam.	intermediate	non-planktotrophic		1
4	shell mineralogy and microstructure	U	aragonite, crossed-lamellar only	aragonite, with outer irregular-prismatic calcite	crossed-foliated calcite only	aragonite, crossed-lamellar, outer spherulitic-prismatic	aragonite, crossed-lamellar, outer fine layer	3
5	opercular shape	—	paucispiral	mesospiral	—	—	—	0
6	opercular ridge	—	absent	present	—	—	—	0
7	opercular calcification	—	like *Pomatias**	uncalcified	like *Cremnoconchus**	—	—	1
8	propodial groove	—	present	absent	—	—	—	0
9	longitudinal division of foot	—	absent	present	—	—	—	0
10	opercular tentacles	—	absent	present	—	—	—	0
11	ovipository flange	—	absent	present*	—	—	—	0
12	eye peduncles	—	absent	present*	—	—	—	0
13	colour pattern of head	—	not so	*Nodilittorina* pattern	—	—	—	0
14	osphradium	—	straight	terminal flexure	—		—	0
15	hermaphroditism	—	gonochoristic	protandrous*	—		—	0
16	prostate	—	closed tube	open groove	—	—	—	0
17	prostate gland cells	—	absent*	epithelial	subepithelial*	—	—	1
18	anterior vas deferens over head	—	closed tube	open groove	—	—	—	0

19	penial vas deferens	U	deep closure	open groove	superficial closure	—	—	0
20	opening of penial vas deferens	—	terminal	subterminal	—	—	—	0
21	bifurcation of penial base	—	absent	present	—	—	—	0
22	penial filament	—	extended	retracted into base*	—	—	—	0
23	simple penial glands	—	absent	scattered	glandular disc	infolded disc*	—	0
24	mamilliform penial glands	U	absent	1 or 2, uniform	many, uniform	1 or 2 and many small	many, not uniform	0
25	muscular papillae on penis	—	absent	present	—	—	—	0
26	paraspermatic nurse cells	U	absent	present, no rods	present, with rods	—	—	0
27	nurse cell flagella	—	absent	present*	—	—	—	0
28	duct to seminal receptacle	—	short	long	—	—	—	0
29	oviducal sperm groove	—	open	partially closed*	—	—	—	0
30	anterior bursa	U	absent	anterior	further back	—	—	1
31	seminal receptacle	—	present	absent	—	—	—	0
32	opening of renal oviduct	—	posterior	anterior*	—	—	—	0
33	capsule gland	—	absent	present	—	—	—	0
34	size of jelly gland	—	large	small	—	—	—	0
35	histology of albumen and capsule glands	—	glandular epithelium	subepithelial gland cells	—	—	—	0

TABLE 5 (*cont.*)

no.	character	un-ordered	character states 0	1	2	3	4	plesio-morphic state
36	coiling of egg groove	–	straight	1 spiralled loop	2 spiralled loops	3 spiralled loops	—	1
37	loop of jelly gland	—	straight	backward loop	—	—	—	0
38	egg capsules	U	absent	pill box	biconvex disc	cupola	—	0
39	eggs per capsule	–	usually 1	several	—	—	—	0
40	ovoviviparity	–	oviparous	spawning of veligers	crawling young	—	—	0
41	littorinid notch in lateral tooth	—	present	absent	—	—	—	0
42	rachidian tooth proportions	—	square	normal	narrow	vestigial*	—	1
43	rachidian tooth outline	—	rectangular	hexagonal	—		—	0
44	rachidian tooth cusps	—	7 or 5	3 or 1	—	—	—	0
45	rachidian tooth hooded	-	not hooded	hooded	—	—	—	0
46	rachidian base plate	—	plain	pair of denticles*	—	—	—	0
47	lateral tooth cusps	—	3 or more, subequal	1 major cusp and denticles	1 cusp only*	—	—	0
48	inner marginal tooth cusps	—	3 or more	1 or 2*	—	—	—	0
49	outer marginal tooth shape	—	greatly widened*	elongate rectangular	neck and basal projection		—	1
50	jaws	—	present	absent	—		—	0
51	position of salivary glands	—	posterior to nerve ring	constricted by nerve ring	anterior to nerve ring		—	1
52	size of salivary glands	—	normal	enlarged	—	—	—	0
53	pleuro-suboesophageal connective	—	long	short	—	—	—	0

Autapomorphic characters (numbers 7, 11, 12, 15, 17, 22, 27, 29, 32, 46, 48) and autapomorphic, terminal, character states (one state each of characters 3, 23, 42, 47, 49) were removed before analysis, for these would artificially increase the consistency index of the cladogram, but not provide any information on relationships. All characters were unweighted. Where there was uncertainty in the probable transformation sequence of character states, the characters were specified as unordered (numbers 3, 4, 19, 24, 26, 30 and 38; see §4). With such a large matrix it was not possible to use the exact algorithm (BANDB) that guarantees to find the shortest (most parsimonious) tree or trees. Instead, the heuristic algorithm (SWAP = GLOBAL MULPARS option) was employed, as suggested by Platnick (1987). For rooting the ingroup tree the ROOT = OUTGROUP option was used, permitting the inclusion of two outgroup taxa and enabling the program to polarize the character states in a manner ensuring global parsimony (Maddison *et al.* 1984; Swofford 1985). The MINF option was employed for character-state reconstruction (Swofford & Maddison 1988) and specified in the GO command. The default options of HOLD = 1 and ADDSEQ = CLOSEST were used in the preliminary analysis, and a range of values in subsequent runs, as discussed below. The entire analysis was repeated using either the Pomatiasidae or Skeneopsidae alone as the outgroup.

(*b*) *Results*

A preliminary analysis of the set of data produced at least 100 equally parsimonious trees (the default maximum for the program) of length (*l*) 147 steps and consistency index (*c*) 0.408 (indicating that 59.2% of the character state changes could be ascribed to homoplasy). Inspection of these trees showed considerable uniformity. The taxa *Pellilitorina*, *Lacuna* (*Lacuna*), *L.* (*Epheria*), *Cremnoconchus*, *Bembicium* and *Risellopsis* together always formed a monophyletic group (the term 'monophyletic' is here used in the sense of Hennig (1966), equivalent to 'holophyletic'). This clade (the Lacuninae) showed a constant topology and made the first branch at the base of the ingroup. The next branch or branches comprised the five subgenera of *Laevilitorina*, either as a monophyletic or a paraphyletic group. The remaining taxa always formed a monophyletic clade (the Littorininae), within which three taxa were responsible for terminal or near-terminal trichotomies.

The PAUP program represents an unresolved polychotomy as several separate, fully bifurcating trees, which in reality are not topologically distinct. Therefore, to examine the range of tree topologies, and to search for alternatives, the number of equally parsimonious trees was reduced by removal of the three taxa causing terminal trichotomies (*Tectarius viviparus*, *Littoraria* (*Lamellilitorina*), *Nodilittorina* (*Fossarilittorina*)) and three of the subgenera of *Laevilitorina* (*Rissolittorina*, *Rufolacuna*, *Pellilacunella*). As discussed by Platnick (1987), the order in which taxa are added together to construct the initial estimate of the tree (ADDSEQ option) and the number of equally parsimonious cladograms held in memory at each stage in the construction (HOLD option) can affect the result of the PAUP program. Therefore eight runs of the reduced data set of 30 taxa were done, representing the combinations of HOLD values of either 1 or 25 (the maximum available) with the four available ADDSEQ options (SIMPLE, ROOTLESS, ASIS, CLOSEST). Five combinations (CLOSEST or SIMPLE with HOLD = 1 or 25, and ASIS with HOLD = 25) each produced the same set of six equally parsimonious trees ($l = 132$), whereas the other combinations found only longer trees. These six trees were topologically identical, because of an unresolved trichotomy of *Laevilitorina* (*Macquariella*), *L.* (*Laevilitorina*) and the remaining non-lacunine taxa, and the interchangeable positions of the clade consisting of *Tectarius* and

Table 6. Character states for the cladistic analysis of subgenera of Littorinidae

(For list of characters see table 5, and for representative species see table 3. *Skeneopsis* and *Pomatias* are outgroup taxa.)

		character number																									
no.	taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
1	*Skeneopsis*	1	0	3	?	1	0	1	0	0	0	0	0	0	?	0	0	1	0	0	0	0	0	0	0	0	?
2	*Pomatias*	0	1	3	3	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
3	*Pellilitorina*	0	0	3	2	0	1	1	0	0	0	1	1	0	0	0	0	?	0	0	0	0	0	0	0	0	0
4	*Lacuna*	0	0	3	3	0	1	1	0	0	1	0	0	0	1	0	0	?	0	0	0	0	0	1	0	1	0
5	*Epheria*	0	0	2	3	0	1	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0
6	*Laevilitorina*	0	0	3	3	0	0	1	0	0	0	0	0	0	0	0	0	?	0	2	0	0	0	1	0	0	0
7	*Rissolittorina*	0	0	3	?	0	0	1	0	0	0	0	0	0	0	0	0	?	0	2	0	1	0	1	0	0	0
8	*Macquariella*	0	0	3	3	0	0	1	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0
9	*Rufolacuna*	1	0	3	?	0	0	1	0	0	0	0	0	0	0	0	0	?	0	2	0	1	0	1	0	0	0
10	*Pellilacunella*	0	0	3	3	0	0	1	0	0	1	0	0	0	0	0	0	?	0	2	0	0	0	?	0	0	0
11	*Bembicium*	1	1	3	0	0	1	1	0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0
12	*Risellopsis*	1	1	2	1	0	0	1	?	?	0	0	0	0	0	0	1	?	1	1	1	1	0	0	0	1	0
13	*Cremnoconchus*	0	1	3	0	0	1	2	1	0	0	0	0	0	0	0	0	2	0	0	0	0	1	1	0	0	0
14	*Melarhaphe*	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	?	0	2	0	0	0	0	0	0	1
15	*Cenchritis*	1	1	1	0	0	0	1	0	1	0	0	0	0	0	0	1	?	0	2	0	0	0	0	0	0	2
16	*Peasiella*	1	1	1	0	1	0	1	0	0	0	0	0	0	0	0	1	1	1	2	0	0	0	1	1	0	1
17	*Tectarius*	1	1	1	0	1	0	1	0	1	0	0	0	0	0	0	1	?	1	1	0	0	0	?	4	0	?
18	*Tectininus*	1	1	1	0	1	0	1	0	1	0	0	0	0	0	0	1	?	1	1	1	0	0	1	4	0	2
19	*Echininus*	1	1	1	0	1	0	1	0	1	0	0	0	0	0	0	1	?	1	1	1	0	0	1	4	0	?
20	*Tectarius viviparus*	1	1	3	0	1	0	1	0	1	0	0	0	0	0	0	1	?	1	1	1	0	0	?	2	0	?
21	*Littorina keenae*	0	1	1	4	0	0	1	0	1	0	0	0	0	0	0	1	?	1	1	0	0	0	1	1	0	1
22	*Littorina plena*	0	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	1	1	1	0	0	0	1	1	0	1
23	*Littorina*	0	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	1	1	1	0	0	0	1	2	0	1
24	*Neritrema*	0	1	3	1	0	0	1	0	1	0	0	0	0	0	0	1	1	1	1	0	0	0	1	2	0	1
25	*Mainwaringia*	0	1	1	0	0	1	1	0	0	0	0	0	0	0	1	1	?	1	2	0	0	0	1	1	0	1
26	*Liralittorina*	0	1	1	4	0	0	1	0	1	0	0	0	0	0	0	1	?	1	1	0	?	0	1	0	0	1
27	*Fossarilittorina*	0	0	1	4	0	0	1	0	1	0	0	0	1	0	0	1	?	1	2	0	?	0	0	0	0	2
28	*Nodilittorina modesta*	0	1	1	4	0	0	1	0	1	0	0	0	1	0	0	1	?	1	1	0	?	0	1	0	0	2
29	*Nodilittorina*	0	1	1	4	0	0	1	0	1	0	0	0	1	0	0	1	1	1	1	0	1	0	2	3	0	2
30	*Echinolittorina*	0	1	1	4	0	0	1	0	1	0	0	0	1	0	0	1	?	1	1	0	1	0	2	1	0	2
31	*Littoraria pintado*	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	?	1	1	0	0	0	1	0	0	2
32	*Littoraria*	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	1	0	1	0	2	0	0	2
33	*Palustorina*	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	?	1	1	0	0	0	2	0	0	2
34	*Lamellilitorina*	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	?	1	1	0	1	0	2	0	0	2
35	*Littorinopsis*	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	?	1	1	0	1	0	2	0	0	2
36	*Littoraria aberrans*	0	1	3	0	0	0	1	0	1	0	0	0	0	0	0	0	?	1	1	0	1	0	3	0	0	1

no.	taxon	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53
		character number																										
1	*Skeneopsis*	?	0	0	0	0	0	0	0	0	0	0	0	?	0	1	1	0	0	0	0	0	0	1	0	2	0	1
2	*Pomatias*	?	0	0	0	1	0	0	0	0	0	0	0	?	0	1	1	0	0	0	0	0	0	0	1	0	0	0
3	*Pellilitorina*	?	?	0	0	1	0	0	0	0	1	0	0	?	0	0	0	0	0	0	0	0	0	1	0	1	0	0
4	*Lacuna*	?	?	0	1	1	0	0	0	0	1	1	0	?	0	0	0	1	0	0	0	0	0	1	1	1	0	?
5	*Epheria*	?	?	0	1	1	0	0	0	0	1	1	0	?	0	0	0	1	0	0	0	0	0	1	1	1	0	0
6	*Laevilitorina*	?	0	0	1	0	0	0	0	0	2	0	0	?	0	0	1	0	0	0	0	0	0	1	1	1	0	0
7	*Rissolittorina*	?	0	0	1	0	0	0	0	0	2	0	0	?	0	0	1	0	0	0	0	0	0	1	1	1	0	?
8	*Macquariella*	?	0	0	1	0	0	0	0	0	2	0	0	?	0	0	1	0	0	0	0	0	0	1	1	2	0	?
9	*Rufolacuna*	?	0	0	1	0	0	0	0	0	2	0	0	?	0	0	1	0	1	0	0	0	0	1	1	2	0	?
10	*Pellilacunella*	?	0	0	1	0	0	0	0	0	2	0	0	?	0	0	1	1	0	0	0	0	0	1	1	2	0	?
11	*Bembicium*	?	1	0	1	0	1	0	0	0	1	1	0	?	0	0	1	0	1	0	0	0	0	1	1	2	0	1
12	*Risellopsis*	?	1	0	1	0	0	0	0	0	1	1	0	?	0	0	1	0	0	0	0	0	0	1	1	2	0	?
13	*Cremnoconchus*	?	?	0	1	1	0	0	0	1	1	0	0	?	0	0	1	0	0	0	0	0	0	1	1	2	0	1
14	*Melarhaphe*	0	0	0	1	0	0	1	1	0	2	0	1	0	0	0	1	0	1	0	1	0	0	1	1	0	0	?
15	*Cenchritis*	0	0	0	1	0	0	1	1	1	1	0	1	0	0	0	1	0	1	0	0	1	0	1	1	0	0	?
16	*Peasiella*	0	0	0	1	0	0	1	1	1	2	0	3	0	0	0	1	0	1	0	0	0	0	1	1	1	0	?
17	*Tectarius*	?	0	0	1	0	0	1	1	1	1	0	?	?	0	0	2	0	1	0	0	1	0	1	1	0	0	?
18	*Tectininus*	0	0	0	2	0	0	1	1	1	1	0	3	0	0	0	3	0	1	0	0	2	1	1	1	0	0	?
19	*Echininus*	?	0	0	1	0	0	1	1	1	1	0	?	?	0	0	2	0	1	0	0	1	0	1	1	?	0	?
20	*Tectarius viviparus*	?	0	0	1	0	0	0	1	1	1	0	0	?	2	0	2	0	1	0	0	1	0	1	1	0	0	?
21	*Littorina keenae*	0	0	0	2	0	0	1	0	1	2	0	2	0	0	0	1	0	1	0	0	0	0	2	1	0	0	?
22	*Littorina plena*	0	0	0	2	0	0	1	1	1	3	0	2	1	0	0	1	0	1	0	0	0	0	2	1	0	1	0
23	*Littorina*	0	0	0	2	0	0	1	1	1	3	0	2	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0
24	*Neritrema*	0	0	0	1	0	0	1	0	1	2	0	0	?	0	0	1	0	0	0	0	0	0	1	1	0	1	?
25	*Mainwaringia*	0	0	1	1	0	0	1	1	1	3	0	2	0	0	0	0	0	0	0	0	0	0	1	1	1	0	?
26	*Liralittorina*	0	0	0	2	0	0	1	1	1	2	0	3	0	0	0	1	0	1	0	0	0	0	2	1	0	0	?
27	*Fossarilittorina*	0	0	0	2	0	0	1	1	1	1	0	3	0	0	0	1	0	1	0	0	0	0	2	1	0	0	?
28	*Nodilittorina modesta*	0	0	0	2	0	0	1	1	1	1	0	?	?	0	0	1	0	1	0	0	0	0	2	1	0	0	?
29	*Nodilittorina*	0	0	0	1	0	0	1	1	1	1	0	3	0	0	0	1	0	1	0	0	0	0	2	1	0	0	?
30	*Echinolittorina*	0	0	0	2	0	0	1	1	1	1	0	3	0	0	0	1	0	1	0	0	0	0	2	1	0	0	?
31	*Littoraria pintado*	0	0	0	2	0	0	1	1	1	1	0	3	0	0	0	1	0	1	0	0	0	0	1	1	1	0	0
32	*Littoraria*	0	0	0	1	0	0	1	1	1	1	0	2	0	0	0	1	0	0	1	0	0	0	1	1	1	0	?
33	*Palustorina*	1	0	0	2	0	0	1	1	1	1	0	2	0	0	0	1	0	0	1	0	0	0	1	1	1	0	?
34	*Lamellilitorina*	0	0	0	1	0	0	1	1	1	1	0	?	?	0	0	1	0	0	1	0	0	0	1	1	1	0	?
35	*Littorinopsis*	0	0	0	1	0	0	0	1	1	1	0	0	?	1	0	1	0	0	1	0	0	0	1	1	1	0	0
36	*Littoraria aberrans*	0	0	0	1	0	0	0	1	1	1	0	0	?	2	0	1	0	0	1	0	0	0	1	1	1	0	?

Cenchritis and the clade *Littoraria* (either of which could be the sister-group of *Nodilittorina* and *Littorina*). Reanalysis after restoration of the three other subgenera of *Laevilitorina* produced no change in the topology of the rest of the tree. Analysis of the reduced data set did not, therefore, find any alternative topologies, or shorter trees, not included in the 100 trees from the preliminary analysis. The strict consensus tree for the complete set of taxa is shown in figure 15.

