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The Genera *Bembicium* and *Risellopsis* (Gastropoda: Littorinidae) in Australia and New Zealand

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ABSTRACT. The taxonomy of the Australasian littorinid genera *Bembicium* and *Risellopsis* is revised. Five Recent species of *Bembicium* are recognised: *auratum*, *nanum*, *melanostoma*, *vittatum* and *flavescens*, the first four of which occur on the Australian mainland, the last on Norfolk and Lord Howe Islands. *B. melanostoma*, *B. vittatum* and *B. flavescens* are sibling species which have been synonymised as *B. melanostoma* in recent systematic accounts, and are shown to be allopatric and distinguished mainly by characters of the penis. At least three fossil species of *Bembicium* are known, of which one is described as new, and the fossil record extends back to the late Oligocene or early Miocene. The genus is endemic to Australasia and presently extinct in New Zealand and the Kermadec Islands. The genus *Risellopsis* is monotypic, represented only by *R. varia* in New Zealand, and has no fossil record before the Pleistocene. Systematic descriptions of the shell and animal and details of habitat and distribution are given for each species. These genera are abundant in the intertidal zone and the rather large literature on their biology and ecology is reviewed. Relationships with other littorinacean taxa are discussed. It is suggested that *Bembicium* and *Risellopsis* together form a monophyletic group, defined by synapomorphies of anterior salivary glands, anterior position of the junction of the duct of the seminal receptacle with the pallial oviduct, longitudinal division of the jelly gland and trochoidal shell shape. The littorinid genus *Peasiella* is superficially similar in shell characters, but anatomical features show that it is not closely related to *Bembicium* and *Risellopsis*. Interesting features of *Bembicium* include the type of development (the hatching of planktotrophic veligers from benthic egg masses recorded in two species is rare in the family) and the extreme intraspecific variability in the form of the radular teeth.

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The genus *Bembicium* comprises a small group of littorinacean gastropods with characteristically trochoidal shells, which occur only on the coasts of Australia and adjacent islands. *Risellopsis* is represented by a single species from New Zealand, and has long been recognised as a close relative of *Bembicium*. All species are common in the intertidal zone, and some have been the subject of a considerable amount of ecological research. The most recent taxonomic treatment of *Bembicium* was by H. Anderson (1958), but this work provided very little anatomical information, and was based largely upon specimens from South Australia.

Recently the taxonomy of a number of littorinid groups has been reevaluated on the basis of new anatomical evidence (Fretter & Graham, 1980; Mastro *et al.*, 1982; Bandel & Kadolsky, 1982; Reid, 1986). A preliminary analysis of phylogenetic relationships within the Littorinidae has suggested that *Bembicium* may be an early offshoot retaining a number of ancestral characters (Reid, 1986), while other authors have proposed its separation as a distinct family. In the present account, anatomical studies of *Bembicium* and *Risellopsis* have been used both to reconsider the species-level taxonomy, and to provide further information about the relationships of these genera with others in the family. A cladistic analysis of the relationships of littorinid genera is in preparation, and a detailed discussion of phylogeny will be deferred. An additional problem in the past has been confusion of *Bembicium* with the superficially similar littorinid genus *Peasiella*, and the mistaken assumption of a close relationship

between the two. These genera have now been clearly defined, permitting a reconsideration of the fossil record and biogeography of *Bembicium*.

Taxonomic History

In view of the trochoidal shape of the shell of *Bembicium*, it is not surprising that early authors included species in the genus *Trochus* (Gmelin, 1791; Dillwyn, 1817; Lamarck, 1822; Wood, 1828; Quoy & Gaimard, 1834). This practice was occasionally continued even after the littorinid affinity of the shells was recognised (Reeve, 1842 a,b; Deshayes & Milne Edwards, 1843; Philippi, 1843; Gould, 1852). Although Quoy & Gaimard (1834) used the generic name *Trochus*, they recognised that the separate sexes, paucispiral operculum and lack of epipodial tentacles set the animals apart from typical members of the genus, and therefore included them (with *Trochus* [= *Tectarius*] *pagodus* Linnaeus) in a separate, but unnamed, section.

