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THE SYSTEMATICS AND ECOLOGY OF THE MANGROVE-DWELLING *LITTORARIA* SPECIES (GASTROPODA: LITTORINIDAE) IN THE INDO-PACIFIC

VOLUME I

Thesis submitted by

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in May 1984

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the Department of Zoology at

James Cook University of North Queensland

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FRONTISPIECE

Shell colour polymorphism of *Littoraria* species. From top:

Row 1: *L. filosa*, Cockle Bay, Magnetic Island, Queensland; colour forms: Y0, Y2, B4, P0.

Row 2: *L. philippiana*, Cockle Bay, Magnetic Island, Queensland; colour forms: Y0, Y2, B5, P0.

Row 3: *L. pallescens*, Ao Nam-Bor, Phuket Island, Thailand; colour forms: Y0, Y3, B5, P0.

Row 4: *L. luteola*, Kurnell, Botany Bay, New South Wales; colour forms: Y1, Y3, B4, P0.

Row 5: *L. albicans*, Santubong, Sarawak; colour forms: Y0, Y2, Y3, P0.

ABSTRACT

The supposed species '*Littorina scabra* (L.)' has been noted for its extreme variability in shell form and colouration. The project was undertaken with the aim of investigating this variability and its possible adaptive significance.

Recent taxonomic treatments of the '*scabra* group' (comprising the members of the family Littorinidae associated with mangroves in the Indo-Pacific) have recognized three species. Using material personally collected and specimens from fourteen museums, the taxonomy of the *scabra* group was revised, demonstrating the existence of 20 species and one subspecies. Initially, species were defined by the diagnostic morphology of the penis and sperm nurse cells. The form of the pallial oviduct is described in detail, demonstrating that some species are ovoviviparous while others produce egg capsules. In addition, the radula, alimentary system, pallial complex and colouration of the head-foot are described, although less useful for taxonomic purposes than the reproductive anatomy. Once species were defined by anatomical criteria, characters of the shell such as shape, sculpture, columella and protoconch were shown to be rather uniform and adequate for the identification of species in most cases. Systematic descriptions and full synonymies are given for each species.

For comparative purposes, the anatomy of 42 other littorinid species was examined. Employing the method of cladistic analysis, the anatomical data were used to construct a tentative phylogeny of the family Littorinidae. The *scabra* group is classified in the genus *Littoraria*, which is shown to be the sister group of *Nodilittorina*. A cladogram of the 36 Recent species of *Littoraria* is presented, and four subgenera are recognized.

Distribution maps are given for each species in the *scabra* group, and were compiled from a total of 1900 museum collections. The biogeography of the group is discussed. The species can be divided into two classes, characteristic of continental and oceanic habitats respectively, and the members of the latter group show the greatest geographical ranges. The form of the protoconch and data in the literature suggest that both oviparous and ovoviviparous species are widely dispersed as planktotrophic veligers. It is suggested that speciation may be occurring in the peripheral regions of the Indo-Pacific, and that species have accumulated in the central region of highest diversity.

The zonation and abundance of *Littoraria* species were quantified on transects through mangrove forests at 14 localities in Australia, South-east Asia and Hawaii. Species were found to show characteristic patterns of vertical and horizontal zonation, although the degree of overlap between sympatric species was considerable. There was a clear distinction between species dwelling on bark and those on foliage. Densities of *Littoraria* species were very low, except on the trees at the outermost edge of the forest. It is suggested that landward limits of horizontal zonation may be determined by physiological tolerance, and vertical distribution by behavioural responses.

Detailed ecological investigations were carried out at Cockle Bay, Magnetic Island, Queensland. Here five *Littoraria* species were common. From lowest to highest, the order of vertical zonation of these species on *Rhizophora* trees was: *L. articulata* and *L. intermedia*, *L. scabra*, *L. philippiana*, and on *Avicennia* trees: *L. articulata*, *L. filosa*, *L. philippiana*.

The snails were highly mobile, those from the lower levels (*L. articulata*, *L. intermedia*, *L. scabra*) migrating vertically with each tidal cycle, to avoid submersion. Those from the higher levels (*L. filosa*, *L. philippiana*) periodically moved down to the water surface at high tide, and were active during the night, early morning and during light rain. All species occupied higher tidal levels during spring tides, and those from higher levels occurred further up the trees during rain. All species showed a vertical size gradient, with smaller individuals at the lower levels. Intense predation pressure at low levels during high tides is believed to have been the selective force responsible for the vertical migration behaviour.

At Cockle Bay the three species from lower levels were found to be reproductively mature throughout the year, and spawning probably occurred each month. The two species from higher levels were reproductively mature only during the wet summer months. There was no correlation between the method of development (release of either pelagic egg capsules or planktotrophic veligers) and the habitats of the species. Phylogenetic patterns of method of development and of breeding season in the Littorinidae are discussed.

Population dynamics of *L. intermedia*, *L. scabra*, *L. philippiana* and *L. filosa* were investigated by a multiple mark and recapture technique. Despite probably continuous spawning, recruitment of *L. intermedia* and *L. scabra* was only significant following the peak spawning period in January and February. In contrast, recruitment of *L. filosa* was highly successful, perhaps because this species settled on foliage, out of reach of predatory crabs. The subsequent survivorship of *L. filosa*, under more rigorous microclimatic conditions, was relatively low. Survivorships of all species were lowest in the smallest size classes and in the summer months, and all showed a marked drop in survivorship during three weeks of monsoonal rain.

Growth rates, as measured on the individually numbered snails, are the highest recorded for the family. Values of the instantaneous size-specific growth rate (k in the von Bertalanffy growth equation) ranged from 0.05 to 0.25 per month. *L. intermedia* and *L. scabra* attained a size of 6 mm in the first month of growth following settlement, and reached the minimum size for sexual maturity in 3 to 4 and 6 to 8 months respectively. Growth rates were highest during the summer months, with the exception of *L. filosa*, in which the season of maximum growth followed that of spawning. These patterns are related to the zonation and feeding behaviour of the species. Few individuals survived to reach 2 years of age, but maximum longevity may be 6 years.

The major predators of the post-larval stages of *Littoraria* species at Cockle Bay were crabs of the genus *Metopograpsus* and the species *Thalamita crenata*. Direct estimates of the causes of death of snails were obtained for artificial populations of *L. filosa* in exclusion cages. Crabs caused 57% of the total loss, or 86% of the total mortality, of *L. filosa* in the size range 7 to 12 mm, accounting for the loss of 19% of the population per month. Bird predation appeared to be insignificant. The severity of crab predation on *Littoraria* species was supported by an analysis of the repaired breakages of the shell, which indicated sublethal damage by crabs. The average numbers of repairs per adult shell were between 0.7 and 3.5 in the five species at Cockle Bay. The rate of sublethal damage (repairs per whorl per month) was highest in 2 to 5 mm shells of *L. intermedia*, *L. scabra* and *L. philippiana*, although in *L. filosa* the rate was highest in adult shells (23 mm). This pattern is explained by the much lower resistance of the thin-shelled *L. filosa* to attack, as demonstrated in laboratory predation trials. The distribution of crabs on the trees at Cockle Bay suggested a gradient of increasing intensity of predation at lower tidal levels. A corresponding interspecific gradient of increasing shell thickness in the species typical of lower tidal levels was shown at nine out of ten of the localities where zonation was recorded on transects, and this is interpreted as an adaptive trend. Interspecific trends of increasing shell size, stronger sculpture and narrower shells at higher tidal levels are interpreted as adaptations to the more rigorous microclimatic conditions at higher levels.

Within the *scabra* group, nine species show a phenotypically similar colour polymorphism, with yellow, pink or brown shells, while the remaining species are merely variable in the degree of shell pigmentation. The degree of colour variation was greatest in

Littoraria species typically found on foliage at the higher tidal levels, while species from bark substrates at lower levels were brown. In some species there was a suggestion of a direct influence of the substrate upon shell colour. This was not the case in *L. filosa*; in this species the polymorphism was presumed to have a genetic basis, and the mechanisms maintaining the polymorphism were investigated. Evidence is presented for the action of visual selection on *L. filosa* on backgrounds of different colour, although the predators involved were not identified. Climatic selection did not appear to be operating. The shell colour forms did not show significant behavioural differences. Manipulation of the colour proportions of *L. filosa* on isolated trees showed that disappearance of colour forms was frequency-dependent. On the basis of this evidence and the persistent rarity of the conspicuous pink colour form, it is concluded that the polymorphism is maintained by apostatic selection.

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CHAPTER 1: GENERAL INTRODUCTION

Members of the family Littorinidae are to be found in almost all the oceans of the world (Rosewater, 1970), and are often abundant in the intertidal zone on rocky shores. This distribution makes them readily accessible, and they have been studied intensively, perhaps to a greater degree than any other family of prosobranch gastropods. A bibliography of the family by Pettitt (1974a, b, 1979) listed over 900 references, covering many aspects of the biology of the group.

Littorinids are typical of rocky substrates, but it has long been known that a small number of species occur in association with mangrove vegetation. In recent years those from the Indo-Pacific province have been classified as three closely related species, of which '*Littorina scabra* (L.)' was the most familiar (Rosewater, 1970, 1980b). In addition to the peculiarity of their habitat, the '*scabra* group' has been thought to be unusual by virtue of ovoviviparous development, reduction of the gills for respiration in air, and extreme variability in the shape, size, sculpture and colouration of the shell. Beyond the treatment by various taxonomists, based largely on characters of the shell, the *scabra* group has remained virtually unstudied.

The past ten years have seen a considerable growth of interest in the Littorinidae amongst workers in Britain and Europe. A recent review (Raffaelli, 1982) lists more than 40 papers on the ecology and systematics of the group published during this period. This interest was stimulated by the discoveries that two apparently well known, but conchologically variable, species, *Littorina obtusata* and *Littorina saxatilis*, were comprised of two and four species respectively (Chapter 2; review by Raffaelli, 1982). This brought the total number of littorinid species on European coasts to eight, and encouraged research in two main fields. One area of research has involved reexamination of the problem of variation of shell shape and colour. In the light of the reclassification, correlations of shell characters with environmental conditions have started to emerge, which are suggestive of their adaptive significance. The other area of research has compared the population biology of these closely related species, which show a wide range of developmental types.

The present study commenced with the aim of investigating the supposed intraspecific variation of '*Littorina scabra*'. Preliminary work at localities in northern Queensland indicated that at least five species had been confused under this specific name, but that these could be distinguished by details of the shell and soft anatomy. Accordingly, ecological surveys were made in order to describe the habitats and zonation patterns of these previously unrecognized species. A study site at Magnetic Island was chosen for the investigation of aspects of migration behaviour, reproduction, growth rate and population dynamics. Comparisons with the results of studies in Europe, and with the limited work on other tropical littorinids, were interpreted in the light of contrasts between tropical and temperate ecosystems, and between the habitats provided by mangrove forests and rocky shores. It was found that the species of the *scabra* group occupy successive but overlapping vertical zones on the mangrove trees. This provided a suitable situation in which to test the hypotheses of Vermeij (review by Vermeij, 1978) concerning the adaptive significance of shell architecture in relation to predation and temperature control. When the species within the group were correctly distinguished, several showed conspicuous shell colour polymorphism, and the basis and maintenance of this variation were considered.

In order to resolve the taxonomic confusion surrounding the *scabra* group, it was necessary to make a complete revision of all the mangrove-associated species in the Indo-Pacific province. This work, comprising Part I of the thesis, is a slightly abbreviated version of a monograph in press with the British Museum (Natural History). Four new names (*Palustorina* n. subgen., *Littoraria* *vespacea* n. sp., *Littoraria subvittata* n. sp., *Littoraria cingulata pristissini* n. subsp.) and a number of new combinations are introduced. These are employed herein, and descriptions are included, but this does not constitute publication in the meaning of the International Code of Zoological Nomenclature (1964: Articles 8 and 9). The new names will not be available until publication of the monograph.

PART I: SYSTEMATICS

CHAPTER 2: INTRODUCTION AND AN HISTORICAL REVIEW

The taxonomy of the family Littorinidae was until quite recently based exclusively upon the characters of the shell, as in the case of many molluscan groups. Several littorinids, and in particular members of the genus *Littorina* in Europe, have been noted for their extreme variability in shell colour and sculpture. However, the examination of the anatomical features of some of these supposedly polymorphic species has led to a re-evaluation of their classification. The most well known case concerns the *Littorina saxatilis* species complex in Europe. The taxonomic history of this group will be briefly reviewed, since it shows parallels with that of the *scabra* group, and provides an instructive example for further taxonomic work on the family.

During the late eighteenth and early nineteenth centuries nineteen species were described in the *saxatilis* group (Fischer-Piette & Gaillard, 1971), but this diversity was reduced, on the basis of shell characters, to seven subspecies and twelve varieties by Dautzenberg & Fischer (1912). As interest in polymorphism and variation increased, the distribution of the colour and form varieties was studied, notably in the long series of papers by Fischer-Piette & Gaillard (1971, and references therein). James (1968) used anatomical characters, including the penis, radula and pigmentation pattern, as well as shell shape and colour, to define five subspecies, which were said to be distinct in Britain but to interbreed elsewhere. In subsequent investigations greater emphasis was placed on penial anatomy and the method of development, whether oviparous or ovoviviparous, leading to the recognition of three species within the complex (Sacchi, 1975; Heller, 1975a; Raffaelli, 1979a). Genetic analysis based upon isoenzyme patterns has confirmed the interpretation of the morphological evidence, by demonstrating that the species are reproductively isolated (Wilkins & O'Regan, 1980). Most recently, Hannaford Ellis (1979) separated a new species from the well known *Littorina rudis*, primarily on the basis of female reproductive anatomy and the method of development, even though the shells of the two were sometimes indistinguishable. The validity of a species definition based entirely upon reproductive anatomy and method of development has been questioned (Caugant & Bergerard, 1980; Smith, 1982), but in this case is supported by isoenzyme analysis (Ward & Warwick, 1980) and differences in breeding seasons (Hannaford Ellis, 1983). The status of *Littorina saxatilis* (Olivi) itself, described from Venice, remains in doubt, but it will probably prove to be a senior synonym of *Littorina rudis* (Maton) (Smith, 1982; Raffaelli, 1982; Hannaford Ellis, 1983) and is used as such here. The disjunct distribution may be explained by the introduction of the species to Venice (Smith, 1982), as has also occurred in South Africa (Hughes, 1979b). Once discrete species were recognized within the *Littorina saxatilis* complex, it became possible to investigate ecological segregation of species and to consider the adaptive significance and maintenance of the shell polymorphisms (Heller, 1975b, 1976).

Other variable taxa which have recently been shown, on the basis of anatomical characters, to comprise several species, include *Littorina obtusata* (L.) (Sacchi & Rastelli, 1967), *Nodilittorina ziczac* (Gmelin) (Borkowsky & Borkowski, 1969; Bandel & Kadolsky, 1982) and *Littorina scutulata* Gould (Murray, 1979). These case histories set precedents with important implications for any taxonomic work on the family Littorinidae. While certain shell characters are highly variable and subject to local adaptation, the range of variation within species may not be as great as has been supposed. Nevertheless, certain species cannot be separated using shell characters alone, and reproductive anatomy appears to be of primary taxonomic significance. Specimens must be examined from throughout the geographical range to determine the status of distant populations. These considerations have been applied in the taxonomic revision of the *scabra* group.

The following historical review traces the changes in species concepts in the *scabra* group, and demonstrates the degree of confusion which has in the past surrounded these littorinids. The term '*scabra* group' is used to include all species formerly classified in the genus *Littorina* (and here recognized as the genus *Littoraria*, Chapter 8) which occur in mangrove habitats in the Indo-Pacific province. The use of quotation marks for a specific epithet indicates either that the author quoted included several species (as here defined, Chapter 9) under the one name, or otherwise provided insufficient information for the interpretation of his concept of the species.

The specific name *scabra* was published by Linnaeus in 1758, but as early as 1705 Rumphius had described and illustrated '*Buccinum foliorum*', noting its habitat on mangrove trees. Between 1830 and 1857 thirty-one specific and varietal names were introduced for members of the *scabra* group. A further ten names appeared from 1871 until 1900, but previous to the three new taxa described herein only one new variety has been described this century. The first and most discriminating monographic treatment was that of Philippi (1847-1848), who recognized thirteen species in the *scabra* group, of which seven are retained unchanged here. Although the first anatomical drawings were made by Quoy & Gaimard in 1832, Philippi described only shells. He correctly recognized the extreme colour variation of *L. angulifera* from the tropical Atlantic and described seven colour varieties of *Litorina 'scabra'* and three of *Litorina 'intermedia'*. These latter two species are here shown to be rather uniform, and three of Philippi's varietal names are raised to specific rank. The monograph of *Littorina* by Reeve (1857) increased the number of recognized species to eighteen, but since his species concepts were narrow, six of these fall into synonymy. Weinkauff (1878,1882) made some attempt to synonymize, broadening the concept of *Litorina 'scabra'*, but essentially compiled the work of previous authors. The work of Nevill (1885) was not illustrated, his system of varieties and subvarieties is confusing, and his descriptions often inadequate. Nevertheless, with many specimens before him, Nevill was able to make some sensible suggestions concerning variation, sexual dimorphism and synonymy. The concept of *Littorina 'scabra'* as a single, widely variable, pantropical species was established by Tryon (1887). In addition to the nominate form (which covered five of the species here recognized), Tryon admitted a variety *lineata* (the tropical Atlantic species *L. angulifera*), a variety *'intermedia'* (comprising three of the smaller species) and a variety *'filosa'* (including all the colourful ribbed and carinate forms, amongst which seven species can be distinguished). Other names in the *scabra* group were distributed between ten other species. Working at about the same time, von Martens was not influenced by Tryon, but followed Philippi, so that his concepts of species were essentially correct, as shown by his list from the East Indies (von Martens, 1897).

Subsequent work, until 1965, consisted mainly of faunistic lists and, latterly, figures of shells in popular texts. Authors often followed Philippi and von Martens in recognizing several species (Casto de Elera, 1896; Hidalgo, 1904–1905; Annandale & Prashad, 1919; Prashad, 1921; Oostingh, 1927; Dautzenberg, 1929; Yen, 1942; Kuroda & Habe, 1952), but in doing so the earlier errors were perpetuated, particularly in regard to the several species confused under the name *Littorina 'intermedia'*, and few new contributions were made. Some authors followed Tryon's broad species concept (Fischer, 1891; Melvill & Standen, 1901; Dautzenberg & Fischer, 1905; Schepman, 1909). The first use of radular characters in the taxonomy of species of *Littoraria* was by Adam & Leloup (1938) who, on the basis of supposed similarity in radular teeth, reduced *Littorina 'filosa'* (= *L. pallescens*) to a variety of *L. scabra sensu stricto*. A new standard in littorinid taxonomy was set by Abbott (1954) and Whipple (1965), who described not only the characters of the shell, but also of the radula, male reproductive anatomy and egg capsules. Whipple (1965) gave a description of *L. intermedia* (as

Littorina scabra).

The comprehensive monograph of the Littorinidae of the Indo-Pacific by Rosewater (1970, 1972) has provided an invaluable source of reference for all subsequent studies of the family. This work established generic and subgeneric groupings based on penial and radular characters, but returned to Tryon's concept of *Littorina 'scabra'* as a widely variable species. Three species were admitted in the *scabra* complex, and placed together in the subgenus *Littorinopsis*. These were *Littorina 'scabra'* (here divided into seventeen species), *Littorina 'carinifera'* (here divided into two species) and *Littorina melanostoma*. Rosewater (1963, 1970, 1980b, 1981) regarded *Littorina 'scabra'* as a pantropical species, with subspecies *Littorina 'scabra scabra'* in the Indo-Pacific, *Littorina scabra angulifera* in the Atlantic and *Littorina scabra 'aberrans'* in the Eastern Pacific.

The status of *L. angulifera*, described by Lamarck (1822) from the Caribbean, has been the subject of debate since 1832 when Quoy & Gaimard applied the name to the Indo-Pacific *L. scabra s. s.*, whilst in 1842 d'Orbigny determined the Caribbean shells as *Littorina 'scabra'*. Subsequent authors, with such exceptions as Tryon (1887) and Bequaert (1943), have mostly recognized that *L. angulifera* is a distinct species, probably basing this decision largely upon the fact of its geographical isolation from the Indo-Pacific *L. scabra* group, since similarities of the shells have usually been stressed. More recently, the two have been separated on the basis of supposed radular differences (Marcus & Marcus, 1963; Bandel, 1974; but see Rosewater, 1980b, for an illustration of the similarity), and no other anatomical comparisons have been made. Now that species of the *L. scabra* group are more clearly defined, it is evident that *L. angulifera* and *L. scabra s. s.* can easily be separated by shell characters alone, and that the penes of the two species are entirely different (Section 9.2.3.1) The anatomy of *L. aberrans* is as yet unknown, but the shell, and particularly the protoconch (Section 4.3) is sufficiently distinctive that it must be given full specific status also.

Most subsequent authors have adopted Rosewater's classification, with the exceptions of Fischer (1970), Higo (1973) and Brandt (1974). Accounts of reproduction and ecology of some Indo-Pacific *Littoraria* species have been given by Abe (1942), Kojima (1958c), Struhsaker (1966), Berry & Chew (1973) and Muggeridge (1979), but in each case only one species was involved so that no taxonomic problems were raised. However, Nielsen (1976), describing zonation of littorinids in a mangrove forest in Thailand, observed that a large form with a white, wide columella (i.e. *L. scabra s. s.*) occurred only at the seaward edge, while smaller shells (i.e. *L. pallescens* and *L. intermedia*) were found throughout the forest. Cook (1983) examined proportions of colour morphs of *Littoraria* in a mangrove forest in New Guinea and separated three (unnamed) species using shell and penial characters (*L. pallescens, L. scabra, L. intermedia*).

The first part of the thesis comprises a taxonomic revision of the *scabra* group, including all species of the genus *Littoraria* which occur in mangrove forests in the Indo-Pacific province. The remaining species in the genus (as listed, Section 8.1.2) have all been examined, but since the majority are well known, they are discussed here only for purposes of comparison. The arrangement of the chapters is as follows. Firstly, an account is given of the material examined, and of the techniques of measurement and dissection (Chapter 3). The morphology of the shell and of the animal in the genus *Littoraria* are described in Chapters 4 and 5 respectively, and features are evaluated as taxonomic characters. Comparisons are drawn with other genera in the family and, where possible, character states are assessed as ancestral or derived, as a basis for decisions concerning generic classification and for a discussion of phylogenetic relationships (Chapter 8). The reclassification of the *scabra* group has been based entirely upon morphological evidence, but it is consistent with the ecological studies of habitat, zonation, behaviour and reproduction described in Part II. Field observations of copulation behaviour, described in Chapter 6, support the idea that the species as defined by morphological criteria are reproductively isolated. Chapter 7 combines data on geographical distribution (from the species records in Chapter 9) with inferences concerning developmental type and dispersal (as derived from observations of larval shells and reproductive anatomy), in a discussion of the biogeography of the genus *Littoraria*. In Chapter 8, the comparative anatomical studies are synthesized in the suggested phylogenies and formal classification of the genus *Littoraria* and of the family Littorinidae. Finally, the data on which the revision is based are presented as formal descriptions of the species in the *scabra* group, together with full synonymies, lists of material examined and notes on habitats (Chapter 9).

For taxonomic purposes, characters of the shell are the most convenient to use. Once the species in the *scabra* group had been defined by reliable anatomical criteria (Chapter 5), shell colour and size were found to be highly variable within species, but shape and sculpture relatively constant (Chapter 4). Shell characters alone are therefore adequate for the identification of the majority of specimens of *Littoraria*, and have been used in the construction of a key (Section 9.1).

CHAPTER 3: MATERIALS AND METHODS

3.1 Material, types and synonymies

The taxonomic work has been based largely upon material collected personally throughout Australia, in South East Asia and Hawaii. In addition, all the collections of the following institutions have been examined: British Museum (Natural History); National Museum of Wales; Australian Museum; Queensland Museum; National Museum of Victoria; Western Australian Museum; National Museum of Natural History, Smithsonian Institution; Academy of Natural Sciences of Philadelphia; Museum of Comparative Zoology, Harvard University; Natal Museum; Rijksmuseum van Natuurlijke Historie; Zoological Research Collection, National University of Singapore; Sarawak Museum; and Phuket Marine Biological Center, Thailand. In total this material comprised over 1900 collections of species in the *scabra* group.

All type specimens referred to in the synonymies have been examined unless otherwise noted. Holotypes of new species described herein, and also neotypes, have been deposited in the British Museum (Natural History), with the exception of the new subspecies *L. cingulata pristissini*, located in the Australian Museum. Paratypes have been deposited in both institutions, and in the National Museum of Natural History, Smithsonian Institution.

The status of type material of the many species and varieties described by Philippi deserves special comment. In 1846 Philippi published descriptions of new species of *Littorina* in the collection of H. Cuming, and these were subsequently figured in his monograph of the genus (1847-1848). Lectotypes of most of these species were designated by Rosewater (1970) from the Cuming Collection in the British Museum. Often Cuming's original label accompanies the specimens and in all such cases the specific name is inscribed in a different hand and followed, as in Philippi's monograph, by the abbreviation 'Ph.'. The handwriting has been authenticated as that of Philippi himself by comparison with labels in the collection of the Senckenberg Museum, Frankfurt (R. Janssen, pers. comm.). Usually Philippi acknowledged Cuming when he illustrated specimens from his collection, but did not always do so. Several additional species and varieties were described by Philippi in his monograph and in those cases in which material from Cuming was acknowledged, specimens in the British Museum have been identified as types with some confidence. Types of the remaining taxa are not present amongst the collections of Philippi in either the Museum für Naturkunde, East Berlin (R. Kilias, pers. comm.) or in the Museo Nacional de Historia Natural, Santiago, Chile (N. Bahamonde, pers. comm.). Philippi described two species from material received from Largilliert, and in these cases lectotypes (now housed in the MNHNP) have been designated from the Largilliert Collection in the Natural History Museum of Rouen. In a few cases specimens originating from localities mentioned by Philippi and closely resembling his figures, have been discovered in the British Museum, together with Cuming's labels, named by Philippi as described above. On the basis of this evidence these specimens can be accepted as lectotypes. Types of the remaining species must be presumed lost, and Philippi's figures have been designated as lectotypes. Lectotype designation is especially important for the varieties of *Litorina 'scabra'* and *Litorina 'intermedia'* illustrated in Philippi's plate 5, of which figures 6 to 11 were incorrectly cited in the text, as has also been noted by Weinkauff (1878) and Nevill (1885).

Lectotypes of the taxa described by Nevill (1885), housed in the Zoological Survey of India and designated herein, were selected by N.V. Subba Rao on the basis of measurements given by Nevill.

Problems have been encountered in the compilation of synonymies, owing to the frequent confusion in the literature of species of similar appearance. Shell characters are often diagnostic, so that published figures can usually be correctly determined. In the absence of adequate descriptions or figures, references by authors to original descriptions and to earlier figures have aided interpretation of species concepts, and in a few cases the known geographical distributions have also been of use. All new names are included in synonymies, but where an original figure could not be identified with certainty or a description of a new species was inadequate, the entry is preceded by a query. Other doubtful references have been omitted. In each synonymy an attempt has been made to compile the major taxonomic works, significant contributions to the classification of the species and references which contain lengthy synonymies. Certain major faunal lists have been included, while for rare or unusual species the mere recognition of the species as distinct has been a sufficient criterion. Obvious spelling errors in specific names have not been listed separately, but are included under the corrected spelling. Of generic names, *Melarhaphe* and *Littorina* have been emended or misspelt by several authors (Section 8.1.1) and are entered separately in the synonymies.

3.2 Methods

3.2.1 Shell characters

Recent taxonomic studies of littorinids have employed indices of shell shape derived as simple ratios of length, width and aperture size (James, 1968; Heller, 1976; Hannaford Ellis, 1979; Raffaelli, 1979a), but the precise measurements taken have varied. The parameters defined by Raup (1966) from a geometrical analysis of shell coiling have been used to examine shell variation in *Littorina* '*saxatilis*' by Newkirk & Doyle (1975), but are not readily visualised and so are unsuitable for the purposes of descriptive taxonomy.

The measurements taken here are illustrated in Figure 3.1. Shell height (H) is the maximum linear dimension of the shell from the apex to the anterior edge of the lip. Erosion of the shell seldom occurs in the mangrove habitat and apices are usually intact so that shell height is a suitable measure of shell size. The species investigated here possess a prominent peripheral keel or a system of spiral ribs and shell breadth (B) was measured from the junction of the peripheral rib with the outer apertural lip to the corresponding point half a revolution earlier. In species with a flared lip, B was measured just behind the apertural expansion. These measurements of shell height and breadth were preferred to those parallel and perpendicular to the axis of coiling, for they are more accurately reproducible. Apertural length (LA) was measured as the maximum external dimension, and apertural width (WA) as the maximum external dimension perpendicular to LA. These four measurements were combined as follows to give indices of shell shape:

Shell proportion PR = height H / breadth B

Apertural shape (circularity) S

= apertural width WA / apertural length LA

Relative spire height SH = height H / apertural length LA

Dimensions of type specimens and of lectotype figures are given in the species descriptions, together with measurements of a number of shells to indicate the range of size and shape encountered. Approximate columellar width (C) is also given; using a micrometer eyepiece the measurement was made perpendicular to the axis of the columellar pillar, from the mid point of its height to the furthest point of the inner apertural lip. All measurements were made on 'adult' shells, as defined by a thickening or flaring of the apertural lip and a laying down of opaque callus within. This development indicates a slowing or cessation of shell growth and does not necessarily correspond to the point at which sexual maturity is attained (Section 13.4.7). In young, actively growing shells the peristome is thin and brittle.

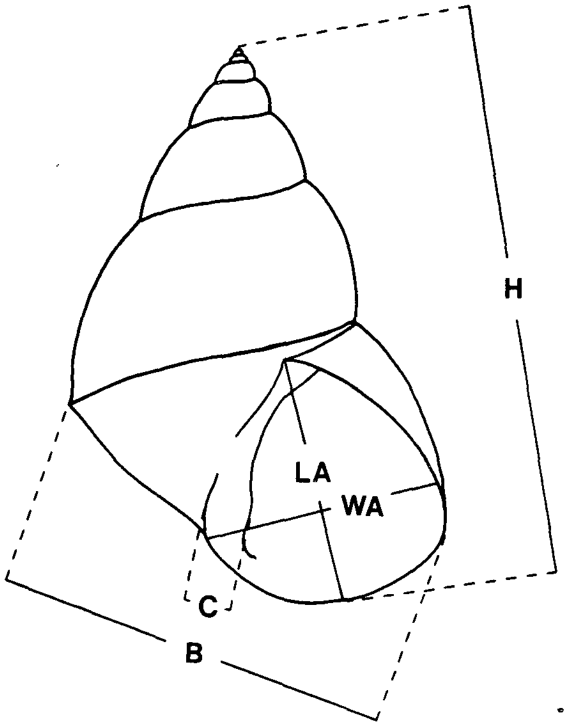


Fig. 3.1 Shell dimensions: B, breadth; C, columellar width; H, height; LA, apertural length; WA, apertural width.

Sexual dimorphism of adult shells was demonstrated by comparison of mean shell heights and of the three shape indices of a random sample of ten male and ten female shells from a representative locality. Ratios were compared using the non-parametric Mann-Whitney U-test, but to compare mean heights the more powerful parametric t-test was used (Zar, 1974). The sample size was small, but the object was to quantify dimorphisms which are often strikingly apparent, rather than to detect minute statistical differences.

In the species descriptions the spire is simply described as relatively tall or low (SH greater than 2.0 or less than 1.7 respectively), depending upon both apical angle and aperture size. Spire outlines are described as convex if the apical angle decreases with whorl number, or as concave if the angle shows an increase. The shell proportion (PR) provides an indication of the acuteness of the apical angle at the last whorl. The number of whorls of the teleoconch was counted from the sinusigera ridge terminating the protoconch (e.g. Fig. 9.22b).

In the descriptions of shell sculpture, spaces between the grooves are referred to as ribs, whether or not they are prominent or rounded. Primary ribs and grooves are defined as those present up to and including the fourth whorl of the teleoconch. Secondary and higher orders of sculpture appear subsequently, formed by division or intercalation of ribs. A similar system of description of orders of sculpture has been used by Rosewater (1982) and Bandel & Kadolsky (1982). The majority of species possess a peripheral keel or an enlarged peripheral rib, at least until the last whorl, where the outline may become more rounded. As the shell grows, the suture with the succeeding whorl overlies the peripheral rib. The number of primary grooves quoted in the species descriptions is that present above the peripheral rib. Usually this will be the number visible on the early spire whorls, but sometimes the most anterior groove is hidden in the suture. It is then necessary to trace the primary grooves to the last whorl in order to be sure of the identification of the peripheral rib. In the few species with a rounded periphery and uniform ribs, the peripheral rib is defined as that to which the suture is attached on the penultimate whorl. Groove width is quoted as a fraction of the average rib width and, since relative groove width increases with whorl number, the figure given is the maximum value. On the last whorl ribs are more prominent than grooves and sculpture is described as the total number of ribs, including those on the base below the periphery. Other descriptions of sculpture on the last whorl refer only to the area between the suture and the periphery.

Details of shell microsculpture and of the protoconch are visible at low magnification, but photographs were taken with the scanning electron microscope after coating of specimens with gold and palladium. The terminology of Thiriot-Quiévreux (1972) and Robertson (1974) was adopted in designating as the protoconch the entire larval shell formed prior to metamorphosis. The embryonic shell, formed by the shell gland, is termed 'protoconch I', and the remainder of the larval shell, deposited by the mantle edge, is termed 'protoconch II' (review by Jablonski & Lutz, 1983). The protoconch is terminated by a strong axial rib, the sinusigera ridge, marking the point at which metamorphosis occurred. The postlarval shell or teleoconch is formed by the mantle edge after metamorphosis.

Where ranges of figures are given, values in parentheses are extremes of the range which are rarely encountered.

3.2.2 Anatomical characters

The colouration of the head-foot was described from living animals when specimens were collected personally (personal collections are indicated by the abbreviation DGR in the lists of locality records, Chapter 9). Pigment is, however, well preserved in material fixed in formalin. Penes were drawn by camera lucida. For species collected personally, living animals, relaxed in a 1% solution of propylene phenoxetol in sea water, were used. Penis length was measured from filament tip to the attachment of the base to the head-foot.

Spermatozoa were removed from the vas deferens of living animals and fixed in a 1% solution of glutaraldehyde in sea water before examination with a light microscope and drawing by camera lucida. Each group of nurse cells illustrated was taken from a single individual. Where living specimens were not available, material fixed in formalin was used; although eupyrene sperm were then agglutinated, nurse cells were often well preserved and comparison with fresh material showed that their shape and structure were normal. Dimensions of nurse cells are maximum lengths including projecting rods, but excluding flagella.

The pallial oviducts were drawn from material fixed in formalin. Their complex structure was investigated by cutting gross serial transverse sections under a dissecting microscope. The sections drawn in the systematic account are those passing through the apex of the spiral of the oviduct. Shading of the several glandular elements of the oviduct follows that used in Figures 5.4 and 5.5. Dimensions of the largest oviduct seen are recorded in each description; the seminal receptacle was not included in the measurement of overall length. The diameter of the spiral section is the maximum in any direction, and the length of the straight section of the pallial oviduct extends from the most anterior whorl of the spiral section to the terminal papilla or pore.

Egg capsules of *L. articulata* from Magnetic Island, Queensland, were released by snails kept in containers half filled with sea water. Spawning occurred on the day after collection from the field.

The following histological techniques were used to investigate penial and oviducal structure: staining in haematoxylin and eosin;

the Mallory-Heidenhain rapid one-step trichrome (Cason, 1950); and the alcian blue-periodic acid-Schiff technique for the histochemical differentiation of mucins (Mowry, 1956).

In order to assess the variability of the anatomical features described, from six to ten specimens of each species, from a wide geographical range, were dissected in detail. Penes were examined in many more animals. For the species *L. scabra*, *L. intermedia*, *L. philippiana*, *L. filosa* and *L. articulata*, the sperm, penes and oviducts of five or ten of each sex were examined each month during the course of a twelve month study of reproductive condition at Magnetic Island, Queensland (Section 13.2.1).