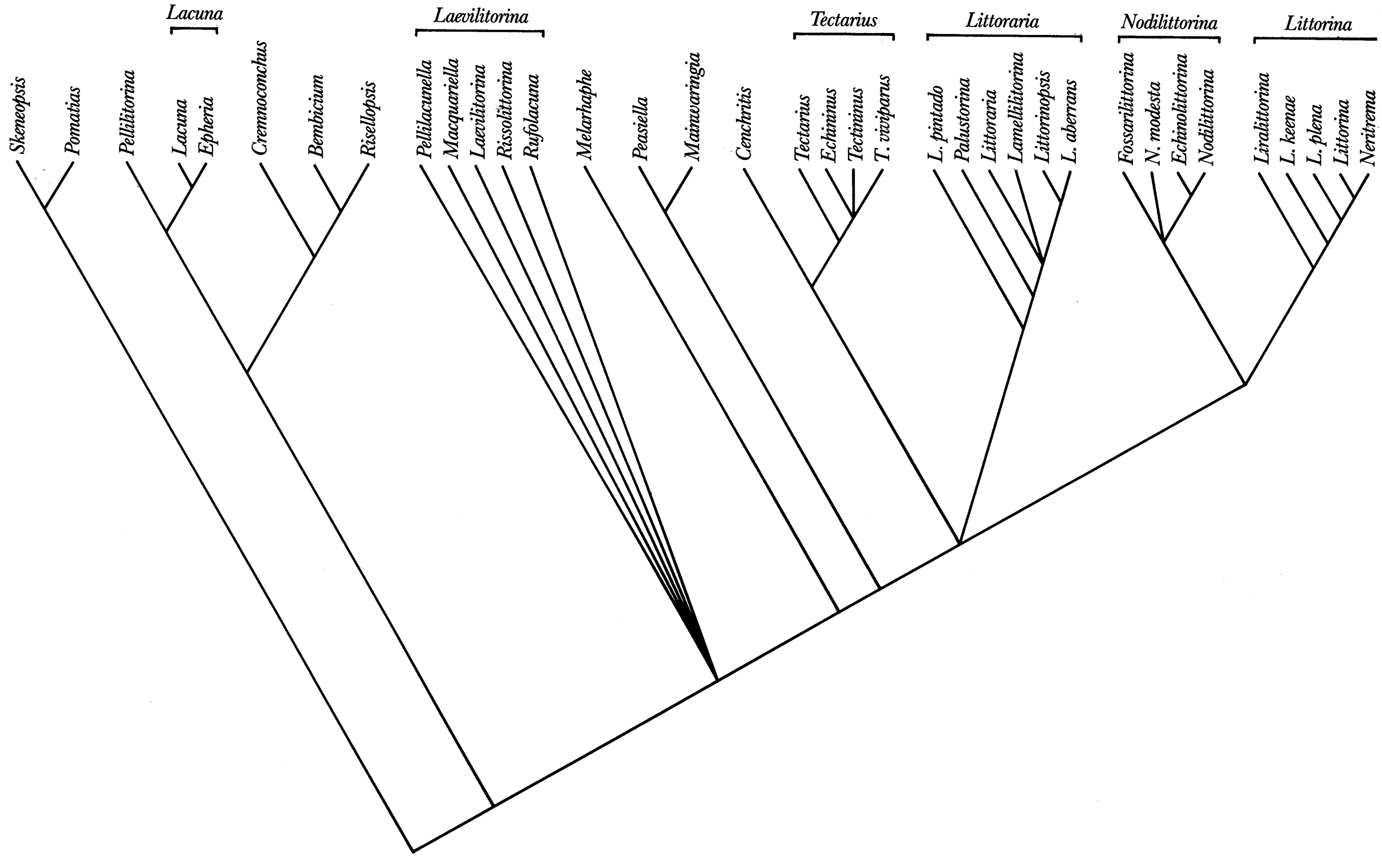

FIGURE 15. Consensus tree of all equally parsimonious cladograms derived from cladistic analysis by PAUP program of data in table 6.

Another source of ambiguity in the cladogram is the reconstruction of character states in the hypothetical ancestors (represented by the nodes of the tree). This translates into ambiguity about the definitions of clades in terms of their synapomorphies. This uncertainty arises because for a given topology there is often more than one equally parsimonious way in which character states can be placed on the tree (a process known as optimization; see Swofford & Maddison (1987) for a discussion of the alternative methods). In some cases alternative reconstructions of characters can support different tree topologies. The CSPOSS option was used to discover cases of ambiguity in character-state reconstruction, and the BLRANGE option used to search for any resulting differences in topology (Platnick 1987). No additional topologies were found by this means. The preferred character state reconstructions are discussed in the following section and shown in figure 16.

By using the Pomatiasidae or Skeneopsidae alone as the outgroup, the range of tree topologies obtained was unchanged.

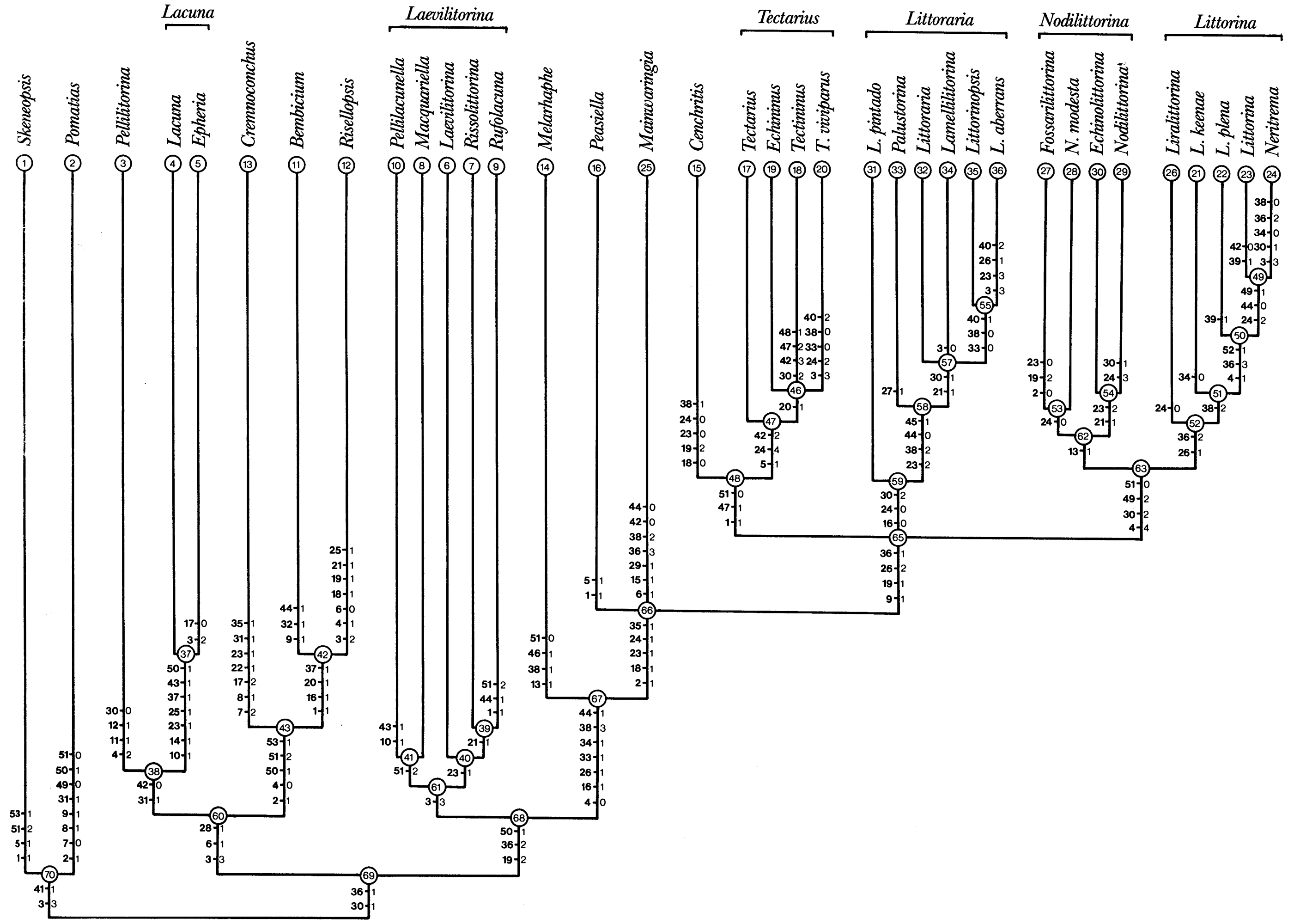

Figure 16. Cladogram of the Littorinidae showing preferred character-state reconstructions (parsimonious for all characters except 3, 24, 39 and 50). Character-state changes between the outgroup (*Skeneopsis* and *Pomatias*) and ingroup (Littorinidae) are polarized by reference to more distant outgroups. Note that position of root of ingroup plus outgroup tree is not known. Synapomorphies are indicated by character number (bold type) and character state (see table 5). Nodes and taxa are numbered arbitrarily for reference. Numbers of taxa correspond to the order of their input to the PAUP program. Consistency index = 0.408, branch length = 147 steps (for completely parsimonious character state reconstruction and excluding autapomorphic characters and autapomorphic terminal character states).

(*c*) *Discussion of the cladogram*

In the first part of this discussion (§5*c*(i)) each character is considered in turn, and the distribution of its character states on the cladogram discussed. Attention is drawn to cases of homoplasy, including parallelism, convergence and reversal in the hypothesized evolutionary sequence of character states. Alternative reconstructions of character states are evaluated. If it can be argued that some character-state reconstructions are more likely than others, it is possible to choose between some of the equally parsimonious cladograms. The topology of the cladogram showing the preferred character-state reconstructions (figure 16) therefore differs slightly from that of the consensus tree (figure 15). In cases where alternative parsimonious reconstructions were judged equally acceptable, that which minimized the *F*-value of Farris (MINF optimization) was chosen. In four cases (characters 3, 24, 39, 50) non-parsimonious reconstructions were preferred. The consistency (*c*) of each character (calculated after exclusion of terminal, autapomorphic states) is given in parentheses after the number and name of the character.

In the second part of this discussion (§5*c*(i)) the individual clades are examined and alternative topologies discussed. Clades are referred to by the numbers of their basal nodes in figure 16, and by their formal names.

(i) *Character analysis*

1. *Shell shape* ($c = 0.200$). The trochoidal shape is shared by Skeneopsidae, *Laevilitorina* (*Rufolacuna*), *Peasiella* and clades 42 and 48, suggesting independent origin in each case.

2. *Shell sculpture* ($c = 0.250$). The reconstruction of this character, showing parallel acquisition of major spiral grooves in Pomatiasidae and clades 43 and 66, implies that absence of such sculpture is plesiomorphic in Littorinidae. *Nodilittorina* (*Fossarilittorina*) shows a reversal. Although nodulose sculpture was not employed as a character in the analysis, it may be noted that the topology of the cladogram suggests that this character shows much homoplasy; either nodulose sculpture is plesiomorphic for clades 43 and 67 and has undergone reversal at least seven times in the latter, or alternatively it has originated independently in clade 43 and at least six times within clade 67.

3. *Protoconch and larva* ($c = 0.333$ for parsimonious reconstruction, $c = 0.250$ for preferred reconstruction). The most parsimonious reconstruction of this unordered character suggests that non-planktotrophy is plesiomorphic in the Littorinidae, and has been lost in clade 67 (state 1) (with subsequent reversal to state 3 in *Tectarius viviparus*, *Littoraria aberrans* and *Littorina* (*Neritrema*)) and in *Lacuna* (*Epheria*) and *Risellopsis* (both state 2). However, it has been argued (see §4 (*a*)) that the primitive state is the production of planktotrophic veligers with sculptured shells (state 1), as found in more distant outgroups. If this is so, non-planktotrophic development (state 3) has evolved independently in the outgroup, and in clades 60 and 61 (perhaps as an adaptation to a cold-water habitat, see §6*d*). This reconstruction is preferred. Interestingly, in both reconstructions the most parsimonious arrangement within clade 60 shows that the 'intermediate' development of *Lacuna* (*Epheria*), *Risellopsis* and some *Bembicium* species (state 2, with unsculptured but planktotrophic veligers) is derived from the non-planktotrophic type (state 3). This parsimony argument is supported by the morphology of the protoconch of the intermediate forms, which is similar to that of the non-planktotrophic species (see §4*a*). Reversion from non-planktotrophy to planktotrophy has hitherto been considered infrequent or impossible in gastropods (Strathmann 1978; Bouchet 1987) (see §6*d*). Character state 0 is an autapomorphy of *Littoraria* (*Lamellilitorina*), derived from state 1.

4. *Shell mineralogy and microstructure* ($c = 0.667$). The reconstruction suggests that the plesiomorphic state was an aragonitic shell with an outer spherulitic-prismatic layer (state 3). From this, shells entirely of crossed-lamellar aragonite (state 0) were developed independently in clades 43 and 67. The fine crossed-lamellar layer (state 4) is a synapomorphy of clade 63, and an outer calcitic layer (state 1) has appeared convergently in *Risellopsis* and clade 50. The shell of crossed-foliated calcite (state 2) is an autapomorphy of *Pellilitorina*.

5. *Opercular shape* ($c = 0.333$). The mesospiral operculum is a parallel development in clade 47 and *Peasiella*, and also occurs in the Skeneopsidae.

6. *Opercular ridge* ($c = 0.333$). The opercular ridge has been developed independently in *Mainwaringia* and clade 60 (with reversal in *Risellopsis*). This implies that it is unlikely to be homologous with the opercular peg of the Cingulopsoidea and Truncatelloidea, but knowledge

of the topology of the outgroup and its relationship to these superfamilies would be necessary to confirm this.

7. *Opercular calcification.* The two types of calcified opercula are autapomorphies of the Pomatiasidae and *Cremnoconchus*.

8. *Propodial groove* ($c = 0.500$). Loss of the propodial groove has occurred independently in the Pomatiasidae and *Cremnoconchus*.

9. *Longitudinal division of foot* ($c = 0.333$). Division of the foot is a synapomorphy of clade 65, which has also arisen in the Pomatiasidae and *Bembicium*. Ditaxic locomotion (a functional division of the sole) is shared by the Pomatiasidae and all Littorinidae, and parallel evolution of a morphological division is not unlikely. It is noteworthy that *Bembicium* occurs at higher levels in the eulittoral zone than most other members of clades 60 and 61, supporting the suggestion that division of the foot may be adaptive in this habitat.

10. *Opercular tentacles* ($c = 0.500$). This character shows parallelism in *Laevilitorina* (*Pellilacunella*) and clade 37. The tree topology supports the suggestion that the opercular tentacles of the Littorinidae are not homologous with those of other families.

11. *Ovipository flange.* Autapomorphy of *Pellilitorina*.

12. *Eye peduncles.* Autapomorphy of *Pellilitorina*.

13. *Colour pattern of head* ($c = 0.500$). The *Nodilittorina*-like pattern appears to have arisen independently in *Melarhaphe* and clade 62.

14. *Osphradium* ($c = 1.000$). The terminal flexure is an unreversed synapomorphy of clade 37.

15. *Hermaphroditism.* Autapomorphy of *Mainwaringia*.

16. *Prostate* ($c = 0.333$). The original premise of a closed prostate being plesiomorphic is supported by the reconstruction. Clades 67 and 42 share the apomorphic open prostate, but in clade 59 this is reversed. No functional explanation can be offered for this curious pattern.

17. *Prostate gland.* Subepithelial glandular tissue and complete absence of glandular cells are autapomorphies of *Cremnoconchus* and *Lacuna* (*Epheria*) respectively.

18. *Anterior vas deferens* ($c = 0.333$). As in the case of character 16, the open condition of this part of the pallial section of the male reproductive tract appears to be apomorphic, with independent origins in *Risellopsis* and clade 66, and reversal in *Cenchritis*.

19. *Penial vas deferens* ($c = 0.400$). This character was specified as unordered in the analysis. The most parsimonious reconstruction suggests that deep closure (state 0) is ancestral, with shallow closure (state 2) having appeared in clade 68, and complete opening (state 1) in clade 65 and *Risellopsis*. Within clade 65 superficial closure has occurred in several lines (*Cenchritis*, *Nodilittorina* (*Fossarilittorina*) and some *Littoraria* (*Littorinopsis*) species). Either state 1 or 2 could be reconstructed at nodes 48 and 65, but MINF optimization is accepted. The transition between an open groove and a superficially closed duct is probably readily accomplished in either direction, accounting for the erratic distribution of these states, although the functional implications are not understood. The direct transition from deep to shallow closure, as in the ancestry of clade 68, could perhaps have been accomplished through an intermediate open state, as found in *Risellopsis*. Parsimony arguments suggest that the entire pallial gonoduct of the male (characters 17, 18, 19) was primitively closed in the Littorinidae, and that opening of the three sections has occurred at different times in the history of the group.

20. *Opening of penial vas deferens* ($c = 0.500$). The opening has independently become subterminal in clades 42 and 46.

21. *Bifurcation of penial base* ($c = 0.250$). Bifurcation has arisen in parallel in clades 39, 54 and

57 and in *Risellopsis*. Either state could be reconstructed at nodes 53 and 62, for *Nodilittorina* (*Fossarilittorina*) and *N. modesta* were coded as unknown (because of the absence of complex penial glands, see §4*d*). The penes of these taxa are in fact not bifurcate, nor are they so in the sister group of clade 62, so it is reasonable to reconstruct state 0 for nodes 53 and 62.

22. *Penial filament.* Autapomorphy of *Cremnoconchus.*

23. *Simple penial glands* ($c = 0.250$). Scattered penial glands have appeared independently in *Cremnoconchus* and in clades 37, 40 and 66, with reversals in *Cenchritis* and *Nodilittorina* (*Fossarilittorina*). The glandular disc has appeared in clades 54 and 58, and an infolded disc is an autapomorphy of *Littoraria aberrans*. Because scattered glands are so widely distributed in the Littorinidae it could be argued that they are plesiomorphic, but this reconstruction would be two steps longer.

24. *Mamilliform penial glands* ($c = 0.571$ for parsimonious reconstruction, $c = 0.400$ for preferred reconstruction). MINF optimization proposes independent origin of mamilliform glands in clades 47, 51, 54 and the clade *Mainwaringia* plus *Peasiella*. This is considered unlikely because of the complex and closely similar structure of these glands, and the known ease with which their numbers (and even their presence) can vary within species. Instead it is proposed that mamilliform glands are a synapomorphy of clade 66, with subsequent loss in clades 53, 59, *Cenchritis* and *Littorina* (*Liralittorina*). One or two penial glands was probably the primitive state (state 1), with multiplication (state 2) in clades 47 and 49, and subsequent size differentiation (state 4) in clade 47 (with reversal to 2 in *Tectarius viviparus*) and differentiation of another kind (state 3) in *Nodilittorina* (*Nodilittorina*). This reconstruction implies that the absence of mamilliform glands in clades 60, 61 and *Melarhaphe* is primitive. Within clade 66, loss of mamilliform glands is to some extent correlated with small size and, in *Littoraria*, with the elaboration of the penial glandular disc that serves the same function.

25. *Muscular papillae* ($c = 0.500$). This character has developed in parallel in clade 37 and in *Risellopsis*. Because of the position of these taxa on the cladogram, it is unlikely that the papillae are the rudiments of mamilliform penial glands.

26. *Paraspermatic nurse cells* ($c = 0.500$). Nurse cells are present only in clade 67. The reconstruction suggests that rods were primitively absent, appeared in clade 65, and have been lost in clade 52 and in *Littoraria aberrans*.

27. *Nurse cell flagella.* Autapomorphy of *Littoraria* (*Palustorina*).

28. *Duct to seminal receptacle* ($c = 1.000$). MINF optimization reconstructs the long duct as a unique synapomorphy of clade 42. However, because the receptacle and its duct are absent in *Pellilitorina*, *Lacuna* and *Cremnoconchus*, this character could not be coded for these taxa. An alternative, equally parsimonious, reconstruction is preferred, in which the long duct is a synapomorphy of clade 60. Lengthening of the duct may have been functionally connected with subsequent loss of the receptacle (see character 31).

29. *Oviducal sperm groove.* Autapomorphy of *Mainwaringia.*

30. *Anterior bursa* ($c = 0.286$). From its absence in more distant outgroups, the anterior bursa appears to be a synapomorphy of the Littorinidae (clade 69), and primitively was in a relatively anterior position (state 1). It has been lost in *Pellilitorina*. The bursa has become relatively posterior (state 2) in *Tectarius* (*Tectininus*) and in clades 59 and 63 (of which it may be a synapomorphy), with subsequent reversal in *Nodilittorina* (*Nodilittorina*), *Littorina* (*Neritrema*) and in clade 57. The reversal in *Littorina* (*Neritrema*) may be explained by the need to separate the bursa from the enlarged jelly gland, and in clade 57 may be connected with elongation of the straight section of the pallial oviduct.