The first author to group species now classified as *Bembicium* with other littorinids was Gray, who in 1839 described two new species in the genus *Littorina*, and noted that because of their shell shape they would probably form a new section. The generic name *Risella* was listed the following year, without diagnosis or included species, in both versions of edition 42 of the *Synopsis of the Contents of the British Museum* (Gray, 1840a, b; see Iredale, 1913). Although in these first usages the genus was a *nomen nudum*, a brief diagnosis was given in edition 44 of the *Synopsis*: '*Risella* is like *Littorina*, but the shell is

top-shaped, the whorls keeled, and the mouth rather square' (Gray, 1842: 60). Iredale (1913) advocated rejection of all the names introduced in this edition, but nevertheless the diagnosis is adequate to define the genus, so that the name *Risella* must take the date of 1842. The type species, *Trochus melanostoma* Gmelin, was subsequently designated by Gray (1847).

The name *Bembicium* was introduced by Philippi (1846) for species with a trochoidal shell and animal like *Littorina*, but differing from *Trochus* in the lack of frontal lobes, of epipodial tentacles and of a multispiral operculum, and in the non-nacreous shell. Herrmannsen (1846) designated *Trochus melanostoma* Gmelin as the type species. The priority of *Risella* was recognised by Philippi (1851, 1853), and thereafter this generic name came into general usage (e.g. Adams & Adams, 1858; Crosse, 1864; Angas, 1865; Fischer, 1879; Tryon, 1887; Kesteven, 1903), although Tenison-Woods (1879) chose to retain *Littorina*. However, in 1912 Iredale reinstated the name *Bembicium*, overlooking Gray's (1842) diagnosis of *Risella*, and claiming that the earliest available introduction was that of Gray (1847). Almost all subsequent workers followed Iredale (1912), although the name *Risella* occasionally appeared in the palaeontological literature (e.g. Speight, 1913; Cossmann & Peyrot, 1918). Despite the priority of *Risella*, it is clear that, pending application to the ICZN for suppression of the name, nomenclatorial stability can best be served by maintaining the existing usage of *Bembicium* (ICZN, 1985, Articles 23b, 79c).

The taxonomic history of *Risellopsis varia* (Hutton) is similar to that of *Bembicium* species, having been described in the supposedly trochid genus *Adeorbis* (Hutton, 1873), then grouped with other littorinids, first tentatively as a *Risella* (Hutton, 1878), then as a *Fossarina* (a genus now placed in the Trochidae, but see Kesteven, 1902, for a discussion of an error in the original description by Adams & Angas, 1863; Hutton, 1880, 1882). Kesteven (1902) recognised the close relationship with *Risella* (= *Bembicium*), but created the new genus *Risellopsis* because of differences in the shell and radula. Subsequent workers have followed this classification.

Several authors have considered *Bembicium* and *Risellopsis* sufficiently distinct from other littorinids to be assigned to a separate family. Kesteven (1903) created the Risellidae on the basis of the closed pallial vas deferens and penial sperm duct, and presence of an ovipositor. All three characters can, however, be found in certain members of the Littorinidae, and the retention of the two genera in this family will be discussed further below. Finlay (1928) renamed the supposed family Bembiciidae. Separate familial status has not received general acceptance by later authors, with some exceptions (Odhner, 1924; Cotton & Godfrey, 1938;

Macpherson & Chapple, 1951; Kershaw, 1955). Rosewater (1970) considered *Bembicium* and *Peasiella* 'at least a separate subfamily' of the Littorinidae. Many *Peasiella* species were initially described in the genus *Risella*, but despite a superficial resemblance between the shells, the two groups are not now thought to be closely related (Reid, 1986).