Radulae from at least four specimens of each species were dissected from material fixed in formalin. The radulae were soaked in 10% potassium hydroxide solution for two hours, cleaned by hand, stored in 70% ethanol and cleaned ultrasonically for 15 seconds before examination with the scanning electron microscope. All radulae were mounted flat and uncoated and were viewed from above. Total radular length was measured and the range of the ratio of radular length to shell height was recorded.

Of the species in the *scabra* group, anatomical data was obtained for all but *L. delicatula* and *L. flammea*. In addition, all other species of the genus *Littoraria* (listed in Section 8.1.2) were dissected, with the exception of *L. aberrans*. For purposes of comparison and discussion of phylogenetic relationships, the following members of other littorinid genera were dissected:

Bembicium : *melanostoma* (Gmelin); *nanum* (Lamarck)
Cenchritis : *muricatus* (L.)
Echininus : *antoni* (Philippi) (= *nodulosus* auctt.); *cumingi* (Philippi)
Fossarilittorina : *meleagris* (Potiez & Michaud); *mespillum* (Mühlfeld)
Littorina : *keenae* (Rosewater) (= *planaxis* Philippi); *littorea* (L.); *obtusata* (L.); *scutulata*

(Gould)

Melarhaphe : *neritoides* (L.)

Nodilittorina : *acutispira* (Smith); *angustior* (Mörch) (= *lineata* (Orbigny)); *australis* (Gray); *aspera* (Philippi); *dilatata* (Orbigny); *hawaiiensis* Rosewater & Kadolsky (=*picta* Philippi); *knysnaensis* (Philippi); *millegrana* (Philippi); *modesta* (Philippi); *praetermissa* (May); *pyramidalis* (Quoy & Gaimard); *sundaica* (Altena); *unifasciata* (Gray); *ziczac* (Gmelin)

Peasiella : sp. (Magnetic I., N. Qld.)

Tectarius : *grandinatus* (Gmelin); *pagodus* (L.)

Species in this list were identified from works by Anderson (1958), Rosewater (1970, 1972, 1981), Keen (1971), Fretter & Graham (1980) and Bandel & Kadolsky (1982). Generic concepts are based upon those of Bandel & Kadolsky (1982) and the results of original research (Chapter 8). Generalizations concerning the characters of littorinid genera are based upon the species listed and upon published accounts by other authors as quoted.

3.3 Zonation and distribution

Except where otherwise acknowledged, notes on habitat and zonation have been based upon personal observations at the localities in the list of records which are followed by the abbreviation DGR. The habitats and zonation patterns of *Littoraria* species are described in detail in Chapter 11.

Species distribution maps were compiled from the localities of the museum specimens seen. The locality records listed are those marked on the distribution maps and are not a complete list of all collections examined. So far as possible only reliable modern records were used; in those few cases in which doubtful records are listed the locality is preceded by a query and plotted as an open circle. Literature records were only included if they extended the known distribution significantly; they are noted as such and plotted as open circles on the maps.

3.4 Abbreviations

The following abbreviations have been used in the text, synonymies and tables:

A	Identification confirmed by anatomical data from preserved specimens (specified for *L. articulata* and *L. strigata* only).
AMS	Australian Museum, Sydney
ANSP	Academy of Natural Sciences of Philadelphia
B	shell breadth
BMNH	British Museum (Natural History), London
BPBM	Bernice P. Bishop Museum, Honolulu
C	columellar width
DGR	collection by the author; majority of material, including all figured specimens, now in BMNH
H	shell height
L.	genus *Littoraria*
LA	apertural length
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Mass.
MHNG	Muséum d'Histoire Naturelle, Geneva
MNHNP	Muséum National d'Histoire Naturelle, Paris
NM	Natal Museum, South Africa
NMV	National Museum of Victoria, Melbourne
NMW	National Museum of Wales, Cardiff
NSMT	National Science Museum, Tokyo
N.S.W.	New South Wales, Australia
N.T.	Northern Territory, Australia

NUS	National University of Singapore
PR	shell proportion = H/B
Qld.	Queensland, Australia
QM	Queensland Museum, Brisbane
RNHL	Rijksmuseum van Natuurlijke Historie, Leiden
S	apertural shape (circularity) = WA/LA
SH	spire height = H/LA
SM	Sarawak Museum, Kuching
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
W.A.	Western Australia
WA	apertural width
WAM	Western Australian Museum, Perth
ZSI	Zoological Survey of India, Calcutta

In particular it should be noted that the abbreviation *L.* refers only to the genus *Littoraria*. The appearance of a specific epithet in quotation marks indicates either that the author quoted included several of the species (as here defined, Chapter 9) under the one name, or otherwise did not provide sufficient information for the subsequent determination of the species.

CHAPTER 4: SHELL CHARACTERS

4.1 Shape, size and thickness

Statistical analyses of shell shape and size have sometimes been used to distinguish between closely related species of littorinids (Borkowski & Borkowski, 1969; Smith, 1981). However, most studies have emphasized the variability of these characters, particularly in relation to the degree of exposure of the habitat to wave action (James, 1968; Newkirk & Doyle, 1975; Heller, 1976; Raffaelli, 1979; Janson, 1982b) and in relation to selection by crab predators (Heller, 1976; Elner & Raffaelli, 1980). The adaptive significance of shape and other aspects of shell form are considered in Chapter 14. In the species of *Littoraria* associated with mangroves, shell shape is relatively constant within species, even in those with the widest geographical ranges, and is therefore a reliable taxonomic character. This constancy is perhaps a consequence of the planktonic dispersal of the species (Section 7.2) combined with the uniformly sheltered conditions prevailing in the mangrove environment. In contrast, the accounts of variability have referred to species with ovoviviparous or benthic development, found on rocky shores subjected to a wide range of exposures.

Although shape may be relatively uniform, adult shell size shows a two- to three-fold variation in most of the species of *Littoraria* in the *scabra* group. In general, individuals from unusual or extreme habitats, such as high level salt marshes, stunted mangrove bushes in full sunlight, or sheltered rocky shores, tend to be of the smallest size. Gallagher & Reid (1974) observed that *L. angulifera* and *L. irrorata* in Florida attain larger size in an apparently more favourable habitat. Trematode parasites are thought to produce gigantism in certain molluscan hosts (Wright, 1966; Sousa, 1983).

However, this effect can be ruled out in *Littoraria* species from mangroves, for of the several thousand specimens examined during the present study only five contained parasites, and these shells were not of especially large size. Muggeridge (1979) found no parasitic infection in *L. luteola* (as *Littorina scabra*) at Patonga, N.S.W.

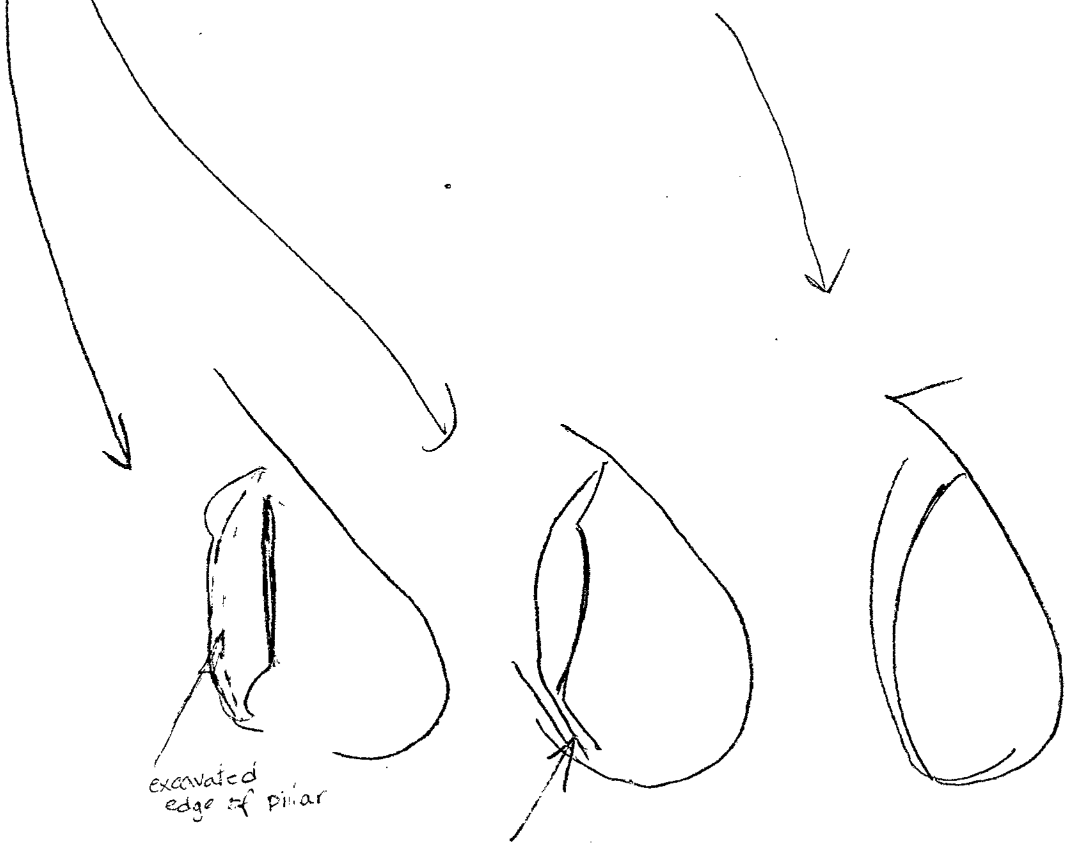
The shape of the aperture does not vary greatly between species of *Littoraria*. In most species the peristome is coplanar and the angle between this plane and the coiling axis of the shell (the angle of elevation of the coiling axis, Vermeij, 1971) is such that the peristome lies flush with a flat surface when the shell is placed upon it. This form may be adaptive for snails living on the predominantly flat surfaces of leaves and trunks. In *L. scabra* the apertural plane is generally hollowed anteriorly to fit the narrow aerial roots of the mangrove trees (*Rhizophora*) upon which it is often found; this is probably a direct mechanical effect of the substrate, as observed in *L. irrorata* by Bingham (1972a).

In young, actively growing shells the apertural lip is thin, sharp and brittle. Certain species of *Littoraria* exhibit a conspicuous flaring and thickening of the outer lip of the aperture when growth slows or ceases, while in other species the lip is merely somewhat thickened from within. If growth is later resumed, a flared lip remains as a prominent varix interrupting the body whorl of the shell. Flaring of the lip is particularly common amongst those species of the subgenera *Littorinopsis* and *Lamellilitorina* with thin shells, which occupy higher tidal levels. Regular measurement of marked individuals in the field at Magnetic Island, Queensland, has shown that in *L. filosa* and *L. philippiana* growth ceases and the lip is flared and thickened during a period coinciding with the annual breeding season (Section 13.3.3). In these two species not every mature individual forms a flared lip when growth ceases, although the majority do so. The tendency to develop a flared lip and varices is more marked in males than in females in all species with this habit, despite the observation of Sewell (1924) to the contrary in a small sample of *Littorina* *'scabra'*. The distribution of varices in *L. luteola*, *L. delicatula* and *L. ardouiniana* suggests that in these species they may also be formed annually. However, *L. albicans* may possess as many as twenty varices and an annual breeding season is perhaps unlikely to account for their formation, unless the species is unusually long lived.

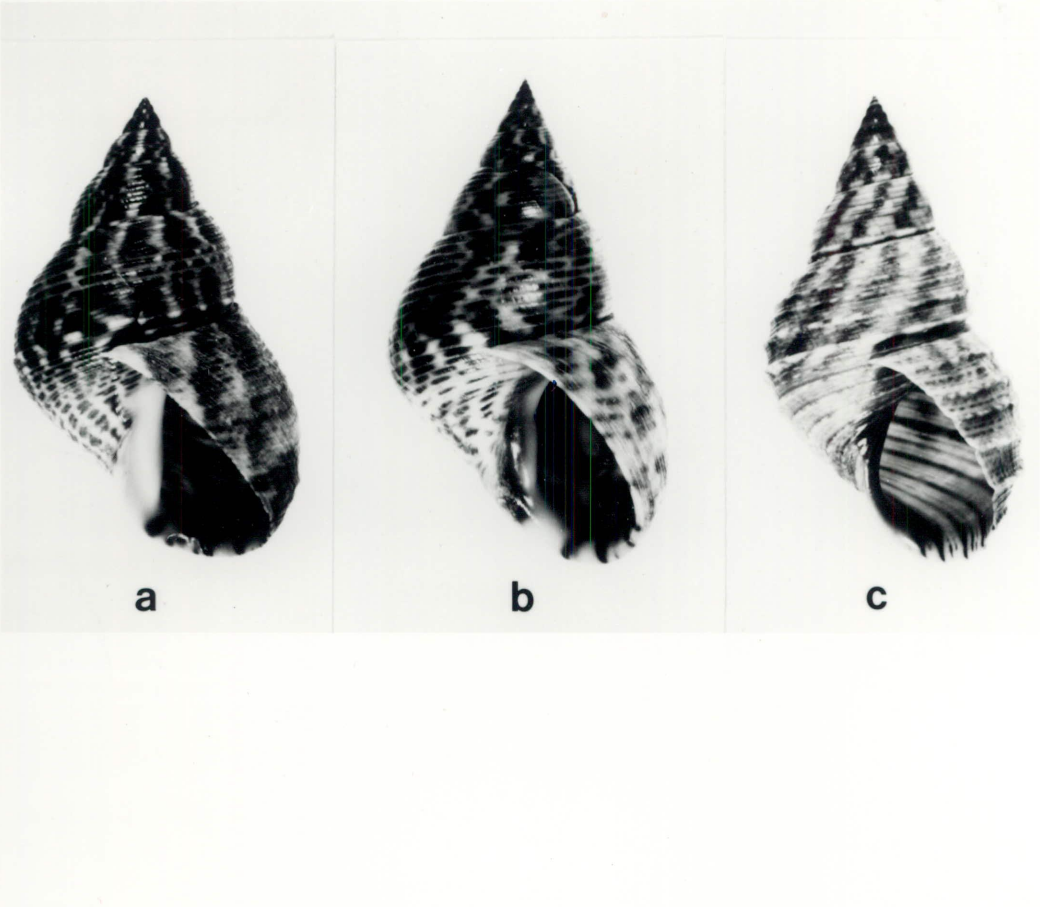
A feature of the aperture which has not hitherto been stressed as an important taxonomic character amongst littorinids is the form, and sometimes also the colour, of the columella. The range of variation of columellar form amongst species of *Littoraria* is illustrated in Figure 4.1. Of especial significance are the relative width of the columella and its shape, whether excavated or rounded. Columellar form is constant within species and can be a useful diagnostic character, as in the separation of shells of *L. filosa* and *L. philippiana*. A narrow and rounded columella is usually, but not invariably, associated with a thin shell.

Shell thickness is described qualitatively in the taxonomic section, but measurements of a thickness index are given in Section 14.3.5. There is considerable variation within the genus, ranging from the thin and fragile *L. delicatula* which is easily crushed between the fingers, to the solid *L. sulculosa*, up to 1.5 mm in thickness at the outer apertural lip, which can only be crushed by several blows of a heavy hammer. Thickness is found to be correlated with the vertical zonation of the species. Those which occur several metres above the ground on the leaves of the mangrove trees typically have thin shells, for example *L. filosa*, *L. luteola* and *L. albicans*, whilst those zoned at the lowest levels have thick shells, as in *L. sulculosa*, *L. intermedia* and *L. articulata* (Sections 14.3.5 and 14.4.4).

Fig. 4.1 Examples of columellar types in *Littoraria* species: (a) *L. scabra*: wide, excavated, with straight pillar; (b) *L. pallescens*: excavated, with convex pillar, pinched at base, and rounded inner apertural lip; (c) *L. filosa*: narrow, rounded, with concave pillar.



97C


a
b
c

4.2 Sexual dimorphism

In the family Littorinidae larger mean size of female shells, or a preponderance of females in the larger size classes, has been reported in many species (Pelseneer, 1926; Struhsaker, 1966; Sacchi, 1968; Daguzan, 1977) and usually explained by greater growth rates of females (Sewell, 1924; Moore, 1937; Lenderking, 1952, 1954; Borkowski, 1974; Underwood & McFadyen, 1983). The same explanation applies in the case of the four species investigated in detail at the Magnetic Island study site (Section 13.3.3). A contributory factor may also be the greater longevity of females, as proposed by Sewell (1924), Pelseneer (1926) and Daguzan (1977). In *Littoraria* species larger females have been recorded in *L. 'scabra'* (Sewell, 1924), *L. pallescens* (Abe, 1942; as *Melaraphe scabra*), *L. luteola* (Muggeridge, 1979; as *Littorina scabra*), *L. intermedia* (Struhsaker, 1966; as *Littorina scabra*), *L. angulifera* (Lenderking, 1952; Gallagher & Reid, 1974) and *L. irrorata* (Bingham, 1972a; Gallagher & Reid, 1974; Hamilton, 1978a).

In the present study dimorphism was examined in each species by comparison of ten adult shells of each sex. Despite small sample size, significant size dimorphism was found in fourteen of the nineteen species and subspecies for which data were available (Table 4.1). In each case male shells were of smaller size.

Dimorphism of shell shape in other littorinids has been noted by several authors (Sacchi, 1968; Daguzan, 1977). Within the genus *Littoraria*, the type and extent of shape dimorphism is variable, as shown by the the shape indices summarized in Table 4.1. Where dimorphism of relative spire height (SH) is significant, males are characterized by a lower spire, as measured by the ratio of shell height to aperture length. The apparently lower spire of males is not the result of a larger apical angle during the course of growth. Rather, it is caused by the distension of the last whorl and or flaring of the lip, which enlarge the aperture relative to the shell

Table 4.1 Summary of sexual dimorphism in the shells of the *Littoraria scabra* group.

Species	Locality	H	PR	S	SH
L. (*Littoraria*) *vespacea*	Santubong, Sarawak	.001 – **	.883 –	.970 –	.218 –
L. (*Lamellilitorina*) *albicans*	Santubong, Sarawak	.028 – *	.280 –	.352 –	.012 – *
L. (*Littorinopsis*) *scabra*	Moa I., Qld.	<.001 – **	.352 –	.630 –	<.001 – **
L. (*Littorinopsis*) *lutea*	Ubin I., Singapore	.001 – **	.740 +	.106 –	.002 – **
L. (*Littorinopsis*) *pallescens*	Ubin I., Singapore	.067 –	.740 –	<.001 – **	<.001 – **
L. (*Littorinopsis*) *philippiana*	Magnetic I., Qld.	.348 –	1.0 +	.657 –	.014 – *
L. (*Littorinopsis*) *intermedia*	Magnetic I., Qld.	<.001 – **	.630 –	.264 –	.004 – **
L. (*Littorinopsis*) *subvittata*	Aldabra	.001 – **	.002 – **	.684 –	<.001 – **
L. (*Littorinopsis*) *filosa*	Darwin, N.T.	.259 –	.166 +	.796 +	.297 –
L. (*Littorinopsis*) *c. cingulata*	Broome, W.A.	.029 – *	.076 –	.854 =	.012 – *
L. (*Littorinopsis*) *c. pristissini*	Denham, W.A.	.027 – *	.106 –	.825 +	<.001 – **
L. (*Littorinopsis*) *luteola*	Kurnell, N.S.W.	.031 – *	.018 – *	.218 +	<.001 – **
L. (*Littorinopsis*) *ardouiniana*	Hong Kong	.021 – *	.004 – **	.218 +	<.001 – **
L. (*Littorinopsis*) *delicatula*[1]	Port Canning, Bengal, India				–
L. (*Palustorina*) *melanostoma*	Kanchanadit, Thailand	.252 +	.106 +	.280 –	.394 +
L. (*Palustorina*) *conica*	Santubong, Sarawak	.008 – **	.712 –	<.001 – **	.028 – *
L. (*Palustorina*) *carinifera*	Sungei Merbok, Malaysia	.852 –	.314 +	.166 –	.166 –
L. (*Palustorina*) *sulculosa*	Broome, W.A.	<.001 – **	.064 –	.218 –	.090 –
L. (*Palustorina*) *articulata*	Broome, W.A.	.001 – **	.394 +	.415 –	.106 –
L. (*Palustorina*) *strigata*	Penang, Malaysia	.032 – *	.970 +	.012 – *	.436 –

H = shell height; PR = shell proportion; S = aperture shape; SH = spire height. Figures are probability levels for comparison of mean values of H (t-test) and shape indices (Mann-Whitney U test) between samples of 10 males and 10 females. +,– or = indicates direction of difference when value for males is compared with that for females. * indicates probability between 0.01 and 0.05; ** less than 0.01. [1] from Nevill (1885).

height. Only if expansion of the last whorl is considerable does this produce a dimorphism of shell proportion (PR). Aperture shape (S) is sometimes more elongate in males, which contributes to the apparent lowering of spire height. It must be emphasized that such dimorphism is only achieved at the last whorl of the shell and is not apparent in younger specimens. In species with significant dimorphism, shells with an adult aperture can, with experience, be immediately identified as male or female on the basis of their shape. Nevill (1885) observed the lower spire and patulous aperture of male shells of *L. delicatula* and *L. scabra*, while Abe (1942) noted the more elongate shell of the male in *L. pallescens* (the elongate aperture of the male of this species does in fact cause the whole shell to appear elongate, although there is no significant difference in shell proportion).

Struhsaker (1966) and Muggeridge (1979) have reported an absence of shape dimorphism in *L. intermedia* and *L. luteola* respectively, both species for which highly significant dimorphism has been found in the present study. Probable explanations for this discrepancy are that both authors used the ratio of shell height to breadth, which does not measure the most obvious aspect of dimorphism, and furthermore that shape dimorphism is only evident in adult shells, which were not specifically selected by these authors.

4.3 Protoconch

The protoconch is of similar form in most of the species of *Littoraria* in the *scabra* group (e.g. Figs 9.10b, 9.22b, 9.69b, 9.73b). The first whorl (protoconch I) is smooth, but thereafter (protoconch II) is sculptured by strong spiral ribs of which five are usually visible, and by oblique axial ridges which are most obvious in the middle of the whorls. After a further three whorls the termination of the protoconch is marked by a prominent sinusigera ridge, by a discontinuation of sculpture and often also by a change from the horn colour of the larval shell to a colour closer to that of the adult shell. Only in *L. albicans* is the protoconch distinctive (Fig. 9.6b), being low spired, sculptured by low spiral ribs only, and of unusually large size. In the majority of species the length of the protoconch is 320–415 μm, but in *L. albicans* 610–660 μm. The apical angle of the protoconch is usually similar to or greater than that of the first teleoconch whorl; only in *L. conica* is it smaller, producing a papillose apex (Fig. 9.61a). Species of *Littoraria* from mangrove forests are unusual amongst littorinids in that the protoconch is not infrequently intact even in adult shells, presumably as a consequence of the sheltered nature of the environment.

Characters of the protoconch would not appear to be useful for classification at the generic level in this family, for amongst species with planktotrophic development the protoconch is rather uniform, varying only in the degree of sculpture of the protoconch II. In species of *Littorina*, *Melarhaphe* and *Nodilittorina* in which the adult shell is rather smooth, the protoconch II is sculptured by spiral rows of minute tubercles (Pilkington, 1971; Thiriot-Quiévreux & Babio, 1975; Fretter & Manly, 1977; Fish & Fish, 1977). In strongly sculptured *Nodilittorina* species, as in many species of *Littoraria*, the tubercles tend to fuse, forming spiral ribs which are often discontinuous or undulating (Rosewater, 1981; Bandel & Kadolsky, 1982). Several authors have reported variability within species in the degree of fusion of tubercles and development of spiral ribbing (Struhsaker & Costlow, 1968; Bandel & Kadolsky, 1982). Within the genus *Littoraria* most species show strong sculpture of the protoconch, but in the western Atlantic *L. irrorata* the tubercles are not fused into spiral ridges (Thiriot-Quiévreux, 1980). A pattern of more or less fused tubercles on the protoconch II appears also in some rissoacean genera (Thiriot-Quiévreux & Babio, 1975) and in certain other mesogastropods and neogastropods (Bandel, 1975).

The length of the protoconch formed by planktotrophic larvae of littorinids ranges from 250 to 450 μm in the accounts quoted above, so that the 610 to 660 μm protoconch of *L. albicans* would seem to be exceptional for the family. Although the shape of the protoconch in this species is unusually broad, the small size of protoconch I and the strong sinusigera ridge terminating protoconch II suggest that the larva does undergo planktotrophic development (Shuto, 1974). Protoconchs of species of the subgenus *Littorinopsis*, which are ovoviviparous, are not distinguishable from those of oviparous species of *Littoraria* which spawn pelagic egg capsules, for the larvae of the former are retained only until the early veliger stage and a long phase of planktotrophic development ensues (Section 7.2). In littorinids which undergo nonplanktotrophic, so-called 'direct', development (in which larvae are brooded or encapsulated until hatching as benthic juveniles; see Jablonski & Lutz, 1983) the protoconch is of relatively large size, almost smooth, composed of two whorls or less, and lacks a sinusigera ridge (Rosewater, 1982). Amongst the species of *Littoraria* such a protoconch is seen only in the Eastern Pacific *L. aberrans*. Although the anatomy and method of development of this species is unknown, a nonplanktotrophic larval form can be predicted.

4.4 Shell sculpture

The sculpture of the teleoconch is the most important of the taxonomic characters of the shell of *Littoraria* and is diagnostic for the majority of the species. In previous taxonomic studies shell sculpture has usually been described only in general terms, although in the *Nodilittorina ziczac* species complex of the western Atlantic the number of spiral grooves has been used to distinguish several similar species (Borkowski & Borkowski, 1969; Bandel, 1974; Bandel & Kadolsky, 1982). No detailed comparisons, of the type presented here for *Littoraria*, have hitherto been made for any other group of littorinids, perhaps because in other species the character is often too variable to be diagnostic. Many studies have emphasized variability of sculpture in the family (Fischer-Piette & Gaillard, 1971; Borkowski, 1975) especially in relation to exposure of the habitat to wave action (James, 1968; Struhsaker, 1968; Heller, 1975a; Smith, 1981; see Section 14.4.4). These accounts have concerned species from exposed rocky shores and it appears that *Littoraria* species from sheltered mangrove habitats are less variable in this respect. Even in this genus there is considerable variation within some species, often between geographically distant populations, as in *L. carinifera* and *L. filosa*, but occasionally also within local populations, as in *L. cingulata pristissini* and *L. pallescens*.

From the faint axial growth lines visible on the apical whorls and from newly settled shells collected in the field, it is evident that in the genus *Littoraria* growth of the postlarval shell begins by the infilling of the areas on each side of the beak of the larval aperture, thus forming a planar aperture. In many species the first one to three whorls of the postlarval shell are smooth and in the species descriptions the number of such whorls before the appearance of spiral sculpture is recorded. In several species spiral sculpture begins immediately after the sinusigera ridge formed at metamorphosis, but the sculpture produced is clearly different from that of the larval shell. Wherever spiral sculpture develops, it consists of from six to twenty-six narrow grooves visible above the suture with the following whorl. Often the more posterior of these grooves appear first and may be deeper and more closely spaced than the rest, but all are developed over the space of one to two revolutions. These grooves are here termed primary grooves, and the spaces between, the primary ribs. The point of appearance of the primary grooves, their number and spacing, are characteristic of each species.

On subsequent whorls the number of ribs is increased by either or a combination of two processes: primary ribs may become divided by secondary grooves (each division forming a continuing primary rib and an anterior secondary rib), or secondary ribs may appear in the primary grooves by intercalation of small riblets which may expand into ribs. Occasionally one or more ribs may be added by intercalation or division on the early whorls; the convention is adopted that all ribs present on the fourth whorl of the postlarval shell are regarded as primary. Secondary sculpture does not occur in all species, but if and when it is formed it usually develops over most of the surface of the whorl in the space of one revolution. Division of primary ribs by secondary grooves occurs either centrally or towards the anterior face of the rib. Division and intercalation may occur side by side on the same whorl, at different stages on the same shell, or one process may occur exclusively. Where tertiary and higher orders of sculpture appear, the scale is so small and the ribs so numerous that the distinction between formation by intercalation or division can be difficult to draw. Furthermore, towards the end of the last whorl spiral sculpture may become indistinct as axial growth lines become stronger.

On the last whorl of the adult shell, grooves often become wider and ribs prominently rounded. The relative width of ribs and grooves is an important character. In species with the strongest sculpture the primary ribs may become especially prominent on the last whorl, developing into raised carinae (e.g. *L. carinifera*, *L. filosa*, *L. pallescens*). In many species the peripheral rib is the largest and most prominent, and enhances the natural angulation of the shell, thus imparting a strongly keeled appearance. The basal part of the shell below the keel is sculptured in rather similar fashion to the area above the periphery, although the ribs become smaller and more closely spaced anteriorly. Since only the last whorl of the base is visible, primary and secondary sculpture cannot always be distinguished; also, differences in rib width are less pronounced on the base. For these reasons basal sculpture is of lesser importance as a taxonomic character and is not considered in detail in the species descriptions.

Nodulose sculpture is entirely lacking in all known species of *Littoraria,* although it is conspicuous in the littorinid genera *Tectarius, Echininus, Cenchritis* and *Bembicium,* in many species of *Nodilittorina* and a few of *Littorina* and *Melarhaphe.* The distribution of nodulose sculpture in the family has been reviewed by Bandel & Kadolsky (1982) and, as pointed out by these authors, the character cannot be used as evidence of close phylogenetic relationship. In the genus *Nodilittorina,* sculpture is especially variable between species, ranging from regular spiral ribbing to strong nodulation. Spiral sculpture is present in most littorinid genera, although it is weak or absent in *Melarhaphe* (Rosewater, 1981).

The significance of shell sculpture has been related by various authors to temperature control, hydrodynamic properties and defence against predation, as reviewed by Vermeij (1978) and in Section 14.4.4.

In addition to the conspicuous spiral sculpture described, microsculpture is visible under low magnification, especially on the last two whorls where the scale is larger. In the subgenus *Littorinopsis* regular spiral striae are visible in the grooves, but are faint or absent on the ribs (e.g. Fig. 9.10d). If the grooves are narrow, microsculpture may be visible only in the wider posterior grooves. In the subgenus *Palustorina* spiral striae are restricted to the ribs, while the grooves contain strong, regular axial lines. The axial sculpture is most clearly visible in species with wider grooves (e.g. Fig. 9.78b); when narrow the grooves appear pitted (e.g. Fig. 9.56d). In *L.* (*Lamellilitorina*) *albicans* spiral microsculpture is absent and axial striae are prominent in the grooves (Fig. 9.6e). Other species of the genus show spiral striae developed over the whole surface of the shell. The form of the microsculpture can be a useful diagnostic feature, as for example in the differentiation of shells of *L. cingulata* and *L. sulculosa.*

In most species the surface appears glossy under low magnification; the periostracum is not evident and is presumably thin and closely adherent. In *L. melanostoma, L. carinifera* and *L. flammea* the layer is thicker and occasionally flakes off, showing that in these three species the spiral microsculpture on the ribs is largely produced by ridges on the periostracum. Reimchen (1981) has described spiral ridges on the periostracum of *Littorina mariae*. In *L. vespacea* the periostracum is occasionally produced into short bristles.

4.5 Shell colour

Most of the authors writing on the *Littoraria scabra* complex since Philippi (1847–1848) have commented on the wide range of shell colour forms. Despite the recognition of many species within the group in the present revision, the majority still show considerable colour variation (see Frontispiece). In all *Littoraria* species shell colour is best described as a ground colour, either a shade of white to yellow, or of orange pink, with a superimposed pattern of dark pigment, usually brown or black. Dark pigment is deposited in the form of spiral dashes, usually confined to the shell ribs. The dashes are often discrete, but if very dense, they may run together or appear smudged. In most species the dark dashes are aligned to some degree, especially at the suture and periphery of the whorls, to form axial flames. This alignment is often most apparent on the spire whorls, and some shells show complete alignment from suture to base, which produces oblique axial stripes. Within most species the development of dark pigmentation is variable, ranging from complete absence, through faint mottling, to dark dashes and stripes which sometimes cover the surface. Continuous spiral colour bands are unusual, occurring commonly only in *L. pallescens*.

Although variation in these species is striking, not all can be described as polymorphic, since strictly the term can only be used of discrete variation (Ford, 1945). In *Littoraria* species the variation of the dark pattern is apparently continuous, but, at least in paler shells, the ground colour is seen to be either pale yellow or orange pink, with no intermediate shades. In shells with the darkest patterning, the ground colour is obscured and appears brown. For convenience of description, those species in which shells may be either predominantly yellow, pink or brown are termed 'polymorphic' in the species descriptions, as opposed to 'variable' species in which only the degree of patterning changes. Amongst the polymorphic species the same range of colour forms is encountered in each and the polymorphisms may be homologous (see Frontispiece; Section 15.5.1).

Colour polymorphism is most striking in members of the subgenus *Littorinopsis*, being shown in all or part of their range by ten of the twelve species (the exceptions are *L. scabra* and *L. subvittata*). In the other subgenera of *Littoraria*, the only strikingly polymorphic species is *L. (Lamellilitorina) albicans*. Pink shells are very occasionally found in *L. (Palustorina) melanostoma* and *L. (P.) articulata*, but these species are not described as polymorphic (Section 15.2). The adaptive significance of colour polymorphism is discussed in Chapter 15, and its occurrence is correlated with habitat rather than probable phylogenetic grouping.

In general, shell colour is so variable in *Littoraria* species as to be a poor guide to identification. Nevertheless, the relative abundance of colour forms, the size of the pigment dashes, their degree of alignment and the number of axial stripes per whorl, may serve to characterize species. A few species show a more or less constant shell colour and pattern (e.g. *L. carinifera*, *L. vespacea*, *L. cingulata cingulata*).

The columellar pillar is pale or white in most specimens, but the colour of the excavated area, and sometimes also of the parietal callus, can be useful in distinguishing species. Columellar colour was used as a taxonomic character in the *Nodilittorina ziczac* species complex (Borkowski & Borkowski, 1969). In polymorphic species columellar colour is often correlated with external shell colour, being white in unpigmented yellow or pink shells, and purple in darkly patterned shells. Internal shell colour usually reflects the external pattern.

Since shell colouration is so variable in many members of the family, the character cannot be regarded as of great significance in a consideration of relationships at the generic level. Outside the genus *Littoraria*, true colour polymorphism is found only in the genus *Littorina* (reviews by Sacchi, 1974; Raffaelli, 1982), although anatomical characters suggest that these genera are not closely related (Section 8.2). It is noteworthy that a pattern of spiral dashes aligned to form axial markings is common to species of *Littoraria* and to those of *Nodilittorina* which lack nodulose sculpture (see figures in Bandel & Kadolsky, 1982). In the genus *Littorina*, however, spiral bands of colour predominate. Of possible phylogenetic significance is the presence or absence of an unpigmented spiral band in the anterior part of an otherwise dark brown aperture. This pattern is typical of the genera *Nodilittorina* and *Melarhaphe*, and is seen also in *Laevilitorina* and *Rissolittorina* (Ponder, 1966; Ponder & Rosewater, 1979) and in some species of the family Lacunidae. In other groups this pale apertural stripe is generally absent, although *Littorina keenae* appears to be an exception. In the genus *Littoraria* this pattern is often visible in specimens of *L. pintado* and *L. mauritiana*, both of which show several ancestral character states (Fig. 8.2), and is also seen in *L. carinifera*. Conceivably, the white apertural stripe is an ancestral character in the genus.

4.6 Operculum

Several authors have used characters of the operculum in the taxonomy of littorinids (Abbott, 1954; Rosewater, 1972, 1981; Bandel & Kadolsky, 1982). Members of the genera *Tectarius* and *Cenchritis* possess a mesospiral operculum, and *Echininus* and *Peasiella* a multispiral one. In *Nodilittorina* both paucispiral and mesospiral opercula are found, and Bandel & Kadolsky (1982) have argued that tighter coiling of the operculum is an adaptation to fit a more circular aperture and to thicken the operculum, in order to reduce water loss. Other littorinids, as reviewed by these authors, show a paucispiral operculum, which appears to be the ancestral condition in the family. In the genus *Littoraria* the operculum is thin and paucispiral (as illustrated by Rosewater, 1981) and no differences could be detected between the opercula of different species.