31. *Seminal receptacle* ($c = 0.333$). MINF optimization reconstructs parallel loss of the seminal receptacle (state 1) in clade 38 and *Cremnoconchus*. The receptacle is also absent in the Pomatiasidae, so an alternative is the reconstruction of state 1 at nodes 43, 60, 69 and 70. This is not acceptable, because, as mentioned in the discussion of character 28, the loss of the receptacle in clade 28 and *Cremnoconchus* was probably a consequence of lengthening of its duct in the common ancestor (node 60). The MINF reconstruction supports the homology of the seminal receptacle of littorinids with that in more distant outgroups; the alternative does not.

32. *Opening of renal oviduct*. Autapomorphy of *Bembicium*.

33. *Capsule gland* ($c = 0.333$). This is a synapomorphy of clade 67, reversed only in the ovoviviparous taxa (*Tectarius viviparus* and clade 55).

34. *Size of jelly gland* ($c = 0.333$). Reduction in size is a synapomorphy of clade 67, with reversals in *Littorina keenae* and *L.* (*Neritrema*) which produce gelatinous egg masses.

35. *Histology of albumen and capsule glands* ($c = 0.500$). The glands of the pallial oviduct have independently become subepithelial in *Cremnoconchus* and in clade 66.

36. *Coiling of egg groove* ($c = 0.429$). A coiled egg groove is a synapomorphy of the Littorinidae (as argued from more distant outgroups) and primitively there was only a single spiralled loop in the coil (state 1). A second loop (state 2) has arisen in clade 68, with reversal in clade 65. A second loop has appeared again in clade 52, and a third (state 3) in *Mainwaringia* and clade 50, with a reversal to state 2 in *Littorina* (*Neritrema*). This reconstruction for clade 50 is preferred to the MINF reconstruction of parallel evolution of state 3 in *Littorina plena* and *L.* (*Littorina*), because it is supported by a species-level cladogram of the genus (Reid 1989*a*).

37. *Loop of jelly gland* ($c = 0.500$). This has appeared independently in clades 37 and 42.

38. *Egg capsules* ($c = 0.333$). The presence of capsules is a synapomorphy of clade 67. The primitive state is unclear, because either state 1 or 3 could be reconstructed at node 67. If MINF optimization is accepted, the cupola shape (state 3) is primitive, having given rise to the pill-box type (state 1) in *Cenchritis* and *Melarhaphe*. The biconvex disc (state 2) has arisen independently in clades 51, 58 and *Mainwaringia*. Capsules have been lost in the ovoviviparous or non-planktotrophic taxa *Littorina* (*Neritrema*), *Tectarius viviparus* and clade 55. The alternative reconstruction of state 0 at the junction of clade 55 with *Littoraria* (*Lamellilitorina*) is not acceptable, because *L.* (*Lamellilitorina*) possesses a large capsule gland and is therefore oviparous. The reconstruction predicts state 2 in *Littoraria* (*Lamellilitorina*) and state 3 in *Tectarius* (*Tectarius*), *T.* (*Echininus*) and *Nodilittorina modesta*.

39. *Eggs per capsule* ($c = 1.000$ for parsimonious reconstruction, $c = 0.500$ for preferred reconstruction). This character is reconstructed by the program as a synapomorphy of clade 50, because the state cannot be specified for the type species of *Littorina* (*Neritrema*), which lacks capsules. However, a species-level cladogram of *Littorina* suggests that more than one egg per capsule may have been achieved independently in *L. plena* and the type species *L. littorea* (Reid 1989*a*).

40. *Ovoviviparity* ($c = 0.500$). Retention of veligers in the mantle cavity has appeared in clade 55, proceeding to release of crawling young in *Littoraria aberrans* and, independently, in *Tectarius viviparus*.

41. *Littorinid notch in lateral* ($c = 1.000$). The polarity of this character is uncertain; absence of the notch may be a synapomorphy of the outgroup (see §4*h*).

42. *Rachidian tooth proportions* ($c = 0.500$). The reconstruction suggests that the plesiomorphic state is the normal shape (state 1), with parallel evolution of a square rachidian (state 0) in clade 38, *Mainwaringia* and *Littorina* (*Littorina*). A narrow rachidian (state 2) is a unique

synapomorphy of clade 47, and a reduced rachidian (state 3) is an autapomorphy of *Tectarius* (*Tectininus*).

43. *Rachidian tooth outline* ($c = 0.500$). A hexagonal outline has appeared independently in *Laevilitorina* (*Pellilacunella*) and in clade 37.

44. *Rachidian tooth cusps* ($c = 0.167$). Reduction in the number of cusps is a synapomorphy of clade 67, with a parallel reduction in *Bembicium* and *Laevilitorina* (*Rufolacuna*). The reversals in clades 49, 58 and *Mainwaringia* are correlated with a habitat on wood and macroalgae.

45. *Rachidian tooth hooded* ($c = 1.000$). This is a unique synapomorphy of clade 58.

46. *Rachidian base plate*. Autapomorphy of *Melarhaphe*.

47. *Lateral tooth cusps* ($c = 1.000$). Cusp reduction (state 1) has occurred uniquely in clade 48, with further reduction (state 2) being an autapomorphy of *Tectarius* (*Tectininus*).

48. *Inner marginal tooth cusps*. Autapomorphy of *Tectarius* (*Tectininus*).

49. *Outer marginal tooth shape* ($c = 0.500$). Greatly widened outer marginal teeth (state 0) are an autapomorphy of the Pomatiasidae. Within the Littorinidae the *Nodilittorina*-type tooth (state 2) is a synapomorphy of clade 63, with a reversal to the plesiomorphic normal type (state 1) in clade 49.

50. *Jaws* ($c = 0.500$ for parsimonious reconstruction, $c = 0.250$ for preferred reconstruction). The MINF optimization suggests parallel acquisition of jaws in the Skeneopsidae and *Pellilitorina*. However, from their frequent presence in more distant outgroups, jaws are likely to be plesiomorphic in the ingroup plus outgroup, suggesting that parallel loss may have occurred in the Pomatiasidae and three clades of Littorinidae (37, 43, 68), a non-parsimonious solution.

51. *Position of salivary glands* ($c = 0.250$). The most parsimonious reconstruction suggests that constricted glands (state 1) are plesiomorphic in the ingroup plus outgroup, with parallel acquisition of anterior glands (state 2) in the Skeneopsidae, *Laevilitorina* (*Rufolacuna*), and clades 41 and 43. Glands have become entirely posterior (state 0) in the Pomatiasidae and (according to the MINF optimization) in *Melarhaphe* and in clades 48 and 63 (of which this may be a synapomorphy). In an alternative reconstruction, posterior glands are primitive in clade 67, with reversal to state 0 in clade 59, *Mainwaringia* and *Peasiella*. The former is accepted. As would be expected on morphological grounds, the change from anterior to constricted or posterior glands does not appear to have occurred. Constricted glands of the proposed primitive type do indeed occur in the Eatoniellidae and some Cerithioidea (see §4*i*).

52. *Size of salivary glands* ($c = 1.000$). Enlarged salivary glands are a unique synapomorphy of clade 50.

53. *Pleuro-suboesophageal connective* ($c = 0.500$). A short connective is a synapomorphy of clade 43 (although the state in *Risellopsis* is not known), but is also present in the Skeneopsidae.

(ii) *Clade analysis*

In this section the principal clades are discussed (those recognized at generic level or above). In evaluating their respective synapomorphies, the character-state reconstructions advocated in §5*c*(i) are employed. For characters 3, 24 and 50 the reconstructions are not those of maximum parsimony. Each clade (numbered as in figure 16) is followed by its name or included taxa and by a list of its synapomorphies by character number and, in parentheses, character state (table 5). Synapomorphies which are both unique and unreversed are in bold type. The appropriate taxonomic rank of clades is discussed, but owes more to convention and to subjective assessment of 'degree of difference' than to strict application of the rules of phylogenetic classification (Wiley 1981). The correspondence between the cladogram and the formal classification of the family is discussed in §6*b*.

Clade 69: Littorinidae [30 (1), **36 (1)**]. The family is defined by two synapomorphies, the anterior bursa and coiled egg groove, of which only the latter is unreversed.

Clade 60: Lacuninae [3 (3), 6 (1), **28 (1)**]. The monophyly of this clade is supported by the synapomorphies of the opercular ridge and long duct to the seminal receptacle (leading to its eventual loss, see §5*c*(i)). Non-planktotrophic development is a common response to cold-water conditions, which is believed to have arisen in parallel in other clades. The topology of this clade is constant and completely resolved in all the equally parsimonious cladograms. It is not considered sufficiently distinct from other littorinids to warrant familial status.

Clade 38: Pellilitorina, Lacuna [31 (1), 42 (0)]. The loss of the seminal receptacle is remarkable, but has occurred in parallel in *Cremnoconchus*.

Pellilitorina [**4 (2), 11 (1), 12 (1)**, 30 (0)]. Loss of the bursa has also occurred in some *Peasiella* species.

Clade 37: Lacuna [10 (1), **14 (1)**, 23 (1), 25 (1), 37 (1), 43 (1), 50 (1)]. This genus is well defined by seven synapomorphies, but only two characters distinguish the two subgenera.

Clade 43: Cremnoconchus, Bembicium, Risellopsis [2 (1), 4 (0), 50 (1), 51 (2), 53 (1)]. Despite the unusual freshwater habitat and four autapomorphies of *Cremnoconchus*, its inclusion in this clade is strongly supported by characters 4, 51 and 53. It does, however, share apomorphic states of characters 8 and 31 with the Pomatiasidae. Loss of the propodial groove is unique to *Cremnoconchus* and the Pomatiasidae and, together with the analogous calcification of the operculum, could be associated with terrestrial and freshwater life in these taxa.

Cremnoconchus [**7 (2), 8 (1), 17 (2), 22 (1)**, 23 (1), 31 (1), 35 (1)]

Clade 42: Bembicium, Risellopsis [1 (1), 16 (1), 20 (1), 37 (1)]

Bembicium [9 (1), **32 (1)**, 44 (1)]

Risellopsis [3 (2), 4 (1), 6 (0), 18 (1), 19 (1), 21 (1), 25 (1)] The entirely open male reproductive tract is anomalous, but placement in clade 60 is not in doubt.

Clade 68: Laevilitorininae, Littorininae [19 (2), 36 (2), 50 (1)]. The derived state of the penial sperm duct is important (although an open duct occurs also in *Risellopsis*), but the other synapomorphies of this clade are weak. Uncertainty about the topology of clade 66 makes the reconstruction of character 36 doubtful. Jaws are absent in two other clades. Further characters are required to confirm the monophyly of this clade.

Clade 61: Laevilitorininae, *Laevilitorina* [3 (3)]. Among the equally parsimonious cladograms there are numerous topologies, all paraphyletic, for the five subgenera of *Laevilitorina*. The monophyly of the genus is supported by a non-parsimonious reconstruction of character 3 and, depending on the topology of clade 66, might also be supported by character 36. The spiral pattern of the pallial oviduct is indeed characteristic (similar only to that of *Peasiella*, which is distantly related; see §4*f*). Four of the component subgenera have been treated as full genera by previous authors (table 1), but few anatomical characters separate them. The recognition of this genus as a subfamily is appropriate because it is desirable to retain the subfamily Littorininae for clade 67 alone, which is clearly defined by important synapomorphies and corresponds with a major ecological shift (see §6*d*).

Clade 67: Littorininae [4 (0), 16 (1), **26 (1)**, 33 (1), 34 (1), 38 (3), 44 (1)]. All the alternative cladograms support the coherence of this subfamilial clade, which is clearly defined by its unique synapomorphy of sperm nurse cells, probably correlated with the largely open pallial reproductive tract of the male. The presence of the capsule gland and egg capsules are also unique, although reversed in ovoviviparous species. Members of this clade are also distinguished by their shift to a supralittoral habitat and occurrence in warm and tropical waters (see §6*d*).

Melarhaphe [13 (1), 38 (1), **46 (1)**, 51 (0)]. The epithelial structure of the oviducal glands is a plesiomorphic character strongly supporting the basal position of *Melarhaphe* in the Littorininae.

Clade 66: Peasiella, Mainwaringia, Cenchritis, Tectarius, Littoraria, Nodilittorina, Littorina [2 (1), 18 (1), 23 (1), 24 (1), 35 (1)]. The histology of the oviducal glands is the most important synapomorphy of this clade, being shared only with *Cremnoconchus*. The reconstruction of mamilliform penial glands as a synapomorphy here is non-parsimonious, but justified by the probable homology of the glands throughout the clade. Of the other synapomorphies listed, only that of shell sculpture is independent of the internal topology of the clade. Relationships among the component taxa are uncertain. In all the equally parsimonious cladograms *Peasiella* and *Mainwaringia* appear as one clade, but because its only synapomorphy is the presence of mamilliform penial glands, this topology reverts to a trichotomy at node 66 if the non-parsimonious reconstruction of character 24 is accepted.

Mainwaringia is an anomalous taxon, showing a peculiar mixture of apomorphic and plesiomorphic states. It is excluded from clade 65 by plesiomorphies in characters 9, 19 and 26, and from clade 52 by additional plesiomorphies in characters 4, 30 and 51. However, in characters 26, 36, 38, 44 and 49 it shows states that are apomorphic within clade 52. Other characters that support placement of *Mainwaringia* in the genus *Littorina*, although not included in the analysis, include shell shape (similar to *Littorina plena*; figure 2), shape of the paraspermatic nurse cells (see §4*e*), medial position of the bursa (see §4*f*) and double rim of the biconvex egg capsule (Reid 1989*a*). In a species-level cladogram of *Littorina*, *Mainwaringia* would occupy a position between *L. plena* and *L. brevicula* (Reid 1989*a*), but if it is forced into this position in the family cladogram (figures 16 and 17), four more steps are added to the total branch length (151 steps). The geographical distribution of *Mainwaringia* is consistent with placement in *Littorina* (Reid 1989*b*). Some of the characters that appear to exclude *Mainwaringia* from *Littorina* could be associated with its relatively small size, unusual muddy and brackish habitat, and the fact that it would be the only *Littorina* with an entirely tropical distribution (which could have resulted in loss of a calcitic layer, see §4*a* and Taylor & Reid (1989)). In summary, inclusion of *Mainwaringia* within *Littorina* is considered to be the more probable of the alternatives, because of the subjective weight given to characters of the nurse cells, oviduct, egg capsules and radula. Nevertheless, until more evidence is available *Mainwaringia* is retained at generic rank. If inclusion of *Mainwaringia* in clade 52 is accepted, various topologies become possible for *Peasiella*, *Cenchritis*, *Tectarius*, *Littoraria* and clade 63; in a consensus tree these clades would make a polychotomy between nodes 63 and 67 (figure 17).

The affinities of *Peasiella* are also uncertain. Synapomorphies in characters 1 and 5 support a sister-group relationship with clade 47. However, plesiomorphies in 9, 19, 26 and 36 dictate its basal position in clade 66. Its similarities to *Mainwaringia* are believed to be plesiomorphies, not indicative of close relationship.

Clade 65: Cenchritis, Tectarius, Littoraria, Nodilittorina, Littorina [9 (1), 19 (1), 26 (2), 36 (1)]. The synapomorphy of paraspermatic nurse cells with rods is an important one (reversed in *Littorina* and *Littoraria aberrans*). Only two characters have a bearing on the trichotomy at node 65: character 30 supports the monophyly of clades 59 and 63, character 51 that of clades

48 and 63. Both characters show considerable homoplasy on the cladogram, and do not permit clear choice between these alternative topologies.

Clade 48: Cenchritis, Tectarius [1 (1), **47 (1)**, 51 (0)]. Only character 47 supports the monophyly of this clade.

Cenchritis [18 (0), 19 (2), 23 (0), 24 (0), 38 (1)]. All the characters listed as apomorphies would be plesiomorphic at the level of node 67. Consequently, *Cenchritis* appears in a basal position in clade 66 in some of the alternative trees when *Mainwaringia* is forced into clade 52. This uncertainty, and differences in eight characters, preclude placement of *Cenchritis* in the genus *Tectarius*.

Clade 47: Tectarius [5 (1), 24 (4), **42 (2)**]. The shape of the rachidian tooth is a good synapomorphy, and shell shape and sculpture are similar throughout the genus. Of the four subgenera, two are differentiated by several characters, but in *Tectininus* these are mostly modifications of the radula, and in *Tectarius viviparus* they are largely concerned with ovoviviparous reproduction. Node 46 is an unresolved trichotomy. Traditionally, *Echininus* and *Tectarius* have been accorded generic or subfamilial rank, on the basis of the more tightly wound operculum of the former. This is regarded as a minor difference, as is character 20 which separates nodes 46 and 47.

Clade 59: Littoraria [16 (0), 24 (0), 30 (2)]. Although none of the synapomorphies of this genus is unique, together they make a well-defined clade. Within clade 59, clade 58 is defined by four synapomorphies, and subgenera *Littoraria*, *Lamellilitorina* and clade 55 form an unresolved trichotomy, because of the reconstruction of character 38.

Clade 63: Nodilittorina, Littorina [**4 (4)**, 30 (2), 49 (2), 51 (0)]. The shell microstructure and shape of the outer marginal teeth clearly define this clade. In characters of the oviduct, egg capsule, radula and shell, *Littorina* (*Liralittorina*) and, to a lesser extent, *Littorina keenae*, are striking intermediates, showing how more typical *Littorina* species may have evolved from a *Nodilittorina*-like ancestor.

Clade 62: Nodilittorina [13 (1)]. Coloration of the head is a weak synapomorphy, shared with *Melarhaphe* and some *Littorina* (*Neritrema*) species. Other similarities between members of the genus, which made them easy to recognize before the analysis, have proved to be symplesiomorphies (characters 26, 38, 49). Other features such as shell coloration and a spiral egg groove with less than 1.5 whorls support the recognition of the clade. Subgenera *Nodilittorina* and *Echinolittorina* (clade 54) are the typical members of the genus (sharing a bifurcate penis and penial glandular disc), and, if the parsimonious (but improbable) reconstruction of character 24 is allowed, form an unresolved trichotomy with *Fossarilittorina* and *Nodilittorina modesta*. Although *N. modesta* differs from *N.* (*F.*) *meleagris* in three character states, it has been included in the same subgenus in the proposed classification, awaiting further information on relationships within the genus *Nodilittorina*.

Clade 52: Littorina [26 (1), 36 (2)]. The nurse cells without rods and coiling of the oviduct support the integrity of this clade. The possibility of inclusion of *Mainwaringia* in this clade has been discussed above.

6. Discussion and conclusions

(*a*) *Relationships of the Littorinidae with other families*

In his review of the phylogeny of the littorinoidean–truncatelloidean radiation, Ponder (1988) showed that existing character sets are inadequate to resolve clearly the relationships of the superfamilies Cingulopsoidea, Littorinoidea and Truncatelloidea, and even to demonstrate their monophyly unequivocally. One possibility is that the Cingulopsoidea are a paraphyletic basal group, from a member of which the other two superfamilies (both monophyletic and sharing a common ancestor) have been derived (Ponder 1988, figure 7).

Only one strong character supports the monophyly of the Littorinoidea, the penis with pedal innervation. The pedal and cephalic penes of the Truncatelloidea are believed to have evolved independently from an aphallate ancestor (see §4*d*). Other characters common to the littorinoidean families are a closed pallial and penial vas deferens, loss of neck lobes and absence of opercular tentacles, but these characters are not unique and often not constant within the superfamily.

Relationships within the Littorinoidea are also uncertain. The most probable sister-group of the Littorinidae is the Pomatiasidae, because the two families share the synapomorphies of ditaxic pedal waves and assumed loss of the internal chitinous layer of the shell. However, the Pomatiasidae share with the Skeneopsidae the synapomorphies of short dorsal folds in the anterior oesophagus and loss of the oesophageal gland. The Littorinidae and Skeneopsidae show a synapomorphy in the loss of the crystalline style and perhaps in the anterior position of the salivary glands of primitive littorinids. In some of the alternative phylogenies presented by Ponder (1988) the Skeneopsidae clustered with the Truncatelloidea, because of the anterior salivary glands, inner chitinous layer of the shell and concentrated nervous system. One relationship within the Littorinoidea that is firmly established is that between the Pomatiasidae and Annulariidae. Arguments for the maintenance of separate familial status have been summarized by Thompson (1978), but in view of the diversity of the Littorinidae reviewed herein, the only character of significance at the family level was the supposed difference in penial innervation. New information on the Pomatiasidae has diminished this difference (see §4*d*), and the Annulariinae are here considered a subfamily of the Pomatiasidae.