At the specific level, variability in shell characters in the genus *Bembicium* is so great that opinions on the classification of the species have differed considerably. A total of 21 names are available for the Recent species, 19 of which were described between 1828 and 1866. In 1834, Quoy & Gaimard classified the forms from the Australian mainland and Tasmania into four species: *luteus* (includes two species as defined in the present revision, separable only by anatomical characters), *nanus*, *planus* (here regarded as juvenile *B. nanum*) and *auratus*, and so came close to the system proposed here. In a monograph of *Bembicium*, Philippi (1846) took more account of variation in shell form, and accepted eight species, to which he later added four more (Philippi, 1851). This made a total of 12, which were finely illustrated in a second monograph (Philippi, 1853). Crosse (1864) produced a third monograph, and with a similar species concept to that of Philippi, enumerated nine species (making no reference to Philippi, 1851 or 1853). Smith (1884) made some attempt to synonymise, but still accepted at least six species. The first suggestion that only one variable species was involved was made by Tenison-Woods (1877, 1879), who also made the extraordinary assertion that though all animals were hermaphrodite, *Risella aurata* functioned as the male and *R. nana* as the female. The concept of a single variable species was maintained by Tryon (1887), Pritchard & Gatliff (1902), Kesteven (1903) and Hedley (1910, 1916, 1918). Other Australian authors have mostly adopted a classification similar to that of Quoy & Gaimard (1834), accepting two or three species in New South Wales (Angas, 1867; Musgrave, 1929; Iredale, 1931; Iredale & McMichael, 1962), two or three in Tasmania (May, 1921, 1923; Kershaw, 1955), four in Victoria (MacPherson & Chapple, 1951) and three to five in South Australia (Angas, 1865; Verco, 1908; Cotton & Godfrey, 1938). The details of the species concepts of these authors may be found by reference to the synonymies in the systematic section.

Since 1958 the basis for the modern classification of the species of *Bembicium* has been the revision by H. Anderson. In defining species, Anderson placed most emphasis on characters of the shell, and using material largely from South Australia, she recognised three species: *B. melanostoma*, *B. auratum* and *B. nanum*. This conclusion was supported by a study of the egg masses of the first two, and by limited anatomical descriptions. The presence of three species in South Australia is confirmed by the

present study. However, Anderson's concept of *B. melanostoma* has been modified by its exclusion from the faunas of Queensland and New South Wales, and by its division into two conchologically similar, but anatomically distinct, species: *B. melanostoma* s. s. from Victoria and Tasmania and *B. vittatum* from South and Western Australia. The concepts of *B. auratum* and *B. nanum* remain unchanged, but an additional species, *B. flavescens*, is recognised from Norfolk and Lord Howe Islands.

Despite the work of H. Anderson (1958), there has still been confusion of the identity of the *Bembicium* species. Although *B. nanum* is distinctive, *B. auratum* and *B. 'melanostoma'* have often been misidentified in museum collections, perhaps because the latter is usually the more golden in colouration, while the former frequently has a black aperture.

Materials and Methods

This taxonomic work has been based largely upon the collections of the following institutions: Australian Museum, Museum of Victoria, South Australian Museum, Western Australian Museum, National Museum of New Zealand, New Zealand Geological Survey, British Museum (Natural History), Muséum National d'Histoire Naturelle (Paris) and National Museum of Natural History (Washington).

Except where otherwise stated in the synonymies, all available type material has been examined. The types of the species described by Philippi (1846, 1851) are not located in either the British Museum (Natural History) or the Museum für Naturkunde, East Berlin (R. Kilius, pers. comm.), nor could information be obtained about their possible presence in the Museo Nacional de Historia Natural, Santiago, Chile. The figures published by Philippi in 1853 have therefore been designated as lectotypes.

Only taxonomic, faunistic and anatomical works have been listed in the synonymies; references to ecological studies are given in the introductory sections.