CHAPTER 5: ANATOMICAL CHARACTERS

5.1 Colouration of head-foot

The colouration of the animal has sometimes been used as a taxonomic character in littorinids, for example in the descriptions of supposed subspecies of *Littorina 'saxatilis'* by James (1968). Amongst the Indo-Pacific species of *Littoraria* treated here, pigmentation of the animal is seldom of use in distinguishing species since in the majority the pattern is the same. The sole of the foot is pale, usually whitish or cream, and the sides mottled with grey or black pigment. The head is grey to black, paler at the tip of the snout and often with an unpigmented, short, longitudinal streak between the tentacles, which is most conspicuous in the largest individuals. The red buccal mass is visible within the head. Irregular bands of pigment reach almost to the tips of the tentacles; the bases are darkly pigmented but for a prominent white stripe on inner and outer sides. This pattern is illustrated by *L. scabra* (Fig. 5.1) and is characteristic of most members of the genus. The pattern may be contrasted with that typical of *Nodilittorina*, *Echininus*, *Melarhaphe* and *Fossarilittorina*, with an unpigmented patch or band over the eye and sometimes an absence of pigment on the distal parts of the tentacles (pers. obs.).

In species of *Littoraria* with colour polymorphic shells the pigmentation of the animal is correlated with the colour of the shell, as has been observed in *Littorina obtusata* in Europe (Barkman, 1955; Bakker, 1959). For example, in *Littoraria filosa* the animals with pure yellow shells are entirely unpigmented, in darker shells animal pigmentation becomes more pronounced, especially on the head, until animals are dark grey in brown shells.

Only in *L. albicans*, with red tentacles lacking basal stripes, is the colouration of the animal entirely diagnostic.

5.2 Male reproductive tract

The anatomy of the male reproductive system of *Littoraria* (e.g. *L. scabra*, Fig. 5.1) is similar to that of the European *Littorina* species described in detail by Linke (1933) and Fretter & Graham (1962). Lobules of the testis, orange or red brown in colour, ramify in the digestive gland and join to form a duct running close to the surface of the visceral mass against the columella of the shell. The more distal, convoluted portion of the testicular duct is distended with stored sperm during the breeding season, functioning as a seminal vesicle, and leads to the pallial vas deferens via a short renal section. In species of *Littoraria* the pallial section is a closed tube with a central slit-like lumen, surrounded by a swollen, glandular prostate. This condition has been reported previously in *L. angulifera* and *L. flava* by Marcus & Marcus (1963) and in *L. melanostoma* by Berry & Chew (1973) and contrasts with the open prostate found in most other genera of littorinids, as discussed below. In the majority of *Littoraria* species the prostate opens to a ciliated groove which carries sperm forward over the lateral surface of the head-foot to the conspicuous penis, situated on the right side of the head behind the eye. In a few species the entire vas deferens is a closed tube, the groove over the head-foot and penial groove being closed as a shallow duct, leaving only a minute pore communicating with the mantle cavity adjacent to the distal end of the prostate.

The form of the penis shows considerable variation within the Littorinidae and is perhaps the single most important taxonomic character of the anatomy of the family. It has been used to define the generic groups of the family by Rosewater (1970, 1972, 1981) and in the revision of his classification by Bandel & Kadolsky (1982),

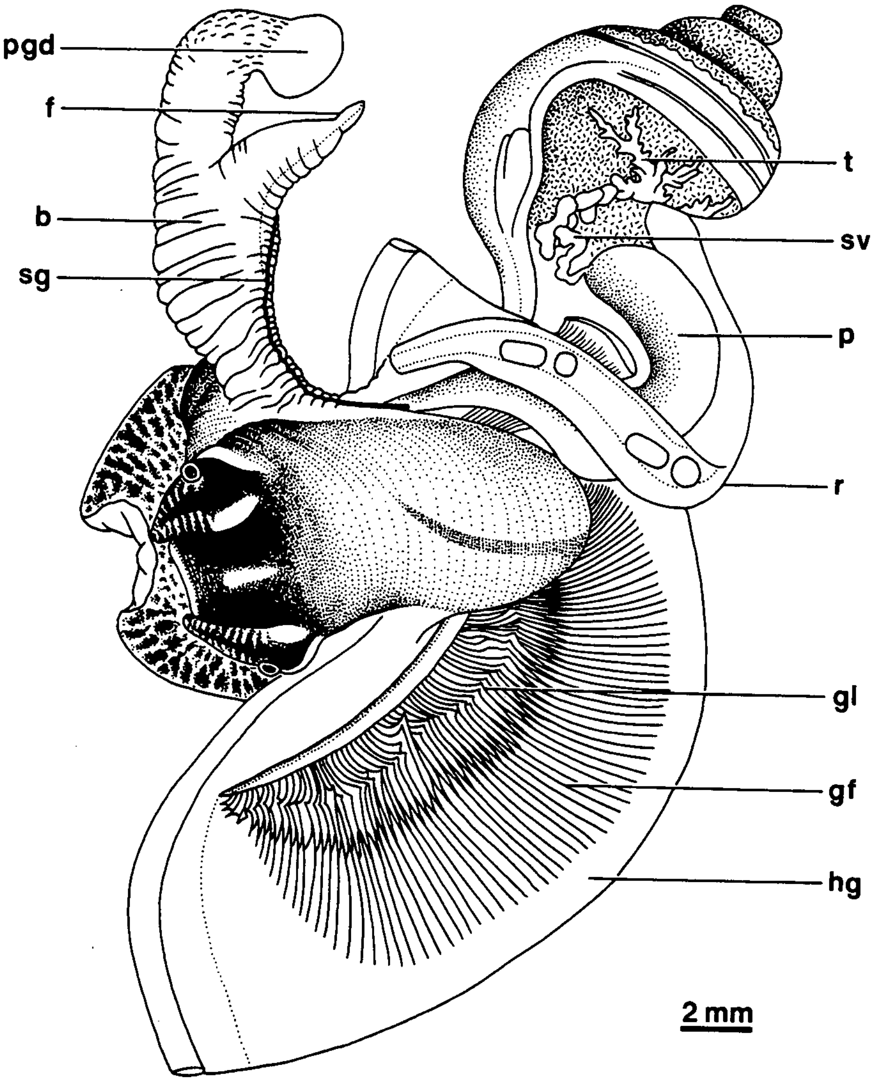


Fig. 5.1 *Littoraria (Littorinopsis) scabra*: male reproductive tract; mantle cavity opened between rectum and hypobranchial gland; b, base of penis; f, filament of penis; gf, gill fold; gl, gill leaflet; hg, hypobranchial gland; p, prostate gland; pgd, penial glandular disc; r, rectum; sg, penial sperm groove; sv, seminal vesicle; t, testis.

besides being employed as a specific character in most other recent taxonomic studies (Whipple, 1965; Heller, 1975a; Ponder & Rosewater, 1979). In two cases dimorphism of penial shape has provided the first indication of the existence of a pair of sibling species (Sacchi & Rastelli, 1967; Murray, 1979).

In general the littorinid penis is differentiated into a thick, wrinkled and muscular basal region, often with glandular appendages, and a narrow, smooth, distal filament, along which sperm passes in a deep, but usually open, groove at the posterior (dorsal) edge. The conspicuous glandular elements are of two types. In all species of *Littorina*, *Nodilittorina*, *Tectarius*, *Echininus* and *Peasiella* penial glands are found. Each gland is visible externally as a papilla, within which the duct may appear hyaline and is referred to as an 'accessory flagellum' by Abbott (1954) and Rosewater (1970, 1981). The internal structure of penial glands has been described by Linke (1933) and by Marcus & Marcus (1963). The small penial papillae of *Tectarius*, *Echininus* and *Nodilittorina pyramidalis*, as well as the very large basal glands of *Echininus antoni*, show the same structure as penial glands. The second glandular element occurs in the genera *Littoraria* and *Nodilittorina* and has been variously described as a 'disk or sucker' (Leidy, 1846), 'clasper' (Lenderking, 1954), 'haftlappen' (Marcus & Marcus, 1963), 'penial gland' (Whipple, 1965), 'lateral thickened appendage' or 'basal flap' (Rosewater, 1970, 1981), 'attachment gland' (Bingham, 1972b) and as an 'adhesive flagellum' (Bandel & Kadolsky, 1982). It is suggested that all these terms refer to a similar, probably homologous, structure, for which the name penial glandular disc seems appropriate. Only in species of *Nodilittorina* do both glandular types occur on the penis together.

The structure of the penial glandular disc has not hitherto been described in detail. When relaxed, the penis is folded back into the mantle cavity, lying against the head-foot, with the filament nearest the mid-line. In species of *Littoraria* the glandular disc appears bulbous or resembles a sucker, and in the resting position the secretory surface is lowermost. During the present study, histological sections of four species were examined: *L. scabra*, *L. philippiana*, *L. melanostoma* and *L. articulata*. In each case the epithelium of the penis is columnar and, except in the sperm groove, unciliated. The penial disc is composed of glandular tissue lying below the epithelium, staining dark pink in haematoxylin and eosin, blue in Mallory-Heidenhain trichrome and magenta (indicating neutral mucins) by means of the alcian blue-periodic acid-Schiff (ABPAS) technique. The granular secretion is discharged through numerous fine cyloplasmic extensions passing between the epithelial cells. Over most of the base the epithelium stains magenta in ABPAS and is not secretory, but the epithelium overlying the secretory surface of the disc is taller and contains numerous goblet cells staining bright blue in ABPAS (indicating acidic mucins). Elsewhere these cells are abundant on the penial filament, where they extend also beneath the epithelium, and presumably their secretion serves for lubrication. Similar goblet cells are found in the female oviduct, especially in the sperm groove. The subgenera *Littorinopsis* and *Palustorina*, as represented by the four species examined, differ slightly in that the disc of *Littoraria* is composed almost solely of glandular cells, whilst in *Palustorina* the glandular tissue is interspersed amongst the muscle fibres and blood spaces within the penial base.

The penis of *Littoraria* species is differentiated into filament and base, penial glands are absent, the penial glandular disc is well developed and the sperm groove usually, but not always, open. Within the genus penial shape varies widely, but is in the majority of cases diagnostic of the species (Fig. 5.2, and Figures in Chapter 9). Specific differences can be seen in the relative lengths of filament and base, position of the glandular disc, colouration of both disc and base, and in the closure of the sperm groove. There are few clear trends in penial form above the species level. In the subgenus *Littorinopsis* (as in the type species, *L. angulifera*, Fig. 5.2o) the base is bifurcate, the glandular disc being carried on a limb well separated from the penial filament; the junction of filament and base is marked by a constriction, and although relative

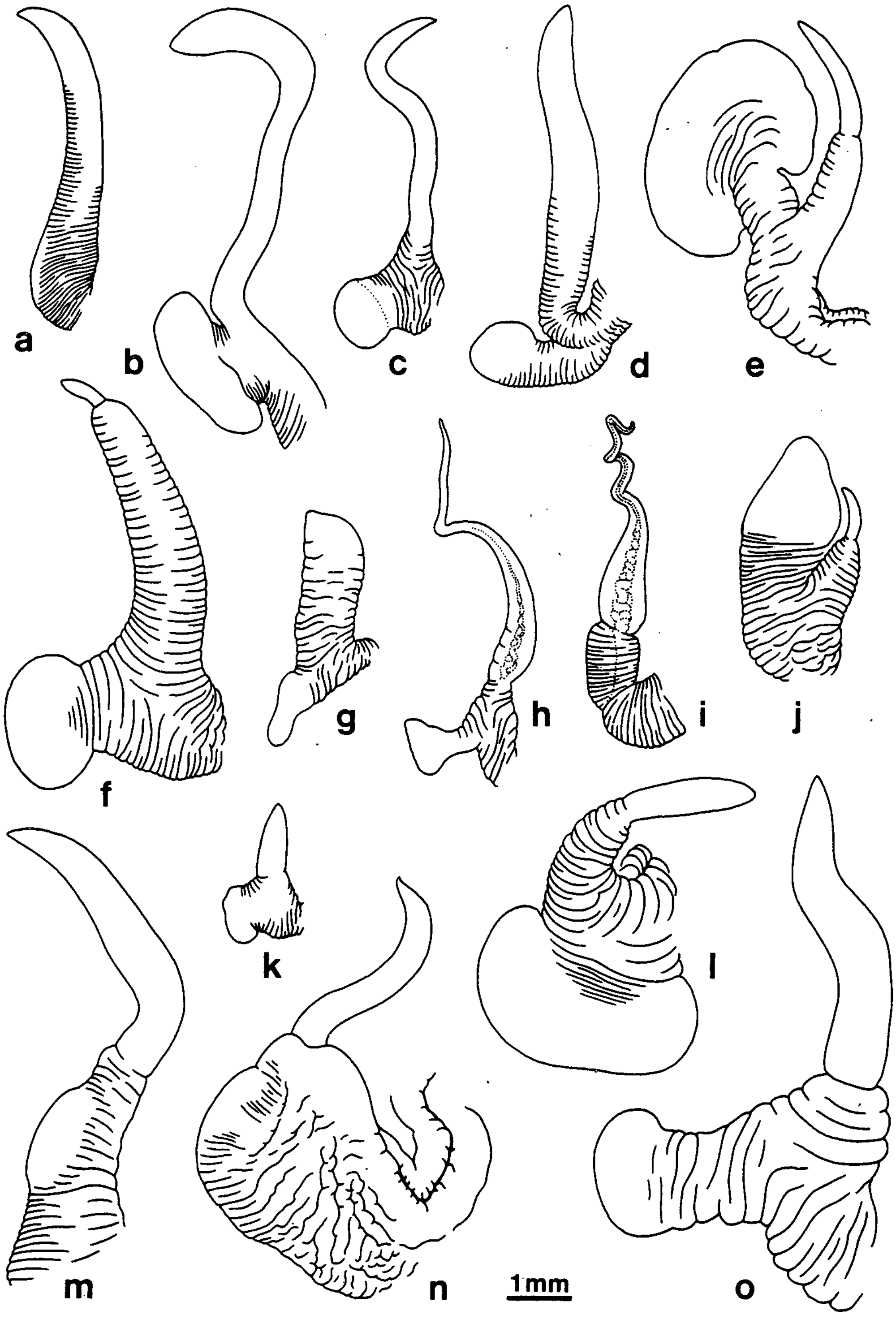


Fig. 5.2 Penes of *Littoraria* species other than those described in Chapter 9: (a) *L. pintado*; (b) *L. coccinea*; (c) *L. glabrata*; (d) *L. mauritiana*; (e) *L. undulata*; (f) *L. nebulosa*; (g) *L. cingulifera*; (h) *L. tessellata*; (i) *L. flava*; (j) *L. varia*; (k) undescribed species from tropical Eastern Pacific; (l) *L. zebra*; (m) *L. irrorata*; (n) *L. fasciata*; (o) *L. angulifera*.

proportions of base and filament vary between species, the entire penis is, even in the relaxed state, of large size relative to the length of the shell. In three species of this subgenus (*L. intermedia*, *L. philippiana*, *L. subvittata*) the sperm groove is closed as a duct. Penes of four Indo-Pacific species of *Littorinopsis* (*L. scabra*, *L. intermedia*, *L. luteola*, *L. pallescens*) have been illustrated by previous authors, as indicated in the synonymies, and that of the Atlantic *L. angulifera* by Leidy (1845), Marcus & Marcus (1963) and Rosewater (1981).

Members of the subgenus *Palustorina* (as represented by the type species, *L. melanostoma*, Fig. 9.57a-g) show a rather characteristic penial shape. In this group the penis is not bifurcate, the glandular disc being closely incorporated into the base, the penis is of relatively small size and the sperm groove is always open. Penes of species placed in the subgenus *Palustorina* have not hitherto been figured.

Amongst species of the subgenus *Littoraria*, penial form is rather diverse (Figs 5.2, 9.3a-f). The base is often clearly bifurcate, although not so in *L. pintado*, *L. flava*, *L. fasciata*, *L. irrorata* and *L. vespacea*, in which species the penial glandular disc is closely incorporated into the base. In this subgenus the sperm duct is internal in *L. flava*, *L. tessellata* and in an undescribed species from the Eastern Pacific.

Despite the undoubted taxonomic importance of penial characters, there are several difficulties to be considered. Most serious is that although shapes are diagnostic to an experienced eye, it is usually necessary to examine a number of specimens in order to gain the necessary appreciation of the range of variation and of the aspects of shape which are most significant. A morphometric approach (as used by Hannaford Ellis, 1979) might be of use in the initial separation of certain difficult species, but is hardly appropriate in a broad taxonomic treatment, since not only are penes irregular and hard to measure precisely, but their shapes are influenced by the degree of relaxation and method of fixation of the specimens. In the present study most penes have been drawn from living specimens removed from the shell and relaxed in a 1% solution of propylene phenoxetol, of which the shapes are the same as those seen when the shells of crawling animals are lifted. If animals are dropped into boiling water the penes are also fixed in a similarly extended state. The penes of animals fixed in alcohol or formalin without prior relaxation are often somewhat contracted and usually contorted. Therefore, to illustrate penial shapes several examples have been drawn for each species.

Once artificial differences in shape due to contraction or contortion are recognized, penial form is found to be rather constant. Although immature males lack a fully developed penis, once maturity is reached there is little change in shape of the organ with increasing size of the animal. Penes of smaller animals are sometimes paler in colour. In certain temperate littorinids the penis is reduced in size, or even shed, outside the breeding season (Linke, 1933; Berry, 1961; Palant & Fischelson, 1968; Grahame, 1969; Le Breton, 1970). However, in the study of reproductive condition of five species of *Littoraria* at Magnetic Island, Queensland, over one year (see Section 13.3.1), males were found to be mature virtually throughout the year in *L. scabra*, *L. intermedia* and *L. articulata*, while in *L. filosa* and *L. philippiana* with more restricted breeding seasons the change in size and shape of the penis with reproductive condition was slight. Even in *L. luteola*, with one of the most temperate distributions of the Indo-Pacific species, no significant reduction in size of the penis occurs (Muggeridge, 1979). It is possible that trematode parasitism may reduce penis size (Lysaght, 1941), but this condition is rare in *Littoraria* species.

Although the species-specific form of the penis is so striking in many littorinid groups, its functional significance is not clear. Linke (1933) suggested that the secretion of the penial glands secures the base of the penis in position in the mantle cavity of the female, while only the elongated filamentous tip enters the bursa copulatrix. Bingham (1972b) suggested a similar function for the penial glandular disc of *L. irrorata*. This possibility is strengthened by the discoidal or sucker-like shape of the appendage and by personal observation of the application of its secretory surface to the roof of the mantle cavity (or occasionally to the inside of the shell or side of the head-foot) of the female during copulation, in the species of the subgenus *Littorinopsis* in Queensland.

Heller (1975a) was so impressed by the differences in penial morphology of four sympatric European *Littorina* species that he suggested that penial shape is of importance in species recognition and perhaps as an isolating mechanism preventing interspecific mating. In several littorinids males are rather indiscriminate in their choice of mate (Section 6.2) and the success of copulation may depend upon the recognition response of the female, which could be based on penial shape. However, as pointed out by Raffaelli (1979) there is much variation in the number and arrangement of the penial glands in the species considered by Heller, which would make specific recognition by this means difficult. Amongst other *Littorina* species, Sacchi & Rastelli (1967) found a conspicuous difference in penial shape between the two species in the *obtusata* group, with very similar conchological characters, and Hannaford Ellis (1979) found penial shapes to be characteristic, but not entirely diagnostic, of two species in the *saxatilis* group. There is stronger evidence for penial morphology as an isolating mechanism in certain other gastropod groups, for example in endodontid land snails Solem (1976) reported character displacement of penial shapes in localities where congeneric species are sympatric. In the genus *Littoraria* penial shape is more consistent than in *Littorina* and might therefore indeed be a species recognition character.

Fretter & Graham (1962, p. 352) have described examples of correspondence in structure of penis and pallial oviduct in several prosobranchs. In *Littoraria* there is no very obvious correspondence, at least when the penis is relaxed. For example, the bursa copulatrix of *L. scabra* is large, despite the small size of the penial filament (Figs 5.7, 9.11). In the conchologically similar pair *L. philippiana* and *L. pallescens*, as in the pair *L. articulata* and *L. strigata*, relative length of the filament is the most important diagnostic character, yet in neither case do the oviducts show corresponding differences (Figs 9.23, 9.19 and 9.74, 9.79). The more posterior position of the bursa copulatrix in many *Littoraria* species is not associated with any particular penial shape. However, the shape of the penis during copulation may be very different from that at rest, as illustrated by Bingham (1972b) for *L. irrorata*.

Although characters of the male reproductive anatomy are of importance in classification at both generic and specific levels, they do not permit more than speculation upon phylogenetic relationships, at the present state of knowledge. The pallial genital ducts of prosobranchs have evolved from open grooves (Fretter & Graham, 1962) and the retention of an open prostate in at least seven littorinid genera (Fig. 8.1) is probably primitive. In all species of *Littoraria*, and in *Melarhaphe*, the prostate is closed, a condition probably derived independently in the two groups, which show few other derived characters in common (Fig. 8.1). Similarly, the closed penial sperm duct found in a few species of the subgenera *Littoraria* and *Littorinopsis*, and elsewhere in the family in *Melarhaphe*, *Fossarilittorina*, *Bembicium* and also in *Rufolacuna* (Ponder, 1976), has probably been independently derived in each case.

Of the glandular elements of the penis, the histology of the penial glands described by Linke (1933) in *Littorina* and by Marcus & Marcus (1963) in *Nodilittorina* (as *Littorina ziczac*, but = *Nodilittorina lineolata* (Orbigny) *fide* Bandel & Kadolsky, 1982) is so similar that the glands are almost certainly homologous. In *Littorina* the number of penial glands ranges from zero (in *Littorina scutulata* Gould *s. s.*; Murray, 1979) to 59 (in *Littorina obtusata* (L.); Linke, 1933; Sacchi & Rastelli, 1967). Both within species (Linke, 1933; Raffaelli, 1979) and to a certain extent also between species, the number is correlated with shell size. Almost all species of *Nodilittorina* show a single penial gland (Bandel & Kadolsky, 1982), although in *N. lineolata* the number varies from zero to two (Marcus & Marcus, 1963) and in *N. pyramidalis* from zero to one (pers. obs.). There are neither penial glands nor glandular disc in '*Nodilittorina*' *striata* (King & Broderip) (Rosewater, 1981), but this species should perhaps be placed in the genus *Melarhaphe*. Penial glands of identical external appearance occur in *Echininus*, numbering two to twelve (Rosewater, 1972), in *Tectarius*, numbering approximately 100, and occur singly in *Peasiella*. The variation in number of penial glands between genera is correlated with shell size, and is possibly connected with the allometric relationship of gland number and size seen in *Littorina*. The distribution of penial glands in the family (Fig. 8.1) suggests that they are probably an ancestral feature of the genera considered here, with the exception of *Bembicium*. The variation in number of glands within genera, and even within species, implies that they might readily be lost, to derive the condition found in the genera *Littoraria*, *Cenchritis*, *Melarhaphe* and *Fossarilittorina*.

Another noteworthy feature of the littorinid penis is the presence of numerous small papillae on the filament of species of *Tectarius* and *Echininus* (Rosewater, 1972; pers. obs.) and in *Nodilittorina pyramidalis* (Rosewater, 1970; pers. obs.). The presence of papillae seems correlated with large size of the shell, for they are found in all *Tectarius* species, absent in the small *Echininus viviparus* (Rosewater, 1982), and present in only one relatively large *Nodilittorina* species.

The homology of the penial glandular disc is more difficult to determine, since the gross appearance is less characteristic. Amongst *Littoraria* species the disc varies in appearance from a prominent sucker to a thin flap, or even a gland so closely incorporated into the base as to be scarcely visible from the surface. However, judging by the four species examined histologically, the structure is similar in each case. The secretion of both glandular types consists of acidophil granules (Linke, 1933; pers. obs.), although in the glandular disc these are secreted through cytoplasmic extensions between epithelial cells, while in penial glands the secretion passes into intercellular canals. Amongst other littorinid genera, glandular structures of similar external appearance to the glandular disc occur only in the genus *Nodilittorina*, although their histology has not been examined. Penes of *Nodilittorina* species have been illustrated by Abbott (1954), Marcus & Marcus (1963), Rosewater (1970) and Ponder & Rosewater (1979), and show a range of differentiation of the glandular disc, from a swelling adjacent to the penial gland, to a well defined disc very similar to that in *Littoraria* species (e.g. *N. tuberculata* (Menke), Abbott, 1954). If the penial glandular discs are homologous in *Littoraria* and *Nodilittorina*, a close relationship is indicated between these genera.

In the littorinid genus *Bembicium* the penis bears distal, presumably glandular swellings, and in *Rissolittorina* (Ponder, 1966) and *Rufolacuna* (Ponder, 1976) long penial appendages have been described. In *Laevilitorina* and *Macquariella* the penis is simple (Ponder, 1976; Ponder & Rosewater, 1979) and no glandular appendages have been noted in the European Lacunidae (Fretter & Graham, 1962). Consideration of the relationships of these groups must await further information on their anatomy.

The functional significance of the evolutionary modifications of the penis remains obscure. The presence of glandular elements is not correlated with habitat, being absent in *Cenchritis muricatus* and *Melarhaphe neritoides*, both from the supralittoral zone, but present in *Nodilittorina* from similar habitats. As discussed above, the presence of glandular elements is to some extent correlated with size, and possibly tied to it by an allometric relationship in the case of penial glands, but again *Cenchritis muricatus* is an exception. This correlation with size suggests that the main function of glandular elements may be support of the organ by adhesion, as suggested by Linke (1933) and Bingham (1972b). The penial glandular disc might fulfill this role more effectively when carried on a projection of the base; if so, this adaptation appears to have arisen repeatedly in *Littoraria* species (compare Figs 5.2 and 8.2). If, however, the principal function of the glands is concerned with species recognition, then penial shapes cannot be interpreted as mechanical adaptations.

5.3 Sperm cells

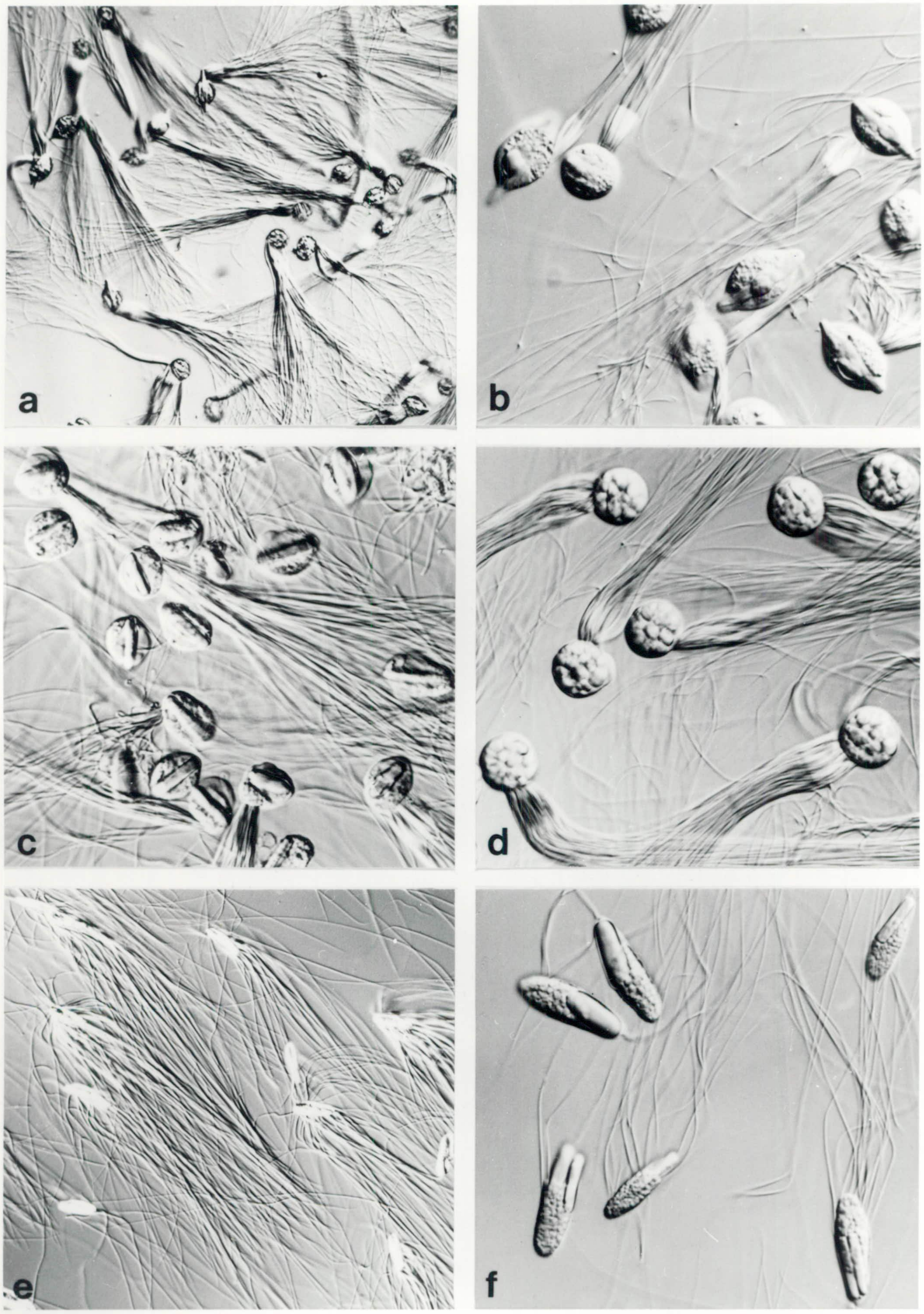
In many littorinids, as in certain other prosobranchs (reviewed by Fretter & Graham, 1962), the testis produces not only the typical (or eupyrene) sperm responsible for fertilization, but also atypical sperm. The typical sperm of *Littoraria* appear thread-like, 100 to 350 µm in length, with further details only visible at the highest magnifications of the light microscope. Typical sperm of *L. angulifera* and *L. nebulosa* were described by Reinke (1912), while Buckland-Nicks (1973) gave an account of the ultrastructure of the spermatozoa of *Littorina scutulata*.

The atypical sperm of littorinids are known as nurse cells and are rounded, 8 to 55 µm in diameter, and packed with yolk granules. The development of the nurse cells in the testis has been described for several littorinid species (Reinke, 1912; Ankel, 1930; Linke, 1933; Woodard, 1942a; Battaglia, 1952; Buckland-Nicks & Chia, 1977). To summarize, they are derived from the germinal epithelium in the tubules of the testis by an unusual reductional division. Each nurse cell is initially attached to the tubule wall by a stalk, and by pseudopodia to developing spermatids. As the cell detaches, the nucleus degenerates and yolk accumulates in the cytoplasm. In certain littorinids, including the majority of species of *Littoraria*, the nurse cells contain conspicuous rod-shaped inclusions, which according to Woodard (1942a, in *L. irrorata*) are formed from eupyrene sperm heads, which enter the nurse cells in a process analogous to fertilization. Numerous typical sperm become attached by their tips to the nurse cells (Fig. 5.3) and the composite bodies, called spermatozeugmata, are transferred to the female in a mucous spermatophore (Woodard, 1942b; Buckland-Nicks, 1973). Within the bursa copulatrix the nurse cells degenerate and the sperm reattach to the epithelium of the bursa (Fretter & Graham, 1962, p. 342) before eventual storage in the seminal receptacle.

Most authors have stressed the probable role of the nurse cells in the nutrition of the eupyrene sperm, while Grahame (1973) has suggested that the yolk of the nurse cells may contribute to the energetic cost of egg production in the female. In addition, the coordinated beating of the flagella of the attached sperm may propel the unit more effectively (Borkowski, 1971; Buckland-Nicks, 1973). Woodard (1942b) observed that nurse cells may also control sperm agglutination and ingest excess sperm in the oviduct.

The possible taxonomic significance of nurse cells was first pointed out by Borkowski (1971), who noted that the cytoplasmic rods were present in some littorinids and absent from others. Further, Borkowski suggested that the position of attachment of the spermatozoa to the nurse cell, whether perpendicular or parallel to the rod, was characteristic of each species. Differences in the shape of nurse cells have been mentioned by Marcus & Marcus (1963) and Jordan & Ramorino (1975). In the present study the appearance of the nurse cells has been found to be a useful taxonomic character, often diagnostic of the species. In particular there is interspecific variation in the size and shape of the nurse cells, the size of the contained yolk granules, and the shape and number of the rods. There is also a rather wide range of variation within species and even within individuals. This does not greatly detract from the usefulness of the character, but means that spermatozoa of several individuals should be examined if the nurse cells are to be used to confirm identification. This variability is partly due to the not uncommon malformations of the nurse cells, which are hardly surprising in view of the abortive and variable processes described

Fig. 5.3 Spermatozeugmata of *Littoraria* species (differential interference contrast illumination): (a,b) *L.* (*Littorinopsis*) *scabra*, Magnetic I., Qld. (×190, ×490); (c) *L.* (*Littorinopsis*) *cingulata pristissini*, Denham, W.A. (×490); (d) *L.* (*Littorinopsis*) *philippiana*, Magnetic I., Qld. (×490); (e,f) *L.* (*Palustorina*) *articulata*, Magnetic I., Qld. (×190, ×490).


a
b
c
d
e
f

by Woodard (1942a) during the course of their development. Small and malformed nurse cells seem to become more common in the seminal vesicle outside the main breeding season. Most *Littoraria* species examined usually possess more or less distinct rods, although within certain species they are sometimes small or apparently absent. Although the position of attachment of the spermatozoa to the nurse cell was stressed by Borkowski (1971), in *Littoraria* this is variable, even within individuals, as also found by Marcus & Marcus (1963) in *L. flava*. Most commonly, attachment is perpendicular to the rod, but this orientation is seldom determined by a direct attachment of sperm to the rod itself (as stated by Reinke, 1912). Rather, the spermatozoa attach to the region of the cell occupied by the yolk granules, as evident from species in which granules do not entirely pack the cell (Fig. 5.3a,b).

Within the genus *Littoraria* the form of the nurse cells is not only a useful specific character, but is diagnostic of the new subgenus *Palustorina*. In the subgenera *Littoraria*, *Littorinopsis* and *Lamellilitorina* the nurse cells are round or oval, rarely more than 30 µm in length, and the rods, if present, usually extend the full length of the cells or even appear to project from them. In addition to the species described in detail in the present work, nurse cells of this form are known in *L. nebulosa* (Reinke, 1912; rods absent), *L. irrorata* (Woodard, 1942a; pers. obs.), *L. angulifera* (Lenderking, 1954), *L. flava* (Marcus & Marcus, 1963), *L. pintado*, *L. undulata*, *L. coccinea*, *L. zebra*, *L. fasciata* and *L. varia* (all pers. obs.).

In contrast, in the species of the subgenus *Palustorina* the nurse cells are elongate or fusiform, 30 to 55 µm in length, and the rods and the yolk granules are concentrated at opposite ends of the cell. Most importantly, each nurse cell bears a single flagellum, 160 to 250 µm in length, arising from the end occupied by the rods (referred to as basal simply for convenience of description). Flagellate nurse cells have not previously been reported in the family, and their occurrence supports the probable homology of nurse cells with the apyrene sperm of other prosobranchs (Fretter &

Graham, 1962, p. 342; Buckland-Nicks & Chia, 1977). The eupyrene spermatozoa are attached at the opposite end of the nurse cell to the flagellum, their orientation either in the same or opposite direction to that of the flagellum. In either case the flagellum is unlikely to contribute significantly to locomotion of the nurse cell once eupyrene sperm are attached, since each of the many spermatozoa is comparable in length to the single flagellum and their combined beat must outweigh that of the latter. It is not known whether the flagellum is a compound structure, consisting of a number of fibres as in the atypical sperm of some other mesogastropod families such as Strombidae (Reinke, 1912) and Cerithiopsidae (Fretter & Graham, 1962, p. 340). This is likely, since the flagellum appears broad and ribbon-like near the base, and can occasionally be seen to fray into several strands. The mucronate tip conspicuous in the nurse cells of *L.* (*P.*) *conica* is reminiscent of the stalk by which nurse cells are attached to the germinal epithelium in the early stages of their formation (Reinke, 1912; Linke, 1933; Woodard, 1942a).