The systematic position of the Aciculidae remains uncertain. They have been variously classified in the Truncatelloidea or Littorinoidea, but Ponder (1988) advocated their removal to the Cyclophoroidea (Architaenioglossa) (see §4*j*).

(*b*) *Phylogeny and classification of the Littorinidae*

The cladistic analysis presented here supports the monophyly of the Littorinidae, identifying the coiled egg groove and anterior bursa of the pallial oviduct as synapomorphies defining the family (the former being unreversed). Previous definitions have relied heavily on features of the 'littorinid' radula, none of which is unique, and among anatomists there was only a vague concept of a group sharing many characters with truncatelloideans and lacking the specializations of the 'higher mesogastropods'. The best summary of the results of the phylogenetic analysis, with generic and subfamilial groupings, is shown in figure 17.

Several authors have recommended that the Lacunidae should be united with the Littorinidae (Ponder 1976; Arnaud & Bandel 1978; Reid 1988), having assumed that *Lacuna* and the Antarctic genera that resemble it are primitive littorinids. Reid (1988) discussed the

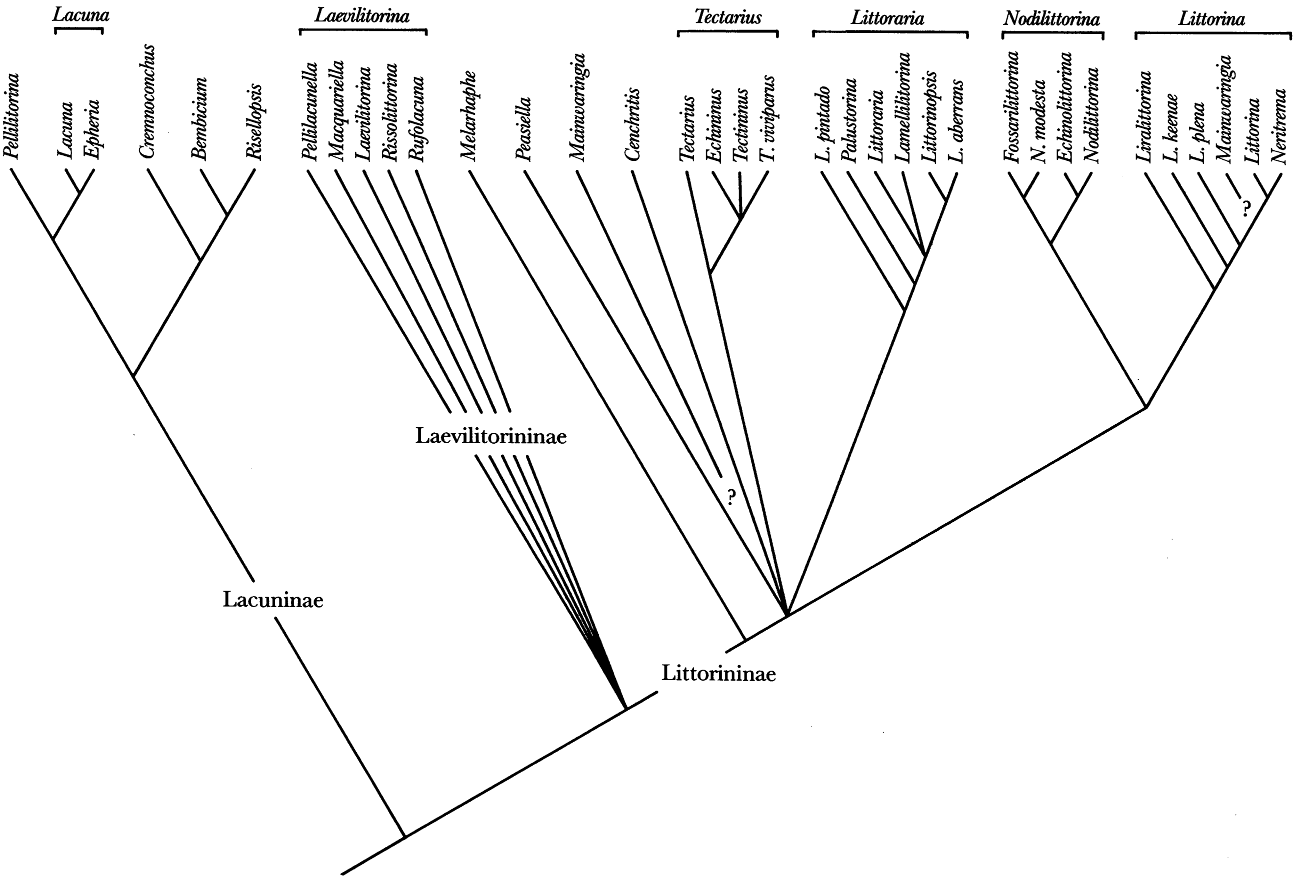

FIGURE 17. Summary of the results of the phylogenetic analysis of the Littorinidae, showing subfamilial groupings. See §5*c*(ii) for discussion of uncertain position of *Mainwaringia*.

limited anatomical evidence then available for the relationships among four littorinid groups believed to be of possible subfamilial status (lacunines, bembiciines, littorinines, *Cremnoconchus*). The phylogeny of these groups is now clarified. The cladogram supports the monophyly of both the Lacuninae and the Littorininae, but separate familial status for the former is not desirable, because of the intermediate position of *Laevilitorina*. The recognition of the subfamilies Tectariinae and Echinininae (Rosewater 1972) was based on characters of the shell and operculum, and is not supported by the anatomical evidence.

The only previous attempt at a cladistic analysis of the Littorinidae is that of Reid (1986*a*). This employed 11 characters for the analysis of 10 taxa, and was consequently poorly resolved. The presence of paraspermatic nurse cells was correctly assessed as an important synapomorphy of the group here defined as the Littorininae, but within this clade there was little resemblance to the topology given here. The purpose of this preliminary analysis was to identify an outgroup for a species-level cladogram of *Littoraria*. *Nodilittorina* was chosen, on the basis of the supposed synapomorphy of the penial glandular disc, but the present analysis indicates parallel evolution of this character in the two genera. Nevertheless, the relationships among the subgenera of *Littoraria* have been confirmed.

Several studies have compared allozyme frequencies in littorinid species as a means of estimating genetic difference, but so far only a few species have been examined. Most of the results are consistent with the phylogenetic hypothesis presented here. Jones (1972) examined variation of two enzymes and myoglobin in 12 species from Panama. These were classified in five subgenera of *Littorina* (following Rosewater (1970)) and the results failed to support the implied relationships. Following the classification presented here, it can be seen that two genera were represented, namely *Nodilittorina* and *Littoraria*. The dendrogram based on malate dehydrogenase clearly discriminates the two groups, with the possible exception of '*Littorina penicillata*' (the identity of the species thus identified is uncertain). Janson (1985) compared the genetic identity between '*Littorina*' *angulifera* and three species of the '*Littorina ziczac* species-complex', and found it to be at the lower extreme of the expected range for congeneric species. This is not surprising if they are classified according to the present scheme, in the genera *Littoraria* and *Nodilittorina* respectively. In electrophoretic comparisons of seven northern Atlantic species (Warmoes 1986; Ward 1989) '*Littorina*' *neritoides* has been found to show the greatest difference from the rest, whereas *L. littorea* was less distinct, and the remainder were similar. This is precisely the relationship that would be predicted from the cladogram presented here, and is reflected in the classification of the species as *Melarhaphe*, *Littorina* (*Littorina*) and *L.* (*Neritrema*) respectively.

A cladogram can be converted into a hierarchical Linnaean classification that exactly reproduces the hypothesized phylogenetic relationships (see, for example, Wiley 1981). However, unless the cladogram is markedly asymmetrical the resulting classification is liable to be cumbersome, requiring many new names and the use of non-mandatory taxonomic ranks. The character set presently available for the Littorinidae is insufficient to give a single unambiguous topology for the cladogram, and addition of new characters can be expected to improve the resolution. For these reasons the classification presented here does not exactly reflect a particular branching pattern. It is consistent with the phylogenetic hypothesis (figure 17) in that each subfamily and genus is believed to be monophyletic (but see §5*c*(ii) for a discussion of the status of *Mainwaringia*). Some subgenera are known to be paraphyletic, as shown by cladograms at the species level (Reid 1986*a*, 1989*a*). Decisions as to the generic or subgeneric status of taxa have been made with the two aims of reflecting 'degree of difference', as subjectively assessed, and of preserving taxa in their accustomed uses as far as possible (see §5*c*(ii)).

The new classification is summarized in table 2. These generic concepts agree quite closely with those of Bandel & Kadolsky (1982) and Reid (1986*a*) (although fewer full genera are accepted), but differ from those of earlier authors (table 1). Taxonomic diagnoses are given in Appendix 1, where one new subfamily and four new subgenera are described. The new subgenera are all monotypic, and were considered necessary to indicate noteworthy differences from congeners, of a magnitude recognized elsewhere in the family at subgeneric level. An annotated list of the 173 extant species, complete at the present state of knowledge, is included in Appendix 1.

(*c*) *Fossil record and historical biogeography*

The fossil record is a potential source of corroborative evidence for a cladistic phylogeny based on extant taxa. In practice the record is rarely sufficiently complete to provide evidence of relative apomorphy of characters, and can only be used to estimate a timescale for the phylogenetic tree. The first appearance of a synapomorphic character gives a minimum age for the origin of the clade it defines.

Unfortunately, the fossil record of the Littorinidae provides little information, for two reasons. Firstly littorinids commonly inhabit hard substrates in intertidal or shallow subtidal areas, and gastropod assemblages from such habitats are rarely preserved as fossils. The fossil record is therefore very incomplete. It is also biased towards those genera that occur in sheltered embayments, in or near to depositional environments. Thus the genus *Littoraria*, of which most Recent species inhabit mangrove forests, has the most extensive fossil record. *Littorina* and *Peasiella* are also relatively frequent as fossils, but genera from the high intertidal of exposed rocky shores, such as *Nodilittorina* and *Tectarius*, are extremely rare (Oyama 1953). The second reason for the poor fossil record of littorinids is the common difficulty of making generic assignments, even for Recent specimens, on the basis of shells alone. Consequently lineages may be difficult to trace even if specimens are available. The origin of the family itself is obscured by the resemblance of the shells to those of other groups, such as the Naticoidea and Ampullarioidea (= Viviparoidea (Ponder & Warén 1988)).

The oldest fossil that could be a member of the Littorinidae is *Lemniscolittorina berryi*, from the Upper Campanian of the late Cretaceous of Mississippi and Tennessee (Sohl 1960). However, the pustulose sculpture and sinuous form of the growth lines are unlike those of any modern littorinids and the familial assignment is therefore doubtful. An unidentified *Littorina* species has been recorded from a deposit of probable Palaeocene age in Baja California (Woods & Saul 1986). This material has not yet been examined, but if it is indeed a member of the derived genus *Littorina* the origin of the Littorinidae must have been considerably earlier, despite the absence of unequivocal fossils. For comparison, the earliest members of the Rissoidae are known from the Middle Jurassic, and the more derived members of the Truncatelloidea probably radiated in the Cretaceous (Ponder 1985*a*, 1988). The earliest records of littorinid genera are listed in table 7.

Even without the support of an extensive fossil record, a cladogram is a source of hypotheses about historical biogeography (see, for example, Wiley 1981). In comparing the cladogram of the Littorinidae (figures 16, 17) with modern distributions (see Appendix 1), it can be seen that members of the Lacuninae and Laevilitorininae all share a southern temperate or antarctic distribution, with the exceptions of *Lacuna* from the equivalent zone in the Northern Hemisphere and *Cremnoconchus* from India. One *Bembicium* species reaches the tropics in northern Queensland (Reid 1988). On the basis of the predominantly Southern Hemisphere distribution of the Eatoniellidae and Cingulopsidae, Ponder (1988) has proposed a southern, cool-water origin for the common ancestors of the Cingulopsoidea, Littorinoidea and Truncatelloidea. If primitive taxa, with a high proportion of plesiomorphic characters, are more likely to be found near the centre of origin of a group (a dispersalist view; see, for example, Brundin (1981)), then the distribution of the Lacuninae and Laevilitorininae could be regarded as supporting a southern temperate origin of the Littorinidae as a whole. In contrast, the Littorininae are a largely tropical and subtropical group (an exception is *Littorina*, discussed below), and it is tentatively suggested that this clade diversified in the tropical Tethys Ocean, perhaps in the early Cretaceous (see Howarth (1981) for summary of Mesozoic palaeogeography). It is notable that the primitive littorinines *Melarhaphe* and *Cenchritis*, as well as the more primitive subgenera of *Nodilittorina* and *Littorina*, occur in the Atlantic, as if this were a relict area. The fossil record and biogeography of each of the littorinid genera will now be considered in turn.

The Lacuninae and Laevilitorininae have a poor representation in the fossil record. The Antarctic genera *Laevilitorina* and *Pellilitorina* are not known as fossils, whereas *Risellopsis*,

TABLE 7. EXAMPLES OF FOSSIL LITTORINIDAE, TO SHOW EARLIEST OCCURRENCES AND GEOGRAPHICAL RANGES OF GENERA

(? Indicates doubtful generic or familial assignment.)

genus	species	locality	formation or stage	epoch	approx. age (Ma)	reference
?*Lemniscolittorina*	*berryi* (Wade, 1926)	Mississippi; Tennessee	Ripley Form.	U. Cretaceous	75	Sohl (1960)
Lacuna	*carpenteri* Anderson & Martin, 1914	Kern R., California		L. Miocene	22	Anderson & Martin (1914)
	japonica Masuda, 1966	Noto Penin., Japan	Higashi–Innai Form.	L. Miocene	22	Masuda (1966)
	intermedia Makiyama, 1927	Totomi, Japan		Pliocene	2–5	Makiyama (1927)
	crassior (Montagu, 1803)	E. England	Icenian Crag	Pleistocene	1	Harmer (1920–5)
	Recent species	California		U. Pliocene–Pleistocene	3	Grant & Gale (1931)
Bembicium	*altum* (Tate, 1894)	Victoria	Janjukian	U. Oligocene	25	Reid (1988)
Risellopsis	*varia* (Hutton, 1873)	Wanganui, New Zealand		Pleistocene	0.3	Reid (1988)
Melarhaphe	*mausseneti* (Cossmann, 1907)	Paris	Thanetian	U. Palaeocene	55	D. Kadolsky, personal communication
	obtusangula (Sandberger, 1859)	Waldböckelheim	Rupelian	M. Oligocene	35	Kadolsky (1973)
	sacyi (Cossmann & Peyrot, 1919)	Aquitaine	Aquitanian	L. Miocene	22	Cossmann & Peyrot (1919)
	ligeriana (Kadolsky, 1973)	Loire; Banat	Pontilevian; Tortonian	U. Miocene	8	Kadolsky (1973)

Peasiella	*minuta* (Deshayes, 1824)	Loire	Lutetian	M. Eocene	45	D.G.R., personal observation
	cf. *roepstorffiana* (Nevill, 1885)	Gore, New Zealand	Duntroonian	U. Oligocene	28	D.G.R., personal observation
Tectarius	*elegans* (Faujas, 1817)	Aquitaine	Stampian	U. Oligocene	30	Lozouet (1986)
	?*rehderi* Ladd, 1966	Bikini Atoll		L. Miocene	22	Ladd (1966)
Littoraria	*densestriata* (Deshayes, 1861)	Paris	Cuisian (U. Ypresian)	L. Eocene	50	Cossmann & Pissarro (1907–13)
	tricostalis (Deshayes, 1833)	Paris	Lutetian	M. Eocene	45	Cossmann & Pissarro (1907–13)
	subangulata (Deshayes, 1861)	Paris	Bartonian	M. Eocene	40	Cossmann & Pissarro (1907–13)
	cf. *angulifera* (Lamarck, 1822)	Panama	Culebra Form.	L. Miocene	22	Woodring (1957)
	alberti (Dujardin, 1837)	Loire	Tortonian	U. Miocene	8	Glibert (1949)
	sheaferi (Olsson, 1967)	Florida	Pinecrest Beds	Pliocene	2–5	Olsson (1967)
Nodilittorina	*kostejanus* (Boettger, 1901)	Banat		M. Miocene	15	Zilch (1934)
	iwakiana (Nomura & Hatai, 1936)	N. Honshu	Tanagura Beds	M. Miocene	15	Nomura & Hatai (1936)
Littorina	?sp.	Baja California	Sepultura Form.	U. Palaeocene	55	Woods & Saul (1986)
	?*mountsoloensis* Weaver & Palmer, 1922	Washington State	Cowlitz Form.	U. Eocene	40	Weaver (1942)
	sookensis Clark & Arnold, 1923	Vancouver I.	Sooke Form.	L. Miocene	22	Weaver (1942)
	petricola 'Dall' Arnold, 1908	Oregon	Empire Form.	U. Miocene–L. Pliocene	5–10	Weaver (1942)
	littorea (Linnaeus, 1758)	E. England	Red Crag	U. Pliocene	2	Harmer (1920–5)

restricted to New Zealand, is recorded only as a single Pleistocene occurrence (Reid 1988). *Bembicium* has a more extensive fossil record, perhaps because of the opportunities for preservation in its habitat on sheltered shores and mudflats. Although presently restricted to Australia, fossils occur also in New Zealand, and the earliest are from the Upper Oligocene (Reid 1988).

Recent species of the genus *Lacuna* occur in the northern Pacific, northern Atlantic and Arctic Oceans, in contrast to its sister-group *Pellilitorina* with a circum-Antarctic distribution. Many Cainozoic fossils, especially from the Palaeogene of northwestern Europe, have been assigned to *Lacuna* (see, for example, Cossmann & Pissarro 1907–13; Gougerot & le Renard 1982), or other genera such as *Cirsope* and *Medoriopsis*, which have been included in the Lacunidae (Wenz 1939; Kadolsky 1973). The affinities of these fossils are uncertain. The frequent spiral sculpture and occurrence in warm-water assemblages militates against close relationship with *Lacuna*. In fact, it is considered unlikely that these forms are members of the Littorinidae, because of the development of a more or less conspicuous angulation or canal at the anterior edge of the peristome, which is not found in any modern littorinids. Lozouet (1986) has made the suggestion that *Cirsope* is a member of the Elachisinidae (Truncatelloidea, see Ponder (1985*b*)), and that *Medoriopsis* resembles certain Trichotropidae (Calyptraeoidea). Allowing that these fossils are not *Lacuna*, the earliest probable records of the genus are *L. carpenteri* from California (Anderson & Martin 1914) and *L. japonica* from Japan (Masuda 1966), both of Lower Miocene age. Bipolar distributions, such as that of the clade comprising *Lacuna* and *Pellilitorina*, can be explained in terms of either vicariance or dispersal (see, for example, Crame 1986; Briggs 1987). A vicariant explanation would require the disjunction of a formerly continuous distribution or extinction of a once cosmopolitan ancestor in the intervening temperate and tropical regions. There is, however, no evidence of this from the meagre fossil record. The alternative dispersalist view is that migration may have occurred between the polar regions, perhaps in deep, cool water ('isothermal submergence'). This is possible, because *Lacuna* and *Pellilitorina* extend to greater depths than most other littorinids (see §6*d*). In the early Cainozoic, latitudinal temperature gradients were less pronounced, and evidence from foraminiferan distributions suggests that in the eastern Pacific either the thermocline was shallower or the surface waters cooler than in the western part (Kennett *et al.* 1985). It is possible, therefore, that *Lacuna* dispersed northwards in relatively deep water along the west coast of South America, before the steepening of temperature gradients during the Miocene. *Lacuna* may have reached the Atlantic relatively recently, migrating across the Arctic through the Labrador Sea in the late Pliocene, as in the case of *Littorina*, discussed later.