Measurements were made of adult shells, which showed a slightly thickened and non-growing apertural lip. Shell height was measured parallel to the axis of coiling, and shell diameter as the maximum dimension perpendicular to the axis. The height/diameter ratio was calculated as a measure of shell shape. The number of whorls of the teleoconch was counted from the slight ridge terminating the protoconch, or, if the apex was eroded, by comparison with well-preserved juveniles from the same locality. The number of whorls of the protoconch was counted by constructing a line tangential to and a continuation of the tip of the sutural spiral, and counting three-quarters of a whorl the first time the sutural spiral crossed the line, and an additional one whorl for each subsequent

intersection, with the final whorl estimated as a fraction of a revolution. For example, the protoconch illustrated in Fig. 14d has 1.5 whorls. This method gives results similar to that described by Jablonski & Lutz (1980), but is more accurate, since it defines precisely the extent of the first whorl.

Preserved material in museum collections was used for anatomical studies. From the observation of living animals of *Bembicium nanum* and *B. auratum* at Sydney, New South Wales, and Magnetic Island, Queensland, it appears that the shape of the penis of preserved animals is very similar to that in the living state. Drawings of penes and pallial oviducts were made using a camera lucida, from animals with mature gonads showing no evidence of parasitism by trematodes. The complex structure of the pallial oviduct was investigated both by serial histological sectioning and by cutting gross serial transverse sections under a dissecting microscope. For each species the reproductive anatomy was examined in ten to 30 males and five to ten females, from the widest available range of localities.

Serial histological sections were cut of a single mature penis of each species, of two pallial oviducts of *B. auratum*, and one each of *B. nanum* and *Risellopsis varia*. Sections were cut at 5 µm and were stained using either Masson's trichrome (Luna, 1968) or the alcian blue-periodic acid-Schiff technique for the histochemical differentiation of mucins (Sheehan & Hrapchak, 1973). The latter stains acidic mucins blue and neutral mucins magenta, while mixed mucins appear purple.

Spermatozoa were examined from two specimens each of *B. auratum* and *B. nanum* from North Harbour, Sydney, and *B. auratum* from Magnetic Island, Queensland. Samples were removed from the seminal vesicle of living, mature, unparasitised males, and fixed in a 1% solution of glutaraldehyde in sea water before examination with a light microscope.

The radulae of five, and in the case of *B. auratum* ten, specimens of each species were examined with a scanning electron microscope. The specimens used were mature examples of both sexes, from a wide geographical range. Radulae were treated with hot 50% potassium hydroxide solution for 15 minutes, rinsed, cleaned ultrasonically for ten seconds, and mounted flat. Although side and top views of some species are also shown, the standard view adopted for showing the shape of tooth cusps was from the posterior end at an angle of 45° to the horizontal. Only teeth from the central region of the radular ribbon were photographed. The total length of each intact radula was measured, and its relative length recorded as the ratio of total length to shell diameter.

Comparisons with other littorinid genera are based on published accounts as quoted, on the species listed by Reid (1986, pp. 5–6) and on new observations of *Mainwaringia leithii* and *Lacuna vincta* (Reid, in prep.).

The locality records are not complete lists of all material examined, but are lists of only those records plotted on the distribution maps.

Abbreviations

ABPAS	Alcian blue – periodic acid – Schiff stain
AIM	Auckland Institute and Museum
AMS	Australian Museum, Sydney
BMNH	British Museum (Natural History), London
DGR	Collection by author, material now in BMNH
MHNG	Muséum d'Histoire Naturelle, Geneva
MNHNP	Muséum National d'Histoire Naturelle, Paris
MT	Masson's trichrome stain
NMNZ	National Museum of New Zealand, Wellington
NMV	Museum of Victoria, Melbourne
NZGS	New Zealand Geological Survey, Lower Hutt
SAM	South Australian Museum, Adelaide
TM	Tasmanian Museum, Hobart
USNM	National Museum of Natural History, Washington, D.C.
WAM	Western Australian Museum, Perth
ZMB	Museum für Naturkunde, East Berlin