The subgenera of *Littoraria* also differ in the lengths of the eupyrene sperm, 205 to 350 µm in *Palustorina* species, 100 to 187 µm in the subgenus *Littorinopsis*, while in species of the nominate subgenus lengths are more variable, from 60 to 303 µm.

Amongst other genera of the family Littorinidae, cytoplasmic rods occur in the nurse cells of most species of *Nodilittorina* which have been examined (Borkowski, 1971; Jordan & Ramorino, 1975; pers. obs.) and in *Cenchritis muricatus* (Borkowski, 1971). Variation in the shape of the nurse cells in *Nodilittorina* is such that, as in *Littoraria*, the character may prove to be diagnostic of species. Accounts of the nurse cells of *Littorina* species (Reinke, 1912; Ankel, 1930; Linke, 1933; Buckland-Nicks & Chia, 1977) and of *Melarhaphe neritoides* (Battaglia, 1952) have failed to record the presence of rods in these genera. Only typical eupyrene sperm have been found in the seminal vesicle of two *Bembicium* species (*B. melanostoma* from Magnetic I., Qld., and from Sydney Harbour, N.S.W.; and *B. nanum* from Sydney Harbour, N.S.W., pers. obs.). This result requires confirmation, since Bedford (1965) reported nurse cells in *Bembicium nanum*, although without providing clear figures. It is tentatively suggested that the absence of nurse cells in *Bembicium* and of rods in *Littorina* might be primitive character states (Fig. 8.1). Confirmation must await descriptions of sperm in other littorinacean groups. In a few *Littoraria* species and in *Melarhaphe neritoides*, rods may have been secondarily lost. The flagellate nurse cells of the subgenus *Palustorina* are apparently uniquely derived in the family.

5.4 Female reproductive tract

In its basic plan the anatomy of the ovary and oviduct of *Littoraria* is closely similar to that of the European *Littorina* species described in detail by Linke (1933) and Fretter & Graham (1962) (Figs 5.5, 5.7). The branched lobules of the ovary ramify through the digestive gland, and from the gonad a thin, transparent oviduct runs just beneath the surface epithelium against the columellar pillar of the shell. This portion of the duct is of gonadial origin, and is followed by the short, convoluted and rather thick-walled renal section. The organogenesis of the gonoduct of *Littorina saxatilis* has been described by Guyomarc'h-Cousin (1976). In several littorinids (*Littorina littorea*, Fretter & Graham, 1962, p. 45; *Littoraria angulifera*, *L. flava*, *Nodilittorina lineolata*, Marcus & Marcus, 1963; *L. melanostoma*, Berry & Chew, 1973) a small gonopericardial duct has been observed, joining the oviduct at the proximal end of the renal section. However, no pericardial connection was found during dissections of *Littoraria* species in the present study. Close to the seminal receptacle, the renal section joins the pallial oviduct, which is derived from the mantle wall. This final section is concerned with transport and storage of sperm and with production of egg capsules, and opens to the mantle cavity at a small, distal aperture.

The structure of the pallial oviduct is complex and can best be understood by reference to the schematic drawing of Figure 5.4a. The basic form is a laterally flattened tube, giving off a blind sac, the bursa copulatrix, near the anterior opening. Posteriorly, a narrow duct leads to the seminal receptacle and is joined by the renal oviduct. Internally, both grooves of the slit-like lumen are ciliated, and the dorsal groove is surrounded by a lobe of glandular tissue. From the functional account of the system in *Littorina littorea* given by Fretter & Graham (1962) it is evident that during copulation sperm are deposited in the bursa and subsequently pass along the ventral sperm groove to the receptaculum for storage. Eggs enter the pallial oviduct close to the receptaculum, and it is probably at this point that fertilization occurs. By a combination of ciliary and muscular action, eggs are passed along the dorsal egg groove and during their passage are successively coated by products of the glands differentiated along the length of the groove.

Before describing the structure of the pallial oviduct in detail, it is necessary to review the nomenclature of the glandular elements, which has been inconsistently applied by previous authors (Table 5.1). Existing accounts of the littorinid oviduct refer only to the European *Littorina* species and to several species of *Littoraria* and *Bembicium*. During the present study, oviducts of species from ten genera (Section 3.2.2) have been dissected and it has been found that in all but *Bembicium* the same three glandular types can be distinguished. Proximally, the albumen gland appears white, pale grey or fawn in fresh or preserved material, and as first noted by Hannaford Ellis (1979) it is differentiated into an initial opaque and a subsequent translucent part. This is followed by the gland variously named capsule, covering or membrane gland. In most species the greater part of this gland is opaque pink, or sometimes cream, while the segment closest to the egg groove, and often the entire distal part of the gland, is a translucent dark red or orange brown. These two components have been distinguished by different names by several authors (Table 5.1). Since the term capsule gland is in general use in other prosobranch groups, has

Table 5.1 Nomenclature of the glandular components of the pallial oviduct in the family Littorinidae.

Author	Species	Albumen gland opaque	 translucent	Capsule gland opaque	 translucent	Jelly gland
Linke (1933)	*Littorina obtusata*	Eiweissdrüse		Kapseldrüse		Gallertdrüse
	Littorina littorea	Eiweissdrüse		Kapseldrüse		Gallertdrüse
	Littorina 'saxatilis'	Eiweissdrüse		Kapseldrüse		Brutraum
Fretter & Graham (1962)	*Littorina littorea*	albumen gland		capsule gland (part)	covering gland	capsule gland (part)
Marcus & Marcus (1963)	*Littoraria flava* *Littoraria angulifera*	Kapseldrüse (part)		Kapseldrüse (part)		
Berry & Chew (1973)	*Littoraria melanostoma*	albumen gland		covering gland	capsule gland (part)	capsule gland (part)
Sacchi (1975)	*Littorina nigrolineata*	albumen gland		capsule gland		jelly gland
	Littorina saxatilis	albumen gland		capsule gland		brood pouch
Hannaford Ellis (1979)	*Littorina arcana*	opaque albumen gland	translucent albumen gland	capsule gland		jelly gland
	Littorina rudis			capsule gland		brood pouch
Fretter (1980)	*Littorina* spp. with benthic egg mass	opaque albumen gland	translucent albumen gland	membrane gland		jelly gland
	Ovoviviparous *Littorina* spp.	opaque albumen gland	translucent albumen gland	membrane gland		brood pouch
	Littorina littorea	opaque albumen gland	translucent albumen gland	jelly gland	shell gland	capsule gland

capsule

jelly gl

historically been applied to both these glandular components in littorinids, and since the two components are intimately associated, the terms opaque and translucent capsule glands will be adopted here. The third and final section of the pallial oviduct has been variously modified in littorinids according to the method of development; the possible homology of structures in this position in the various littorinid genera is uncertain, but they will be referred to as the jelly gland.

The names given to the various glands of the pallial oviduct reflect their supposed contributions to the coverings of the eggs, although there has as yet been no detailed histological study relating structures of the egg capsule to the glands producing them. Berry & Chew (1973) reported that the staining reactions of the egg albumen, covering and capsule in *L. melanostoma* corresponded to those of the glands of the same names (Table 5.1), although neither the composition of the egg capsule, nor the structure of the final parts of the oviduct, were described in detail.

The probable functions of the glands can, perhaps, be deduced from the correlation of oviducal structure with the type of spawn produced. In *Littorina littorea* and *Melarhaphe neritoides*, both producing pelagic capsules (Linke, 1933; Lebour, 1935; Fretter & Graham, 1962), the egg is coated with albumen, surrounded by a covering membrane, and embedded in a viscous fluid within the firm outer capsule. In these two species all glandular types are present; the opaque capsule gland occupies a relatively large volume of the oviduct (pers. obs.) and, as suggested by Linke (1933), probably produces the most voluminous component of the spawn, the viscous fluid. In contrast, in *Littorina arcana* and *Littorina obtusata*, which produce a benthic gelatinous spawn (Hannaford Ellis, 1979; Fretter, 1980), the opaque capsule gland is considerably smaller in relation to the albumen gland. The reduction of the opaque capsule gland has proceeded even further in the ovoviviparous *Littorina saxatilis* (Fretter, 1980) and in none of these three species has a translucent portion of the capsule gland been described. Fretter &

Graham (1962, pp. 389, 425) reported that embryos of *Littorina saxatilis* and *Littorina obtusata* are enclosed in thin egg coverings, but that no capsule is present. It seems possible, therefore, that the translucent capsule gland is concerned with production of the outer egg capsule, while the opaque capsule gland produces the material between the capsule and the albumen layer, including the so-called egg covering. Although, as discussed below, capsule glands are absent in the ovoviviparous species of *Littoraria*, the embryos are still enclosed within a thin, spherical covering, the origin of which is unknown. Linke (1933) suggested that the capsule may be produced by the ovipositor. However, this seems unlikely, since Fretter & Graham (1962, p. 387) found fully formed capsules within the oviduct of *Melarhaphe neritoides*, while in *Littoraria* species an ovipositor is apparently lacking. The secretion of the ovipositor may merely harden the capsule (Linke, 1933; Fretter & Graham, 1962, p. 47).

In species of *Littorina* (Linke, 1933; Hannaford Ellis, 1979; Fretter, 1980) and *Bembicium* (Anderson, 1958; Bedford, 1965) which produce benthic gelatinous egg masses, the final section of the pallial oviduct is greatly enlarged by glandular folds thrown into the lumen and is named the jelly gland (Table 5.1). In the ovoviviparous *Littorina saxatilis* this section is also folded internally and functions as the brood pouch. As suggested by Hannaford Ellis (1979), brood pouch and jelly gland are homologous in the genus *Littorina*. In *Littorina littorea*, *Melarhaphe neritoides* and the other littorinid genera examined during the present study which are known to produce pelagic capsules, this final glandular section is relatively poorly developed. It follows the translucent capsule gland and is visible only as a small whitish lobe around the egg groove, sometimes with a pale yellow or brown proximal region. From its position, it is to be expected that this final glanduar element will produce material found externally to the egg capsule. Such a substance has been described in *Littorina sitkana* Philippi (in which capsules are embedded in a benthic gelatinous egg mass; Buckland-Nicks *et al.*, 1973), in *Littorina keenae* Rosewater (in which capsules are initially embedded in a pelagic, gelatinous egg mass; Schmitt, 1979, as *Littorina planaxis*) and in *Littoraria nebulosa* (in which capsules are shed in mucous strings; Bandel, 1974). In each case the gelatinous material soon disintegrates to release the capsules and perhaps for this reason has not been observed in other species. It is therefore tentatively suggested that the final glandular component in species with pelagic capsules is similar in function to the jelly gland of species with benthic spawn. The name jelly gland will be used here and the homology thereby implied is strengthened by the occurrence of all three conditions of this gland within the genus *Littorina*. However, confirmation must await further investigation.

Figure 5.4a illustrates in schematic form the arrangement of the components of the pallial oviduct in littorinids which produce pelagic egg capsules. In fact the egg groove and its surrounding glands do not follow a straight course as shown in this figure. In all littorinid genera so far examined the pathway of the eggs has been greatly lengthened and the volume of the glands increased by throwing the egg groove into a series of loops and spirals lying on the right side of the organ. The pattern of the convolutions appears to be characteristic of each of the genera examined (Fig. 5.9). In *Littoraria* the characteristic pattern is a doubly wound spiral, which can be visualized as an elongated loop wound back upon itself (Fig. 5.4b-d). The sperm groove, however, continues to follow a straight course to the seminal receptacle along the morphologically ventral side of the lumen. Throughout its spiral route the egg passage remains an open groove, its lumen continuous with that running the length of the oviduct, and in cross section the common lumen of the spiral whorls can be seen. Although in most previous accounts of the littorinid oviduct the external spiral form has been illustrated, the internal structure has been correctly interpreted only by Berry & Chew (1973) in *Littoraria melanostoma*. Since their account was in some respects incomplete, the oviduct of *L. melanostoma* will be redescribed here, as a typical example of the genus. Amongst other species of *Littoraria*, oviducts have previously

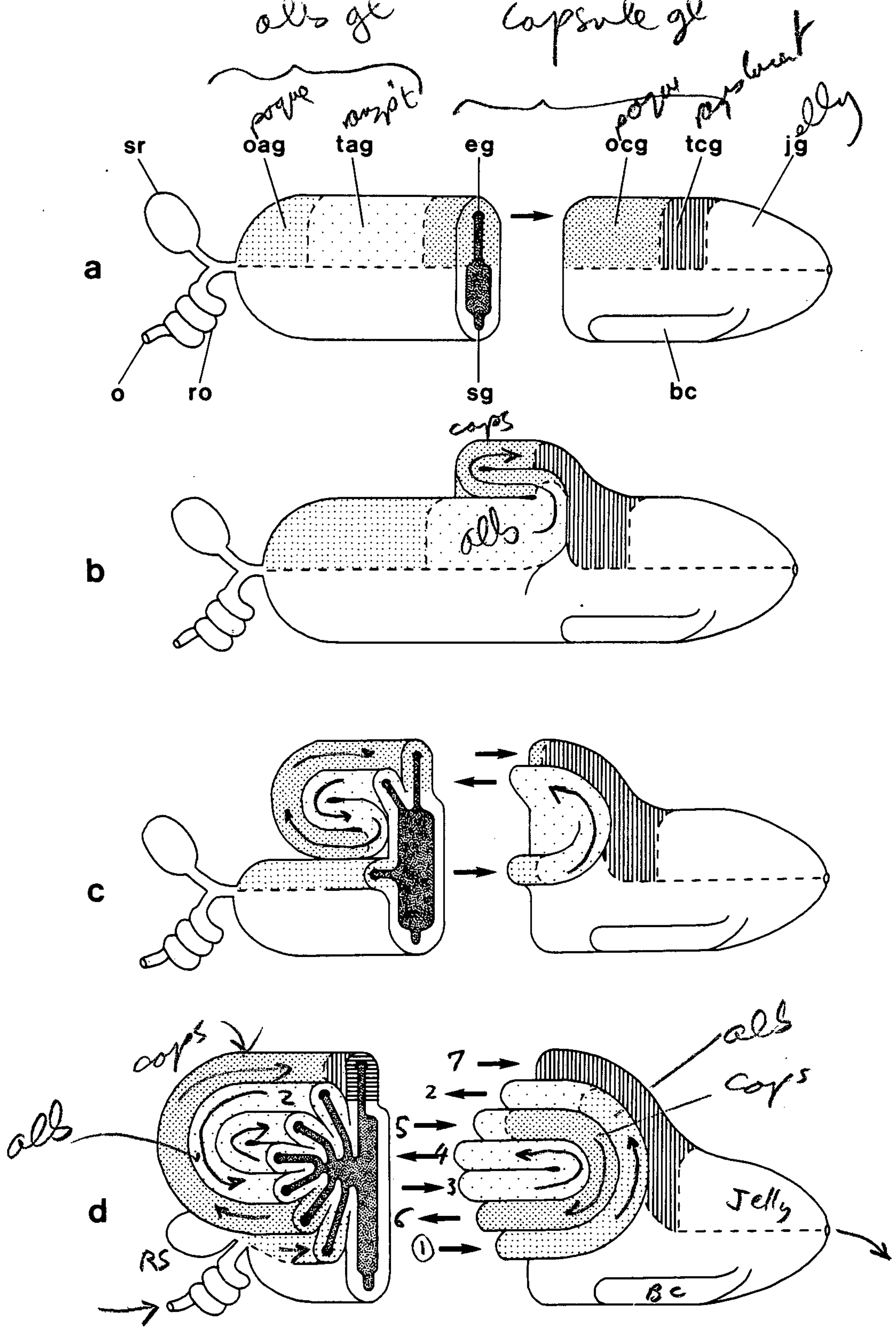


Fig. 5.4 Schematic diagram explaining the form of the pallial oviduct in oviparous *Littoraria* species; (a) to (d) represent hypothetical stages showing progressive lengthening of egg groove by twisting into a double spiral (see text for details); bc, bursa copulatrix; eg, egg groove; jg, jelly gland; o, ovarian oviduct; oag, opaque albumen gland; ocg, opaque capsule gland; ro, renal oviduct; sg, sperm groove; sr, seminal receptacle; tag, translucent albumen gland; tcg, translucent capsule gland; arrows indicate pathway of eggs.

been figured only for *L. angulifera* and *L. flava* from the western Atlantic (Marcus & Marcus, 1963).

Species of *Littoraria* in which development has been observed either spawn pelagic egg capsules or are ovoviviparous, releasing early veliger larvae after brooding the eggs between the lamellae of the gills in the mantle cavity. As a result of the present study it has been found that the method of development is clearly indicated by the structure of the pallial oviduct. Only two species of the *scabra* group, *L. articulata* (pers. obs.) and *L. melanostoma* (Berry & Chew, 1973) are definitely known to spawn pelagic egg capsules. In both species the spiral portion of the oviduct is large, composed of 4½ to 6½ whorls, along which all the glandular types defined above can be distinguished. Six other species of the *scabra* group possess a pallial oviduct of this type (*L. vespacea*, *L. albicans*, *L. conica*, *L. carinifera*, *L. sulculosa*, *L. strigata*); veligers have never been found in their mantle cavities and they can be assumed to be oviparous also. This prediction is strengthened by the discovery of similar oviducts in all other *Littoraria* species of which egg capsules have been described in the literature (*L. undulata*, *L. coccinea*, *L. nebulosa*, *L. flava*, *L. irrorata*, *L. pintado*; Section 5.5). In the remaining ten species of the *scabra* group for which the anatomy is known, the spiral portion of the oviduct is reduced, consisting of 2½ or 3½ whorls, and both opaque and translucent capsule glands are absent. These species are ovoviviparous and retention of embryos in the mantle cavity was observed in eight of them (*L. scabra*, *L. lutea*, *L. pallescens*, *L. philippiana*, *L. intermedia*, *L. subvittata*, *L. filosa*, *L. luteola*).

The pallial oviduct of *L.* (*Palustorina*) *melanostoma* is representative of the oviparous group, which comprises all members of the subgenera *Littoraria*, *Palustorina* and *Lamellilitorina*. When examined externally from the right side (Fig. 5.5a,c) the pallial oviduct is seen to consist of a proximal swelling marked by a conspicuous spiral line of black pigment. This spiral portion partly overlies the rectum, and is followed by a straight portion which

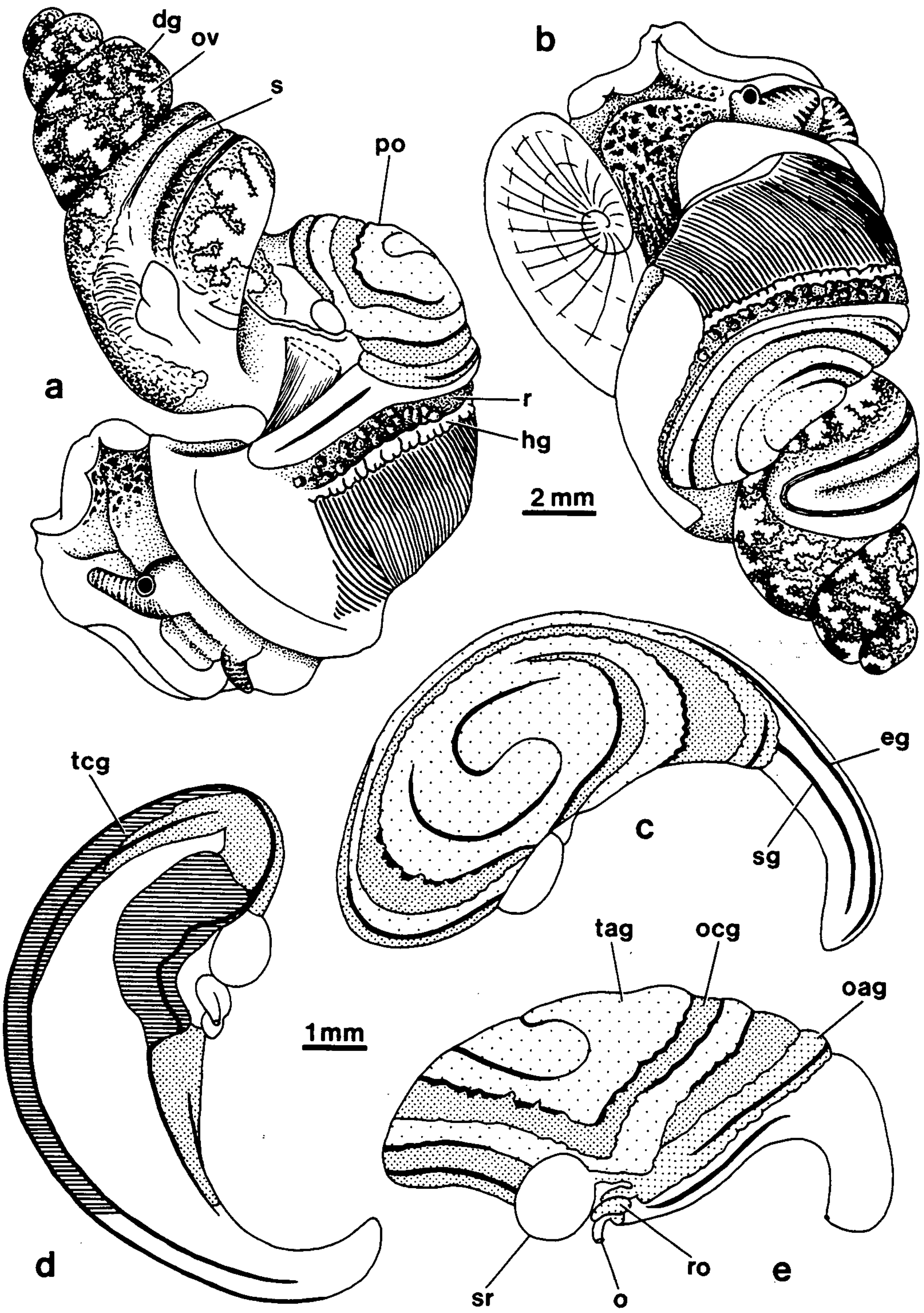


Fig. 5.5 *Littoraria (Palustorina) melanostoma*: female reproductive tract; (a,b) animal removed from shell; dg, digestive gland; hg, hypobranchial gland; ov, ovary; po, pallial oviduct; r, rectum; s, stomach; (c,d,e) lateral, medial and ventral views of pallial oviduct; abbreviations and shading as in Fig. 5.4.

terminates at a pore opening into the mantle cavity to the right of the anal papilla. The internal structure can be understood by cutting successive transverse sections (Fig. 5.6). These may be compared with the diagrams of Figure 5.4. Within the straight portion the lumen is a laterally flattened slit, with a ventral pigmented sperm groove and a dorsal pigmented groove for the passage of eggs. Distally, the bursa copulatrix is represented only by a ventral chamber communicating with the lumen of the oviduct. The bursa only separates as a distinct sac posteriorly, at the level of the most anterior part of the spiral oviduct, and continues posteriorly just to the right of the sperm groove. The bursa opens in a more anterior position in the subgenus *Lamellilitorina* and in some species of the subgenus *Littoraria*, as discussed below. Running beneath the spiral portion, the sperm groove continues posteriorly as a short duct leading to the seminal receptacle. The convoluted renal oviduct enters the pallial section just anterior to the receptacle, from which point the morphologically dorsal egg groove leads forward into the spiral portion. Viewed from the right side, the egg groove runs in an anticlockwise direction through three revolutions to the apex of the spiral, and continues through three descending clockwise whorls, which alternate with the ascending whorls of the groove. Leaving the spiral on the dorsal side, the descending groove runs forward as the dorsal egg groove of the straight portion of the duct.

Within the spiral section the lining of the egg groove is darkly pigmented and all whorls of the groove communicate by a common central lumen, although several serial sections must be examined to demonstrate all interconnections. Nevertheless, the opening of the groove is constricted by the glandular folds between which it runs, so that the egg passage may function effectively as a closed tube. The surrounding glandular tissues can be identified by their colouration even in unstained fresh or preserved material. For the first one third of a revolution the groove runs through opaque white tissue of the albumen gland. The subsequent portion of the albumen gland is translucent pale grey or fawn, and surrounds the $2\frac{1}{2}$

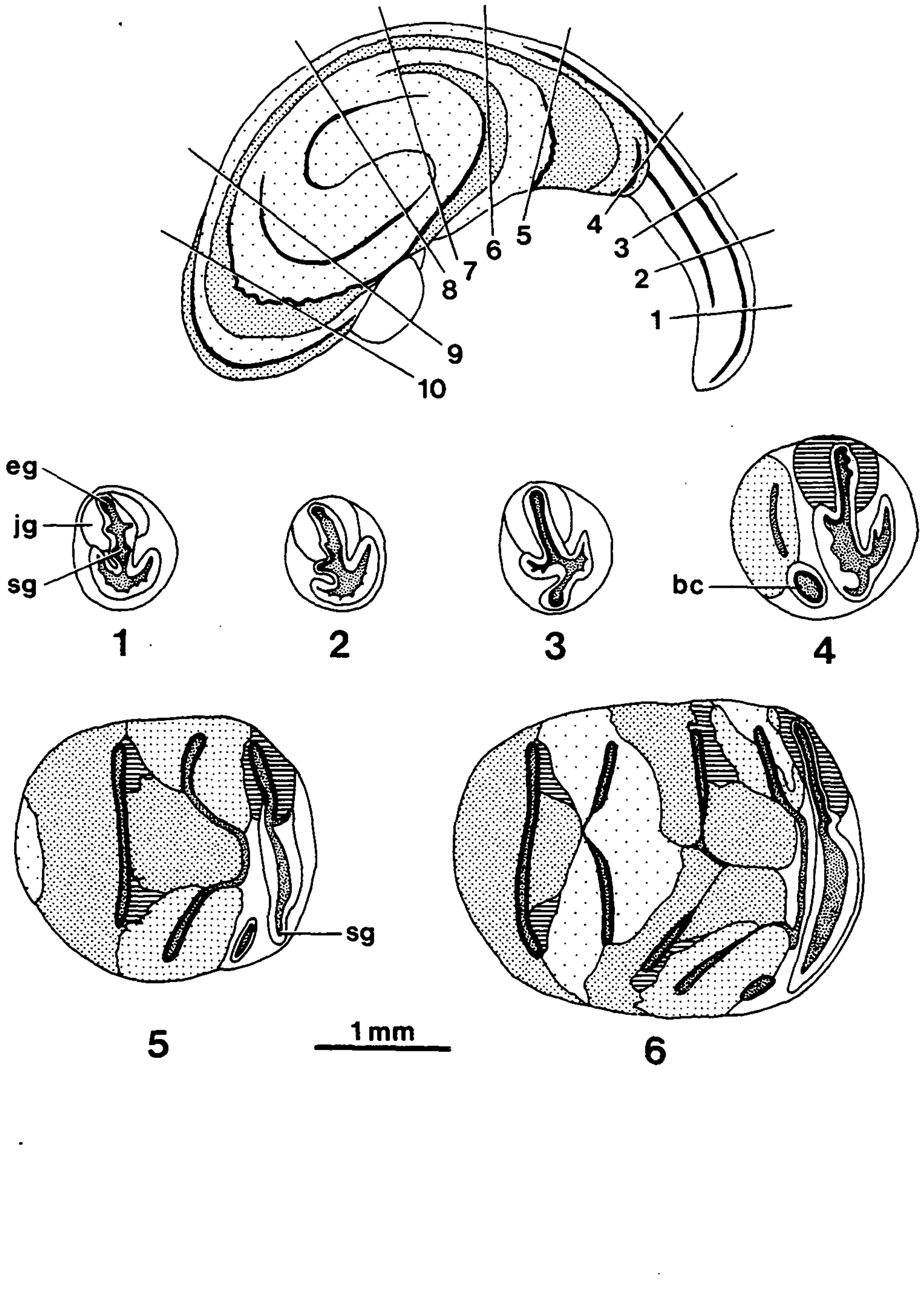
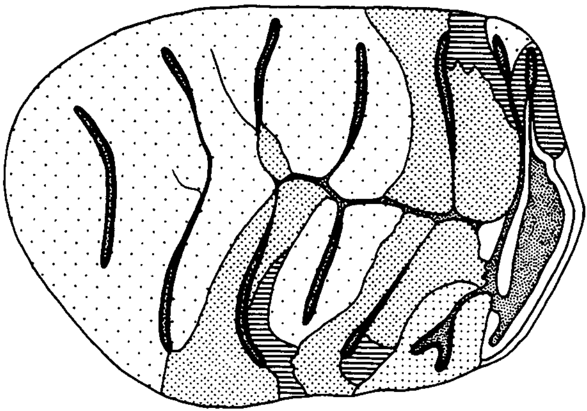


Fig. 5.6 *Littoraria (Palustorina) melanostoma*: serial sections of pallial oviduct; abbreviations and shading as in Fig. 5.4.



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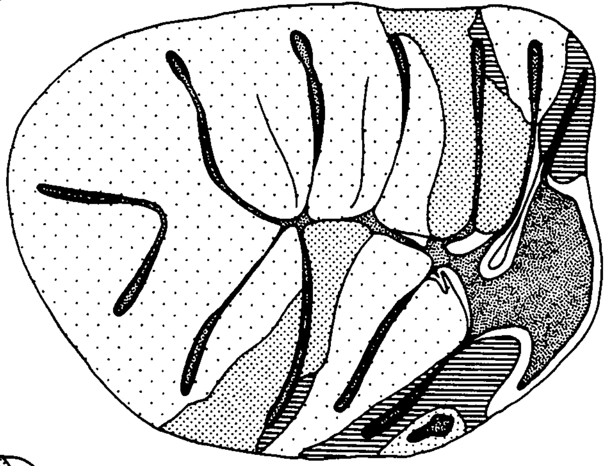

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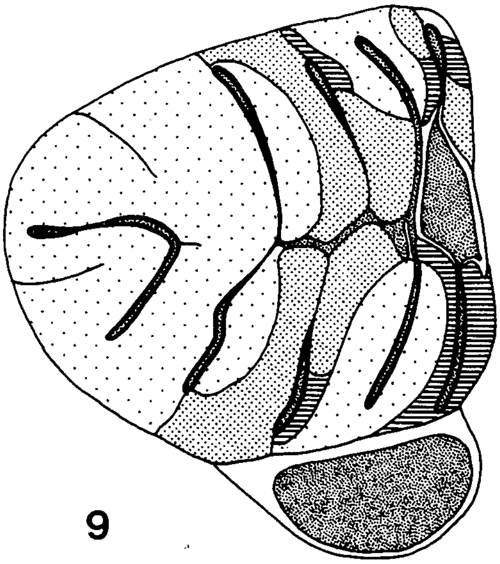

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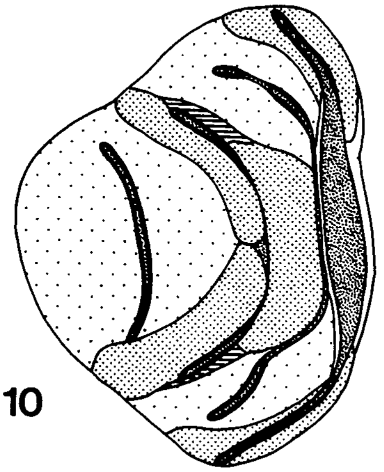

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whorls ascending to the apex, as well as the first whorl of the descending spiral. The following descending whorls are surrounded by the capsule glands, pale pink opaque tissue predominating for the first $1\frac{1}{2}$ whorls and dark red translucent tissue for the last whorl of the spiral, extending around the lowermost chamber. A small amount of translucent whitish jelly gland surrounds the egg groove in the straight portion of the oviduct.

Identification of the glandular components was confirmed by histological techniques. The initial opaque white portion of the albumen gland stained dark pink in haematoxylin and eosin (HE), blue in Mallory-Heidenhain trichrome (MHT) and blue and purple (indicating acidic and mixed mucins) using the alcian blue and periodic acid-Schiff (ABPAS) technique. The following translucent section of the gland stained pale pink in HE, very pale blue or colourless in MHT, and largely magenta but with some blue areas (mainly neutral mucins) in ABPAS. Similar MHT staining reactions of the albumen gland were described by Hannaford Ellis (1979) in two *Littorina* species. The opaque capsule gland is packed with a granular secretion, staining dark pink in HE, red in MHT and magenta to purple in ABPAS (indicating neutral and mixed mucins). The translucent capsule gland stains pink in HE, blue in MHT and purple in ABPAS. Berry & Chew (1973) reported similar trichrome staining reactions for the glandular tissues in this species. Within the whorls of the opaque capsule gland a small patch of cells near the base of the egg groove shows the reactions of the translucent albumen gland, whilst an adjacent area is an extension of the translucent capsule gland. The close association of the two regions of the capsule gland is further demonstrated by the appearance of an area of the opaque tissue type within the translucent region of the gland posterior to the seminal receptacle (Fig. 5.6). This complex pattern is found in the other oviparous species also. The staining reactions of the jelly gland are the same as those of the translucent albumen gland. In each type of gland the subepithelial cells are arranged in indistinct, closely packed lobules, each delimited by a very thin connective tissue envelope, with a single layer of secretory cells surrounding the narrow central lumen. This structure has been illustrated by Linke (1933, figs 57, 62) and Fretter & Graham (1962, p. 335). The arrangement applies also to the jelly gland, which is thus in contrast to the glandular epithelial folds of this region in *Littorina* (Linke, 1933) and *Bembicium* (pers. obs.)

The lumen of the pallial oviduct is lined throughout by an epithelium, supported by a thin basement membrane which clearly separates it from the glandular subepithelial cells. In the final and largest chamber of the spiral the epithelium is ciliated and columnar, with cells up to 70 µm tall, and is thrown into closely packed folds up to 150 µm in height. In the remaining spiral portions of the oviduct ciliated columnar epithelium is found only within the grooves, while the lining of the common central lumen is low and lacks cilia. Most of the ciliated cells within the grooves contain granules of black pigment, which is responsible for the black spiral clearly visible on the right side of the intact oviduct. The secretion of the subepithelial glandular cells reaches the spiral groove through fine cytoplasmic extensions terminating between the ciliated epithelial cells. Consequently the epithelial layer appears to show the same staining reactions as the glandular tissue beneath it, although close examination shows that the epithelial cells are not themselves glandular.The secretory pathway is shown most clearly by the granular secretion of the covering gland. In the final chamber of the spiral there is no glandular tissue beneath the epithelium. Here the surface area is much increased by folding of the epithelial layer and the cells contain clear vesicles. These cells stain strongly magenta in ABPAS and may well serve a secretory function. The structure and staining reaction of the epithelium of the bursa are similar. In contrast, in the sperm groove the epithelium contains numerous goblet-shaped cells, colourless in MHT, but bright blue (indicating acidic mucins) in ABPAS, and these are clearly secretory. A layer of circular muscle 20 to 80 µm in thickness underlies the epithelium in the final chamber, while a thinner layer surrounds both bursa and oviduct in the straight section.

In the ovoviviparous species, comprising the subgenus *Littorinopsis*, the spiral form of the pallial oviduct is similar to that of the oviparous species, although the glandular region is relatively smaller in size and consists of fewer whorls. The spiral structure is usually less clear externally owing to the small amount of black pigment in the ciliated spiral groove. In comparison with the oviparous species of *Palustorina* the bursa copulatrix is situated further anteriorly, lying beside the straight section of the oviduct, which it joins near the opening to the mantle cavity. Throughout its length the pallial oviduct runs along the right side of the rectum, and the straight portion terminates in a raised papilla to the right of the anus. This papilla is presumably concerned with positioning the ova in the mantle cavity for brooding, and is absent in the oviparous species. *L.* (*Littorinopsis*) *scabra* is representative of the ovoviviparous group (Fig. 5.7). In this species the opaque region of the albumen gland occupies the first anticlockwise ascending whorl of the spiral and is followed by the translucent albumen gland which continues for half a revolution to the apex, and through a further two descending clockwise whorls into the straight portion of the oviduct (Fig. 5.8). The two parts of the albumen gland are similar in appearance and staining reactions to the homologous glands in *L.* (*Palustorina*) *melanostoma*. The small amount of glandular tissue around the egg groove running through the straight section appears to be the reduced jelly gland; staining reactions are similar to those of the translucent albumen gland, although in ABPAS the tissue stains red rather than magenta. Both types of capsule gland are absent. The epithelial lining of the pallial oviduct is closely similar to that described for *L. melanostoma*, except for the fact that the goblet cells staining blue in ABPAS (indicating acidic mucins), whilst still concentrated in the sperm groove, are also found in smaller numbers through the convoluted epithelium of the final chamber and straight section.