The freshwater littorinid *Cremnoconchus* has no fossil record, and is presently restricted to western India. The sister-group of *Cremnoconchus* consists of *Bembicium* and *Risellopsis*, and it is possible that it shares with them an origin in the Southern Hemisphere and has been carried northwards by the movement of the Indian plate since the Lower Cretaceous (see Davis (1979) for the similar case of the Pomatiopsidae).

Shells of the genus *Melarhaphe* are distinguished by their rounded aperture and lack of spiral grooves, but species of *Nodilittorina* and some truncatelloideans can be similar, so that identification of fossils is doubtful. The fossil history of this, the most primitive of the littorinine genera, may extend back to the Middle Oligocene in Europe (Kadolsky 1973) or even to the Upper Palaeocene (D. Kadolsky, personal communication). The only extant species, *M. neritoides*, is found in the temperate waters of the northeastern Atlantic and Mediterranean.

The molluscan assemblages with which the fossil species occur support the suggestion that they were inhabitants of warm waters. The group may have been excluded from the tropics by the abundant, speciose genus *Nodilittorina*, which occurs in a similar habitat.

Cenchritis is now represented by a single species, *C. muricatus*, in the Caribbean region, and, like *Melarhaphe*, may be a relict genus, a surviving descendant of the early littorinine stock which, it is hypothesized, radiated in the Tethys Ocean. No fossils can be unequivocally assigned to this genus, but '*Littorina*' *coislinensis* Cossmann, 1902, from the Eocene of France, bears a resemblance to it.

The trochoidal, umbilicate shells of *Peasiella* are highly distinctive, and first occur in the Eocene of France. Modern species are widely distributed in the tropical Indo-Pacific.

Recent species of *Tectarius* occur at supralittoral levels on exposed coasts, probably accounting for their scarcity as fossils, but at least two species are recorded from the Upper Oligocene of France (Lozouet 1986) and a doubtful one from the Lower Miocene of Bikini Atoll (Ladd 1966). Extant species are distributed in the central Indo-Pacific, with a single species in the Caribbean.

Typical *Littoraria* species can usually be distinguished by a tall spire, angulate periphery, and strong spiral ribs or carinae, but can be very similar to species of *Nodilittorina* and *Littorina*. Several species from the Eocene of France (table 7) are, however, so close to modern species that they can be assigned to the subgenus *Littorinopsis*. The status of the fossil 'subgenera' *Styloplocus*, *Eulimene*, *Prosthenodon* and *Touzinia* is uncertain; the first two are probably correctly placed in *Littoraria* (see, for example, Wenz 1939), but the others may not be littorininds. Modern species of *Littoraria* occur in all tropical and warm temperate seas, often in association with mangroves in sedimentary environments, which explains their relatively frequent preservation as fossils. The phylogeny of this genus has been investigated at the specific level (Reid 1986*a*), but correlations with modern distribution and the fossil record are obscure. The species with most plesiomorphic characters, *L. pintado*, has a very wide, disjunct distribution in the western Indian Ocean, central Pacific and Baja California, and other primitive members of the subgenus *Littoraria* occur in the Indo-Pacific also. Although the subgenera *Palustorina* and *Lamellilitorina* are restricted to the central Indo-Pacific, the remaining subgenera *Littoraria* and *Littorinopsis* have an essentially pantropical distribution. Perhaps this group is too ancient and widely dispersed to show patterns of distribution that can be easily related to geological events during the Cainozoic, as is possible for the more recently derived genera *Littorina* and *Nodilittorina*.

In the case of *Littorina*, comparison of modern distributions with the cladogram shows a more obvious pattern. The most primitive species, *L.* (*Liralittorina*) *striata*, is found in the subtropical islands of the eastern Atlantic, *L. keenae* and *L. plena* occur in the northeastern Pacific and other *L.* (*Littorina*) and *L.* (*Neritrema*) species in both the northern Pacific and northern Atlantic. Reid (1989*b*) has discussed the biogeography of *Littorina* in detail. A dispersalist interpretation of the pattern would suggest origin of the genus in the Tethys Sea from a common stock with *Nodilittorina*, and westward dispersal to the Pacific (see Adams (1981) for summary of Cainozoic palaeogeography; Berggren & Hollister (1974, 1977) for palaeocirculation). However, trans-Pacific dispersal is unlikely and the distribution of *Littorina* in the Pacific has been explained by a model involving vicariance and speciation in response to climatic deterioration during the Cainozoic (Reid 1989*b*). Reinvasion of the northern Atlantic took place following the opening of the Bering Strait in the late Pliocene. The fossil record provides some support for this hypothesis. The earliest possible *Littorina* is the unnamed species from Baja California, which may be of Palaeocene age (Woods & Saul 1986). Another possible *Littorina* is *L. mountsoloensis* from the Upper Eocene of Washington State (Weaver & Palmer 1922), although the slight anterior canal suggests that this may be incorrectly assigned. *Littorina* next appears in the Lower Miocene of Vancouver Island, where *L. sookensis* closely resembles *L. keenae* (Clark & Arnold 1923). Further species occur in the Miocene and Pliocene of northwest America, but not until the latest Pliocene and Pleistocene are *L.* (*Littorina*) *littorea* and *L.* (*Neritrema*) *saxatilis* recorded from northwestern Europe (Harmer 1920–5).

The biogeography of *Nodilittorina* is less clear, but does show some similarities to that of *Littorina*. The primitive subgenus *Fossarilittorina* inhabits the tropical Atlantic, Caribbean and Pacific coast of Central America, whereas the more derived species occur throughout the tropical Atlantic and Indo-Pacific. As noted in Appendix 1, the separation of the two remaining subgenera is uncertain, but it may be significant that almost all of the Atlantic species retain the primitively posterior position of the bursa (subgenus *Echinolittorina*), whereas in most of the Indo-Pacific species the bursa is anterior (subgenus *Nodilittorina*). Because the Straits of Panama did not close until the Pliocene (Berggren & Hollister 1977), it is not surprising that at least one species of *Echinolittorina* (*N. peruviana*) occurs in the eastern Pacific, and a possible *Nodilittorina* (*N. lineolata*) in the Atlantic. In contrast to *Littorina*, *Nodilittorina* has remained restricted to warmer waters. The fossil record of *Nodilittorina* is meagre, as expected from its habitat in the high intertidal zone of exposed coasts, with one certain species present in Europe and a more doubtful one in Japan, both in the Middle Miocene. In terms of the number of extant species, *Nodilittorina* is the most successful of the littorinid genera.

(*d*) *Phylogenetic perspectives on ecology and life history*

In discussions of comparative ecology and physiology it is common to explain differences between species as adaptations to their environment, without explicit reference to phylogenetic relationships. However, the concept of adaptation is a historical, evolutionary one. Adaptation is apomorphic function promoted by natural selection, which should be identified by comparison with the function of the plesiomorphic state present in the appropriate outgroup (Coddington 1988). Phylogenetic hypotheses are also necessary when invoking developmental constraints that may restrict the range of adaptations produced by natural selection (Gould & Lewontin 1979). As an example, the diversity of life-history strategies in the Littorinidae has received much attention (see, for example, Woodward 1909; Borkowski 1971; Buckland-Nicks *et al.* 1973; Underwood 1974; Mileikowsky 1975; Hughes & Roberts 1980, 1981), and the various types have been discussed in relation to the habitats in which they occur. Examples of the occurrence of different spawn or developmental types in species occupying the same habitat have frustrated efforts to explain the diversity by optimal strategies in each habitat. A phylogenetic hypothesis provides the means to determine relative apomorphy of characters, and thus to distinguish cases of genuine adaptation.

The aim of this discussion is not to review the extensive literature on the ecology of littorinids, but to indicate some of the important inter-relationships between an understanding of phylogeny and the interpretation of ecological data. A phylogenetic tree permits formulation of evolutionary hypotheses to account for the distribution of shared ecological characteristics. Conversely, ecological and developmental characteristics influence phylogeny, by affecting rates of evolution, dispersal and extinction (see, for example, Vermeij 1972; Jablonski & Lutz

1983; Scheltema & Williams 1983; Jablonski 1986). The discussion is arranged in two parts, first considering correlations between habitat and phylogeny (summarized in table 8) and then aspects of larval development and dispersal (see table 4).

Almost all littorinids occur on hard substrates, and the great majority live on rocks (table 8). Although some *Littorina* species can be found on mud and sand, and littorinids from deeper water may occur on sediments, in general soft substrates are unfavourable, because they impede locomotion. Two groups, *Littoraria* and *Mainwaringia*, have an obligate association with mangrove vegetation, although members of other genera can occasionally be found in this habitat. A few of the more primitive members of *Littoraria* are found on rocks, the ancestral habitat, and it is possible that others have been excluded from it by competition with the highly successful genus *Nodilittorina*, which is dominant on rocky shores in tropical and subtropical areas. In colder waters, littorinids of the genera *Laevilitorina*, *Pellilitorina*, *Lacuna* and *Littorina* (*Neritrema*) occur in close association with macroalgae. The substrate is not only the surface for locomotion, but also for grazing, and the form of the radular teeth shows correlations with substrate (see §4*h*).

The range of tidal level and depth occupied by littorinids shows a striking correlation with the phylogenetic hypothesis (table 8). All marine members of the Lacuninae and Laevilitorininae inhabit the eulittoral and sublittoral zones, which are therefore the ancestral habitats. In contrast, almost all members of the Littorininae occupy the littoral fringe, and indeed littorinines are so characteristic of this zone on worldwide coastlines that their occurrence is used to define its extent (Stephenson & Stephenson 1949). Reference to the cladogram (figure 16) indicates the synapomorphies of the subfamily; these are the morphological changes that have accompanied, and perhaps permitted, the colonization of the littoral fringe, and for which adaptive functions can be considered. The Littorininae are distinguished from other littorinids by the possession of capsule glands and production of planktonic egg capsules, which overcome the problem of desiccation that would be faced by the ancestral benthic egg masses in the littoral fringe. The Littorininae are also characterized by the combination of an open prostate (reversed in *Littoraria*) and paraspermatic nurse cells. As suggested previously (see §4*e*), these characters may be functionally related, the nurse cells preventing dispersal of sperm from the open pallial gonoduct. Why the prostate (and, in most cases, also the anterior vas deferens and penial vas deferens) should have become open is mysterious, although it could be related to speed of copulation during exposure at low tide (see §4*d*). In addition, most of the more derived Littorininae possess complex penial glands, which secure the penis during insertion, and may be advantageous when copulation takes place in air or under conditions of wave splash. The longitudinal division of the foot, present in most Littorininae, but in few Lacuninae and no Laevilitorininae, might be related to increased efficiency of locomotion or to adhesion when washed by waves (see §4*c*). In addition to these morphological traits, physiological and behavioural adaptations were obviously required for successful colonization of the rigorous habitat of the littoral fringe.

Although the Littorinidae are primarily inhabitants of the intertidal zones and of shallow water, those genera that occur in the sublittoral have sometimes been recorded at moderate depths (table 8). In the case of *Laevilitorina*, *Pellilitorina* and *Lacuna* the depth range probably represents the normal habitat. However, *Littorina* is characteristic of the intertidal and shallow water over most of its geographical range, and the maximum depths given refer to records from high latitudes (Thorson 1941; Fretter & Graham 1980).

TABLE 8. SUMMARY OF HABITATS OF SUBGENERA OF LITTORINIDAE

(Abbreviations: ×, typical habitat; (×), common occurrence. Data from Preston (1916), Thorson (1941), Macpherson (1971), Bandel (1974), Ponder (1976), Arnaud & Bandel (1978), Picken (1979), Powell (1979), Fretter & Graham (1980), D.G.R., personal observation.)

	substrate			zonation				temperature		
taxon	rocks	macro-algae	mangroves	littoral fringe	eulittoral	sublittoral	maximum depth/m	cold	temperate	tropical
Pellilitorina	.	×	.	.	.	×	60	×	.	.
Lacuna (*Lacuna*)	.	×	.	.	×	×	170	×	×	.
Lacuna (*Epheria*)	.	×	.	.	×	×	208	×	×	.
Cremnoconchus	×	.	.	.	.	.	.	.	.	×
Bembicium	×	.	(×)	.	×	.	.	.	×	.
Risellopsis	×	.	.	.	×	.	.	.	×	.
Laevilitorina (*Pellilacunella*)	.	×	.	.	.	×	30	×	.	.
Laevilitorina (*Macquariella*)	.	×	.	.	.	×	12	×	(×)	.
Laevilitorina (*Laevilitorina*)	×	×	.	.	×	×	30	×	(×)	.
Laevilitorina (*Rissolittorina*)	.	×	.	.	×	.	.	.	×	.
Laevilitorina (*Rufolacuna*)	.	×	.	.	×	×	6	.	×	.
Melarhaphe	×	.	.	×	.	.	.	.	×	.
Peasiella	×	.	(×)	.	×	.	.	.	.	.
Cenchritis	×	.	(×)	×	.	.	.	.	.	×
Tectarius (*Tectarius*)	×	.	.	×	.	.	.	.	.	×
Tectarius (*Echininus*)	×	.	.	×	.	.	.	.	.	×
Tectarius (*Tectininus*)	×	.	.	×	.	.	.	.	.	×
Tectarius viviparus	×	.	.	×	.	.	.	.	.	×
Littoraria pintado	×	.	.	×	.	.	.	.	.	×
Littoraria (*Palustorina*)	(×)	.	×	×	.	.	.	.	.	×
Littoraria (*Littoraria*)	×	.	×	×	.	.	.	.	.	×
Littoraria (*Lamellilitorina*)	.	.	×	×	.	.	.	.	.	×
Littoraria (*Littorinopsis*)	.	.	×	×	.	.	.	.	.	×
Littoraria aberrans	.	.	×	×	.	.	.	.	.	×
Nodilittorina (*Fossarilittorina*)	×	.	.	.	×	.	.	.	.	×
Nodilittorina (*Echinolittorina*)	×	.	.	×	.	.	.	.	×	×
Nodilittorina (*Nodilittorina*)	×	.	.	×	.	.	.	.	×	×
Littorina (*Liralittorina*)	×	.	.	×	.	.	.	.	×	×
Littorina keenae	×	.	.	×	.	.	.	.	×	.
Littorina (*Littorina*)	×	.	.	×	×	(×)	60	(×)	×	.
Littorina (*Neritrema*)	×	×	.	×	×	(×)	150	×	×	.
Mainwaringia	.	.	×	×	×	.	.	.	.	×

It has been suggested (see §6*c*) that the Littorininae diversified in the tropical Tethys Ocean. Colonization by intertidal organisms of the tropics and of the littoral fringe are connected, for similar adaptations to avoid desiccation and temperature stress are required for each. These adaptations in littorinines include strong shell sculpture for convective heat loss, reduction in relative size of the aperture, and attachment to the substrate by a film of mucus when the operculum is closed (Vermeij 1973).

The genera of Littorinidae tend to be restricted to particular climatic zones (table 8). The main reason is probably because different reproductive strategies (which often characterize clades) are favoured in polar and tropical waters, as discussed below. Only *Littorina*, with the widest range of developmental types, extends to all climatic zones. Another important factor, still poorly understood, may be the role of temperature as a stimulus or inhibitor of gametogenesis. Warm-water species, for example, may be limited in their spread to cooler waters by a minimum temperature requirement for spawning (Raffi *et al.* 1985). Temperature requirements may be evolutionarily conservative; at a given locality, invertebrates with cool-water origins tend to breed in the winter, and those ranging into warmer waters tend to breed the summer (Moore 1972). An example of this phenomenon in two littorinids with planktotrophic development is the breeding of *Melarhaphe neritoides* in the winter and *Nodilittorina punctata* in the summer, at the same locality in Israel (Palant & Fishelson 1968). Purely ecological explanations of breeding seasons, for example in terms of abundance of phytoplankton (Underwood 1974), could not account for this difference.

Despite their colonization of the littoral fringe, none of the Littorininae has become truly terrestrial in habits. In fact, one of the developments that permitted their successful colonization of the littoral fringe, the pelagic egg capsule, has tied them to the marine environment. The few examples of non-planktotrophic development in the Littorininae are apparently of recent origin and have not produced terrestrial radiations. *Cremnoconchus* is the only littorinid to be found outside the marine environment, inhabiting wet cliffs beside streams in the Western Ghats of India (Blanford 1863). As the sister-group of *Bembicium* and *Risellopsis*, with a possible origin in Gondwanaland, this genus is of ancient origin (see §6*c*).

Much theory has developed to account for the evolution of different life-history strategies (reviews by Stearns (1977), Calow (1983), Jablonski & Lutz (1983), Olive (1985), Grahame & Branch (1985) and Strathmann (1985)), providing a framework within which to consider the diversity of developmental types in the Littorinidae. The reproductive strategies of marine invertebrates have been related to aspects of ecology (the demographic theory), the isolation of the habitat, latitude, depth and body size. The demographic theory of life-history evolution is based on the two postulates of resource limitation and optimization of reproductive strategy by natural selection. Different strategies are seen as the optimal solutions resulting from different systems of selection (the *r*–*K* model), of mortality schedules (bet-hedging model) and of environmental instability. Reproductive characteristics typical of '*r*-strategists' (e.g. numerous, small, planktotrophic larvae) are predicted in opportunistic species, in cases where adult survivorship is unpredictable, and in unstable environments. Under the opposite conditions, characteristics of '*K*-strategists' (e.g. few, large, non-planktotrophic larvae, sometimes with parental care) are predicted. The isolation of the habitat may also influence life history, for survival of offspring may be maximized by low dispersal in habitats that are highly geographically restricted, and, conversely, by large-scale dispersal if habitats are patchy but widespread. Nevertheless, one theoretical model predicts little or no short-term advantage to wide dispersal of marine larvae (Palmer & Strathmann 1981), so that consideration of potential for dispersal may not be relevant to discussion of the merits of planktotrophy and non-planktotrophy (Strathmann 1985). Another pattern in the distribution of developmental types is the prevalence of non-planktotrophy and brooding at high latitudes, and of planktotrophy in the tropics. When first observed, this was explained in terms of short periods of algal productivity and slow developmental rates induced by low temperatures, which caused suppression of planktotrophy in polar waters (Thorson 1950). More recently, Highsmith (1985) has proposed that the greater abundance of pelagic predators and benthic filter feeders at high latitudes selects for the elimination of planktonic stages, whereas these are favoured by intense benthic predation in the tropics. Non-planktotrophy also becomes more common in deep-sea molluscs (Jablonski & Lutz 1983). An additional consideration is the relation between body size and reproductive strategy: because planktotrophy entails severe larval mortality, there may be a size limit below which sufficient numbers of eggs to ensure recruitment cannot be produced.

A major difficulty in the application of these general theories is that all make the assumption that life-history traits are free to evolve, taking no account of possible physiological, developmental and evolutionary constraints, which may preclude optimal solutions. Where patterns of reproduction have a strong systematic bias, such constraints may be inherent in the body plan or be a consequence of ancestral specialization (Stearns 1984). It must also be recognized that developmental strategy may influence evolutionary history: species with planktotrophic larvae are widely dispersed, reducing the probability of both extinction and speciation, and consequently are geologically long-lived, whereas the reverse is true of non-planktotrophic forms that have lost or reduced the duration of the planktonic stage (reviews by Jablonski & Lutz (1983) and Jablonski (1986)).

Planktotrophy is almost certainly the plesiomorphic type of development in the Littorinidae. In the common ancestor of the family, veliger larvae with multispiral, sculptured shells probably emerged from benthic egg masses, although this hypothetical condition is not present in exactly this form in any of the known living littorinids (see §4*g* and 5*c* (i)).