It is possible to speculate upon the evolution of the pallial

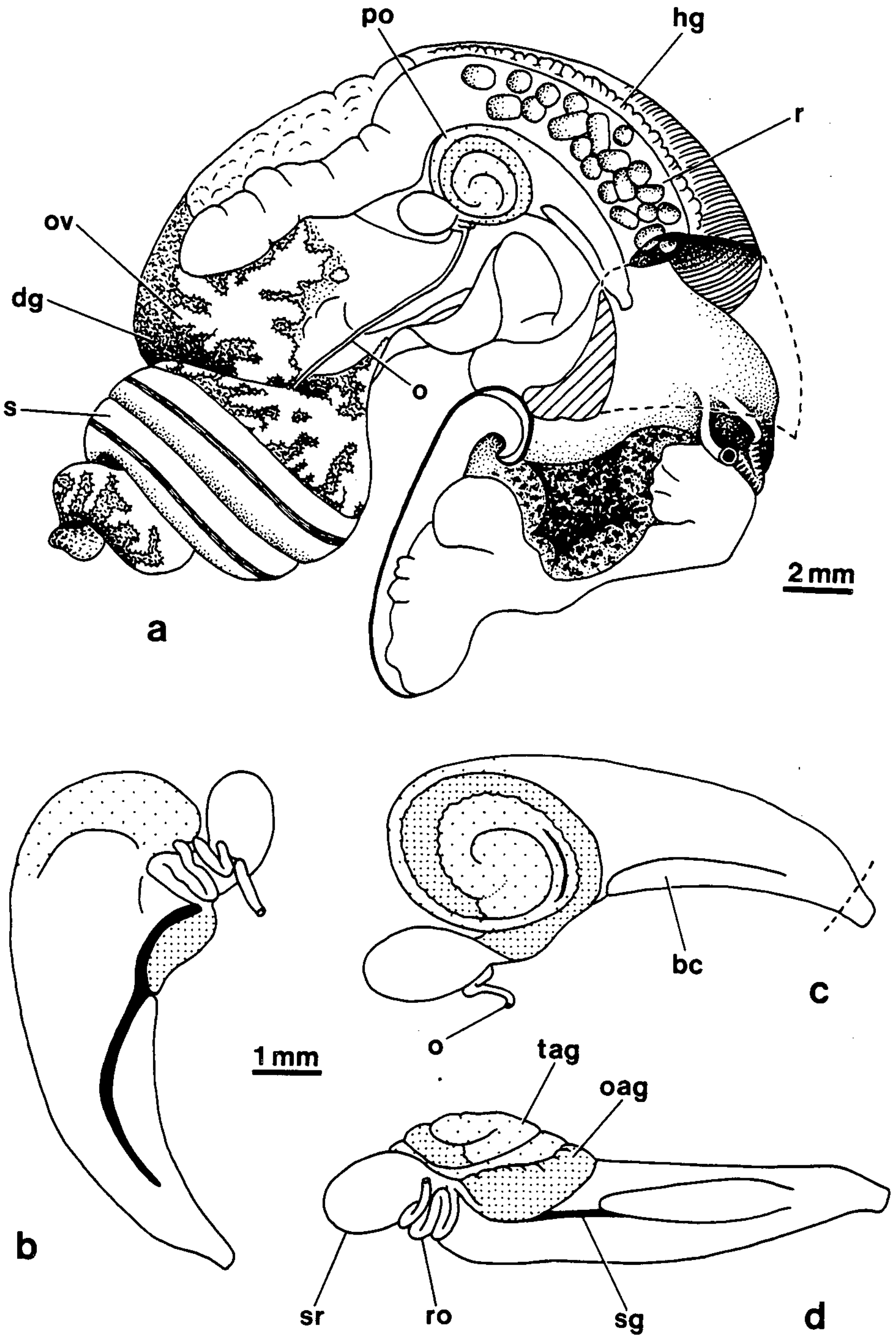

Fig. 5.7 *Littoraria (Littorinopsis) scabra*: female reproductive tract; (a) animal removed from shell; (b,c,d) medial, lateral and ventral views of pallial oviduct; abbreviations and shading as in Figs 5.4 and 5.5; dashed lines indicate cut mantle tissue.

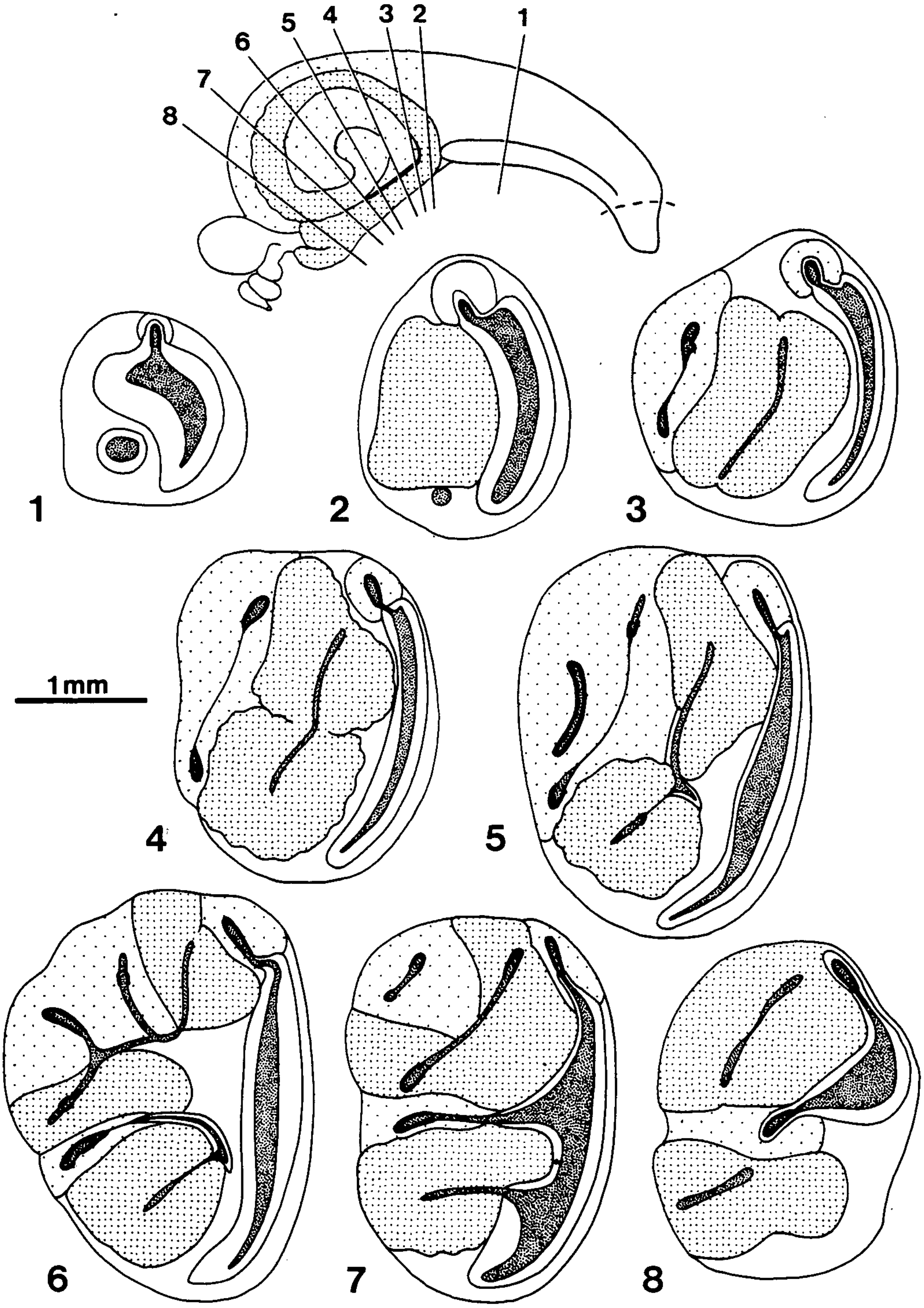

Fig. 5.8 *Littoraria (Littorinopsis) scabra*: serial sections of pallial oviduct; shading as in Fig. 5.4.

oviduct in the family Littorinidae. It is likely that the pallial oviduct of prosobranchs arose as a straight, elongate gutter in the pallial wall (Fretter & Graham, 1962; Ponder, 1968) which in most groups has closed ventrally to form a tube, as represented diagrammatically in Fig. 5.4a. Amongst the various littorinid genera examined during the present study, certain species of *Nodilittorina* (*N. angustior*, *N. australis*, *N. dilatata*, *N. hawaiiensis*, *N. millegrana*, comprising 'group 1' in Fig. 5.9), of *Fossarilittorina* and *Peasiella*, and also *Echininus antoni*, approximate most closely to this hypothetical ancestral condition. In these forms the albumen gland occupies a proximal loop of the egg passage, while capsule glands and jelly gland follow an almost straight course to the genital opening. Although there is as yet no evidence to support the suggestion that this form of the oviduct is in fact primitive for the family, it is nevertheless possible to arrange the oviducts of other species in a morphological sequence suggesting how progressive elaboration of a simple oviduct might have occurred (Fig. 5.9).

The single spiral form found in *Littoraria* is not unique to the genus, for very similar oviducts are seen in *Cenchritis muricatus* and *Tectarius grandinatus*. The spiral oviduct of *Bembicium* is only superficially similar, and lacks capsule glands (pers. obs.; see also Anderson, 1958; Bedford, 1965). The condition in *Echininus cumingi* and *Nodilittorina ziczac* is intermediate between that of *Tectarius grandinatus* and the simplest form of the oviduct. In some species of *Nodilittorina* the capsule gland is thrown into a loop (*N. pyramidalis*, *N. unifasciata*, comprising 'group 2' in Fig. 5.9), while in others both capsule gland and jelly gland are each thrown into a loop (*N. knysnaensis*, *N. praetermissa*, comprising 'group 3' in Fig. 5.9) and in *Melarhaphe neritoides* the jelly gland is elaborated into a spiral. The condition in *Littorina* is distinctive, with albumen and capsule glands each forming a spiral, while the jelly gland follows a relatively straight course. Whilst the sequence of Figure 5.9 should not be interpreted as indicative of evolutionary relationships between the species illustrated, it does suggest that derivation of the oviduct of *Littoraria* can most

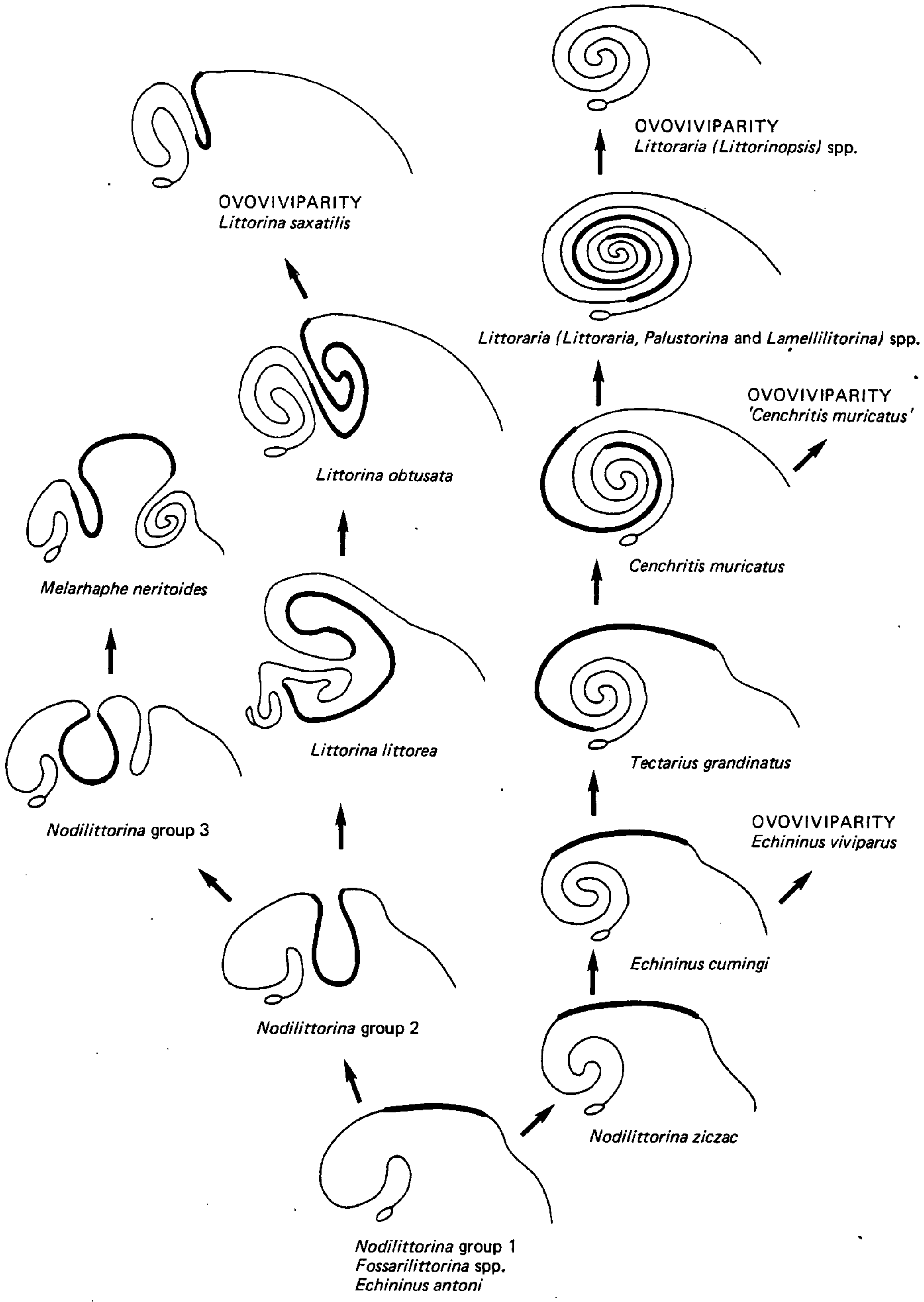

Fig. 5.9 Diagrammatic representations of the pallial oviducts of some genera of Littorinidae, arranged in morphological sequence, showing how progressive elaboration of the path of the egg groove may have occurred; opaque capsule gland indicated by thick line; see text for details.

reasonably be postulated from the condition found in the genera *Nodilittorina, Fossarilittorina, Peasiella, Echininus, Tectarius* and *Cenchritis*, rather than from the specialized forms found in modern species of *Littorina* and *Melarhaphe*.

Amongst the oviparous species of *Littoraria*, the simplest oviduct is that of *L. pintado*, with only 3½ whorls in the spiral portion. In other respects also this species displays characters regarded as primitive in this genus (Fig. 8.2). The most elaborate oviducts are found in the Eastern Pacific species *L. zebra* and *L fasciata*, the latter showing a spiral of 9½ whorls. The degree of separation of the bursa from the straight section of the oviduct appears to be another character of phylogenetic significance in the genus. In the subgenus *Littorinopsis* all species of which the anatomy is known show a bursa of the type described above in *L. scabra*. This condition, in which the bursa joins the oviduct close to the genital aperture, is also found in five species of the subgenus *Littoraria* (Fig. 8.2). In contrast, in other members of this subgenus and in *Palustorina*, the bursa is not fully separated from the oviduct until a point close to the anterior part of the spiral section, and this condition appears to be primitive in the genus *Littoraria*. Amongst the other littorinid groups examined, the bursa shows the more posterior opening in most but not all species of *Nodilittorina* and in *Littorina littorea*. Marcus & Marcus (1963) described two bursae in *Nodilittorina lineolata* (as *Littorina ziczac*, but see Bandel & Kadolsky, 1982), but this observation is probably erroneous.

The subgeneric division of *Littoraria* proposed here (Section 8.3) separates the ovoviviparous species as the subgenus *Littorinopsis*. Within the genus, as in the family as a whole, oviparity is certainly the ancestral condition. Little structural modification of the pallial oviduct has occurred with the development of ovoviviparity; the oviduct has merely been simplified by the loss of capsule glands and reduction in number of whorls of the spiral groove. Since the form of the oviduct, and also the method of brooding in the mantle cavity to the early veliger stage, are similar in the species of *Littorinopsis*, they may be a monophyletic group (Fig. 8.2). The anatomy of *L. aberrans* from the eastern Pacific is as yet unknown, and so, consequently, is its subgeneric assignment, but in view of the character of its protoconch (Section 4.3) it would appear to undergo nonplanktotrophic development. The thin and colour polymorphic shell of this species suggests a high supratidal zonation (Sections 14.3.5, 15.4.1), so that ovoviviparity (rather than a benthic egg mass) might be predicted, but whether embryos are brooded in the oviduct or in the mantle cavity remains to be discovered.

It may be noted that the ovoviviparous habit has evolved independently in several other littorinid groups. In *Littorina* it has been described in the species *saxatilis* and *neglecta* (Fretter, 1980), in which embryos are retained within the brood pouch, formed from the distal section of the pallial oviduct, until after metamorphosis (Linke, 1933; Fretter & Graham, 1962, p. 343). Rosewater (1982) described *Echininus viviparus*, which broods its young in a similar fashion, although not closely related to *Littorina* (Fig. 8.1). The brooding of embryos to the early veliger stage between the lamellae of the gills has only been described in the subgenus *Littorinopsis*. However, Bandel (1974) noted the release of veligers by *Cenchritis muricatus*, although other authors have found this species to release egg capsules (Lebour, 1945; Borkowski, 1971).

Variation of the type of larval development within a single species (reviews by Robertson, 1974; Jablonski & Lutz, 1983) is extremely rare in gastropod molluscs. Most reported cases have subsequently been explained by the existence of unrecognized sibling species (Jablonski & Lutz, 1983). Several littorinids have been cited as examples of species with variable development. In *Littorina* '*saxatilis*' (Fretter & Graham, 1962; Robertson, 1974) the ovoviviparous and oviparous forms are now recognized as distinct species, partly on the basis of oviducal anatomy (Heller, 1975a; Sacchi, 1975; Hannaford Ellis, 1979). Although the taxonomic significance of developmental type and the associated oviducal anatomy is still disputed in the case of the pair of species *Littorina saxatilis* and *Littorina arcana* (Gaugant & Bergerard, 1980; Smith, 1982), differences in allele frequency have been demonstrated in sympatric populations (Ward & Warwick, 1980), supporting the case for a specific difference. A report of a short pelagic stage in *Littorina 'obtusata'* by Tattersall (1920) has never been confirmed, for although two closely related species are now recognized (Sacchi & Rastelli, 1967), subsequent observations have been of nonplanktotrophic development in benthic egg masses. The variation in development of *Cenchritis muricatus* noted by Bandel (1974) suggests that the form requires taxonomic study.

In the genus *Littoraria* the following species have been reported to release both veligers and earlier developmental stages: *L. pallescens* (Abe, 1942, as *Melaraphe scabra*; c.f. pers. obs. of veligers in mantle cavity); *L. angulifera* (Lenderking, 1954; c.f. Gallagher & Reid, 1974) and *L. intermedia* (Struhsaker, 1966, as *Littorina scabra*). As suggested by Struhsaker (1966), release of embryos rather than veligers may be an abnormal response to laboratory conditions. In the present study females of ovoviviparous species have occasionally been found to release embryos prematurely upon disturbance. In each of these three species the embryonic stages shed were devoid of egg capsules, so that this habit represents only a very minor modification of the normal ovoviviparous habit. Anatomical examination has provided no suggestion that any species of *Littoraria* is able to show both oviparous and ovoviviparous modes of development. In conclusion, the release of veligers as opposed to egg capsules, and the associated differences in anatomy of the oviducts described above, must be accepted as evidence of at least specific difference in *Littoraria*, as in other littorinids.

In the present study the form of the pallial oviduct has been used principally to define generic and subgeneric groups and to suggest the method of development in species for which it is unknown. Although not one of the most useful characters at the specific level, variation between species of the same subgenus can be observed in such details as the number of whorls of the spiral section, extent of the glandular components, and relative lengths of the bursa, spiral and straight portions. Usually the details of the arrangement of the spiral egg groove and relative sizes of glandular lobes, as seen in transverse section, are not of great importance, for these vary somewhat between individuals and are dependent upon the exact plane of the section. Use of the anatomy of the pallial oviduct as a taxonomic character is complicated by the reduction in size and darkening in colour of the organ, to grey or brown, which takes place outside the breeding season. However, these changes are largely a consequence of a decrease in thickness of the glandular walls of the duct; the form and structure do not change. Likewise, in females infected with parasitic trematodes the gonad and oviduct may be reduced in size, but trematode infections are rare in *Littoraria* species.

5.5 Egg capsules

As discussed in Section 5.4, species of *Littoraria* in which spawning has been described produce either pelagic egg capsules or release veligers after a period of development in the mantle cavity. *L. aberrans* is an apparent exception, with some form of nonplanktotrophic development (Section 4.3). Spawning and development of the western Atlantic *L. angulifera* have been investigated by Lebour (1945), Lenderking (1954) and Gallagher & Reid (1974), and of *L. irrorata* by Bingham (1972b) and Gallagher & Reid (1974), while the egg capsules alone have been described in *L. flava* (Marcus & Marcus, 1963) and *L. nebulosa* (Bandel, 1974). Of the Indo-Pacific species only the following have been examined in any detail: *L. pallescens* (Abe, 1942, as *Melaraphe scabra*); *L. pintado* and *L. intermedia* (Struhsaker, 1966, the latter as *Littorina* *scabra*); *L. melanostoma* (Berry & Chew, 1973); and *L. luteola* (Muggeridge, 1979, as *Littorina scabra*). The egg capsules of *L. coccinea* and *L. undulata* have been illustrated by Rosewater (1970) and of *L. articulata* by Kojima (1958c; as *L. strigata*). From these accounts the duration of brooding in ovoviviparous species varies from four days in the tropical *L. angulifera* to seventeen days in the temperate *L. luteola*, while capsules of *L. irrorata* hatch in one to two days, *L. pintado* in three, and *L. melanostoma* in seven days. Gallagher & Reid (1974) suggested a planktotrophic life of eight to ten weeks before settlement in *L. angulifera*.

In the ovoviviparous species of *Littoraria* the embryo is contained within an egg covering alone and no capsule is produced. Amongst the oviparous members of the genus, the egg capsules have been described in eight species, as illustrated in Figure 5.10. In each case the capsule is a more or less symmetrical biconvex disc, ranging from 150 to 400 µm in diameter, and typically containing a single ovum. The capsule is surrounded by a circumferential flange or lamella, which in *L. coccinea* and *L. glabrata* (= *L. kraussi*) is turned down to form a flotation skirt (Rosewater, 1970). The capsule of *L. pintado* (Struhsaker, 1966) differs somewhat from the others in the genus and is considered below.

The utility of the form of the egg capsule as a taxonomic character has been disputed in the past (Borkowski, 1975). However, revised species concepts based upon detailed anatomical studies have shown that in several groups of littorinids the form of the egg capsule is a useful diagnostic character (Murray, 1979; Bandel & Kadolsky, 1982). In the genus *Littoraria* the published drawings suggest that egg capsule form might be species specific in many cases, although at least in *L. articulata* there appears to be some variation within a species (Section 9.2.4.6).

The range of capsule types produced by members of the family Littorinidae has been reviewed by Bandel (1974) and by Jordan & Ramorino (1975). Systematic trends in capsule form above the species level have been denied (Rosewater, 1970), but in the light of new generic concepts (Bandel & Kadolsky, 1982) some generalizations can be made. The capsules of oviparous species of the genus *Littoraria* are rather distinctive (Fig. 5.10, after authors quoted above), although similar to those described in *Cenchritis muricatus* (Lebour, 1945; Borkowski, 1975; figures given by these authors differ, as illustrated in Fig. 5.10). Species of *Littorina* with planktotrophic development show capsules of similar form again (Buckland-Nicks *et al.*, 1973; Kojima, 1957, 1958b; Linke, 1933; Murray, 1979; Schmitt, 1979; illustrated in Fig. 5.10), although usually of larger size and frequently enclosing several eggs. The capsules of *Nodilittorina* contain single eggs and are more elaborate, with a cupola sculptured by concentric rings, the edge of the cupola overhanging the lower half of the capsule as a peripheral band or skirt (Struhsaker, 1966; Borkowski, 1971; Pilkington, 1971; Bandel, 1974; Jordan & Ramorino, 1975; Bandel & Kadolsky, 1982). Similar shapes have been reported by Borkowski (1971) for *Echininus antoni* (as *E. nodulosus*) and *Fossarilittorina meleagris* (Fig. 5.10).

These trends in capsule form have to a certain extent been overlooked, because in several littorinid groups closely related species may show a range of developmental types, as exemplified by the genus *Littorina*, with species producing pelagic capsules, benthic egg masses or retaining embryos in the oviduct. Littorinids known to produce a benthic gelatinous spawn without individual egg capsules include six species of the genus *Littorina*, three of *Bembicium* and one of *Risellopsis* (Section 13.4.1). This type of spawn has also been described in several Antarctic littorinaceans (Picken, 1979) and in members of the family Lacunidae from Europe (Fretter & Graham, 1962, p. 388). On the basis of the spawn in Lacunidae, 'the most primitive family of the Littorinacea', Fretter (1980) suggested that production of this type of benthic gelatinous egg mass was the primitive condition in the Littorinidae. If these families are sister groups in the sense of Hennig (1966), this is a reasonable assumption. However, their relationship is uncertain, and Ponder (1976) has questioned whether the two groups should be

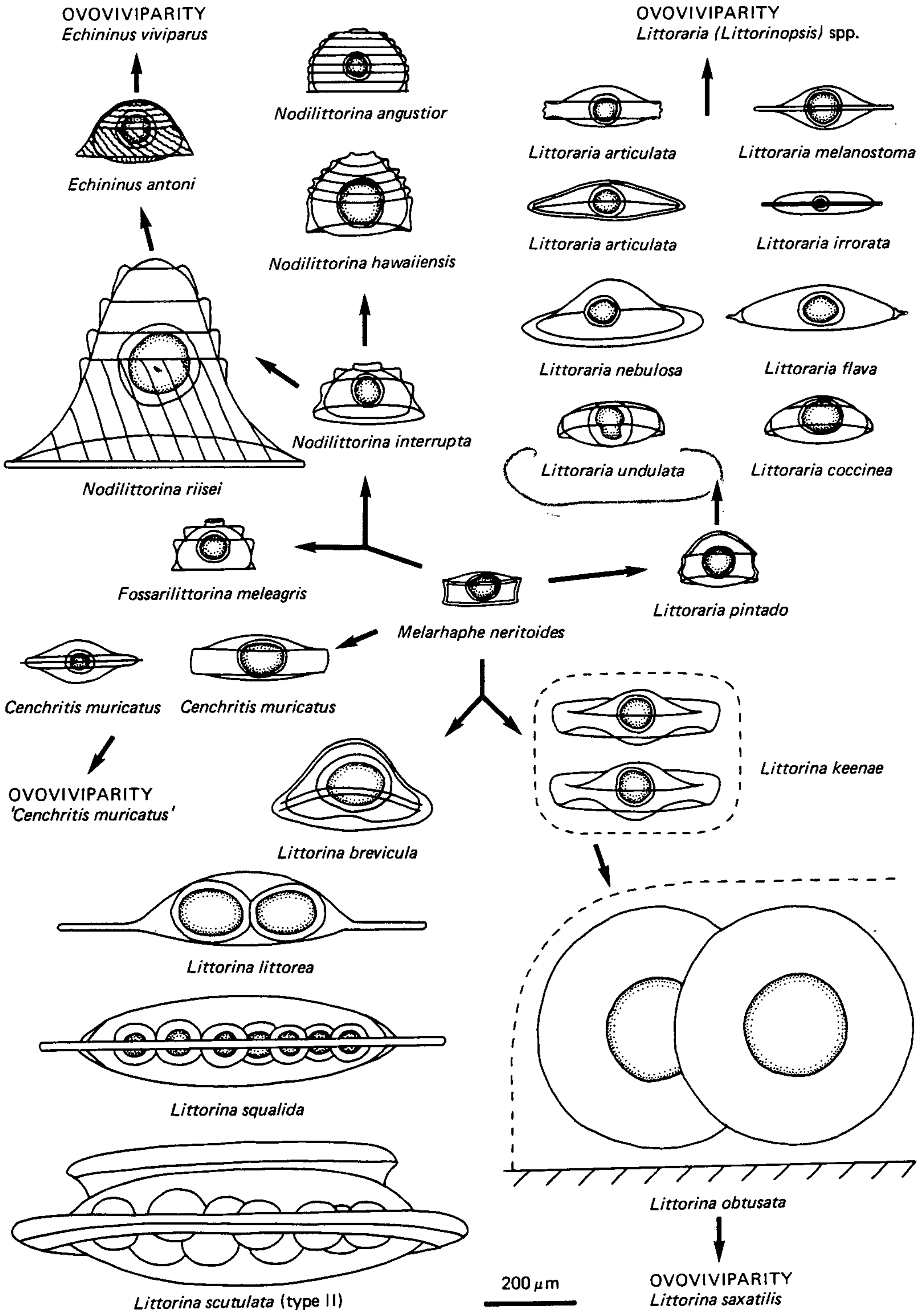

Fig. 5.10 Egg capsules of Littorinidae, arranged to show possible derivation of the forms characteristic of several genera from a simple pelagic capsule (represented by that of *Melarhaphe neritoides*). (After Bandel, 1974; Bandel & Kadolsky, 1982; Berry & Chew, 1973; Bingham, 1972b; Borkowski, 1971; Kojima, 1957, 1958a, c; Lebour, 1935, 1945; Linke, 1933; Marcus & Marcus, 1963; Murray, 1979; Rosewater, 1970; Schmitt, 1979; Struhsaker, 1966).

maintained as distinct families. It is also noteworthy that benthic egg masses are only known to occur in littorinaceans from cold or temperate latitudes. Various prosobranch and other invertebrate groups show a tendency to eliminate planktonic developmental stages at high latitudes (review by Picken, 1979), and the distribution of benthic spawn in littorinaceans may be the result of adaptation to similar ecological conditions rather than retention of an ancestral character. The ecological significance of the type of development is discussed further in Section 13.4.1.

If a benthic spawn is indeed primitive in the Littorinidae, then as suggested by Fretter (1980) the pelagic capsule of, for example, *Littorina littorea* could be derived from the ancestral state, as represented by *Littorina obtusata*, via the intermediate condition shown by *Littorina mandschurica* Schrenk (Kojima, 1958c) and *Littorina squalida* Broderip & Sowerby (Kojima, 1958b) in which a large capsule contains up to fourteen eggs. Reduction in the number of eggs to one, and modification of the capsule shape, could then have given rise to the condition of *Melarhaphe neritoides*, from which other forms could be derived. One difficulty in this scheme is that the similarity between a benthic gelatinous egg mass lacking capsules and the pelagic capsules of *Littorina* species containing many eggs is deceptive. If the interpretation of the function of the glands of the pallial oviduct given in Section 5.4 is correct, then the jelly of the benthic egg mass is produced by the jelly gland, whilst that in the capsule is a product of the opaque capsule gland. Accordingly, derivation of the pelagic capsule from the gelatinous spawn would require the following modifications of the oviduct: increase in size of the opaque capsule gland, development of a new gland (the translucent capsule gland, to secrete the capsule) and reduction in size of the jelly gland.

In view of the characteristics of the spawn of *Littorina sitkana* (Buckland-Nicks *et al.*, 1973) and of *Littorina keenae* (Murray, 1979, as *Littorina planaxis*), a new interpretation can be offered. If release of pelagic capsules were the ancestral state, elaboration of the jelly gland would have allowed production of a spawn mass with embedded capsules. The spawn mass of *Littorina keenae* is pelagic and soon disintegrates to release the individual capsules, while in *Littorina sitkana* it is attached to the substrate and benthic juveniles emerge. When hatching takes place within the spawn mass, the need for a protective egg capsule must be reduced and loss of the translucent capsule gland may follow, thereby deriving a spawn like that of *Littorina obtusata*, without individual egg capsules (Goodwin, 1979). In support of this suggestion it can be argued that, as discussed above, benthic development may be a response to environmental conditions at high latitudes. Further, in most genera a few species show capsule forms which could have been derived from a generalized ancestral type. This type may be represented by *Melarhaphe neritoides*, with a simple 'pill box' shaped capsule (Lebour, 1935), closely similar to that of *Cenchritis muricatus* (Lebour, 1945). Only slight modification by development of the lower rim as a narrow skirt, and duplication of the upper rim as rings of sculpture on a cupola, would be required to form capsules like those of *Littoraria pintado* (Struhsaker, 1966), *Fossarilittorina meleagris* (Borkowski, 1971) and *Nodilittorina interrupta* (C.B. Adams in Philippi) (Bandel, 1974, as *Littorina* sp., but see Bandel & Kadolsky, 1982). This scheme is illustrated in Figure 5.10.

Although this second scheme is the more attractive on the basis of available evidence, it is highly speculative. Much more information is required, especially concerning the anatomy and relationships of the lacunids and of the small littorinacean forms from the Antarctic. The two schemes may not even be mutually exclusive, for the pelagic capsule might be ancestral with respect to the genera discussed , and yet derived in the superfamily as a whole.

Whichever scheme is considered more likely, it appears that within the genus *Littoraria* the rather *Nodilittorina*-like capsule of *L. pintado* may be ancestral and the symmetrically biconvex capsule forms derived. This suggestion is in agreement with the cladogram of

Figure 8.2. The scheme of Bandel (1974) shows similarities to Figure 5.10, but places the ovoviviparous species without capsules in a central position. This cannot be accepted, since these species are undoubtedly derived from closely related oviparous species. Ovoviviparous species of *Littorina* were probably derived from those with large jelly glands producing benthic spawn (Fretter, 1980), whilst in the genus *Littoraria* the cladogram of Figure 8.2 suggests derivation of ovoviviparous species from those producing symmetrically biconvex capsules containing single eggs. Ovoviviparous species of *Echininus* and *Cenchritis* were presumably likewise derived from ancestors with pelagic capsules.

5.6 Radula

The littorinid radula is of the generalized taenioglossate type. Each transverse tooth row consists of a central rachidian, flanked on each side by a lateral and an inner and outer marginal tooth, all bearing posteriorly directed cusps. The range of variation within the family in the form of the radular teeth can be appreciated from the figures of Rosewater (1970, 1972) and Bandel (1974). The function of the littorinid radula has been described by Ankel (1936, 1938) and the mechanical relationships of the teeth by Bandel & Kadolsky (1982). Rosewater (1980a) has classified littorinid radulae into five major types, on the basis of the form of the rachidian tooth, and has correlated each type with a particular habitat and food source. The importance of radular characters in taxonomic studies has been emphasized by Rosewater (1970, 1972, 1981), but he has made use of them only at subgeneric and higher levels of classification. Recently, Bandel & Kadolsky (1982) have discriminated between species of *Nodilittorina* solely on the basis of radular characters.