The modern Lacuninae and Laevilitorininae all reproduce by the ancestral benthic egg mass, which can be viewed as a phylogenetic constraint precluding their establishment in the tropics and in the littoral fringe. The majority are non-planktotrophic, with no planktonic larval stage, and when contrasted with the Littorininae this is in broad agreement with the predictions of the general theories of life-history strategy reviewed above. Little is known about the demography of the Lacuninae and Laevilitorininae, or about the predictability and stability of the environments in which they live, but their low eulittoral and sublittoral habitats are likely to be more predictable and adult mortality less variable than in the rigorous environment of the high intertidal. The subtidal habitat is relatively continuous, so that dispersal by a planktonic stage might not increase survival of offspring. Furthermore, many species of these subfamilies are associated with macroalgae, on which rafting of adults or egg masses could occur, providing a means of passive dispersal without a planktonic stage (Highsmith 1985). The marine species are restricted to temperate and polar waters, so their loss of planktotrophy is consistent with the latitudinal pattern of developmental strategies. Adaptation to a cold-water habitat may well have been the major factor in the loss of planktotrophy in the Laevilitorininae and Lacuninae. Some members of these groups are of small adult size, and some occur at moderate depths. It is notable that ovoviviparity has not been recorded in Lacuninae or Laevilitorininae, despite its supposed advantages at high latitudes.

Some lacunines (*Risellopsis*, *Lacuna* (*Epheria*) and some *Bembicium*) do, however, have planktotrophic larvae. Although it is commonly believed that evolutionary loss of a planktotrophic veliger is irreversible (Bouchet 1987), arguments from both parsimony (see §5*c*(i)) and the morphology of the protoconch (see §4*a*) suggest that in these cases planktotrophy has indeed been developed from a non-planktotrophic (and probably non-planktonic) condition. If non-feeding, non-planktonic embryos still retain the velar feeding apparatus (as, for example, in *Lacuna* (*Lacuna*) (see Thorson 1946, figure 93*d*)), reduction in the amount of yolk in the egg could permit a reversion to planktotrophy (Strathmann 1978; Ponder 1985*a*). Reversion to planktotrophy in *Bembicium* and *Risellopsis* could be explained by their temperate, rather than polar, distribution, and it may also be significant that they do not occur in association with macroalgae. The distribution of larval development in *Lacuna* species is poorly known; Grahame (1977) has interpreted the planktotrophy of *Lacuna* (*Epheria*) *vincta* and non-planktotrophy of *L.* (*L.*) *pallidula* in terms of the *r*–*K* selection model. Although perhaps developed as an adaptation to cold water, loss of a planktonic larva must have pre-adapted the ancestors of *Cremnoconchus* for life in freshwater.

The Littorininae occupy the upper eulittoral and littoral fringe, a rigorous and unpredictable habitat in which the size of adult populations can show marked fluctuations (Hughes & Roberts 1981; McQuaid 1981). The high intertidal is a patchy but widespread habitat, in which wide dispersal might be advantageous (although geographical variability in the high intertidal habitat may militate against this, see Vermeij (1972)). The subfamily is largely tropical and temperate in distribution, body size is seldom very small, and the wide range of developmental types suggests no obvious developmental or evolutionary constraints. The predominance of planktotrophic development in the Littorininae is therefore consistent with theoretical predictions. The absence of benthic egg masses is also to be expected, for these would be susceptible to desiccation at high tidal levels, and to intense benthic predation in the tropics. There are, however, exceptions to these two predictions about development and eggs.

Among the tropical Littorininae, brooding of embryos has originated in three clades: *Tectarius viviparus*, *Cenchritis muricatus* and the clade comprising *Littoraria* (*Littorinopsis*) and *Littoraria aberrans*. In *L.* (*Littorinopsis*) the embryos are retained for only a few days, to be spawned as planktotrophic veligers of the same size as those hatching from the pelagic capsules of other *Littoraria* species. This represents only a minor modification of the typical littorinine pattern of pelagic eggs and planktotrophic larvae. Larval survival may be slightly increased by this means, at no cost in terms of fecundity, and the energetic cost may even be reduced, because no capsule gland is present. Perhaps more importantly, this short-term brooding permits storage of eggs, produced over a period of hours or even days, for rapid release (see Gallagher & Reid (1974) for a comparison of spawning rate in an oviparous and an ovoviviparous *Littoraria* species). Species of *L.* (*Littorinopsis*) inhabit high supratidal levels in mangrove forests, where the period of contact with high spring tides may be brief, and predation at low levels by crabs is severe (Reid 1984), so that rapid spawning is advantageous. Brooding in *Cenchritis* is possibly facultative (see §4*g*); again the supralittoral habitat may make rapid spawning necessary.

Brooding to the crawling stage is rare in tropical littorinids, occurring only in *Tectarius viviparus* and *Littoraria aberrans*. Both occur at the highest levels of the littoral fringe, *T. viviparus* on cliffs (Rosewater 1982) and *L. aberrans* in the landward fringe of mangrove forests. Ovoviviparity in these two cases is probably a geologically recent adaptation to a nearly terrestrial habitat. The disadvantage of such a strategy is the limitation on dispersal. Indeed, both species are restricted in distribution, *T. viviparus* to the Mariana Islands and *L. aberrans* to the Pacific coast of Panama and Costa Rica, where it is rare. As a consequence of poor dispersal, non-planktotrophic species are evolutionarily short-lived, with an increased probability of extinction and speciation (Jablonski & Lutz 1983; Jablonski 1986). This may explain why non-planktotrophic development is not more common in the littorinids of the littoral fringe.

The genus *Littorina* presents an especially interesting example of correlation between phylogeny, developmental type and latitudinal distribution (see §§4*g*, 6*c*; Reid 1989*a*, *b*). The primitive species, found in warmer water (*L.* (*Liralittorina*) *striata*, *L. keenae*, *L.* (*Littorina*) *brevicula*, and, if a member of this clade, *Mainwaringia rhizophila*), produce pelagic capsules containing single eggs. At higher latitudes, other species of the subgenus *Littorina* produce large pelagic capsules containing several eggs, whereas non-planktotrophic, non-planktonic development, in either benthic gelatinous egg masses or in the oviduct, is the rule in *Neritrema*. These apomorphic types of spawn and development are believed to be adaptations to the cold-water habitat. The larger size of the egg capsules of *L.* (*Littorina*) species supports the suggestion by Highsmith (1985) that predation on planktonic stages may be a significant selective pressure at high latitudes. Suppression of planktotrophy, as in *L.* (*Neritrema*), may be explained either by this hypothesis or by the limited availability of phytoplankton and slow growth rates in cold water (Thorson 1950). In contrast to the two tropical littorinines that are non-planktotrophic and ovoviviparous, the two *Littorina* species with similar development (*L.* (*Neritrema*) *saxatilis* and *L.* (*N.*) *neglecta*) are both abundant and widespread in the northern Atlantic. Perhaps this is because dispersal is accomplished by the rafting of adults on macroalgae, which are only present at high latitudes (Highsmith 1985).

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APPENDIX 1. DIAGNOSES OF SUPRASPECIFIC TAXA OF THE LITTORINIDAE, WITH LISTS OF THE RECENT SPECIES

This is not a fully sequenced phylogenetic classification (see §6*b*). The genera and subfamilies are believed to be monophyletic, but there is some doubt about the rank of *Mainwaringia* (see §5*c*(ii)). Four new subgenera and one new subfamily are described, and many new combinations and new synonymies are created. Complete synonymies (excluding misspellings) are given for supraspecific taxa. Only taxa with living representatives are considered.

In the following lists a query preceding a generic taxon indicates that its placement in synonymy is doubtful; for a specific taxon a query indicates doubtful inclusion in a subgenus. Doubtful specific status is indicated by '? stat.' following a taxon. The equality sign is used for both junior and senior synonyms. Type species are given, in square brackets, with an indication of original designation (OD), subsequent designation (SD, with authority), monotypy (M) or tautonymy (T).

When reading the diagnoses it can be assumed that subordinate taxa possess the characters listed for their superior taxa. Where the term 'usually' is employed, subordinate taxa possess the characters concerned unless otherwise stated. Similarly, if the term 'occasionally' is used, subordinate taxa lack the characters unless otherwise indicated.

For each subgeneric taxon a short list of the principal taxonomic references is provided. In the species lists, annotations are given in square brackets, and are usually references to some of the junior synonyms in common usage.

Since the compilations of gastropod classification by Thiele (1929) and Wenz (1938), the following generic taxa have been excluded from the Littorinidae.

Benthonella Dall, 1889 [Rissoidae (Ponder 1985*a*)]
Boetica Dall, 1918 [?Elachisinidae (Ponder 1985*b*)]
Epheriella Pallary, 1914 [Phasianellidae (Gofas 1982*b*)]
Ersilia Monterosato, 1872 [Eulimidae (Warén 1983)]
Iphitus Jeffreys, 1883 [= *Iphitella* Thiele, 1925; Epitoniidae (Bouchet & Warén 1986)]
Nilsia Finlay, 1927 [Fossaridae (Ponder 1967)]
Problitora Iredale, 1931 [?Naticidae (Rosewater 1970)]
Stenotis A. Adams, 1863 [Vanikoridae (A. Warén, personal communication)]
Zelaxitas Finlay, 1927 [Rissoellidae (Ponder 1966*b*)]

FAMILY LITTORINIDAE Anon., 1834

Shell: inner chitinous layer absent; usually entirely aragonitic, of crossed-lamellar structure. Operculum: peg absent; usually corneous. Head-foot: posterior pedal gland absent; locomotion usually by retrograde ditaxic pedal waves; accessory tentacles absent, except on opercular lobe in some genera; neck lobes absent; cephalic tentacles long, tapering, mobile; osphradium a simple ridge with lateral ciliated zones, usually straight. Usually gonochoristic. Male: penis with pedal innervation, on right side of head. Female: pallial oviduct closed; oviducal sperm groove usually open (i.e. oviduct monaulic); egg groove twisted into spiral; anterior bursa copulatrix usually present; seminal receptacle usually present. Radula: radular sac long and coiled; rachidian outline usually rectangular, with lateral wings and plain base plate; lateral teeth with littorinid notch in broad base; lateral and inner marginal usually with three or more cusps; outer marginal usually elongate rectangular; cusps of all teeth usually pointed. Alimentary system: jaws usually absent; one pair of oesophageal pouches; glandular mid-oesophagus with folds delimiting food groove; crystalline style absent. Nervous system: circumoesophageal ganglia not concentrated; pleuro-supraoesophageal connective long; pleuro-suboesophageal connective usually long.

SUBFAMILY LACUNINAE Gray, 1857
RISELLINAE Kesteven, 1903
BEMBICIINAE Finlay, 1928

Shell: periostracum usually thick; protoconch non-planktotrophic or intermediate. Operculum: paucispiral; usually corneous; internal ridge usually present. Head-foot: mesopodial sole not usually longitudinally divided. Male: penial vas deferens usually deeply closed; penis not usually bifurcate; mamilliform penial glands absent. Sperm: nurse cells absent in seminal vesicle. Female: seminal receptacle absent or, if present, reached by long duct from anterior end of pallial oviduct; capsule gland absent; jelly gland large; glands usually of epithelial structure. Spawn: benthic, gelatinous, lacking capsules. Radula: usually five to seven cusps on rachidian. Alimentary system: salivary glands constricted or anterior.

Genus *Pellilitorina* Pfeffer, in von Martens & Pfeffer, 1886 [*Littorina setosa* E. A. Smith, 1875; SD, Thiele (1929)]

Shell: turbinate; macroscopically smooth; protoconch non-planktotrophic; entirely calcitic, of crossed-foliated structure; thick, bristly periostracum. Operculum: paucispiral A. Head-foot: ovipository flange in females; eyes on short peduncles. Male: prostate closed; anterior vas deferens closed; penial vas deferens deeply closed; subepithelial penial glands absent. Female: bursa absent; seminal receptacle absent; egg groove coiled in one spiral. Radula: rachidian square; three cusps on outer marginal. Alimentary system: jaws present; salivary glands constricted.

Distribution: Antarctic.
References: von Martens & Pfeffer (1886); Powell (1951); Arnaud & Bandel (1978).
Species:
pellita (von Martens, 1885)
setosa (E. A. Smith, 1875)

Genus *Lacuna* Turton, 1827

Shell: macroscopically smooth; protoconch non-planktotrophic or intermediate; aragonitic, with outer spherulitic-prismatic layer. Operculum: paucispiral A. Head-foot: two opercular tentacles; osphradium with short terminal flexure. Male: prostate closed; anterior vas deferens closed; penial vas deferens deeply closed; penis with scattered simple glands, muscular papillae on adaxial surface. Female: seminal receptacle absent; egg groove coiled in one spiral, backward loop in jelly gland. Radula: rachidian with square proportion, hexagonal outline; one to four cusps on outer marginal. Alimentary system: salivary glands constricted.

Remarks: The number of valid species and the status of genera listed as synonyms are uncertain, because only five species have been examined anatomically and shell characters show considerable intraspecific variation. The species lists are adapted from the references given.

Subgenus *Lacuna* Turton, 1827 [*Helix lacuna* Montagu, 1803 = *Lacuna parva* da Costa, 1778; T]
Medoria Leach, in Gray, 1847 [*Turbo crassior* Montagu, 1803; SD, Gray (1847); not Robineau-Desvoidy, 1830]
?*Lacunella* Dall, 1884 [*Lacunella reflexa* Dall, 1884; M; not Deshayes, 1861]
?*Lacunaria* Dall, 1885 [not Conrad, 1866; new name for *Lacunella* Dall, 1884]
?*Aquilonaria* Dall, 1886 [*Aquilonaria turneri* Dall, 1886; M]
?*Haloconcha* Dall, 1886 [new name for *Lacunaria* Dall, 1885]
?*Sublacuna* Pilsbry, 1895 [*Lacuna stentomorpha* Pilsbry, 1895 = *L. latifasciata* A. Adams, 1863; M]
Temanella Rovereto, 1899 [new name for *Medoria* Leach, in Gray, 1847]
?*Carinolacuna* Thiele, 1929 [*Lacuna carinifera* A. Adams, 1851; M]
?*Lacunitunica* Golikov & Gulbin, 1978 [*Lacunitunica lukinii* Golikov & Gulbin, 1978; OD]

Shell: conical, depressed or auricular. Spawn: hemispherical or reniform gelatinous mass. Development: non-planktotrophic.

Distribution: northern Atlantic, northern Pacific, Arctic.

References: Habe (1953); Abbott (1974); Golikov & Kusakin (1978); Fretter & Graham (1980).

Species:

carinifera A. Adams, 1851
crassior (Montagu, 1803)
latifasciata A. Adams, 1863
lepidula A. Adams, 1863
lukinii (Golikov & Gulbin, 1978)
marmorata Dall, 1919
minor (Dall, 1919)
orientalis (Golikov & Gulbin, 1985)
pallidula (da Costa, 1778)
parva (da Costa, 1778)
reflexa (Dall, 1884)
setonaikaiensis (Habe, 1958)
smithii Pilsbry, 1895
succinea Berry, 1953
turneri (Dall, 1886)
uchidai (Habe, 1953)

Subgenus *Epheria* Leach, in Gray, 1847 [*Turbo vinctus* Montagu, 1803; SD, Gray (1847)

Shell: conical. Male: prostate not glandular. Spawn: annular gelatinous mass. Development: planktotrophic.

Distribution: northern Atlantic, northern Pacific, Arctic.

References: Habe (1953); Abbott (1974); Golikov & Kusakin (1978); Fretter & Graham (1980).

Species:
- *decorata* A. Adams, 1861
- *porrecta* Carpenter, 1864
- *turrita* A. Adams, 1861
- *unifasciata* Carpenter, 1856
- *variegata* Carpenter, 1864
- *vincta* (Montagu, 1803)

Genus *Cremnoconchus* Blanford, 1869 [new name for *Cremnobates* Blanford, 1863]
Cremnobates Blanford, 1863 [*Cremnobates syhadrensis* Blanford, 1863; M; not Swainson, 1855]
Lissoconchus Thiele, 1929 [*Cremnoconchus conicus* Blanford 1870; M]

Shell: turbinate; smooth or with major spiral grooves; protoconch non-planktotrophic. Operculum: paucispiral A or B; calcified, with proteinaceous layer internally and externally. Male: prostate closed; prostate gland subepithelial; anterior vas deferens closed; penial vas deferens deeply closed; penial filament retracted into cavity in base; simple penial glands in base. Female: seminal receptacle absent; oviducal glands subepithelial; egg groove coiled in one spiral. Radula: five cusps on rachidian; three cusps on outer marginal. Alimentary system: salivary glands anterior. Nervous system: pleuro-suboesophageal connective short.

Distribution: freshwater, western India.

Remarks: Shell characters are variable and anatomical study will be required to confirm the status of the species.

References: Blanford (1863, 1870).

Species:
- *conicus* Blanford, 1870 [? = *carinatus* (Layard, 1854) not Anthony, 1840]
- *syhadrensis* (Blanford, 1863)

Genus *Bembicium* Philippi, 1846 [*Trochus melanostoma* Gmelin, 1791; SD, Herrmannsen (1846)]
Risella Gray, 1842, *nom. obl.* [*Trochus melanostoma* Gmelin, 1791; SD, Gray (1847)]

Shell: trochoidal; major spiral grooves present; periostracum thin; protoconch intermediate. Operculum: paucispiral A. Head-foot: mesopodial sole divided longitudinally. Male: prostate open; anterior vas deferens closed; penial vas deferens deeply closed, opening subterminal; penis lacking subepithelial glands, filament swollen. Female: duct to seminal receptacle long; opening of renal oviduct anterior; egg groove coiled in one spiral, backward loop in jelly gland. Development: non-planktotrophic or planktotrophic. Radula: three cusps on rachidian; two to four cusps on outer marginal. Alimentary system: salivary glands anterior. Nervous system: pleuro-suboesophageal connective short.

Distribution: Australia.

Reference: Reid (1988).

Species:
- *auratum* (Quoy & Gaimard, 1834)
- *flavescens* (Philippi, 1851)
- *melanostoma* (Gmelin, 1791)
- *nanum* (Lamarck, 1822)
- *vittatum* Philippi, 1846

Genus *Risellopsis* Kesteven, 1902 [*Adeorbis varius* Hutton, 1873; OD]

Shell: trochoidal; major spiral grooves present; periostracal bristles; protoconch intermediate; aragonitic with outer calcitic layer of irregular-prismatic structure. Operculum: paucispiral B; no ridge. Male: prostate open; anterior vas deferens open; penial vas deferens open, opening just subterminal; penis with small lateral appendage; penis lacking subepithelial glands, filament short, swollen. Female: duct to seminal receptacle long; opening of renal oviduct posterior; egg groove coiled in one spiral, backward loop in jelly gland. Development: planktotrophic. Radula: five cusps on rachidian; three cusps on outer marginal. Alimentary system: salivary glands anterior.

Distribution: New Zealand.

Reference: Reid (1988).

Species:

varia (Hutton, 1873)

SUBFAMILY LAEVILITORININAE **n. subfam.**

Shell: thick periostracum; macroscopically smooth; protoconch non-planktotrophic; entirely aragonitic, with outer spherulitic-prismatic layer. Operculum: usually paucispiral A; no ridge. Head-foot: mesopodial sole not longitudinally divided. Male: prostate closed; anterior vas deferens closed; penial vas deferens superficially closed; mamilliform glands absent. Sperm: nurse cells absent in seminal vesicle. Female: capsule gland absent; jelly gland large; glands of epithelial structure; egg groove coiled in two spirals, each of half a whorl. Spawn: benthic, gelatinous, lacking capsules.

Genus *Laevilitorina* Pfeffer, in von Martens & Pfeffer, 1886.

Diagnosis: as for subfamily.

Subgenus *Pellilacunella* Powell, 1951 [*Pellilitorina bennetti* Preston, 1916; OD]

Shell: turbinate. Head-foot: eight opercular tentacles. Male: penis not bifurcate, filament small. Radula: rachidian proportion normal, outline hexagonal; nine cusps on rachidian; one cusp on outer marginal. Alimentary system: salivary glands anterior.

Distribution: Antarctic.

Reference: Powell (1951).

Species:

bennetti (Preston, 1916) **n. comb.**

Subgenus *Macquariella* Finlay, 1926 [*Paludestrina hamiltoni* E. A. Smith, 1898; OD]
Laevilacunaria Powell, 1951 [*Pellilitorina bransfieldensis* Preston, 1916; OD]

Shell: large aperture. Operculum: paucispiral A or B. Male: penis not bifurcate, longitudinal ridge at base, small filament, subepithelial glands absent. Radula: one to five cusps on rachidian; two to ten cusps on outer marginal. Alimentary system: salivary glands usually anterior.

Distribution: Antarctic, southern New Zealand, southern Australia.

References: von Martens & Pfeffer (1886); Powell (1951, 1979); Ponder (1976).

Species:

antarctica (von Martens, 1885) **n. comb.** [? = *bransfieldensis* (Preston, 1916)]
aucklandica (Powell, 1933) **n. comb.**
?*delli* (Powell, 1955) **n. comb.**
hamiltoni (E. A. Smith, 1898)
kingensis (May, 1924) **n. comb.**
?*macphersonae* (Dell, 1964) **n. comb.**

Subgenus *Laevilitorina* Pfeffer, in von Martens & Pfeffer, 1886 [*Littorina caliginosa* Gould, 1849; SD, Suter (1913)]
?*Corneolitorina* Powell, 1951 [*Littorina coriacea* Melvill & Standen, 1907; OD]

Shell: conical. Male: penis not bifurcate, longitudinal ridge at base, short filament, scattered simple glands. Radula: three to seven cusps on rachidian; seven to ten cusps on outer marginal. Alimentary system: salivary glands constricted.

Distribution: Antarctic, Subantarctic, southern Australia.

References: von Martens & Pfeffer (1886); Powell (1951, 1979); Dell (1964); Ponder (1976); Arnaud & Bandel (1978); Ponder & Rosewater (1979).

Remarks: This is a poorly known group in which taxonomy is based on shell and radular characters, with little knowledge of intraspecific variation or geographical distribution. A systematic revision would probably reduce the number of recognized species. Subgeneric allocation at present doubtful for most species.

Species:

antarctica (E. A. Smith, 1902) [not von Martens, 1885]
antipodum (Filhol, 1880)
bifasciata Suter, 1913
caliginosa (Gould, 1849)
claviformis Preston, 1916 [? stat.]
coriacea (Melvill & Standen, 1907)
elongata Pelseneer, 1903 [? stat.]
granum Pfeffer, in von Martens & Pfeffer, 1886 [? stat.]
heardensis Dell, 1964
johnstoni (Cotton, 1945)
latior Preston, 1912 [? stat.]
mariae (Tenison Woods, 1876)
pygmaea Pfeffer, in von Martens & Pfeffer, 1886 [? stat.]
umbilicata Pfeffer, in von Martens & Pfeffer, 1886 [? stat.]
venusta Pfeffer, in von Martens & Pfeffer, 1886 [? stat.]

Subgenus *Rissolittorina* Ponder, 1966 [*Zelaxites alta* Powell, 1940; OD]

Shell: high conical. Male: penis bifurcate, probably with scattered simple glands. Radula: five cusps on rachidian; ten cusps on outer marginal. Alimentary system: salivary glands constricted.

Distribution: New Zealand.

Reference: Ponder (1966*b*).

Species:
alta (Powell, 1940)

Subgenus *Rufolacuna* Ponder, 1976 [*Cyclostrema bruniensis* Beddome, 1883; OD]

Shell: depressed, umbilicate. Operculum: paucispiral B. Male: penis bifurcate, probably with scattered simple glands. Radula: three cusps on rachidian; seven cusps on outer marginal. Alimentary system: salivary glands anterior.

Distribution: southern Australia.
Reference: Ponder (1976).
Species:
bruniensis (Beddome 1883)

SUBFAMILY LITTORININAE Anon., 1834
TECTARIINAE Rosewater, 1972
ECHINININAE Rosewater, 1972

Shell: periostracum usually inconspicuous; major spiral grooves usually present; protoconch usually planktotrophic. Operculum: usually paucispiral A, corneous; ridge usually absent. Head-foot: mesopodial sole usually longitudinally divided. Male: prostate usually open; penial vas deferens never deeply closed; subepithelial penial glands usually present, sometimes as glandular disc or mamilliform glands. Sperm: nurse cells present, usually with rods. Female: capsule gland usually present; albumen and capsule glands usually subepithelial; jelly gland usually small. Spawn: usually pelagic capsules containing single ova, occasionally benthic gelatinous or ovoviviparous. Radula: usually three cusps on rachidian. Alimentary system: salivary glands usually posterior, occasionally constricted.

Genus *Melarhaphe* Menke, 1828 [*Turbo caerulescens* Lamarck, 1822 = *Turbo neritoides* Linnaeus, 1758; M]

Shell: conical; macroscopically smooth. Head-foot: mesopodial sole not longitudinally divided; head with two longitudinal black lines on tentacles. Male: anterior vas deferens closed; penial vas deferens superficially closed; penis not bifurcate, subepithelial glands absent. Sperm: nurse cells lack rods. Female: albumen and capsule glands epithelial; egg groove coiled in two spiral loops. Spawn: pill-box capsules. Radula: pair of denticles on rachidian base plate; six cusps on outer marginal.

Distribution: northeastern Atlantic, Mediterranean, Black Sea.
Reference: Rosewater (1981).
Species:
neritoides (Linnaeus, 1758)

Genus *Peasiella* Nevill, 1885 [*Trochus tantillus* Gould, 1849; OD]

Shell: trochoidal; umbilicate; periostracum occasionally with bristles. Operculum: multispiral. Head-foot: mesopodial sole not longitudinally divided. Male: anterior vas deferens open; penial vas deferens superficially closed; penis not bifurcate, filament long; usually a single mamilliform penial gland; scattered simple penial glands. Sperm: nurse cells lack rods. Female: bursa present or absent; egg groove coiled in two spiral loops, each of half a whorl. Spawn: cupola capsules. Radula: three to six cusps on outer marginal. Alimentary system: salivary glands constricted.

Distribution: Indo-Pacific.

Reference: Reid in prep.

Species:

conoidalis (Pease, 1868)
infracostata (Issel, 1869)
isseli (Semper, in Issel, 1869).
roepstorffiana (Nevill, 1885)
tantilla (Gould, 1849)
n. sp. Reid, in prep.

Genus *Cenchritis* von Martens, 1900 [*Turbo muricatus* Linnaeus, 1758; OD]

Shell: trochoidal; granular sculpture. Operculum: paucispiral B. Male: anterior vas deferens closed; penial vas deferens superficially closed; penis not bifurcate, subepithelial glands absent. Female: egg groove coiled in one spiral. Spawn: pill-box capsules. Radula: single major cusp on lateral; three cusps on outer marginal.

Distribution: Caribbean.

References: Clench & Abbott (1942); Abbott (1954).

Species:

muricatus (Linneaus, 1758)

Genus *Tectarius* Valenciennes, 1832

Shell: trochoidal; nodulose or spinose. Operculum: meso- or multispiral. Male: anterior vas deferens open; penial vas deferens open; penis not bifurcate; mamilliform glands five or more, usually of two or three sizes; scattered simple penial glands. Female: egg groove coiled in one spiral. Spawn: cupola capsules predicted in most species. Radula: rachidian narrow, occasionally vestigial; single major cusp on lateral; two to four cusps on outer marginal.

Subgenus *Tectarius* Valenciennes, 1832 [*Trochus coronatus* Valenciennes, 1832; SD, Clench & Abbott (1942)]
Cidaris Röding, 1798 [*Trochus pagodus* Linnaeus, 1758; SD, Herrmannsen (1847); not Leske, 1778]
Pagodus Gray, 1839 [*Monodonta pagodus* 'Lamarck' = *Trochus pagodus* Linnaeus, 1758; M]
Pagodella Swainson, 1840 [*Trochus pagodus* Linnaeus, 1758; SD, Rosewater, (1970)]
Echinella Swainson, 1840 [*Monodonta coronaria* Lamarck, 1816 = *Trochus grandinatus* Gmelin, 1791; M; not Bory St Vincent, 1824]
Hamus 'Klein' H. & A. Adams, 1858 [*Trochus pagodus* Linnaeus, 1758; SD, Rosewater, (1970)]
Echinellopsis Rovereto, 1899 [new name for *Echinella* Swainson, 1840]

Operculum: mesospiral. Male: 25 or more large, and numerous small, mamilliform penial glands; opening of penial vas deferens terminal.

Distribution: central Indo-Pacific.

Reference: Rosewater (1972).

Species:
coronatus (Valenciennes, 1832)
grandinatus (Gmelin, 1791)
pagodus (Linnaeus, 1758)
rusticus (Philippi, 1846)
tectumpersicum (Linnaeus, 1758)

Subgenus *Echininus* Clench & Abbott, 1942 [new name for *Nina* Gray, 1850]
Nina Gray, 1850 [*Trochus cumingii* Philippi, 1846; M; not Horsfield, 1829]

Shell: umbilicate. Operculum: multispiral. Male: opening of penial vas deferens subterminal; 2–12 large, and numerous small, mamilliform penial glands.

Distribution: central Indo-Pacific.

References: Rosewater (1972, 1982).

Species:
cumingii (Philippi, 1846)
spinulosus (Philippi, 1847) [? stat.]

Subgenus *Tectininus* Clench & Abbott, 1942 [*Litorina nodulosa* Pfeiffer, 1839 = *Litorina antonii* Philippi, 1846; OD]

Operculum: mesospiral. Male: two very large, basal, mamilliform penial glands with common opening; plus one or two large, and numerous small, mamilliform penial glands. Female: bursa in relatively posterior position. Radula: rachidian vestigial; one cusp on lateral; one cusp on inner marginal.

Distribution: Caribbean.

References: Clench & Abbott (1942); Abbott (1954); Bandel & Kadolsky (1982).

Species:
antonii (Philippi, 1846) **n. comb.** [= '*nodulosus* (Pfeiffer, 1839)']

Subgenus *Echininiopsis* **n. subgen.** [type species *Echininus viviparus* Rosewater, 1982]

Etymology: From resemblance to *Echininus*.

Characters as for genus, with the following additions and modifications. Shell: nodulose; not umbilicate; protoconch non-planktotrophic. Male: five to eight mamilliform penial glands all of large size; opening of penial vas deferens just subterminal; penial filament short. Female: capsule gland absent. Development: ovoviviparous; embryos brooded in mantle cavity and released as crawling young.

Distribution: Mariana Is.

Reference: Rosewater (1982).

Species:
viviparus (Rosewater, 1982) **n. comb.**

Genus *Littoraria* Griffith & Pidgeon, 1834

Shell: conical; never nodulose. Male: prostate closed; anterior vas deferens usually open; penial vas deferens usually open; penis sometimes bifurcate; penial glandular disc usually present; mamilliform penial glands absent. Female: egg groove coiled in one spiral. Spawn: usually biconvex discoidal capsules, or ovoviviparous. Radula: three or five cusps on rachidian; rachidian usually hooded. Alimentary system: salivary glands constricted.

Subgenus *Protolittoraria* **n. subgen.** [type species *Turbo pintado* Wood, 1828]

Etymology: From its apparently primitive status within the genus.

Characters as for genus, with the following additions and modifications. Male: penis not bifurcate; scattered simple penial glands not forming glandular disc. Female: bursa in relatively posterior position. Spawn: cupola capsules sculptured by one concentric ring. Radula: three cusps on rachidian; rachidian not hooded; outer marginal lacks strongly narrowed neck and outer basal projection; six cusps on outer marginal.

Distribution: Indo-Pacific, Baja California.

Reference: Rosewater (1970).

Species:

pintado (Wood, 1828) [= *pullata* (Carpenter, 1864)]

Subgenus *Palustorina* Reid, 1986 [*Littorina melanostoma* Gray, 1839; OD]

Male: penis not bifurcate; penial glandular disc present. Sperm: nurse cells flagellate. Female: bursa in relatively posterior position. Spawn: biconvex discoidal capsules. Radula: five cusps on rachidian; rachidian hooded; two to four cusps on outer marginal.

Distribution: central Indo-Pacific.

Reference: Reid (1986*a*).

Species:

articulata (Philippi, 1846)
carinifera (Menke, 1830)
conica (Philippi, 1846)
flammea (Philippi, 1847)
melanostoma (Gray, 1839)
strigata (Philippi, 1846)
sulculosa (Philippi, 1846)

Subgenus *Littoraria* Griffith & Pidgeon, 1834 [*Littorina pulchra* 'Gray' Sowerby, 1832 = *Turbo zebra* Donovan, 1825; M]

Shell: periostracum occasionally with bristles. Male: penis bifurcate; penial glandular disc present. Female: bursa in relatively posterior or anterior position. Spawn: biconvex discoidal capsules. Radula: three or five cusps on rachidian; rachidian usually hooded; four or five cusps on outer marginal.

Distribution: worldwide tropics and sub-tropics.

References: Bequaert (1943); Rosewater (1970); Keen (1971); Reid (1986*a*).

Remarks: This is probably a polyphyletic assemblage (Reid 1986*a*).

Species:

cingulifera (Dunker, 1845)
coccinea (Gmelin, 1791)
fasciata (Gray, 1839)

flava (King & Broderip, 1832)
glabrata (Philippi, 1846) [= *kraussi* (Rosewater, 1970)]
irrorata (Say, 1822)
mauritiana (Lamarck, 1822)
nebulosa (Lamarck, 1822)
tessellata (Philippi, 1847)
undulata (Gray, 1839)
varia (Sowerby, 1832)
vespacea Reid, 1986
zebra (Donovan, 1825)
n. sp. Reid in prep.

Subgenus *Lamellilitorina* Tryon, 1887 [*Littorina albicans* Metcalfe, 1852; SD, Wenz (1938)]

Shell: numerous axial varices in large specimens; protoconch planktotrophic, large (> 0.5 mm diam.). Male: penis bifurcate; penial glandular disc present. Female: bursa anterior. Radula: five cusps on rachidian; rachidian hooded; five cusps on outer marginal.

Distribution: Borneo.
Reference: Reid (1986*a*).
Species:
albicans (Metcalfe, 1852)

Subgenus *Littorinopsis* Mörch, 1876 ['*Littorina subangulata* Lamarck', error for *Phasianella angulifera* Lamarck, 1822; OD]

Male: anterior and penial vas deferens occasionally closed; penis bifurcate; penial glandular disc present. Female: bursa anterior; capsule gland absent. Development: ovoviviparous; embryos brooded in mantle cavity, released as planktotrophic veligers. Radula: five cusps on rachidian; rachidian hooded; five cusps on outer marginal.

Distribution: worldwide tropics and subtropics.
Reference: Reid (1986*a*).
Species:
angulifera (Lamarck, 1822)
ardouiniana (Heude, 1885)
cingulata (Philippi, 1846)
delicatula (Nevill, 1885)
filosa (Sowerby, 1832)
intermedia (Philippi, 1846)
lutea (Philippi, 1847)
luteola (Quoy & Gaimard, 1833)
pallescens (Philippi, 1846)
philippiana (Reeve, 1857)
scabra (Linnaeus, 1758)
subvittata Reid, 1986

Subgenus *Bulimilittorina* **n. subgen.** [type species *Littorina aberrans* Philippi, 1846]

Etymology: from its resemblance to the pulmonate snail *Bulimus*.

Characters as for genus, with the following additions and modifications. Shell: protoconch non-planktotrophic. Male: penis bifurcate; penial glandular disc infolded to form two structures superficially resembling mamilliform glands. Sperm: no rods in nurse cells. Female: bursa anterior; capsule gland absent. Development: ovoviviparous; embryos brooded in mantle cavity, released as crawling young. Radula: five cusps on rachidian; rachidian hooded; four cusps on outer marginal.

Distribution: western Central America.

Reference: Philippi (1847).

Species:

aberrans (Philippi, 1846)

Genus *Nodilittorina* von Martens, 1897

Shell: conical; major spiral grooves usually present; smooth or nodulose; aragonitic, of crossed-lamellar structure with fine outer layer. Head-foot: tentacles usually pale with two or three longitudinal black stripes. Male: anterior vas deferens open; penial vas deferens usually open. Female: bursa in relatively posterior or anterior position; egg groove coiled in one spiral of one whorl. Spawn: cupola capsules. Radula: outer marginal teeth with narrowed neck and basal projection, four to eight cusps.

Subgenus *Fossarilittorina* Rosewater, 1981 [*Phasianella meleagris* Potiez & Michaud, 1838; OD]

Shell: smooth, often without major spiral grooves. Male: penial vas deferens open or superficially closed; penis not bifurcate; scattered simple penial glands sometimes present; mamilliform penial glands absent. Female: bursa in relatively posterior position.

Distribution: Caribbean, West Africa, western Central America.

References: Bequaert (1943); Keen (1971); Rosewater (1981).

Species:

meleagris (Potiez & Michaud, 1838) **n. comb.**
mespillum (Mühlfeld, 1824) **n. comb.**
?*modesta* (Philippi, 1846)

Subgenus *Echinolittorina* Habe, 1956 [*Litorina tuberculata* Menke, 1828; OD]

Shell: sometimes nodulose. Male: penis bifurcate; penial glandular disc usually present; single mamilliform penial gland. Female: bursa in relatively posterior position. Radula: rachidian occasionally narrowed; cusps of inner marginal tooth occasionally reduced to two.

Distribution: tropical and warm temperature zones of Atlantic, Caribbean, western South America, ?South Africa.

References: Rosewater (1970, 1981); Keen (1971); Bandel & Kadolsky (1982).

Remarks: This subgenus is distinguished from *N.* (*Nodilittorina*) by the posterior bursa; because this is a plesiomorphic character in the genus, *Echinolittorina* is probably a paraphyletic group. The validity of the distinction between these two subgenera is doubtful, but is supported by geographical distribution. At the specific level the taxonomy of several species is in doubt, because distinctions based on radular characters alone are not always supported by anatomical differences.

Species:

?*africana* ('Krauss' Philippi, 1847) [? = *knysnaensis* (Philippi, 1847)]
angustior (Mörch, 1876)
dilatata (d'Orbigny, 1842)
granosa (Philippi, 1848)
interrupta (C. B. Adams, in Philippi, 1847)
miliaris (Quoy & Gaimard, 1833) [? = *helenae* ('Melliss' E. A. Smith, 1890); ? = *vermeiji* Bandel & Kadolsky, 1982]
peruviana (Lamarck, 1822)
punctata (Gmelin, 1791)
riisei (Mörch, 1876) [? = *glaucocincta* (Mörch, 1876); ? = *mordax* Bandel & Kadolsky, 1982]
tuberculata (Menke, 1828)
ziczac (Gmelin, 1791)

Subgenus *Nodilittorina* von Martens, 1897 [*Littorina pyramidalis* Quoy & Gaimard, 1833; SD, Abbott (1954)]

Granulilittorina Habe & Kosuge, 1966 [*Granulilittorina philippiana* Habe & Kosuge, 1966, ? = *Littorina vidua* Gould, 1859; M]

Shell: major spiral grooves; sometimes nodulose. Male: penis bifurcate; penial glandular disc present; single mamilliform gland, occasionally also with numerous minute mamilliform glands on filament. Female: bursa usually in relatively anterior position.

Distribution: tropical and warm temperate zones of Indo-Pacific, eastern Pacific, southwestern Atlantic.

References: Rosewater (1970); Keen (1971); Bandel & Kadolsky (1982).

Remarks: See remarks under *N.* (*Echinolittorina*). At least three species (marked by queries in species list below) apparently have the bursa in a relatively posterior position and are doubtfully included in this subgenus. The taxonomy of this group has previously been based principally on shell characters, but anatomical investigations during the present study have revealed 10 additional species that had either been synonymized in recent accounts or are undescribed.