In all twenty species of the *scabra* group the radulae were found to be of the type defined by Rosewater (1980a) as 'hooded', that is with a frontal plate anterior to the cusps of the rachidian tooth. Rosewater has suggested that this radular type may be adapted for feeding upon the algal flora of mangroves, driftwood and marsh grass. It is indeed striking that the majority of species known to possess radulae of the hooded type are found upon these substrates, and in addition to the species of the *scabra* group there can be listed the following: *L. angulifera* (Marcus & Marcus, 1963; Bandel, 1974; Rosewater, 1980b), *L. nebulosa* (Troschel, 1858; Bandel, 1974), *L. irrorata* (Troschel, 1858; Allen, 1953), *L. flava* (Marcus & Marcus, 1963), *L. aberrans* (Rosewater, 1980b), *L. varia*, *L. zebra* and *L. fasciata* (all Rosewater, 1980a). Nevertheless, species with hooded radulae occur also on rocky shores, for example *L. undulata* (Adam & Leloup, 1938; Rosewater, 1970) and *L. cingulifera* (Rosewater, 1981). Amongst the species living upon mangrove trees several can be found also upon sheltered rocks (e.g. *L. articulata*, *L. strigata*; Section 11.4.4). Since all the species known to possess a hooded radula are members of the genus *Littoraria*, and because they are not entirely restricted to mangrove and similar habitats, it seems likely that this specialized radular type is not only of ecological, but also of phylogenetic significance, supporting the classification of these species in a single generic group.

The radulae of *L. pintado*, *L. coccinea*, *L. glabrata* and *L. mauritiana*, all illustrated or described by Rosewater (1970), are apparently not hooded. Since a hooded rachidian is unknown in other littorinid genera, the species of *Littoraria* lacking this feature appear to retain the ancestral character state (Fig. 8.2). Within the family Littorinidae there has been a tendency towards reduction of the width of the rachidian tooth in several lines (Bandel, 1974; Bandel & Kadolsky, 1982). A wide rachidian, referred to as 'rhomboidal' by Rosewater (1980a), appears to be the ancestral type and is found in the genera *Littorina*, *Ldevillitorina*, *Pellilitorina* (review by Rosewater, 1980a) and in some species of the Lacunidae also (Troschel, 1858).

Amongst the species of *Littoraria* described here, two different forms of the hooded radula can be recognized, which for convenience will be referred to as 'saw-toothed' and 'chisel-toothed'. The radulae of *L. scabra* (Fig. 9.10e,f) and *L. cingulata cingulata* (Fig. 9.39b) may be used as examples of the saw-toothed form; the rachidian tooth has three well developed cusps, the larger central cusp being pointed or spade shaped; the paired teeth bear cusps of almost equilaterally triangular shape and all of roughly similar size; cusps on the lateral teeth are five in number, of which the central one is the largest, in front of which is a more or less prominent gap, and the other cusps on the laterals are also clearly visible; the inner marginal has four subequal cusps; the outer marginal bears up to six small cusps, of which the outermost is the largest. In the chisel-toothed form, typified by *L. melanostoma* (Fig. 9.56b), the number of cutting edges is much reduced; the rachidian bears a single, broad, straight, cutting edge, formed from the widened central and two small lateral cusps; the cusps of the paired teeth are obliquely triangular, with their points directed towards the midline, so that the cutting edges are effectively long blades rather than pointed teeth; the lateral bears five cusps, but only two of these are large, with a wide gap between, the inner one and outer two cusps being reduced to denticles; the inner marginal has four cusps, of which again only the central two are large; the outer marginal bears only two large cusps. There are, however, intermediates between the extreme saw- and chisel-toothed types.

These two main radular forms lend partial support to the subgeneric classification adopted here. The chisel-toothed type as described is found only in *L.* (*Palustorina*) *melanostoma* and *L.* (*P.*) *conica*, while other species in the subgenus show radulae of intermediate type. In the subgenus *Littorinopsis* the majority show typical saw-toothed radulae, with the exceptions of *L. pallescens* and *L. lutea* which are intermediate. *L.* (*Lamellilitorina*) *albicans* is of the chisel-toothed type, but for its unique rachidian and somewhat toothed outer marginal. *L.* (*Littoraria*) *vespacea* is of the saw-toothed type. The two main morphological types do not correspond with habitat differences, since both include leaf and trunk dwelling species.

From the present study it appears that radular characters are of use mainly in separating groups of species, which from other evidence seem to be closely related. Taxonomic studies of the genus *Littorina* (Heller, 1975a; Raffaelli, 1979) have likewise not revealed useful differences between closely related species. Bandel (1974) was able to distinguish between the radulae of eighteen Atlantic species of the family, although these included members of seven genera, while Bandel & Kadolsky (1982) separated the radulae of twelve species of the genus *Nodilittorina* from the Atlantic and defined some species solely on this basis. Small differences can sometimes be found between species in each of the categories of the hooded radula described above. Characteristics of the rachidian tooth are especially obvious, for example that of *L. albicans* is unique in bearing three equal cusps, while in three species of the subgenus *Littorinopsis* (*L. filosa, L. cingulata, L. subvittata*) the central cusp is rather elongated. Other subtle differences seem to exist in the details of cusp sizes and shapes, but these are difficult to measure or to describe. It is possible that accurate measurement of cusps with the light microscope (as made by Borkowski, 1975) might permit finer discrimination, but are beyond the scope of this work.

There are several difficulties to be considered when comparing the details of the radular cusps. Although all radulae were mounted flat and viewed from above it was found that even slight differences in the orientation of individual teeth altered their appearance considerably. Furthermore, the natural orientation of the teeth obscured certain details of the cusps. These difficulties are demonstrated in Figure 9.10e,f, showing standard and side views of the same radula. Light microscopy is more suitable for detailed comparisons of cusp shapes (Hickman, 1977). Because of these difficulties it is hard to judge the extent of variation between the four specimens examined for each species, but in general the range is apparently small. Of previous studies of littorinid radulae only those of Borkowski (1975) and Goodwin & Fish (1977) have made attempts to describe intraspecific variation and both showed a considerable range. Borkowski also pointed out possible regional variations from comparisons with published figures. However, so much depends on tooth orientation that it is very difficult to make comparisons between the figures given by different authors, and especially to compare camera lucida drawings with scanning electron micrographs. All specimens examined here were taken from large adults, since changes in tooth form with size have been recorded by Borkowski (1975) and Raffaelli (1979).

Radulae of *L. 'scabra'* have been figured by several authors, but because of the similarities within the group it is not usually possible to assign the figures to the correct species in the absence of other information. In two cases radulae have been used in discussions of the classification of the *scabra* complex. Adam & Leloup (1938) figured the tooth row of *L. scabra s. s.* (as 'forme typique') and of *L. pallescens* (as *Littorina scabra* var. *filosa*). Despite the obvious differences between the figures, these authors commented that the radulae were 'almost completely identical'. Rosewater (1980b) gave scanning electron micrographs of *L. scabra s. s.*, *L. angulifera* and *L. aberrans*; of which the first two were closely similar, while the last showed certain differences. Nevertheless, in considering the three species as subspecies of *L. scabra*, Rosewater stressed their similarities in his descriptions. In conclusion, if radular characters are to be used for taxonomy at the specific level in this family, then differences finer than those admitted by most previous authors must be sought, and validated by adequate studies of intraspecific variation.

Littorinids from mangroves are known to have relatively shorter radulae than those of rocky shore species (Peile, 1937; Marcus & Marcus, 1963), presumably because of the need for more rapid tooth replacement when the radula abrades a harder surface. The present study supports this observation, radular lengths varying from 0.58

to 1.35 times the height of the shell, which may be compared with a mean value of 2.2 in the rock dwelling *Littorina saxatilis* complex (James, 1968) and an extreme value of 8.2 in a *Nodilittorina* species (Peile, 1937, as *Littorina 'ziczac'*). The three species found mainly upon the leaves of *Avicennia* trees showed amongst the shortest radulae (mean relative lengths: *L. filosa* 0.77; *L. albicans* 0.67; *L. luteola* 0.58), whilst five out of six species occurring largely on *Rhizophora* trunks had radulae approximately equal to or exceeding the length of the shell. Relative radular length may have some value as a taxonomic character, but although quoted in the descriptions has not been used as such in the present work. James (1968) found a change in relative radular length with age, although Allen (1953) found no correlation between lengths of the shell and radula.

5.7 Alimentary system

The alimentary system of *Littoraria* species (as represented by *L. scabra*, Fig. 5.11a) is in most respects similar to that of *Littorina littorea* as described by Johansson (1939) and Fretter & Graham (1962, pp. 28-32). Werner (1950, 1951) described the morphology and histology of the tract of *L. irrorata*, but his morphological account was inaccurate in several respects. In the foregut (Fig. 5.11b,c) a pair of pouches arises from the ventral side of the anterior oesophagus just behind the red buccal mass. These oesophageal pouches are usually bilobed, the anterior lobe being the larger, so that they may appear four in number. They are hollow, separated from the food channel by darkly pigmented longitudinal folds, and are themselves pale, or sometimes black in darkly pigmented animals. In most species the pouches are thin walled, but in *L. carinifera* and *L. conica* they are thick walled, red, enlarged and apparently glandular. The paired salivary glands are pale pink in colour and lie in a dorsal position between the buccal mass and the glandular mid-oesophagus; they are constricted into two parts by the nerve

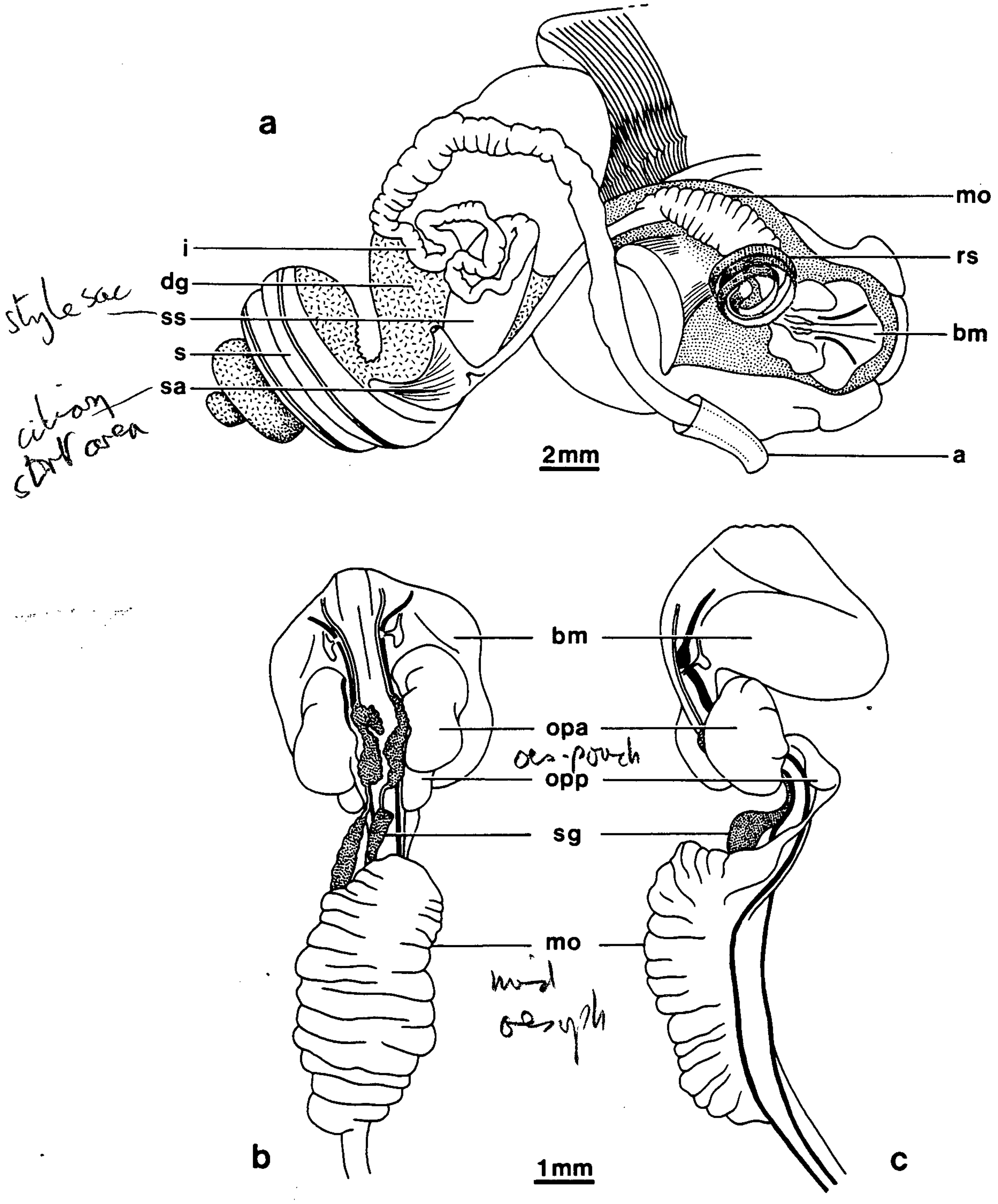

Fig. 5.11 *Littoraria* (*Littorinopsis*) *scabra*: (a) dissection of alimentary system; (b,c) dorsal and lateral views of foregut; a, anus; bm, buccal mass; dg, digestive gland; i, intestine; mo, glandular mid-oesophagus; opa, anterior lobe of oesophageal pouch; opp, posterior lobe of oesophageal pouch; rs, radular sac; s, proximal region of stomach; sa, ciliary sorting area; sg, salivary gland; ss, distal style sac of stomach.

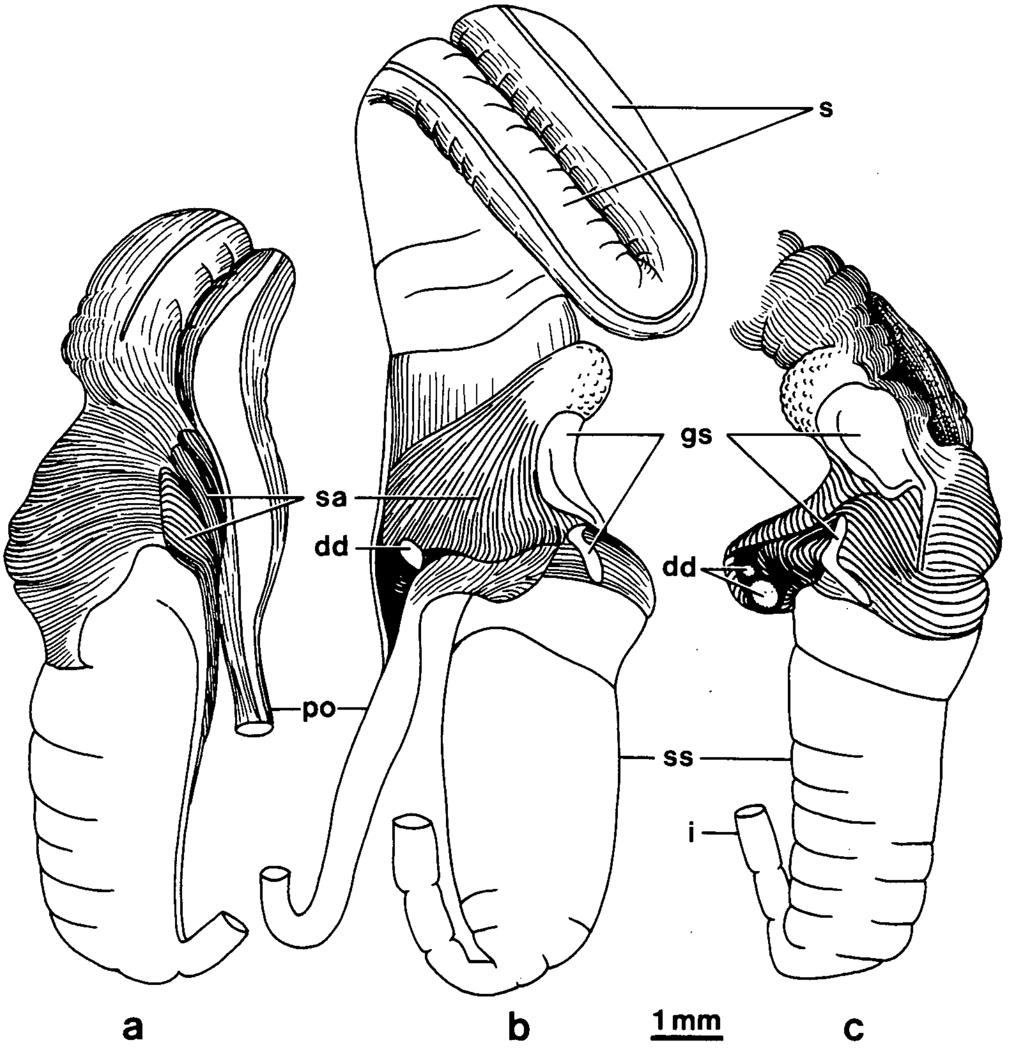

Fig. 5.12 *Littoraria* (*Littorinopsis*) *scabra*: stomach dissected away from digestive gland; (a,b,c) outer, inner and dorsal views; dd, ducts of digestive gland; i, intestine; gs, gastric shield; po, posterior oesophagus; s, proximal region of stomach; sa, ciliary sorting area; ss, distal style sac of stomach.

ring around the oesophagus. The details of the oesophageal pouches and salivary glands thus differ slightly from the condition in *Littorina littorea*, as described by Fretter & Graham (1962), in which the openings of the pouches are constricted and the salivary glands lie entirely posterior to the nerve ring.

Johansson (1939) and Fretter & Graham (1962, p. 30) have described the littorinid stomach in detail, and that of *L. flava* was illustrated by Marcus & Marcus (1963). Stomachs of all the *Littoraria* species examined agree with these accounts. By careful dissection, details of ciliary tracts are visible from the outside. There are three ducts from the digestive gland and the cuticle forming the gastric shield is thickened in two places (Fig. 5.12). Shapes of the ciliary sorting areas and of the shield show individual variation and no consistent differences between species were detected. In a few species (e.g. *L. melanostoma*, *L. articulata*, *L. strigata*) the blind upper end of the stomach is relatively shorter, but this character was not correlated with habitat.

5.8 Pallial complex

The ctenidium of *Littoraria* species consists of triangular leaflets attached to the left side of the roof of the mantle cavity (Fig. 5.1), numbering 60 to 80 in the smaller species (such as *L. strigata*, *L. articulata*, *L. vespacea*) and 100 to 120 in the larger species. Anatomical details have been given by Marcus & Marcus (1963) for *L. angulifera*. The leaflets extend only about halfway across the roof of the mantle cavity and all but the most anterior leaflets are continued as folds as far as the hypobranchial gland adjacent to the rectum. The left edge of each leaflet is white and a little thickened, while the remaining area of the gill, including the folds, is usually black or grey, or white in entirely unpigmented animals. The proportions of the individual leaflets show some small variations between species, but in the subgenus *Littorinopsis* most species show proportions similar to the following for *L. cingulata*: left edge 0.5 mm, right edge 1.2 mm, height of leaflet 0.4 mm, length of fold 2.0 mm. In the subgenus *Palustorina* the leaflets occupy a somewhat greater width of the mantle cavity, as in *L. melanostoma*: left edge 1.3 mm, right edge 1.8 mm, height of leaflet 0.7 mm, length of fold 1.8 mm. In the ovoviviparous species the developing eggs are retained in the mantle cavity, embedded in a thin sheet of mucus over and between the leaflets and folds. At least in some species (*L. pallescens*, *L. lutea*) the leaflets of females brooding larvae are about twice the usual height.

Several authors have suggested that the littorinids living at supratidal levels on mangrove trees and rocky shores represent an intermediate stage in the evolution of terrestrial from marine gastropods, being adapted for aerial respiration by reduction in the size of the gill leaflets (Quoy & Gaimard, 1832, p. 476; Prashad, 1925; Risbec, 1942; Berry, 1963). The gill leaflets of *Littoraria* species are smaller than those of the intertidal *Littorina littorea* (illustrated by Johansson, 1939), but differences from other species are less marked. Remmert (1969) examined the gills of European *Littorina* species and found that the apparent decrease in gill size upshore was explained simply by the positive allometric growth of the gills in combination with the smaller size of the high level species. This cannot account for the relatively smaller gills of *Littoraria* species, which cover a wide size range and show no obvious correlation between gill proportions and adult shell size, at least when comparisons are made between species. No correlation was found between an index of relative gill area and the habitat of the species, so that gill area is not reduced further in the *Littoraria* species living at the higher tidal levels. Since *Littoraria* species on mangroves climb upwards in order to remain above the water level throughout the tidal cycle (Section 12.3.1), respiration must take place in air in all species, explaining the similarity in gill structure.

On the roof of the mantle cavity, between the gill folds and the rectum, lies the hypobranchial gland. In comparison with the intertidal *Littorina littorea* (Johansson, 1939; Fretter & Graham, 1962, p. 22) this is much reduced in *Littoraria* species. The gland is largest in *L. carinifera* (to 2.2 mm wide) and is also relatively large in *L. conica*, *L. articulata*, *L. strigata* and *L. vespacea*. In most species the gland is from 0.5 to 0.8 mm in width, folded, and white, grey or black in colour. In *L. vespacea* it is yellow and conspicuous.

The mantle itself is usually grey to whitish in colour, but in *L. albicans* the entire outer surface is bright yellow.

CHAPTER 6: REPRODUCTIVE ISOLATION

6.1 Introduction

In the present study, only morphological criteria have been used to define the species of *Littoraria* in the *scabra* group, but the implication is that these are biological species, reproductively isolated from each other (Mayr, 1969, p. 26). The morphological approach itself provides some indirect evidence for this assertion, since penial shape is diagnostic of almost all species in the group (Section 5.2), and it has been suggested that the shape of the penis is a species recognition character used during pairing. More direct evidence is provided by observations of copulation in the field.

6.2 Copulatory behaviour

The behaviour of *Littoraria* during copulation is the same as that recorded in other littorinids (Linke, 1933; Abe, 1942; Gibson, 1964; Bingham, 1972b; Gallagher & Reid, 1974). Males search for females, mounting the shell of any other individual encountered, of which they are only able to determine the sex by attempting to insert the penis into the bursa copulatrix (Gibson, 1964; Muggeridge, 1979). If the shell beneath is a male, the pair soon separates. During copulation the male attaches to the right side of the anterior end of the female shell and inserts the penis under the outer lip of the aperture. The act of copulation is probably of short duration, times of less than 40 minutes having been recorded (Gibson, 1964; Bingham, 1972b; Gallagher & Reid, 1974). However, in *Littoraria* the male may remain attached to the female shell in the copulation position for several hours. Under dry conditions both animals withdraw into their shells and attachment is by mucus alone. At the Magnetic Island study site, copulation was only observed under moist conditions, during or after high tide, after rain, or in the early morning. Bingham (1972b) found that high temperatures stimulated copulation in *L. irrorata*.

During the study of reproductive patterns in five *Littoraria* species at Magnetic Island, copulating pairs were recorded at intervals over 12 months, as described in Section 13.2.1. All pairs seen in the copulation position were recorded, and the results are presented in Table 6.1. In the species *L. filosa*, *L. philippiana*, *L. scabra* and *L. intermedia* the penis was inserted under the female shell in 37% of the cases observed, whilst in only 2.9% of these copulating pairs were both partners males. Out of a total of 1198 pairs, in only 43 (3.6%) did the individuals belong to different species. This evidence that the five species (as defined by morphological criteria) copulate preferentially with conspecifics implies a degree of reproductive isolation between species.

It could be argued that the zonation of the species or separate breeding seasons might be responsible for the apparent assortative mating. In fact, the zones of *L. scabra*, *L. intermedia* and *L. articulata* show broad overlap, as do those of the two remaining species (Fig. 11.1; Section 12.3.2), and even within each of these groups the deviation from random mating is highly significant. Although breeding seasons do differ in duration, all the species show maximum reproductive activity during the wet summer months (Section 13.3.1). In view of the indiscriminate behaviour of males in searching for mates, it is not surprising that some attempts at interspecific copulation are found. One male *L. scabra* was even observed attempting to copulate with a *Nerita articulata*. Interspecific mating has been recorded in several studies of the reproduction of co-occurring littorinids (Struhsaker, 1966; Gallagher & Reid, 1974). Raffaelli (1977) found that amongst copulating pairs of *Littorina saxatilis* and *Littorina nigrolineata* almost half were combinations other than male-female intraspecific

Table 6.1 Pairs of *Littoraria* species in copulation position, recorded at Cockle Bay, Magnetic Island, Queensland (September 1980 to September 1981).

	Male				
Female	*L. filosa*	*L. philippiana*	*L. scabra*	*L. intermedia*	*L. articulata*
L. filosa	174	1	10	1	
L. philippiana	8	27	3		
L. scabra	2		37		
L. intermedia				93	8
L. articulata				10	824

Table 6.2 Pairs of *Littoraria* species in copulation position, recorded at Broome, Western Australia (3 November, 1981).

	Male			
Female	*L. filosa*	*L. cingulata cingulata*	*L. sulculosa*	*L. articulata*
L. filosa	36	4		
L. cingulata cingulata	2	55		
L. sulculosa		1	2	
L. articulata				1

pairs.

Copulating pairs were also recorded at Broome, Western Australia, where four species occurred together in broadly overlapping zones (Fig. 11.7; Table 6.2). Here the frequency of interspecific pairing was 6.9%.

6.3 Possibility of hybridization

It is not known whether transfer of sperm occurs during interspecific mating, but no possible hybrids with intermediate shell or anatomical characters have been discovered. Rosewater (1970, 1981) suggested that closely related littorinids may hybridize, but this seems unlikely. If hybrids were frequently produced and were fertile, a complete range of intermediates would be expected. If infertile, a hybrid of intermediate phenotype might appear to be a distinct species. However, all the five species listed in Table 6.1 (and in addition the four other species of the subgenus *Littorinopsis* which were observed to be ovoviviparous, see Section 5.4) were seen to produce progeny which developed at least to the veliger stage.

CHAPTER 7: BIOGEOGRAPHY

7.1 Patterns of distribution

the genus *Littoraria* is largely confined to the tropics. Although several members extend into subtropical regions, the only species with predominantly subtropical or temperate distributions are *L. irrorata* in the western Atlantic (to 39°N) and *L. luteola* in Australia (to 37°S). This restriction to the tropics is not a consequence of dependence on the mangrove habitat, which is itself largely tropical and subtropical in distribution. In subtropical regions *Littoraria* species regularly occur in salt marshes, while in Australasia the distribution of mangroves of the genus *Avicennia* extends to higher latitudes (Saenger *et al.*, 1977) than that of *Littoraria* species. Furthermore, species of *Littoraria* from rocky shores are also absent from temperate zones (Section 8.1.2).

The subgenus *Littoraria* is of worldwide distribution. Species of *Littorinopsis* are largely confined to the Indo-Pacific, with only a single representative in the tropical Atlantic. The subgenera *Palustorina* and *Lamellilitorina* are restricted to Indo-Malaya and Australia (see species list, Section 8.1.2). The term 'Indo-Pacific' is used here to refer to the Indian Ocean and the Pacific Ocean as far east as Easter Island (Springer, 1982).

To a large extent the distributions reported here support the subdivisions of the Indo-Pacific biogeographic region proposed by Macnae (1968) on the basis of the endemic fauna of mangroves (Table 7.1). Two centres of endemicity are conspicuous. Firstly the Malayan Peninsula, eastern Sumatra, western Borneo and southern Vietnam, which is also the focus of highest species richness. Secondly, the north-western coast of Australia, where two species and one subspecies are endemic, while two of the four species shared with

Table 7.1 Comparison of distributions of species of the *Littoraria scabra* group with the subdivisions of the Indo-Pacific province proposed by Macnae (1968) on the basis of mangrove faunas.

Division	Endemic species	Species shared with one other division
1. West Indian Ocean		*L. subvittata*
2. West central	*L. delicatula*	*L. subvittata* *L. conica*
3. East central	*L. vespacea* *L. albicans*	*L. ardouiniana* *L. conica*
4. North-east	*L. flammea*	*L. ardouiniana*
5. East Borneo, Celebes		
6. Qld., New Guinea	*L. philippiana* *L. luteola*	*L. filosa*
7. N.W. Australia	*L. c. cingulata* *L. c. pristissini* *L. sulculosa*	*L. filosa*
8. West Pacific islands		

The eight remaining species are distributed over three or more divisions.

other divisions (*L. articulata, L. filosa*) show rather distinctive shell types not found elsewhere. The isolation of this division is further emphasized by the absence of the widely distributed *L. intermedia,* and by the presence of two further endemic littorinids, *Nodilittorina australis* (Gray) (probably not specifically distinct from *N. nodosa* (Gray)) and *Tectarius rusticus* (Philippi) (Rosewater, 1970, 1972). The eastern limit of the north western Australian endemic littorinids falls between Cape Londonderry and Darwin, whilst the western limit for the eastern Australian endemic *L. luteola* is the Torres Strait and for *L. intermedia* is close to Darwin. These limits correspond with the fact that the Arafura Sea was land during low sea level periods in the Pleistocene, and before that was dry back until the late Tertiary, while the Torres Strait became a seaway only in middle to late Pleistocene times (Doutch, 1972).

Largely on the basis of the distribution of shorefishes, Springer (1982) has proposed that the Pacific Plate should be recognized as a major biogeographic subunit of the Indo-Pacific province. Springer has demonstrated that many fish and other organisms show distributions restricted to either the oceanic or continental lithospheric plates of the Indo-Pacific, and that 20% of the shorefish species occurring on the Pacific Plate are endemic. Springer explained such patterns by proposing a present or historical barrier to dispersal at the western margin of the Pacific Plate, but pointed out that to confirm his vicariance hypothesis it would be necessary to demonstrate sister group relationships between widespread Pacific Plate endemics and species restricted to adjacent continental plates.

Such cladistic data were not available to Springer, but are presented here for the genus *Littoraria*. Of the twenty-five Indo-Pacific species of the genus, only *L. coccinea* could be regarded as a possible Pacific Plate endemic, although its distribution extends across the western margin of the plate as far as Fiji, New Caledonia and Queensland (but not into the Indian

Ocean, *contra* Rosewater, 1970). On the basis of anatomical and conchological similarities (Fig. 8.2), the sister species of *L. coccinea* is believed to be *L. glabrata* (= *kraussi*), endemic to the Indian Ocean. The distribution of *L. pintado*, discussed below, and the variation of *L. carinifera* (Section 9.2.4.4), also suggest a barrier to dispersal between the Indian and Pacific Oceans. Of the remaining widespread Indo-Pacific species of the genus (*L. undulata, L. scabra, L. pallescens, L. intermedia*), all extend far into the Pacific across the western boundary of the Pacific Plate. Sixteen of the species of the *scabra* group are restricted to continental plate areas in the central Indo-Pacific, but none shows an eastern limit of distribution corresponding to the western margin of the Pacific Plate (as figured by Springer, 1982). Distributions of *L. carinifera* (Fig. 9.67) and *L. lutea* (Fig. 9.15) do, however, correspond rather precisely with the margins of the southern part of the Eurasian Plate. In general, the distributions of *Littoraria* species do not lend support to Springer's vicariance hypothesis.

An ecological explanation of the real distinction between the faunas of the Pacific Plate and of its adjacent continental margins, in terms of distribution of high islands and estuarine habitats, was only briefly considered, and set aside, by Springer (1982, p. 123). Nevertheless, in the case of *Littoraria* species, local distribution patterns strongly suggest such an ecological interpretation (Section 11.4.5). On a larger scale, distributions of the most widespread Indo-Pacific *Littoraria* species can also be adequately explained in terms of habitat availability. Of these widespread species, only *L. pallescens* is entirely restricted to mangrove trees, and its distribution in the western Pacific (Fig. 9.20) corresponds with that of mangroves (Macnae, 1968; McCoy & Heck, 1976; Chapman, 1976). *L. scabra* shows a similar distribution, but can occasionally be found on other maritime trees and on driftwood, and probably in consequence there are a few records from the Line and Tuamotu Islands, and also from the Hawaiian Islands (Fig. 9.12), where mangroves have only been introduced this century (Wester, 1981). *L. intermedia* is common on both mangroves and sheltered rocky shores, and *L. undulata* on rocky shores and driftwood, and both species are widely distributed across the Pacific (e.g. Fig. 9.29).

In few cases do the distribution patterns show sudden geographical replacement which could suggest competitive interactions between species. One possible case is the absence of the otherwise widely distributed *L. intermedia* from north-western Australia, where two endemic species occur, but as mentioned above this is more likely to be a result of geological history. Another possible example concerns the two species found on *Avicennia* foliage in eastern Australia; *L. luteola* is abundant in New South Wales and rare in Queensland, while the reverse is true for *L. filosa*, but this is a case of gradual, rather than sudden, replacement. At most localities in the Indo-Pacific region only one leaf dwelling species occurs, or only one occurs commonly. Thus the distributions of *L. filosa*, *L. luteola*, *L. ardouiniana*, *L. delicatula* and *L. albicans* are almost mutually exclusive, and all occur in continental situations. The remaining species known to inhabit foliage is *L. pallescens*, with a wide distribution across the Indo-Pacific, but since it is restricted to oceanic situations it seldom occurs together with the others (Section 11.4.5).

A curious disjunct distribution is shown by the rock-dwelling species *L. pintado*. The typical form of the species occurs in the tropical north-western Pacific (including the Hawaiian, Ryukyu and Caroline Islands) and in the south-western Indian Ocean (Mascarene Islands, Madagascar, South Africa). Despite much collecting in the central Indo-Pacific, the only records from intervening localities are single shells from Bombay and Bali (both MCZ) which are of doubtful provenance. Shells are identical from the two main areas of distribution, although preserved animals have not been seen from the Indian Ocean. Rosewater (1970) recognized a subspecies *L. pintado schmitti* (Bartsch & Rehder) from Clipperton Island in the Eastern Pacific and mentioned that *L. pullata* (Carpenter) from Baja California was an analogue of *L. pintado*. *L. schmitti* and *L. pullata* differ from *L. pintado* only in their more heavily pigmented shells and specimens of *L. pullata* are anatomically identical to *L. pintado* from the western Pacific. Consequently both are here regarded as conspecific with *L. pintado*, and the species becomes the only member of the family known to occur on both sides of the Pacific Ocean. It is of interest that *L. pintado* retains many characters regarded as ancestral within the genus (Section 8.3), and conceivably may be of more ancient origin than other members of the genus. Amongst other species of *Littoraria* from the Indo-Pacific only *L. intermedia* might possibly extend into the Eastern Pacific province, a single shell being recorded from the Galapagos Islands (Section 9.2.3.5). Few other molluscs are known to cross the Eastern Pacific barrier (Emerson, 1967).

Vermeij (1972, 1973b) has suggested that amongst molluscs of mangroves and other intertidal habitats, those of the supralittoral zone are more restricted in distribution as a result of their adaptation to local atmospheric conditions, which are more geographically variable than hydrological conditions. The high level, mostly leaf-dwelling, species of *Littoraria* are indeed sometimes narrowly distributed (e.g. *L. albicans*, *L. luteola*, *L. delicatula*), although *L. pallescens* is widespread, and there is no clear correlation between zonation level and distribution in the genus as a whole. The two species typical of the landward fringes of swamps, *L. carinifera* and *L. conica*, may be more dependent upon atmospheric moisture than other species, since by reason of their position they cannot descend the trees to reach the water level for most of the lunar cycle. These species are restricted to the high rainfall areas of Indo-Malaya, and species are absent from this zone elsewhere (Section 11.5.2). Whilst this might be one case of climatic limitation, it would seem that Vermeij's suggestion might not be generally applicable to these highly mobile snails which show vertical migration with the tidal cycle (Section 12.3.1).

The most striking correlate of distribution is the occurrence of species in oceanic or continental situations (Section 11.4.5). Of the *Littoraria* species associated with mangroves, only three (*L.*

scabra, L. intermedia, L. pallescens) occur across most of the Indo-Pacific province, and all are typical of oceanic habitats. Species of continental shores are more restricted. A similar correlation has been noted by Abbott (1960) in the genus *Strombus*. This effect might be simply the result of species of promontories and islands having access to stronger currents for dispersal. Alternatively, the explanation of Vermeij (1972, 1973b) might apply in modified form, since the oceanic habitat might be more geographically uniform than the continental margins. Continental species could then be restricted by their adaptation to local environmental conditions.