Species:

?*acutispira* (E. A. Smith, 1892)
albicarinata (McLean, 1970) **n. comb.**
antipodum (Philippi, 1847) **n. comb.**
araucana (d'Orbigny, 1840) [? = *paytensis* (Philippi, 1847)]
aspera (Philippi, 1846) [? = *penicillata* (Carpenter, 1864)]
?*australis* (Gray, 1826) [= *nodosa* (Gray, 1839)]
cincta (Quoy & Gaimard, 1833)
cinerea (Pease, 1869)
fernandezensis (Rosewater, 1970) **n. comb.**
galapagiensis (Stearns, 1893)
hawaiiensis Rosewater & Kadolsky, 1981 [= *picta* (Philippi, 1846)]
lineolata (d'Orbigny, 1840)
millegrana (Philippi, 1848)

natalensis (Philippi, 1847)
novaezelandiae (Reeve, 1857) [= *melanacme* (E. A. Smith, 1876); = *feejeensis* (Reeve, 1857)]
pascua Rosewater, 1970
porcata (Philippi, 1846) **n. comb.** [= *abjecta*, *atrata*, *excavata*, *foveata* all (C. B. Adams, 1852); = *roosevelti* (Bartsch & Rehder, 1939)]
?*praetermissa* (May, 1909)
pyramidalis (Quoy & Gaimard, 1833)
quadricincta (Mühlfeld, 1824) [= *leucosticta* (Philippi, 1847)]
radiata (Eydoux & Souleyet, 1852) [= *exigua* (Dunker, 1860)]
subnodosa (Philippi, 1847)
sundaica (Altena, 1945)
trochoides (Gray, 1839)
unifasciata (Gray, 1826)
vidua (Gould, 1859) [= *ventricosa* (Philippi, 1847)]
4 n. spp. Reid in prep.

Genus *Littorina* Férussac, 1822

Shell: major spiral grooves usually present; occasionally nodulose; protoconch planktotrophic or non-planktotrophic; aragonitic, with outer layer of fine crossed-lamellar structure, or more often with outer layer of irregular-prismatic calcite. Male: anterior vas deferens open; penial vas deferens open; penis not bifurcate; scattered simple penial glands present; one or more mamilliform penial glands of uniform size usually present. Sperm: nurse cell rods absent. Female: egg groove coiled in two or three spirals. Spawn and development: either pelagic capsules, benthic gelatinous masses, or ovoviviparous. Alimentary system: salivary glands usually enlarged.

Subgenus *Liralittorina* Rosewater, 1981 [*Littorina striata* King & Broderip, 1832; OD]

Shell: turbinate; nodulose on early whorls; protoconch planktotrophic; aragonitic, with outer layer of fine crossed-lamellar structure. Male: mamilliform penial glands absent. Female: bursa in relatively posterior position; egg groove coiled in two spirals. Spawn: cupola capsules. Radula: outer marginal with narrowed neck and basal projection, eight cusps. Alimentary system: salivary glands not enlarged.

Distribution: subtropical eastern Atlantic islands.

References: Rosewater (1981), Reid (1989*a*).

Species:

striata King & Broderip, 1832

Subgenus *Planilittorina* **n. subgen.** [type species *Littorina keenae* Rosewater, 1978]

Etymology: Latin *planus*, flat, in reference to flattened parietal area.

Characters as for genus, with the following additions and modifications. Shell: turbinate; major spiral grooves faint; protoconch planktotrophic; aragonitic, with outer layer of fine crossed-lamellar structure. Male: two mamilliform penial glands. Female: bursa in relatively posterior position; egg groove coiled in two spirals; jelly gland enlarged. Spawn: biconvex capsules released in ephemeral, pelagic, gelatinous mass. Radula: outer marginal with narrowed neck and basal projection, seven cusps. Alimentary system: salivary glands not enlarged.

Distribution: California, Baja California.

References: Keen (1971); Rosewater (1978).

Species:

keenae Rosewater, 1978 [= *planaxis* Philippi, 1847]

Subgenus *Littorina* Férussac, 1822 [*Turbo littoreus* Linnaeus, 1758; SD, Anton (1838)]
Bacalia H. & A. Adams, 1854 [*Turbo littoreus* Linnaeus, 1758; SD, Winckworth (1922)]
Isonema 'Hall' Provancher, 1891 [*Turbo littoreus* Linnaeus, 1758; SD, Bequaert (1943); not Meek & Worthern, 1866]
Algaroda Dall, 1918 [*Turbo littoreus* Linnaeus 1758; OD]
Ezolittorina Habe, 1958 [*Littorina squalida* Broderip & Sowerby, 1829; M]

Shell: turbinate or conical; usually with major spiral grooves; protoconch planktotrophic; aragonitic, with outer layer of irregular-prismatic calcite. Male: 1–30 mamilliform glands of equal size, occasionally absent. Female: bursa in relatively posterior position; jelly gland not enlarged; egg groove coiled in 3 spirals. Spawn: biconvex capsules; commonly more than one egg per capsule. Radula: rachidian usually square, three or five cusps; outer marginal teeth usually elongate rectangular, sometimes with narrowed neck and basal projection, five to seven cusps. Alimentary system: salivary glands posterior, enlarged.

Distribution: northern Pacific, northern Atlantic.

References: Golikov & Kusakin (1978); Fretter & Graham (1980); Mastro *et al.* (1982); Reid (1989*a*).

Remarks: This is a paraphyletic group (Reid 1989*a*). If *Mainwaringia* is shown to be a member of the genus *Littorina*, it will fall within this group. It will then be desirable to retain *Mainwaringia* as a subgenus, and to remove *L. plena* and *L. scutulata* to a new subgenus.

Species:

brevicula Philippi, 1844
littorea (Linnaeus, 1758)
mandshurica Schrenck, 1867
plena Gould, 1849
scutulata Gould, 1849
squalida Broderip & Sowerby, 1829

Subgenus *Neritrema* Récluz, 1869 [*Turbo obtusatus* Linnaeus, 1758; SD, Dall (1909)]
Neritoides T. Brown, 1827 [*Nerita littoralis* Linnaeus, 1758, ? = *Turbo obtusatus* Linnaeus, 1758; M; not Meuschen, 1779]
Algamorda Dall, 1918 [*Paludinella newcombiana* Hemphill, 1877, = *Assiminea subrotundata* Carpenter, 1864; OD]
Littorivaga Dall, 1918 [*Littorina sitkana* Philippi, 1846; OD]

Shell: turbinate or globular; usually with major spiral grooves; occasionally nodulose; protoconch non-planktotrophic; aragonitic with outer layer of irregular-prismatic calcite. Male: 6–50 mamilliform penial glands. Female: bursa in relatively anterior position; egg groove coiled in two or three spirals; jelly gland enlarged, sometimes forming brood pouch. Spawn and development: benthic gelatinous mass with or without biconvex capsules with single ova, or ovoviviparous with brooding in oviduct to crawling stage; always non-planktotrophic. Radula: rachidian square or normal, five cusps; four to six cusps on outer marginal. Alimentary system: salivary glands posterior, enlarged.

Distribution: northern Pacific, sub-Arctic, northern Atlantic.

References: Abbott (1974); Golikov & Kusakin (1978); Fretter & Graham (1980); Reid (1989*a*).

Species:

aleutica Dall, 1872
arcana Hannaford Ellis, 1978
kurila Middendorff, 1848
mariae Sacchi & Rastelli, 1966
neglecta Bean, 1844 [possibly a form of *saxatilis* (K. & B. Johannesson, personal communication)]
nigrolineata Gray, 1839
obtusata (Linnaeus, 1758) [= *littoralis* auct.]
saxatilis (Olivi, 1792) [= *rudis* (Maton, 1797)]
sitkana Philippi, 1846 [= *atkana* Dall, 1886]
subrotundata (Carpenter, 1864) [= *newcombiana* (Hemphill, 1877)]

Genus *Mainwaringia* Nevill, 1885 [*Mainwaringia paludomoidea* Nevill, 1885, = *Alaba* (*Diala*) *leithii* E. A. Smith, 1876; OD]

Shell: elongate conical; protoconch planktotrophic; aragonitic; periostracum with bristles. Operculum: ridge present. Head-foot: mesopodial sole not divided, locomotion by ciliary gliding, foot tapered posteriorly. Protandrous hermaphrodite. Male: anterior vas deferens open; penis not bifurcate; penial vas deferens superficially closed; scattered simple penial glands present; one mamilliform penial gland. Sperm: nurse cell rods absent. Female: oviducal sperm groove partially closed; bursa in relatively anterior position; egg groove coiled in three spirals. Spawn: biconvex capsules. Radula: rachidian square, with five cusps; one to three cusps on outer marginal. Alimentary system: salivary glands constricted.

Distribution: India, southeast Asia.

References: Reid (1986*b*, 1989*a*).

Remarks: The affinities of this genus are uncertain; it may prove to be a subgenus of *Littorina*.

Species:

leithii (E. A. Smith, 1876)
rhizophila Reid, 1986

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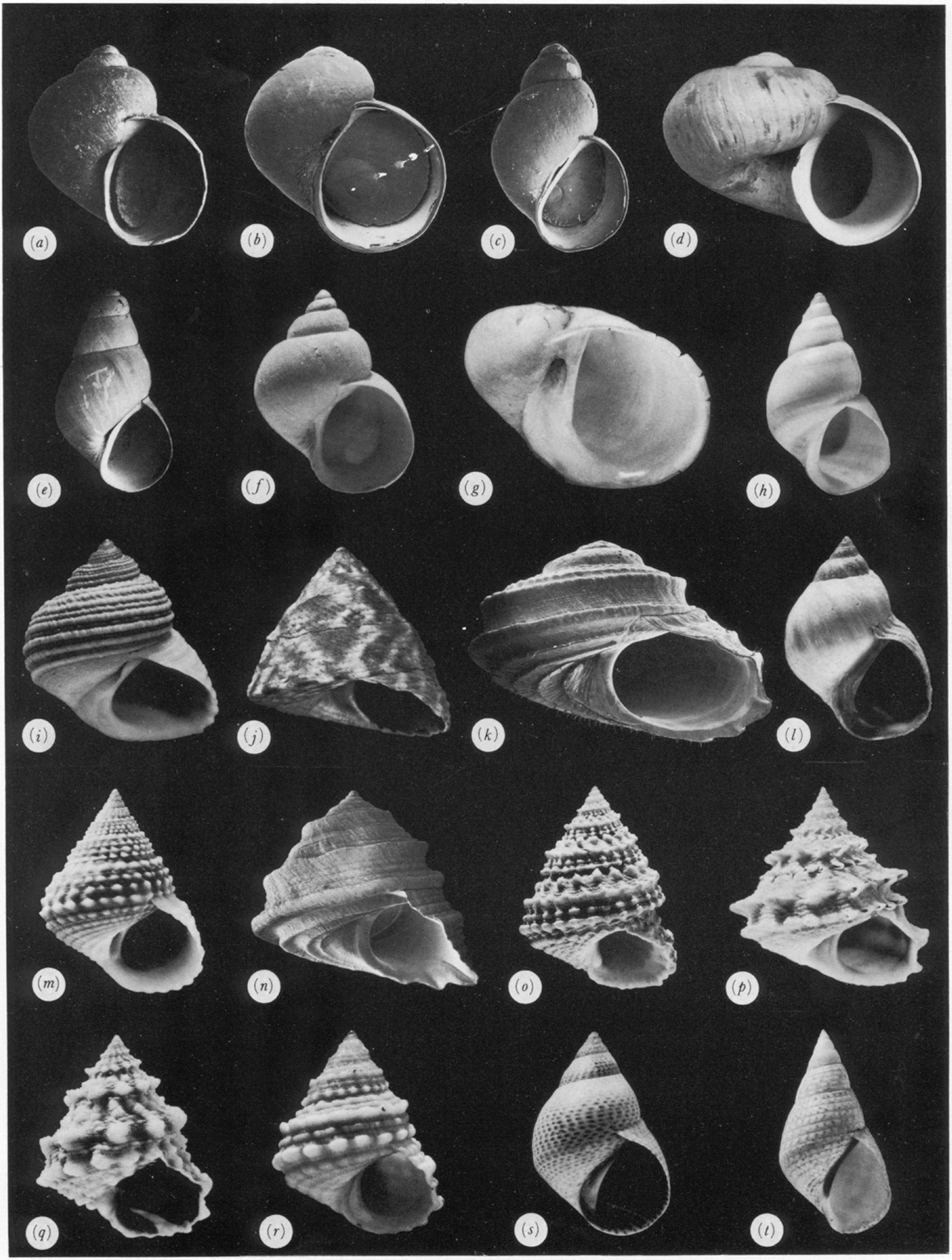

FIGURE 1. For description see opposite.

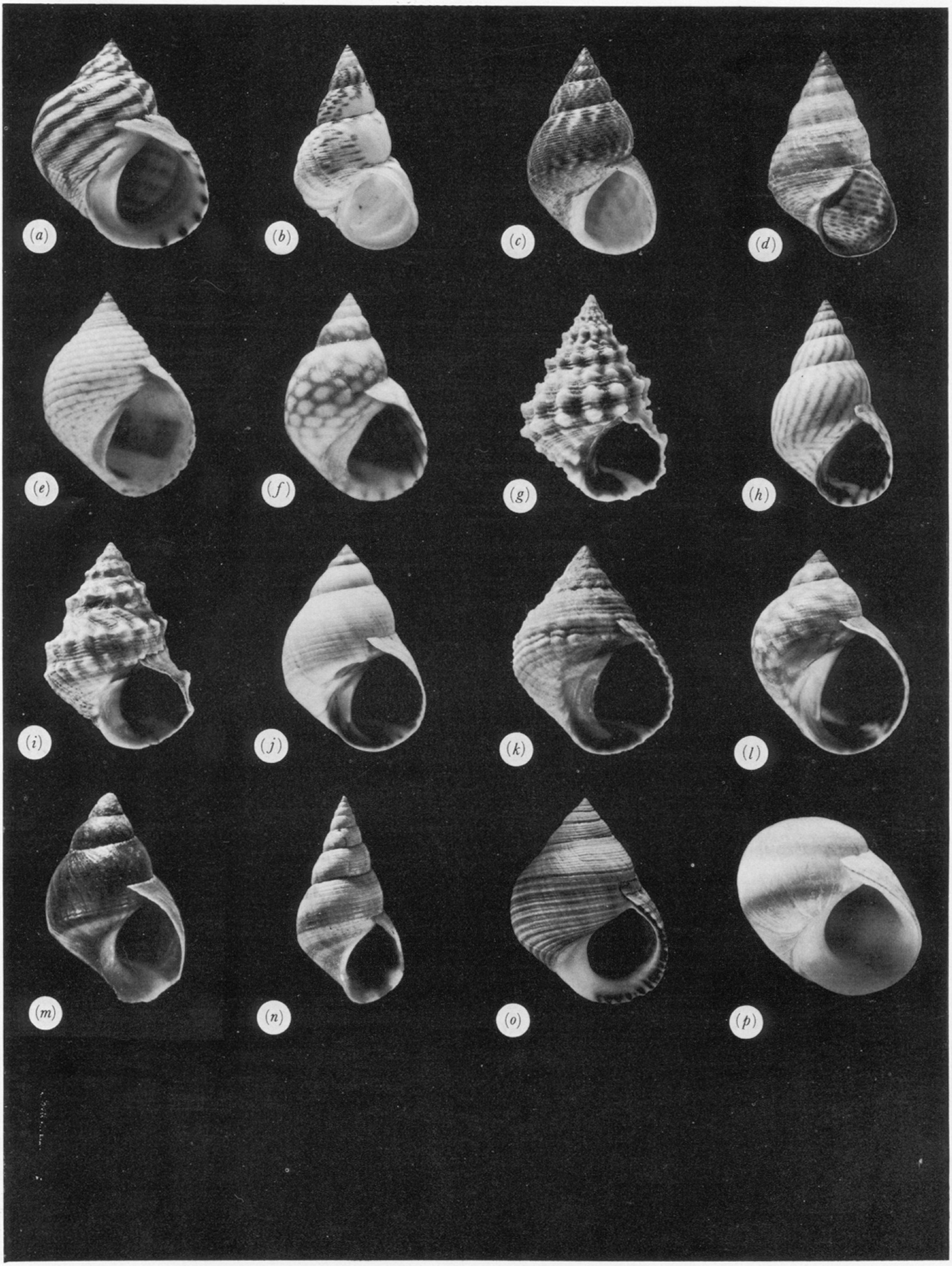

FIGURE 2. For description see opposite.

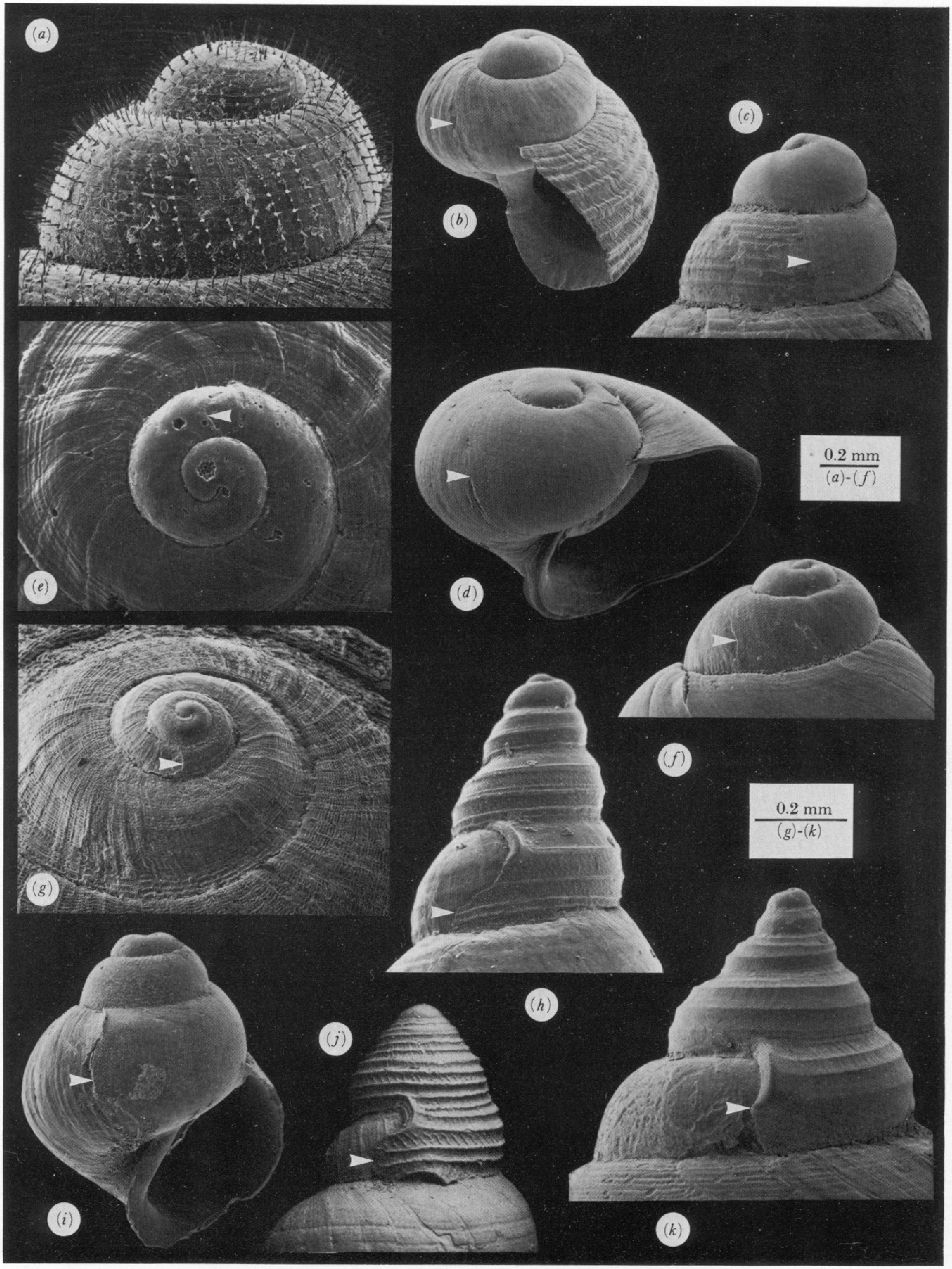

FIGURE 3. For description see opposite.