7.2 Dispersal

There is no direct evidence of the means and distance of dispersal of *Littoraria* species, but some deductions can be made. In the genus *Littorina* the degree of intraspecific variability in shell characters (James, 1968; Heller, 1975a) and enzyme patterns (Berger, 1973; Wilkins & O'Regan, 1980) has been correlated with the potential for larval dispersal suggested by the method of development. *Littorina littorea* releases pelagic egg capsules which hatch into veliger larvae and this presumably widely dispersed species shows rather constant characters. In contrast, the ovoviviparous species of the *Littorina saxatilis* complex lack a planktonic phase and show considerable intra- and inter-population variability. Populations of poorly dispersed species are thought to become precisely adapted to local conditions, explaining variability between populations. In similar fashion, Rosewater (1970) explained the interpopulation variability of *L. 'scabra'* in terms of restriction of gene flow caused by ovoviviparous reproduction. It is now clear that most of the supposed variation between populations of *L. 'scabra'* is in fact variation between species. Within species, shell form is relatively constant. Several *Littoraria* species show striking colour polymorphism, but this is either an adaptive genetic trait constant over wide areas, or is in other cases influenced by environmental effects or by selection from one tree to the next (Chapter 15). Where intraspecific variation in shell form or colour is significant, it is over a considerable geographical range, as discussed in Section 7.3. Therefore shell characters provide no evidence for small scale geographical isolation between populations.

In the two oviparous *Littoraria* species from mangroves of which the egg capsule has been described (Section 5.5), the diameter of the ovum is 76 to 140 μm, whilst in the ovoviviparous species the maximum dimension of the larval shell when spawned from the mantle cavity of the parent is 100 to 140 μm. In all the *Littoraria* species from mangroves, with the exception of *L. albicans*, the height of the shell at settlement and metamorphosis is 320 to 415 μm (from measurements of protoconchs of adults and of newly settled snails collected in the field). These measurements suggest a considerable period of planktotrophic growth between spawning and settlement in both oviparous and ovoviviparous species. The only tropical littorinid for which data on length of larval life are available is *Nodilittorina hawaiiensis* (Struhsaker & Costlow, 1968, as *Littorina picta*), which grows from an 80 μm ovum at spawning to a 250 μm larva at metamorphosis in 24 days, under laboratory conditions. Gallagher & Reid (1979) have estimated the pelagic life of *L. angulifera* as eight to ten weeks, based on the delay between spawning and peak recruitment. The protoconch of *L. angulifera* is closely similar to those of other members of the subgenus *Littorinopsis*, and a similar length of larval life might be predicted for these.

Scheltema (1971) has estimated the maximum time required for transport of larvae across the Atlantic in ocean currents as 60 days from east to west and 96 days in the reverse direction, so that the estimated pelagic life of *L. angulifera* may be just sufficient to permit transatlantic drift. *L. angulifera* is found on both sides of the tropical Atlantic (Rosewater & Vermeij, 1972) and the eastern and western populations are not morphologically distinct (pers.

obs.) so that larval dispersal might occur between them. Despite the probability of long distance dispersal, Gaines *et al.* (1974) have reported significant genetic differences between populations of *L. angulifera* on mangrove islands less than 300 m apart. As observed by these authors this effect was probably due to selection rather than limited dispersal since there was no association between inter-island distance and heterogeneity. Rosewater (1963, 1970, 1981) pointed out that the association of *L. 'scabra'* with mangroves provides the opportunity for dispersal of adults by rafting on floating vegetation, as has been observed by Marcus & Marcus (1963) in *L. angulifera*. All the above evidence suggests that *Littoraria* species have the potential for wide dispersal.

Within the genus *Littoraria* there is no correlation between the range of the distribution and the method of development, whether oviparous or ovoviviparous. This is not unexpected, since both types apparently involve a lengthy planktotrophic phase. In fact, contrary to the usual association of viviparity with restricted distribution, it is three ovoviviparous members of the subgenus *Littorinopsis* (*L. scabra*, *L. intermedia*, *L. pallescens*) which are the most widely distributed of the species associated with mangroves, whilst the oviparous subgenus *Palustorina* shows the more restricted distribution. However, within each subgenus there are examples of wide and narrow geographical ranges. The apparently oviparous *L. albicans* is unique in the genus by virtue of its large protoconch (610-660 μm), which could indicate a long planktotrophic life (Jablonski & Lutz, 1983). Nevertheless, this species is restricted to a small area of Indonesia.

7.3 Variation and speciation

Morphological characters of *Littoraria* species are relatively constant over wide geographical areas, as expected from their presumably wide dispersal. For example, *L. scabra* shows one of the most extensive ranges, and specimens from Hawaii are indistinguishable from those from South Africa. In such uniform and widespread species it is difficult to envisage how sufficient isolation might be achieved to permit speciation. In fact some species of the genus show geographical variation on a large scale, which suggests how peripheral differentiation and vicariance may together lead to speciation in widely dispersing forms (Abbott, 1960; Schuto, 1974).

Clinal variation is shown by several species, for example *L. filosa* and *L. articulata*, which show different shell forms at the extremes of their 6500 km range around the tropical Australian coast. *L. pallescens* shows distinctive shell types in the Arafura Sea and in Malaysia, while across the great range of *L. intermedia* shells from Hawaii and Polynesia can be distinguished from those from the rest of the Indo-Pacific. Thus even where ranges are continuous, regional differentiation can occur over sufficient distance. In such cases, differentiation might proceed to speciation if local extinction or geological events caused vicariance. That this might occur is suggested by a series of examples arranged in order of increasing isolation and differentiation. In the case of *L. carinifera* the distinctive Pacific and Indian Ocean forms are in contact only through the Straits of Malacca (Section 9.2.4.4). In north-western Australia there is evidence that an originally continuous population of *L. cingulata* has become divided into geographically isolated northern and southern populations, which are sufficiently distinct to be recognized as subspecies (Sections 9.2.3.8, 9.2.3.9). Amongst the rock dwelling species, *L. coccinea* is restricted to the Pacific Ocean (as far west as the Philippines) and *L. glabrata* to the Indian Ocean (as far east as the Cocos-Keeling

Islands); although recognized as distinct species, shell and anatomical characters suggest a very close relationship. It should be noted that vicariance does not always lead to differentiation; for instance the Indian and Pacific Ocean forms of *L. pintado* show identical shell characters. Whether differentiation has proceeded to the point of speciation can only be demonstrated if the forms are sympatric over part of their range and remain distinct in the region of overlap. Such is the case for the closely related pair of species *L. articulata* and *L. strigata*. The three species *L. intermedia*, *L. philippiana* and *L. subvittata* may also have originated from a common ancestral species (Fig. 8.2) and now show partial overlap of their ranges.

7.4 Regional diversity

The present taxonomic treatment increases the number of recognized species of littorinids in mangrove forests of the Indo-Pacific province from three (Rosewater, 1970) to twenty. Of this number, up to ten species may be found together in a single mangrove forest, as at Singapore. This change in classification does not significantly alter the pattern of regional diversity of the mangrove fauna as a whole (Vermeij, 1973b), but does considerably change the pattern of distribution of species amongst the genera of mangrove molluscs. Such diversity within a single genus is by no means unusual in the tropics, but stands out as unique amongst the larger mangrove molluscs. Within the family Littorinidae the sympatric occurrence of several congeneric species is common, for example seven species of *Littorina* (and one of *Melarhaphe*) are found on rocky shores in Britain (Raffaelli, 1982).

Within the genus *Littoraria* as a whole, the worldwide pattern of species richness (Fig. 7.1) shows a maximum diversity in the central Indo-Pacific, with progressively fewer species in the Eastern

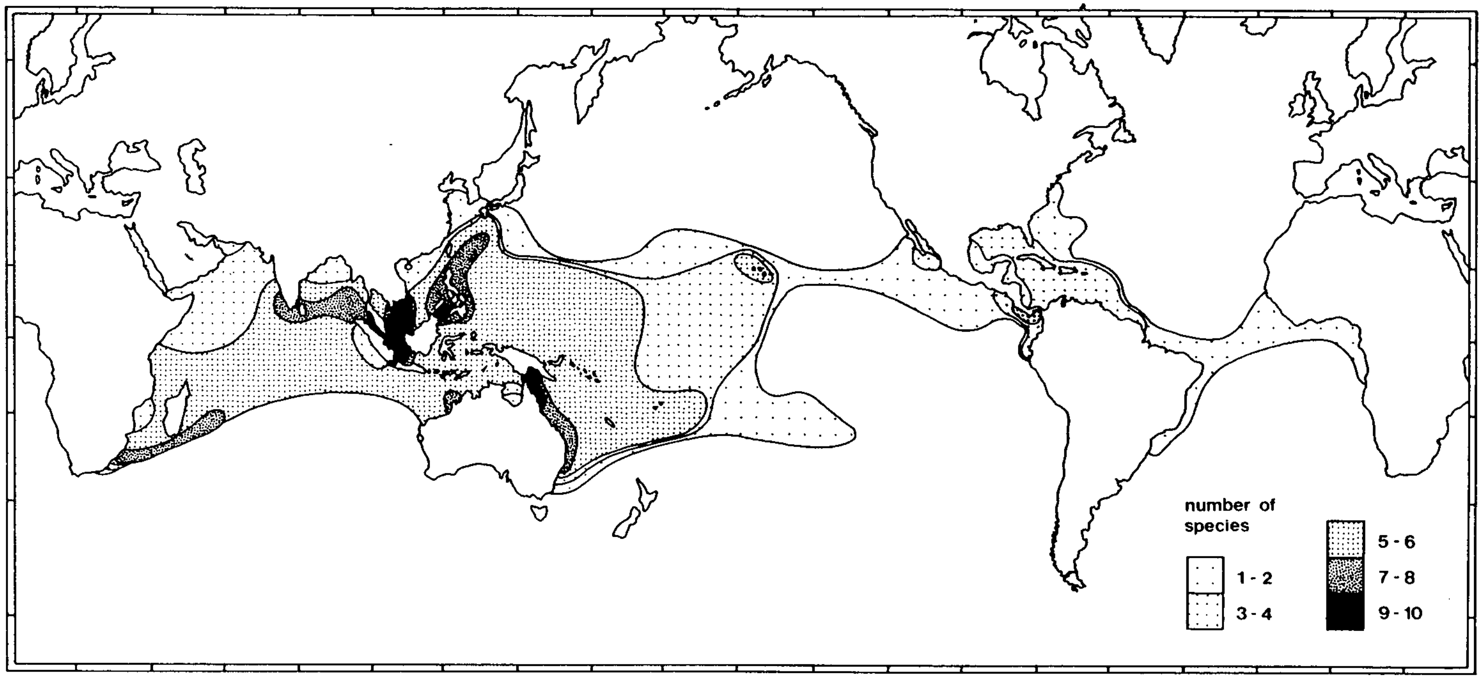

Fig. 7.1 Worldwide contour map of species richness in the genus *Littoraria* (compiled from 2700 distribution records, representing all 36 known species).

Pacific, the western Atlantic and the eastern Atlantic. A similar pattern, with maximum diversity in the central Indo-Pacific, is well known in many marine organisms, such as hermatypic corals (Stehli & Wells, 1971; Rosen, 1981), bivalves (Stehli *et al.*, 1967) and in mangroves and sea grasses (McCoy & Heck, 1976). The various explanations that have been advanced to account for this pattern have been reviewed by Rosen (1981).

The diversity of the mangrove-associated species of *Littoraria* in the Indo-Pacific (comprising the 20 members of the *scabra* group) is illustrated in Figure 7.2. Of the other marine groups mentioned above, the contours of species richness show the closest correlation with those of mangrove tree genera (McCoy & Heck, 1976). Diversity of *Littoraria* species is therefore correlated with a measure of habitat diversity. However, the relationship is probably not a causal one, but rather may be the result of similar factors acting to produce and to maintain high species numbers of the two groups in the same environment. This seems likely, since species of *Littoraria* are seldom restricted to a single tree species, but occupy habitats characterized by substrate and tidal level (Chapter 11). The effect of tree species is evident only in the rather distinct faunas of *Avicennia* and *Rhizophora* zones (Section 11.4.3), but both these genera are very widely distributed throughout the Indo-Pacific (Chapman, 1976).

In comparison with the diversity patterns of corals and seagrasses, the centre of *Littoraria* species richness is located further westwards and does not encompass the archipelagic region of the western Pacific. In part this reflects the continental distribution of mangroves and the oceanic distribution of corals. In the latter group the importance of a large area of suitable habitat and possibilities of isolation, both provided by archipelagos, have been emphasized as explanations for the observed pattern of diversity (Rosen, 1981). The diversity pattern of the gastropod genus *Strombus* (Abbott, 1960) is similar to that shown by corals. In the genus *Littoraria* the highest numbers of co-occurring species are

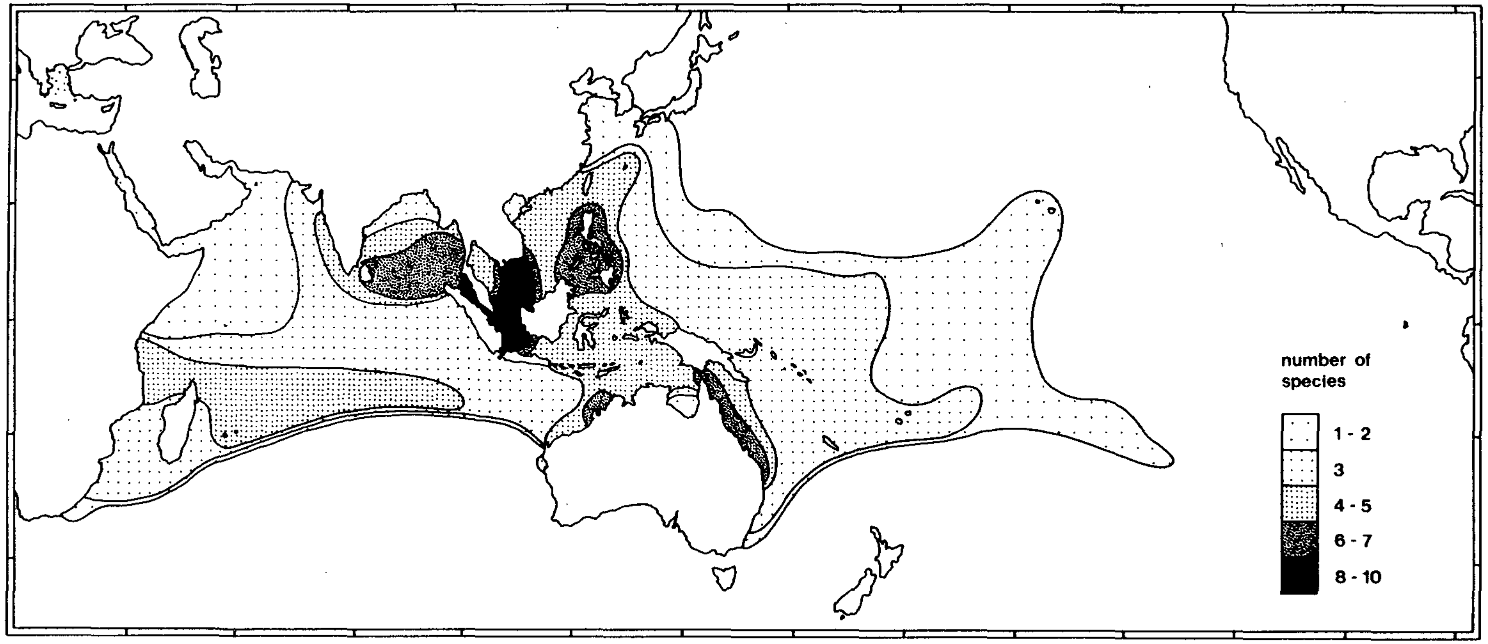

Fig. 7.2 Contour map of species richness of the 20 members of the *Littoraria scabra* group in the Indo-Pacific (compiled from 1900 distribution records).

found in the area of Malaysia, eastern Sumatra, northern Java, western Borneo and southern Vietnam, on the shores of continental land masses, rather than in the central region of Indonesia where continental islands are small and numerous. since the larvae of *Littoraria* species are probably widely dispersed (Section 7.2), archipelagic areas do not provide possibilities for isolation and speciation. In the past the Indo-Malayan centre of diversity has been regarded as a centre of origin from which species have radiated (Ekman, 1953; Stehli & Wells, 1971). However, at least in certain groups, this is a region of accumulation, rather than (or as well as) of generation of species (Taylor, 1971; Kay, in prep.). This appears to be the case in the genus *Littoraria*, in which differentiation and speciation seem to be taking place in the more peripheral areas of the Indo-Pacific province.

Accumulation of species in the Indo-Malayan region may have been favoured by the large area of the mangrove habitat which is available on the shores of large continental land masses, permitting co-occurrence of many species. The effect of predation may also be significant. Vermeij (1978) has argued that predation in marine environments is more intense at lower latitudes (Section 14.1). The major predators of *Littoraria* species are crabs (Chapter 14), and at several localities it has been observed that densities of these snails are greatest in small patches of mangroves or on isolated trees, where tree climbing crabs appear to be scarce (Section 11.5.2). Although no data are available on the local or geographical distribution of crabs, the possibility exists that intense predation in large mangrove forests in equatorial areas may contribute to the maintenance of high species richness in the genus by reducing population size and competitive effects, or by influencing zonation of the snails and overlap between their habitats (Section 11.5).

CHAPTER 8: PHYLOGENY AND GENERIC CLASSIFICATION

8.1 Status of the genus *Littoraria*

Until recently, an emphasis on shell characters in the classification of the family Littorinidae led to the inclusion of all smooth and spirally sculptured forms in the single genus *Littorina*, while species with nodular sculpture were placed in *Nodilittorina*, *Tectarius* or *Echininus*. Even on the basis of shell characters, the group of large, often thin and colourful shells from mangrove habitats was generally recognized as distinct, and following Mörch (1876) was classified as the subgenus *Littorinopsis* (von Martens, 1897; Thiele, 1927). *Littorinopsis* was raised to generic rank by Cossmann (1916), who was followed by Wenz (1938) and by authors in Japan (Kuroda & Habe, 1952; Oyama & Takemura, 1961).

The association of the generic name *Melarhaphe* Menke with the species here placed in *Littoraria* can be traced to the Adams brothers (1858). Tryon (1887) gave *Littorina 'scabra'* as the typical example of his section *Melaraphe*, although the type species is in fact *Turbo neritoides* L. (see Rosewater, 1966, for a discussion of *Melarhaphe*). This error was followed by a number of authors.

The generic name *Littoraria* was first published in an index (Griffith & Pidgeon, 1834) and was neglected until used as a subgenus of *Littorina* (and a senior synonym of *Littorinopsis*) by Bequaert (1943). *Littoraria* has subsequently been accepted as a full genus by Japanese taxonomists (Azuma, 1960; Habe, 1964; Higo, 1973). The type of the genus is *Turbo zebra* Donovan, from the tropical Eastern Pacific, of which the anatomy was hitherto unknown, which may explain the reluctance of some authors to use the generic name. Rosewater (1970, 1981) defined subgenera of *Littorina* partly on the basis of characters of the penis and radula, but still stressed features of the shell. Consequently, he recognized the subgenus *Littoraria* for robust, rather smooth, unicoloured or axially striped shells, which are oviparous and usually found on rocks. The subgenus *Littorinopsis* was retained for species with rather thin, spirally ribbed or carinate, spirally spotted shells, often associated with shore vegetation and mostly thought to be ovoviviparous. Nevertheless, penial and radular characters do not distinguish between these two groups. Placing primary importance on these two anatomical features, Bandel & Kadolsky (1982) united the two as the genus *Littoraria*. From a consideration of the morphological evidence discussed in detail in previous sections, it is clear that the species of *Littoraria* form a natural group, equivalent in rank to the more familiar genera *Littorina* and *Nodilittorina*. Dissection of *L. zebra*, the type species (Fig. 5.2 1), has confirmed that the generic name *Littoraria* is applicable to the group, for previously only shell (Fig. 9.81g) and radula (Rosewater, 1980a) of this species were known. The genus is formally defined in the taxonomic section (Section 9.2).

Bandel & Kadolsky (1982) have proposed a reclassification of the family, using characters of the penis, radula, spawn and shell. The present study, which includes examination of new taxonomic characters of the pallial oviduct and sperm nurse cells, and a reappraisal of information on spawn and penial shape, almost entirely supports the scheme of these authors. The characters of phylogenetic significance in *Littoraria* and other genera are summarized as a cladogram (Fig. 8.1, Table 8.1), which complements the table of characters given by Bandel & Kadolsky. Only one modification of their scheme is made, that *Nodilittorina antoni* is considered a member of the genus *Echininus*. The familiar genus *Littorina* should be restricted to those northern temperate and arctic species which show a pallial oviduct with two consecutive spiral loops (of albumen followed by capsule gland), an open prostate, and a penis lacking a glandular disc and usually with several penial glands.

The synonymy of the genus *Littoraria* given below includes all the genera and the subgeneric combinations which have been used for species of the genus.

8.1.1 Synonymy of the genus *Littoraria*

Helix - Linnaeus, 1758 [in part; not *Helix* Linnaeus, 1758]

Buccinum - Gmelin, 1791 [in part; not *Buccinum* Linnaeus, 1758]

Phasianella - Lamarck, 1822; Menke, 1830 [both in part; not *Phasianella* Lamarck, 1804]

Turbo - Donovan, 1825; Schumacher, 1838 [in part; not *Turbo* Linnaeus, 1758]

Littorina - Lesson, 1831; Philippi, 1846; Reeve, 1857; Nevill, 1885; von Martens, 1887; Annandale & Prashad, 1919; Whipple, 1965; Kay, 1979 [all in part; not *Littorina* Férussac, 1822, type species *Turbo littoreus* Linnaeus, see Melville, 1980]

Littorina (*Littorina*) - Bequaert, 1943 [in part; not *Littorina* Férussac]

Littoraria Griffith & Pidgeon, 1834; Azuma, 1960; Habe, 1964; Habe & Kosuge, 1966; Higo, 1973; Yoo, 1976; Bandel & Kadolsky, 1982

Littorina (*Littoraria*) - Bequaert, 1943; Shikama & Horikoshi, 1963; Rosewater, 1970; Rosewater, 1981

Litorina - Philippi, 1847-48; von Martens, 1871; Lischke, 1871; Weinkauff, 1878, 1882 [all in part; unjustified emendation of *Littorina* Férussac, attributed to Menke, 1828, by Bequaert, 1943]

Littorina (*Melaraphe*) - Adams & Adams, 1858 [in part]; Tryon, 1887; Melvill & Standen, 1901; Dautzenberg & Fischer, 1905; Dautzenberg, 1929; Bequaert, 1943 [in part]; Biggs, 1958 [not *Melarhaphe* Menke, 1828, type species *Turbo neritoides* Linnaeus, see Rosewater, 1966]

Melaraphe (*Litt.*) - Dunker, 1871 [not *Melarhaphe* Menke]

Littorina (*Melaraphis*) - Tapparone-Canefri, 1874; Tryon, 1883 [not

Melaraphis Philippi, 1836 = *Melarhaphe* Menke]

Littorina (*Malaraphe*) - Casto de Elera, 1896 [error for *Melarhaphe* Menke]

Melarhaphe - Hedley, 1918a; Yen, 1942 [in part; not *Melarhaphe* Menke]

Melarapha - Iredale & McMichael, 1962 [in part; see Rosewater, 1966]

Littorina (*Littorinopsis*) Mörch, 1876; Fischer, 1887; von Martens, 1897; Schepman, 1909; Prashad, 1921; Oostingh, 1927; Thiele, 1929; Adam & Leloup, 1938; Rosewater, 1970; Rosewater, 1981

Littorinopsis - Cossmann, 1916; Wenz, 1938; Kuroda & Habe, 1952; Oyama & Takemura, 1961; Brandt, 1974

Melaraphe (*Littorinopsis*) - Hirase, 1934; Abe, 1942

Leptopoma ? - Heude, 1885 [not *Leptopoma* Pfeiffer, 1847]

Littorina (*Lamellilitorina*) Tryon, 1887

Littorinopsis (*Lamellilitorina*) - Wenz, 1938

8.1.2 List of recognized Recent taxa of *Littoraria*

In the following list common synonyms and key taxonomic references are provided for those species not described in detail in the taxonomic section. Habitat and geographical distribution are indicated.

Subgenus *Littoraria* Griffith & Pidgeon, 1834

zebra (Donovan, 1825) [= *pulchra* (Sowerby, 1832)]; Keen (1971); mangroves; tropical E. Pacific

fasciata (Gray, 1839); Keen (1971); mangroves; tropical E. Pacific

varia (Sowerby, 1832); Keen (1971); mangroves; tropical E. Pacific

irrorata (Say, 1822); Bequaert (1943); salt marsh; N.W. Atlantic *vespacea* n. sp.; mangroves; Malaysia

flava (King & Broderip, 1832); Bequaert (1943; as *nebulosa* subsp.); mangroves and rocks; Brazil, Antilles

tessellata (Philippi, 1847); Bandel & Kadolsky (1982); mangroves and rocks; Caribbean

[n. sp. Rosewater (in prep.); salt marsh, mangroves; tropical E. Pacific]

undulata (Gray, 1839); Rosewater (1970); rocks, driftwood; Indo-Pacific

nebulosa (Lamarck, 1822); Bequaert (1943; in part); driftwood, mangroves; Caribbean

cingulifera (Dunker, 1845); Rosewater (1981); mangroves, rocks; W. Africa

coccinea (Gmelin, 179 [= *obesa* (Sowerby, 1832)]; Rosewater (1970); rocks, driftwood; W. Pacific, Polynesia

glabrata (Philippi, 1846) [= *kraussi* (Rosewater, 1970)]; Rosewater (1970); rocks; Indian Ocean

mauritiana (Lamarck, 1822); Rosewater (1970); rocks; S.W. Indian Ocean

pintado (Wood, 1828) [= *schmitti* (Bartsch & Rehder, 1939); *pullata* (Carpenter, 1864)]; Rosewater (1970); rocks; S.W. Indian Ocean, W. and E. Pacific

Subgenus *Lamellilitorina* Tryon, 1887

albicans (Metcalfe, 1852); mangroves; Borneo

Subgenus unknown

aberrans (Philippi, 1846); Rosewater (1980b); mangroves; tropical E. Pacific

Subgenus *Littorinopsis* Mörch, 1876

angulifera (Lamarck, 1822) [= *ahenea* (Reeve, 1857)]; Bequaert (1943); Rosewater (1981); mangroves; tropical E. and W. Atlantic

scabra (Linnaeus, 1758); mangroves; Indo-Pacific

lutea (Philippi, 1847); mangroves; Indonesia, Philippines

pallescens (Philippi, 1846); mangroves; Indo-Pacific

philippiana (Reeve, 1857); mangroves; E. Australia

intermedia (Philippi, 1846); mangroves, rocks; Indo-Pacific *subvittata* n. sp.; mangroves, rocks; W. Indian Ocean

filosa (Sowerby, 1832); mangroves; Australia, Sunda Is.

cingulata cingulata (Philippi, 1846); mangroves; N.W. Australia

cingulata pristissini n. subsp.; mangroves, salt marsh; Shark Bay, W. Australia

luteola (Quoy & Gaimard, 1832); mangroves, salt marsh; E. Australia

ardouiniana (Heude, 1885); mangroves; S. China Sea

delicatula (Nevill, 1885); mangroves; Bay of Bengal

Subgenus *Palustorina* n. subgen.

melanostoma (Gray, 1839); mangroves, salt marsh; Indo-Malaya

flammea (Philippi, 1847); China

conica (Philippi, 1846); mangroves; Malaysia, Indonesia

carinifera (Menke, 1830); mangroves; Indo-Malaya

sulculosa (Philippi, 1846); mangroves, rocks; N.W. Australia

articulata (Philippi, 1846); mangroves, rocks; Indo-Malaya, Australia

strigata (Philippi, 1846); mangroves, rocks; Indo-Malaya

8.2 Relationships of the genus *Littoraria*

Throughout the discussions of morphological characters the attempt has been made to assess which of pairs of character states are likely to be ancestral and which derived, or in the terminology of cladistic analysis, which are plesiomorphic and which apomorphic (Hennig, 1966). These character states are summarized in Tables 8.1 and 8.2. In the absence of information from ontogeny and from a fossil record, out-group comparison has been used to assess plesiomorphies and apomorphies (Wiley, 1981). Insufficient anatomical information is available for the small littorinid forms from southern oceans including *Laevilittorina*, *Rissolittorina* and *Rufolacuna*, and for members of the family Lacunidae (considered by

Ponder, 1976, to be a subfamily of the Littorinidae). Therefore, in considering the relationships of the genus *Littoraria*, only the genera *Nodilittorina*, *Echininus*, *Tectarius*, *Melarhaphe*, *Fossarilittorina*, *Cenchritis*, *Peasiella*, *Littorina* and *Bembicium* have been compared. From the small amount of information available, however, it seems possible that these genera (with the exception of *Bembicium*) may bear closer phylogenetic relationship to each other than to the excluded genera.

In making decisions as to the plesiomorphic and apomorphic states of a character, the conclusion will usually be dependent upon the choice of the out-group with which to draw comparison. That is, a phylogeny must be assumed before it can be tested, which appears to be a circular argument. As discussed by Wiley (1981) this logical difficulty is overcome if sufficient characters are available so that phylogenetic hypotheses can be retested by others in a process of reciprocal illumination.

The character states of the littorinid genera are summarized as a cladogram in Figure 8.1. The distribution of apomorphies shows that considerable parallel evolution has occurred amongst the ten genera, and that most of the branching points are defined by only one or two characters. For these reasons the construction of a dendrogram to indicate recency of common ancestry is highly speculative, and owes more to subjective weighting of characters and estimation of 'overall similarity' than to rigorous application of the criterion of parsimony. The resulting cladogram must be regarded only as an hypothesis, to be tested as further information becomes available. Nevertheless, the cladogram is a useful means of summarizing information visually. Bandel & Kadolsky (1982) have noted a high incidence of parallel evolution in the genus *Nodilittorina*.

The genus *Bembicium* is rather poorly known, but peculiarities of penial form, lack of capsule glands and possible absence of sperm nurse cells, suggest that it is distantly related to the other genera. Of the eight remaining genera, *Littorina* is the most

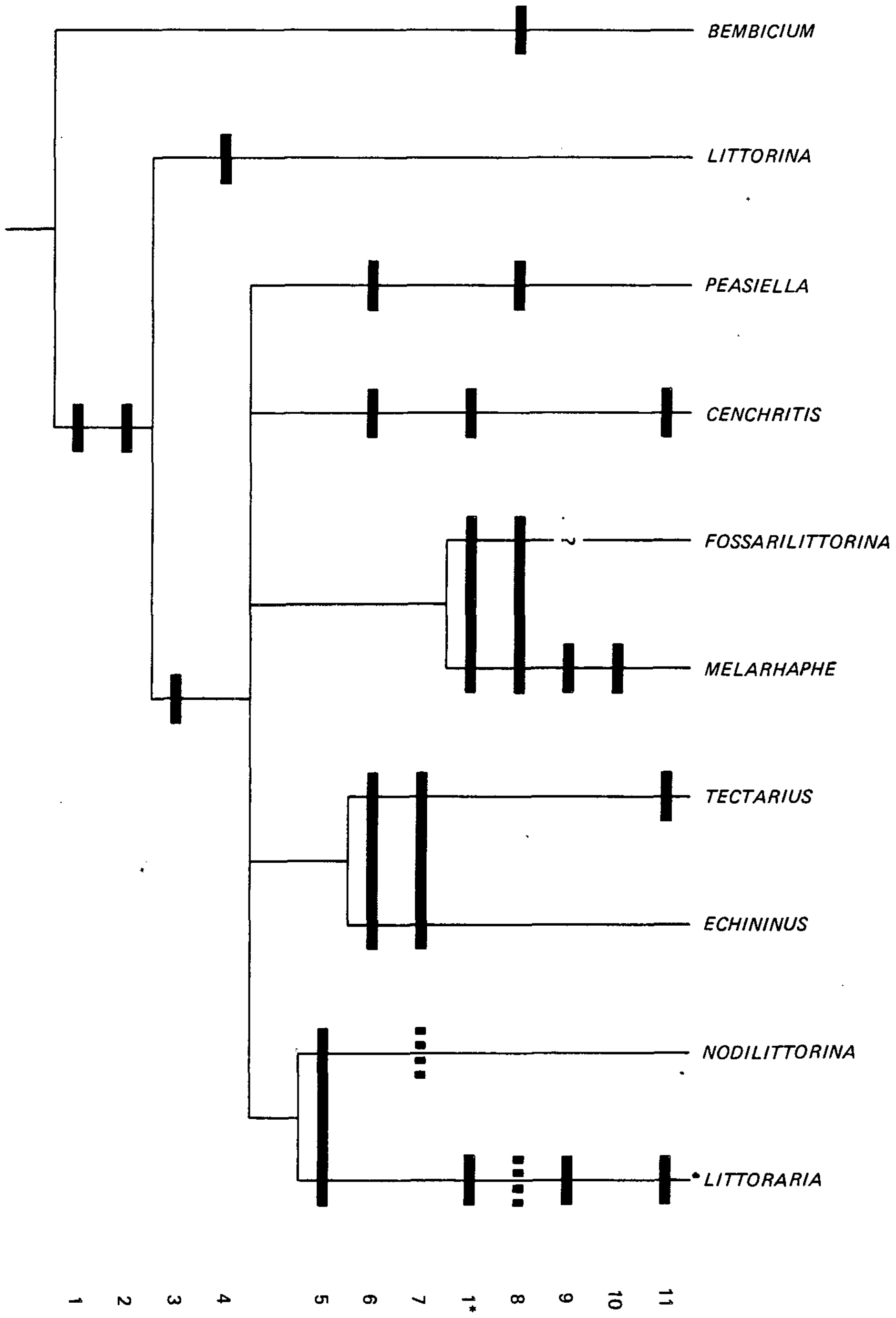

Fig. 8.1 Cladogram representing an hypothesis of phylogenetic relationships amongst 10 genera of Littorinidae; numbers refer to the character states listed in Table 8.1; asterisk indicates a character reversal; solid bars indicate apomorphic states; broken bars indicate occurrence of both character states; query indicates character state unknown.

Table 8.1 Character states in the family Littorinidae.

Character	Plesiomorphic	Apomorphic	Notes
1. penial glands	absent	present	Secondary reversal of character presumed in *Littoraria*, *Melarhaphe*, *Fossarilittorina*, *Cenchritis*.
2. sperm nurse cells	absent	present	Polarity uncertain, no evidence from out-groups.
3. sperm nurse cell rods	absent	present	Polarity uncertain. Secondary loss presumed in *Melarhaphe* and a few *Littoraria* and *Nodilittorina* spp. Unknown in *Tectarius* and *Fossarilittorina*.
4. two consecutive spiral loops in pallial oviduct, of albumen followed by capsule gland	no	yes	
5. penial glandular disc	absent	present	
6. operculum	paucispiral	meso- to multi-spiral	*Tectininus* considered a subgenus of *Echininus*, not of *Nodilittorina*.
7. penial papillae	absent	present	
8. penial sperm groove	open	closed	
9. prostate gland	open	closed	
10. jelly gland a spiral loop	no	yes	
11. single spiral (≥3½ whorls) of pallial oviduct, incorporating capsule gland	no	yes	Secondary loss of capsule gland in ovoviviparous species. *Bembicium* lacks capsule gland.

distantly related to *Littoraria*. The relationships of the remaining genera are less clear, and claims could be made for *Melarhaphe* and *Fossarilittorina*, *Cenchritis* or *Nodilittorina* as the sister group of *Littoraria*. For *Melarhaphe*, possible synapomorphies include the closed prostate and absence of penial glands, while the specialized pallial oviduct, lack of penial glandular disc, specialized radula and smooth shell militate against close relationship.. *Fossarilittorina* is probably closely related to *Melarhaphe*, and the oviduct is less specialised. Evidence for *Cenchritis* includes the spiral oviduct, egg capsules, sperm nurse cells with rods, and lack of penial glands, while the shell, operculum, open prostate and absence of penial glandular disc are conspicuous differences from *Littoraria*. The evidence appears to favour *Nodilittorina* as the genus closest to *Littoraria*. An apparently unique synapomorphy is the penial glandular disc, while similarities of less certain value include the shape, sculpture and colour pattern of the shell of species of *Nodilittorina* which lack nodulose sculpture. The variability in numbers of penial glands in *Nodilittorina* suggests that these might readily be lost to derive the condition in *Littoraria*. Sperm nurse cells are similar in the two genera, as also in *Cenchritis*. The pallial oviduct is of sufficiently generalized structure in some species of *Nodilittorina* not to preclude the derivation of the spiral form shown by *Littoraria*. Egg capsules are divergently specialized in the two genera, although both could be derived from the generalized capsule form of *Melarhaphe neritoides*.

The only study to have applied techniques of biochemical taxonomy to a range of littorinid species from several genera is that of Jones (1972). This study compared the electrophoretic banding patterns shown by three proteins in twelve littorinids from Panama. However, the results were inconsistent and failed to demonstrate the groupings that might have been expected on the basis of the classification adopted in the present work.

8.3 Subgeneric classification

There is no doubt that the genus *Littoraria* is a monophyletic group, for all its members are characterized by the unique combination of four synapomorphies: the presence of the penial glandular disc, the single spiral loop of the pallial oviduct, the closed prostate and the absence of penial glands. Within the genus, derived characters of the oviduct, developmental type, radula, penis and sperm nurse cells can be used in the reconstruction of a hypothetical phylogeny (Fig. 8.2). Within the groups thus defined, shell characters are often similar, although impossible to describe in terms of simple character states. Geographical distribution and habitat also show some correlations with the species groups (see species list, Section 8.1.2).

The most distinctive group of species within the genus is here recognized as the new subgenus *Palustorina*. This group is defined by the unique synapomorphy of its flagellate sperm nurse cells. Sperm nurse cells have not been described in all species of *Littoraria*, but the subgenus is also distinguished by a combination of penial form, position of the bursa copulatrix, and shell microsculpture, which are diagnostic when taken together. This subgenus is restricted to the Indo-Pacific province, and most of its seven members are known to occur exclusively in mangrove habitats, only two species being found also on sheltered rocky shores. Cossmann (1916) proposed the section *Touzinia* of *Littorinopsis*, with *Phasianella prevostina* Basterot, from the Miocene of France, as the type species. Although Cossmann's figures of the species bear a superficial resemblance to *L. melanostoma*, examination of specimens in the BMNH showed that '*Littorinopsis*' *prevostina* is not a member of the same subgenus, and probably not even of the genus *Littoraria*.

The twelve ovoviviparous species known or suspected to brood embryos in the mantle cavity until the early veliger stage, are here recognized as the subgenus *Littorinopsis*. The anatomical difference

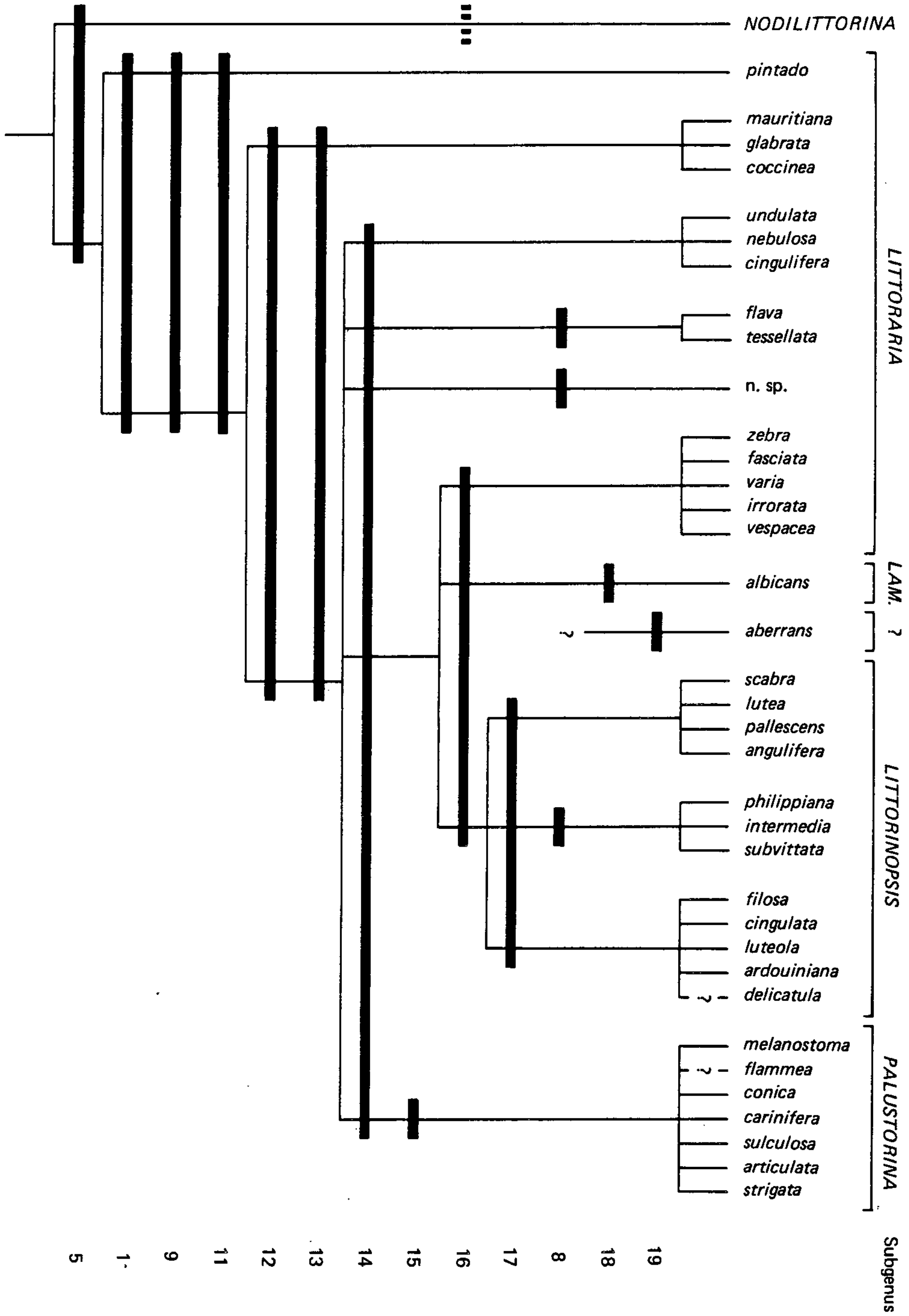

Fig. 8.2 Cladogram of species of *Littoraria*, derived from the character states listed in Table 8.2. *Nodilittorina* is the inferred sister group of *Littoraria*. Terminal groupings are based upon close similarity in the form of the shell and or penis; solid bars indicate apomorphic character states; broken bars indicate the occurrence of both character states; queries indicate uncertainty of position of species of which anatomical characters are unknown; *Lam.*, subgenus *Lamellilittorina*. Note that egg capsules and sperm are undescribed in some species (see text).

Table 8.2 Character states in the genus *Littoraria*.

Character	Plesiomorphic	Apomorphic	Notes
1. penial glands			Absent in all *Littoraria* spp.
5. penial glandular disc			Present in all *Littoraria* spp.
8. penial sperm groove	open	closed	
9. prostate gland			Closed in all *Littoraria* spp.
11. single spiral of pallial oviduct, incorporating capsule glands			Present in all oviparous *Littoraria* spp.; secondary loss of capsule glands in ovoviviparous *Littoraria* spp.
12. egg capsule with spiral rim above flotation skirt or lamella	yes	no	
13. spiral whorls of pallial oviduct ⩾ $3\frac{1}{2}$	no	yes	Secondary reduction of number of whorls to $2\frac{1}{2}$ in a few ovoviviparous *Littoraria* spp.
14. rachidian tooth of radula of 'hooded' type	no	yes	
15. sperm nurse cells flagellate	no	yes	
16. bursa opens in anterior position	no	yes	Condition variable within other littorinid genera
17. brooding of embryos in mantle cavity, loss of capsule glands	no	yes	
18. planktonic protoconch >610 μm	no	yes	
19. direct development	no	yes	Indicated by protoconch of *L. aberrans*.

between ovoviviparous and oviparous species is only a minor modification of the oviduct by the loss of capsule glands, which might, conceivably, have occurred several times during the evolution of the genus. Nevertheless, it seems useful to recognize the group as distinct. The penes are quite uniform, being bifurcate, with a round glandular disc. The shells of the group are also rather distinctive, showing spiral microsculpture in the grooves and being relatively thin in texture, while ten of the members are colour polymorphic. Probably associated with the thin and colourful shells is the habit of many of the species of living at high levels on the foliage of mangrove trees. Only two species occur occasionally on rock substrates. Eleven species occur in the Indo-Pacific and one in the Atlantic.

The subgeneric classification of *L. albicans* and *L. aberrans* is uncertain. *L. albicans* is anatomically close to members of the subgenus *Littoraria*, especially to the *L. zebra* group. However, the species is unique in its large protoconch of the planktotrophic type, equal cusps of the rachidian tooth, large number of primary grooves on the shell, and peculiar colouration of the head-foot. The shell microsculpture, varices and colour polymorphism are also unlike members of the subgenus *Littoraria*. For these reasons, the subgenus *Lamellilitorina* of Tryon (1887) is retained for this single species. In the absence of anatomical information, *L. aberrans* cannot yet be assigned to a subgenus; shell characters are similar to the thin shelled and colour polymorphic species of *Littorinopsis*, but the protoconch shows that the species has nonplanktotrophic development, which is unique in the genus.

The remaining fifteen species are retained in the nominate subgenus. Although this is a paraphyletic and somewhat heterogeneous group, little would be gained by further subdivision. Shells in this group are neither thin nor colour polymorphic. Members occur in all the tropical provinces. *L. pintado* is of interest as the least specialized species in the genus, showing the greatest number of ancestral character states. The penial glandular disc is poorly differentiated, the pallial oviduct shows the least number of whorls amongst the oviparous species of *Littoraria*, the rachidian tooth of the radula is not hooded and the cupola of the egg capsule is sculptured by a single ring. In all these plesiomorph states, *L. pintado* bears greater resemblance to species of *Nodilittorina* and other genera than is shown by any other *Littoraria* species. In addition, the shell is pale and the aperture dark brown with a somewhat paler basal stripe, which is reminiscent of certain smooth shelled *Nodilittorina* species. In common with *L. coccinea*, *L. glabrata*, *L. mauritiana* and *L. undulata*, which also show few derived characters, *L. pintado* typically occurs on exposed rocky shores at high intertidal levels. This is certainly the ancestral habitat of the genus, and that in which most species of *Nodilittorina*, *Melarhaphe*, *Echininus*, *Tectarius*, *Cenchritis* and *Peasiella* also occur. Within the genus *Littoraria* there seems to have been an increasing specialization to the mangrove habitat in species showing more apomorphic characters (compare list of species in Section 8.1.2 with Fig. 8.2). *L. pintado* is also remarkable for its wide and perhaps relict distribution (Section 7.1), which suggests that the species may be of greater age than its congeners.

CHAPTER 9: SYSTEMATIC DESCRIPTIONS

9.1 Key to shells

Shell variation in these species is such that a few rare and atypical shell forms may not conform to the diagnoses given, or may key out incorrectly. Reference should be made to the figures of shells, distribution maps, and, where possible, to anatomical characters. It should be noted that the primary grooves on the spire whorls should be counted on whorl four of the teleoconch or earlier; colour polymorphic shells may be yellow, pink, brown or patterned; columellar colour refers to the excavated area, rather than the pillar which is often white.

1 Columella narrow, rounded, not excavated 2
– Columella excavated or flattened, usually wide 8
2 Sculpture of 9–11 narrow carinae on last whorl; colour polymorphic . . . . . . *L. filosa* (9.2.3.7)
– Sculpture of low or rounded ribs, or numerous fine riblets . 3
3 Ribs on last whorl numbering 40–78 4
– Ribs on last whorl numbering 11–28 5
4 Primary grooves on spire whorls numbering 10–13; secondary sculpture appears on whorl 7; microsculpture indistinct; colour polymorphic . . . . *L. ardouiniana* (9.2.3.11)
– Primary grooves on spire whorls numbering 7–9; secondary sculpture appears on whorls 5–6; microsculpture usually of spiral striae in grooves or over whole surface; colour polymorphic . . *L. cingulata pristissini* (9.2.3.9)
5 On last whorl grooves $\frac{1}{2}$–1 times rib width, containing strong spiral microsculpture; 11–13 prominent, rounded ribs on last whorl; primary grooves on spire whorls numbering 5–6; colour cream marbled with brown . . . . *L. cingulata cingulata* (9.2.3.8)

– On last whorl grooves less than $\frac{1}{3}$ rib width; spiral microsculpture in grooves weak or absent; 15–28 ribs on last whorl; primary grooves on spire whorls numbering 6–10 6

6 Spire outline straight sided, sutures not impressed; colour pale yellow with pattern of brown dots; parietal callus dark purple brown . . *L. melanostoma* (9.2.4.1)

– Sutures impressed, spire whorls rounded 7

7 Sculpture on last whorl of rounded ribs, of which 2 at periphery are most prominent; microsculpture indistinct; colour polymorphic . . . . . *L. luteola* (9.2.3.10)

– Sculpture on last whorl of low ribs of equal width; microsculpture of spiral striae on ribs and pits in grooves; colour pale with oblique, brown, axial stripes . . . . *L. flammea* (9.2.4.2)

8 Primary grooves on spire whorls numbering 17–26; length of protoconch 0.6 mm; up to 20 varices on last whorl; colour polymorphic, fading to white . *L. albicans* (9.2.2.1)

– Primary grooves on spire whorls numbering 4–14; length of protoconch <0.4 mm 9

9 Spire outline almost straight sided, sutures not impressed; strong peripheral keel on last whorl; columella wide 10

– Sutures usually impressed and spire whorls rounded; if not, then columella narrow; last whorl not usually strongly keeled 11

10 Sculpture of 50–70 fine ribs on last whorl; protoconch is a papilla on blunt apex of teleoconch; colour cream with irregular brown pattern . . . *L. conica* (9.2.4.3)

– Sculpture of 1–9 narrow carinae on last whorl, largest at periphery; colour grey with axial red brown lines . . . . . . *L. carinifera* (9.2.4.4)

11 Sculpture on last whorl of 9–11 prominent rounded ribs, separated by grooves 1–3 times rib width 12

– Sculpture on last whorl of more numerous, small or low ribs, separated by grooves less than width of ribs . .13

12 Microsculpture of fine, axial lines in grooves; colour cream, with pale orange brown dashes or bands on ribs . . . . *L. sulculosa* (9.2.4.5)

– Microsculpture of faint spiral lines in grooves, or absent; colour polymorphic . . *L. pallescens* (in part; 9.2.3.3)

13 Columella white and wide 14

– Columella purple, brown or narrow 16

14 Shell colour yellow or orange pink . . . . *L. pallescens* (in part; 9.2.3.3)

– Shell colour pale with more or less dense black or brown pattern 15

15 Microsculpture of spiral striae in grooves; adult size 20–44 mm . . . . *L. scabra* (9.2.3.1)

– Microsculpture of axial striae in the wider grooves, or indistinct; adult size less than 20 mm . . . . *L. articulata* (in part; 9.2.4.6)

16 Sculpture of 13–18 prominent, narrow cords on last whorl . .17

– Sculpture of more numerous, or low and rounded ribs . . .18

17 Secondary sculpture conspicuous between primary cords on last whorl; colour usually brown, sometimes polymorphic . . . . . . *L. philippiana* (9.2.3.4)

– Secondary sculpture faint or absent between primary cords on last whorl; colour polymorphic . . . . *L. pallescens* (in part; 9.2.3.3)

18 Ribs on last whorl numbering 35–60, of equal width . . .19

– Ribs on last whorl usually numbering less than 35, or if not then secondary ribs only half width of primary ribs .20

19 Columella very narrow, excavated; primary grooves on spire whorls numbering 11–14; sutures only slightly impressed; colour polymorphic . . . . *L. delicatula* (9.2.3.12)

– Columella of moderate width; primary grooves on spire whorls numbering 10–12; sutures impressed; colour pale orange brown with dark brown pattern more or less aligned into 8–12 oblique axial stripes . . . . *L. subvittata* (9.2.3.6)

20 Rib at periphery of last whorl more prominent than others,

marking a distinct keel, which is often emphasized by colour pattern; colour polymorphic 21

\- Last whorl rounded and hardly angled at periphery; peripheral rib not more prominent than the rest; colour cream with dark brown or black pattern 22

21 Ribs on last whorl numbering 33–50, comprising primary ribs separated by single secondary ribs of half their width; spiral bands of colour never present . . . . *L. lutea* (9.2.3.2)

\- Ribs on last whorl numbering 21–26; secondary sculpture usually absent or limited to a few inconspicuous riblets; spiral bands of colour may be present . . . . *L. pallescens* (in part; 9.2.3.3)

22 Colour pattern on last whorl of 13–20 axially aligned series of dashes, or axial stripes; posterior rib usually the most prominent, slightly pushed up towards suture; columella purple; spiral microsculpture seldom present on last whorl . . . *L. intermedia* (9.2.3.5)

\- Colour pattern on last whorl of 6–15 more or less axially aligned series of dashes, or axial stripes (alignment may only be evident at sutures and periphery); if axial series number 12–15 then columella usually brown, not purple; ribs of approximately equal width; faint spiral striae usually visible on ribs 23

23 Colour pattern on last whorl of 12–15 well aligned axial series of dashes; faint pale band on middle of base; columella very deeply excavated, brown or dull purple . . . . *L. vespacea* (9.2.1.1)

\- Colour pattern on last whorl of 6–11 axially aligned series of dashes, alignment often interrupted between suture and periphery; columella excavated, purple . . . . *L. articulata* or *L. strigata* (9.2.4.6, 9.2.4.7)

Ponder, 1976, to be a subfamily of the Littorinidae). Therefore, in considering the relationships of the genus *Littoraria*, only the genera *Nodilittorina*, *Echininus*, *Tectarius*, *Melarhaphe*, *Fossarilittorina*, *Cenchritis*, *Peasiella*, *Littorina* and *Bembicium* have been compared. From the small amount of information available, however, it seems possible that these genera (with the exception of *Bembicium*) may bear closer phylogenetic relationship to each other than to the excluded genera.

In making decisions as to the plesiomorphic and apomorphic states of a character, the conclusion will usually be dependent upon the choice of the out-group with which to draw comparison. That is, a phylogeny must be assumed before it can be tested, which appears to be a circular argument. As discussed by Wiley (1981) this logical difficulty is overcome if sufficient characters are available so that phylogenetic hypotheses can be retested by others in a process of reciprocal illumination.

The character states of the littorinid genera are summarized as a cladogram in Figure 8.1. The distribution of apomorphies shows that considerable parallel evolution has occurred amongst the ten genera, and that most of the branching points are defined by only one or two characters. For these reasons the construction of a dendrogram to indicate recency of common ancestry is highly speculative, and owes more to subjective weighting of characters and estimation of 'overall similarity' than to rigorous application of the criterion of parsimony. The resulting cladogram must be regarded only as an hypothesis, to be tested as further information becomes available. Nevertheless, the cladogram is a useful means of summarizing information visually. Bandel & Kadolsky (1982) have noted a high incidence of parallel evolution in the genus *Nodilittorina*.

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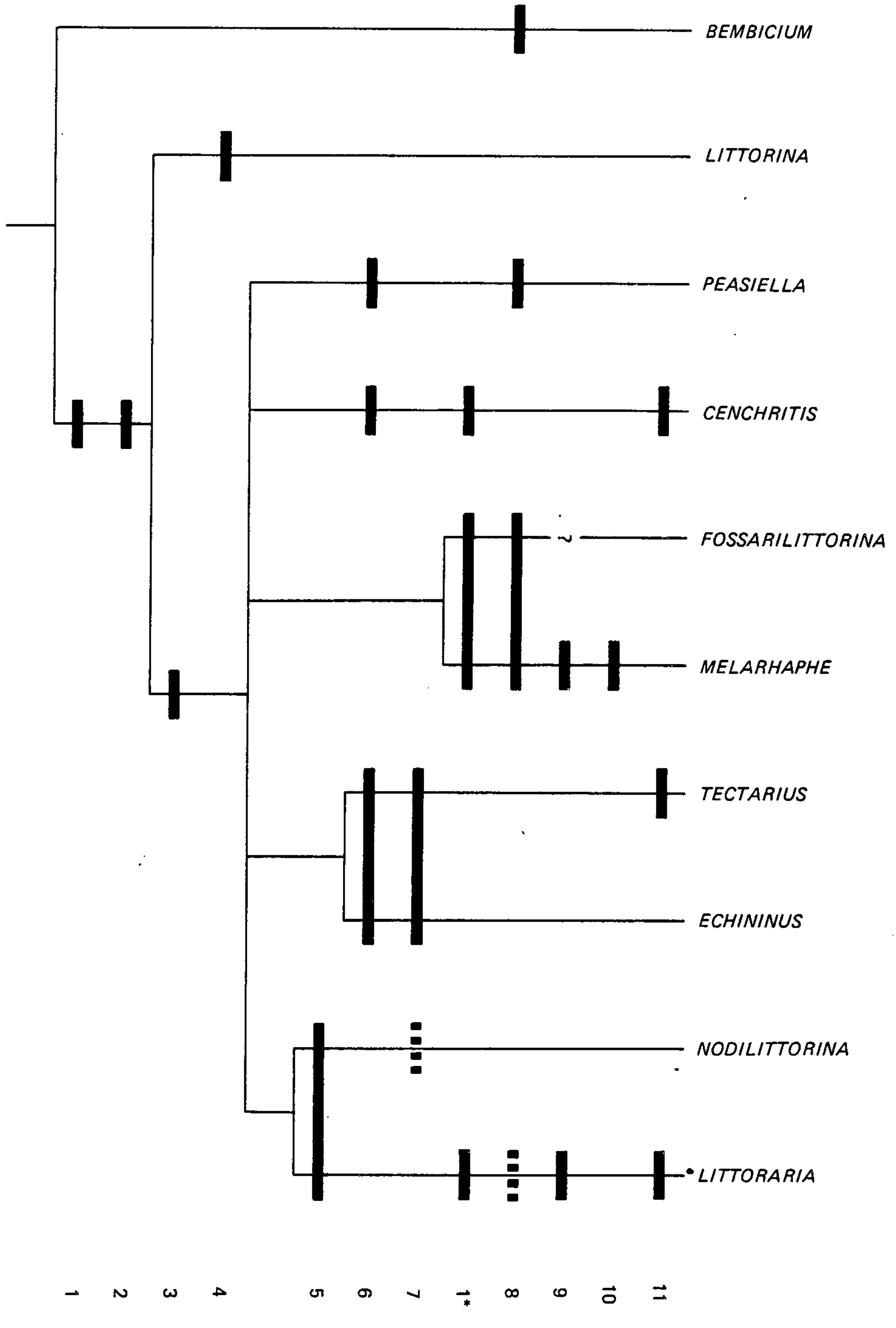

Fig. 8.1 Cladogram representing an hypothesis of phylogenetic relationships amongst 10 genera of Littorinidae; numbers refer to the character states listed in Table 8.1; asterisk indicates a character reversal; solid bars indicate apomorphic states; broken bars indicate occurrence of both character states; query indicates character state unknown.

Table 8.1 Character states in the family Littorinidae.

	Character	Plesiomorphic	Apomorphic	Notes
1.	penial glands	absent	present	Secondary reversal of character presumed in *Littoraria*, *Melarhaphe*, *Fossarilittorina*, *Cenchritis*.
2.	sperm nurse cells	absent	present	Polarity uncertain, no evidence from out-groups.
3.	sperm nurse cell rods	absent	present	Polarity uncertain. Secondary loss presumed in *Melarhaphe* and a few *Littoraria* and *Nodilittorina* spp. Unknown in *Tectarius* and *Fossarilittorina*.
4.	two consecutive spiral loops in pallial oviduct, of albumen followed by capsule gland	no	yes	
5.	penial glandular disc	absent	present	
6.	operculum	paucispiral	meso- to multi-spiral	*Tectininus* considered a subgenus of *Echininus*, not of *Nodilittorina*.
7.	penial papillae	absent	present	
8.	penial sperm groove	open	closed	
9.	prostate gland	open	closed	
10.	jelly gland a spiral loop	no	yes	
11.	single spiral ($\geq 3\frac{1}{2}$ whorls) of pallial oviduct, incorporating capsule gland	no	yes	Secondary loss of capsule gland in ovoviviparous species. *Bembicium* lacks capsule gland.

distantly related to *Littoraria*. The relationships of the remaining genera are less clear, and claims could be made for *Melarhaphe* and *Fossarilittorina*, *Cenchritis* or *Nodilittorina* as the sister group of *Littoraria*. For *Melarhaphe*, possible synapomorphies include the closed prostate and absence of penial glands, while the specialized pallial oviduct, lack of penial glandular disc, specialized radula and smooth shell militate against close relationship.. *Fossarilittorina* is probably closely related to *Melarhaphe*, and the oviduct is less specialised. Evidence for *Cenchritis* includes the spiral oviduct, egg capsules, sperm nurse cells with rods, and lack of penial glands, while the shell, operculum, open prostate and absence of penial glandular disc are conspicuous differences from *Littoraria*. The evidence appears to favour *Nodilittorina* as the genus closest to *Littoraria*. An apparently unique synapomorphy is the penial glandular disc, while similarities of less certain value include the shape, sculpture and colour pattern of the shell of species of *Nodilittorina* which lack nodulose sculpture. The variability in numbers of penial glands in *Nodilittorina* suggests that these might readily be lost to derive the condition in *Littoraria*. Sperm nurse cells are similar in the two genera, as also in *Cenchritis*. The pallial oviduct is of sufficiently generalized structure in some species of *Nodilittorina* not to preclude the derivation of the spiral form shown by *Littoraria*. Egg capsules are divergently specialized in the two genera, although both could be derived from the generalized capsule form of *Melarhaphe neritoides*.

The only study to have applied techniques of biochemical taxonomy to a range of littorinid species from several genera is that of Jones (1972). This study compared the electrophoretic banding patterns shown by three proteins in twelve littorinids from Panama. However, the results were inconsistent and failed to demonstrate the groupings that might have been expected on the basis of the classification adopted in the present work.

8.3 Subgeneric classification

There is no doubt that the genus *Littoraria* is a monophyletic group, for all its members are characterized by the unique combination of four synapomorphies: the presence of the penial glandular disc, the single spiral loop of the pallial oviduct, the closed prostate and the absence of penial glands. Within the genus, derived characters of the oviduct, developmental type, radula, penis and sperm nurse cells can be used in the reconstruction of a hypothetical phylogeny (Fig. 8.2). Within the groups thus defined, shell characters are often similar, although impossible to describe in terms of simple character states. Geographical distribution and habitat also show some correlations with the species groups (see species list, Section 8.1.2).

The most distinctive group of species within the genus is here recognized as the new subgenus *Palustorina*. This group is defined by the unique synapomorphy of its flagellate sperm nurse cells. Sperm nurse cells have not been described in all species of *Littoraria*, but the subgenus is also distinguished by a combination of penial form, position of the bursa copulatrix, and shell microsculpture, which are diagnostic when taken together. This subgenus is restricted to the Indo-Pacific province, and most of its seven members are known to occur exclusively in mangrove habitats, only two species being found also on sheltered rocky shores. Cossmann (1916) proposed the section *Touzinia* of *Littorinopsis*, with *Phasianella prevostina* Basterot, from the Miocene of France, as the type species. Although Cossmann's figures of the species bear a superficial resemblance to *L. melanostoma*, examination of specimens in the BMNH showed that '*Littorinopsis*' *prevostina* is not a member of the same subgenus, and probably not even of the genus *Littoraria*.

The twelve ovoviviparous species known or suspected to brood embryos in the mantle cavity until the early veliger stage, are here recognized as the subgenus *Littorinopsis*. The anatomical difference

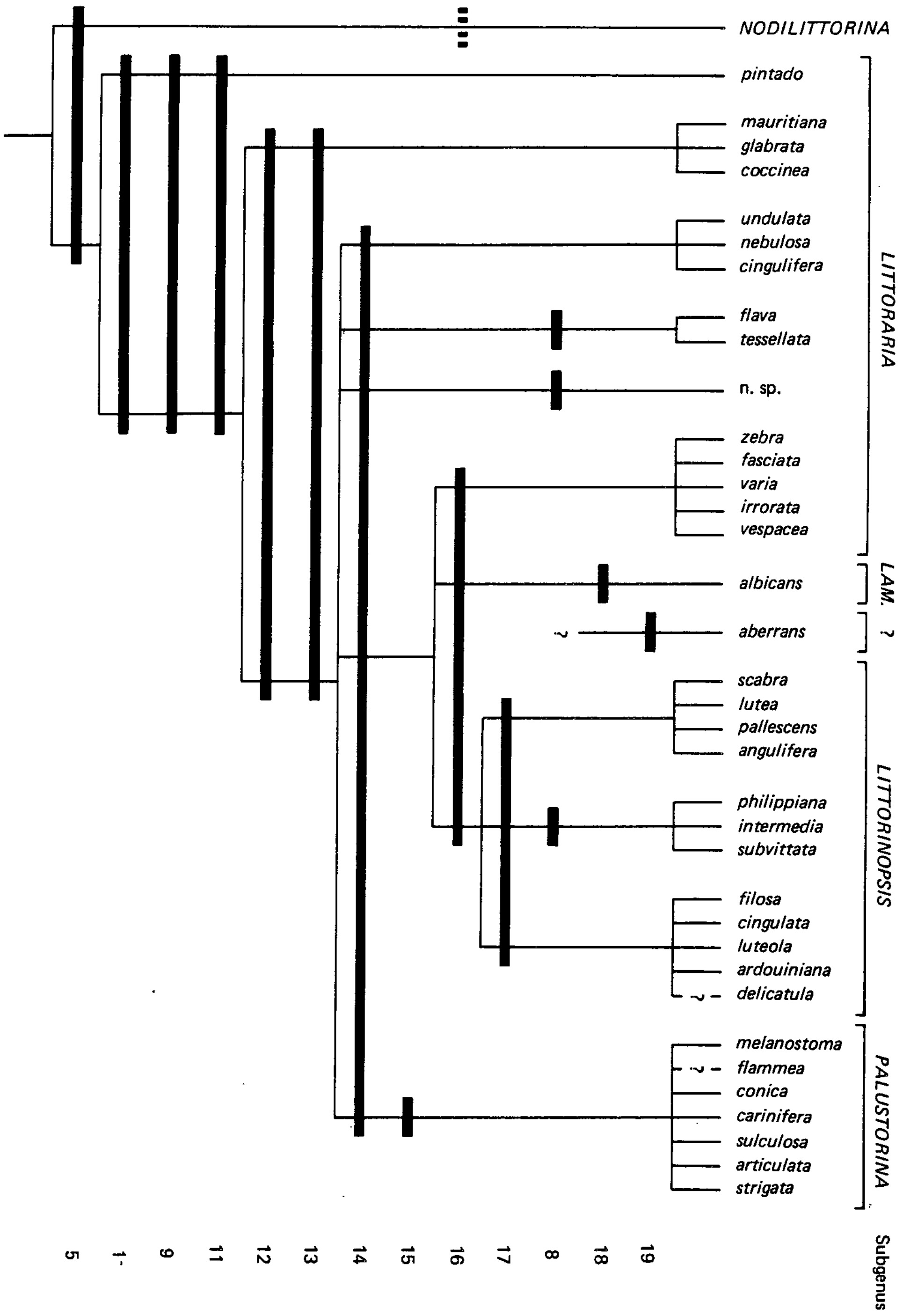

Fig. 8.2 Cladogram of species of *Littoraria*, derived from the character states listed in Table 8.2. *Nodilittorina* is the inferred sister group of *Littoraria*. Terminal groupings are based upon close similarity in the form of the shell and or penis; solid bars indicate apomorphic character states; broken bars indicate the occurrence of both character states; queries indicate uncertainty of position of species of which anatomical characters are unknown; *Lam.*, subgenus *Lamellilitorina*. Note that egg capsules and sperm are undescribed in some species (see text).

Table 8.2 Character states in the genus *Littoraria*.

Character	Plesiomorphic	Apomorphic	Notes
1. penial glands			Absent in all *Littoraria* spp.
5. penial glandular disc			Present in all *Littoraria* spp.
8. penial sperm groove	open	closed	
9. prostate gland			Closed in all *Littoraria* spp.
11. single spiral of pallial oviduct, incorporating capsule glands			Present in all oviparous *Littoraria* spp.; secondary loss of capsule glands in ovoviviparous *Littoraria* spp.
12. egg capsule with spiral rim above flotation skirt or lamella	yes	no	
13. spiral whorls of pallial oviduct $\geqslant 3\frac{1}{2}$	no	yes	Secondary reduction of number of whorls to $2\frac{1}{2}$ in a few ovoviviparous *Littoraria* spp.
14. rachidian tooth of radula of 'hooded' type	no	yes	
15. sperm nurse cells flagellate	no	yes	
16. bursa opens in anterior position	no	yes	Condition variable within other littorinid genera
17. brooding of embryos in mantle cavity, loss of capsule glands	no	yes	
18. planktonic protoconch >610 μm	no	yes	
19. direct development	no	yes	Indicated by protoconch of *L. aberrans*.

between ovoviviparous and oviparous species is only a minor modification of the oviduct by the loss of capsule glands, which might, conceivably, have occurred several times during the evolution of the genus. Nevertheless, it seems useful to recognize the group as distinct. The penes are quite uniform, being bifurcate, with a round glandular disc. The shells of the group are also rather distinctive, showing spiral microsculpture in the grooves and being relatively thin in texture, while ten of the members are colour polymorphic. Probably associated with the thin and colourful shells is the habit of many of the species of living at high levels on the foliage of mangrove trees. Only two species occur occasionally on rock substrates. Eleven species occur in the Indo-Pacific and one in the Atlantic.

The subgeneric classification of *L. albicans* and *L. aberrans* is uncertain. *L. albicans* is anatomically close to members of the subgenus *Littoraria*, especially to the *L. zebra* group. However, the species is unique in its large protoconch of the planktotrophic type, equal cusps of the rachidian tooth, large number of primary grooves on the shell, and peculiar colouration of the head-foot. The shell microsculpture, varices and colour polymorphism are also unlike members of the subgenus *Littoraria*. For these reasons, the subgenus *Lamellilitorina* of Tryon (1887) is retained for this single species. In the absence of anatomical information, *L. aberrans* cannot yet be assigned to a subgenus; shell characters are similar to the thin shelled and colour polymorphic species of *Littorinopsis*, but the protoconch shows that the species has nonplanktotrophic development, which is unique in the genus.

The remaining fifteen species are retained in the nominate subgenus. Although this is a paraphyletic and somewhat heterogeneous group, little would be gained by further subdivision. Shells in this group are neither thin nor colour polymorphic. Members occur in all the tropical provinces. *L. pintado* is of interest as the least specialized species in the genus, showing the greatest number of ancestral character states. The penial glandular disc is poorly differentiated, the pallial oviduct shows the least number of whorls amongst the oviparous species of *Littoraria*, the rachidian tooth of the radula is not hooded and the cupola of the egg capsule is sculptured by a single ring. In all these plesiomorph states, *L. pintado* bears greater resemblance to species of *Nodilittorina* and other genera than is shown by any other *Littoraria* species. In addition, the shell is pale and the aperture dark brown with a somewhat paler basal stripe, which is reminiscent of certain smooth shelled *Nodilittorina* species. In common with *L. coccinea*, *L. glabrata*, *L. mauritiana* and *L. undulata*, which also show few derived characters, *L. pintado* typically occurs on exposed rocky shores at high intertidal levels. This is certainly the ancestral habitat of the genus, and that in which most species of *Nodilittorina*, *Melarhaphe*, *Echininus*, *Tectarius*, *Cenchritis* and *Peasiella* also occur. Within the genus *Littoraria* there seems to have been an increasing specialization to the mangrove habitat in species showing more apomorphic characters (compare list of species in Section 8.1.2 with Fig. 8.2). *L. pintado* is also remarkable for its wide and perhaps relict distribution (Section 7.1), which suggests that the species may be of greater age than its congeners.