SHELL CHARACTERS

Shape, size and sculpture. The keeled, trochoidal shape of *Bembicium* and *Risellopsis* is unusual in the family Littorinidae, being seen elsewhere only in *Peasiella*. The similarity is superficial, however, and *Peasiella* is not closely related. It is not clear why shell shape should be convergent in the two groups. Another unusual feature of *Bembicium* is the presence of a thickened spiral ridge within the aperture, parallel to and just below the peripheral keel (Tenison-Woods, 1877), although this is indistinct in juveniles. Shell growth in *Bembicium* and *Risellopsis* is allometric, the apical angle decreasing with size, so that the spire outline is convex or domed. This is most striking in shells lacking strong radial sculpture, such as *B. nanum* and smooth forms of *B. melanostoma* and *B. vittatum*. Juveniles of *B. nanum* are so much flatter in appearance than adults that they have often been regarded as a separate species, *B. planum* (e.g. Quoy & Gaimard, 1834; Philippi, 1846, 1853; Cross, 1864; Cotton & Godfrey, 1938; MacPherson & Chapple, 1951). The positive allometry of shell height on shell diameter is illustrated graphically in Fig. 1 for a sample of *B. nanum* from Jervis Bay. The phenomenon of doming is common in other littorinids and in gastropods in general (Vermeij, 1980).

The attainment of adult size is not marked by any change in the shape of the aperture, but only by a

slight thickening of the margin when growth slows or ceases. Variation in adult shell size within species is considerable, most showing an approximately two-fold range, and may sometimes be correlated with geographical distribution. Sexual dimorphism has often been reported in littorinids, females being somewhat larger (Reid, 1986). The dimorphism is only slight in *Bembicium* species; for example, the mean diameter of 15 adult male *B. auratum* from Cackle Bay, Magnetic Island, Queensland, was 13.3 mm, and of 13 females 14.2 mm ($t = 2.48$, $P = 0.021$). The larger size of females may be explained by their higher growth rate (Muggeridge, 1979).

Shell shape and sculpture show great variation in both *Bembicium* and *Risellopsis*, as illustrated in the systematic section. As an example, the shell height/shell diameter ratio of *B. auratum* ranges from 0.639 to 1.483, the peripheral keel may be weak or flanged, straight or undulating, the radial folds may be absent or strongly developed (Fig. 16). Much of this variation is on a geographical scale, variation within populations at single localities being much less. *B. auratum*, for example, has a distinctive form in north Queensland. Amongst European *Littorina* species, those with direct, nonplanktotrophic development show a greater degree of interpopulation variability in shell size, shape and sculpture than those with planktonic veliger larvae. The restricted dispersal of nonplanktotrophic species permits adaptation to local conditions of predation and exposure to wave action (review by Raffaelli, 1982). Even in planktotrophic littorinids, selection may maintain striking differences between populations (Struhsaker, 1968). No similar studies of variation in *Bembicium* or *Risellopsis* have yet been carried out. *B. vittatum* is believed to undergo direct development (H. Anderson, 1958), and limited museum collections show that it is a variable species, although not more strikingly so than *B. auratum* with planktonic veligers. Although it may seem superficially that intraspecific variation is comparable with or exceeds interspecific variation in *Bembicium*, three of the five species can usually be identified on the basis of shell characters, of which the number of spiral grooves above the periphery, the number of ridges on the base, and the apertural colouration are most important. *B. melanostoma* and *B. vittatum* are commonly identical and separable only by using anatomical or distributional data.

In addition to the spiral ridges and grooves, both *Bembicium* and *Risellopsis* bear a fine microsculpture of spiral striae. In *Bembicium* the striae are at first parallel to the major grooves, but become somewhat oblique by the last whorl. In many specimens microsculpture, and even the major grooves, may be obscured by erosion. The periostracum of *Bembicium* species is not noticeable. In small or well-preserved shells of *Risellopsis* the periostracum may be produced into pointed bristles 0.2 mm long on the ribs, and are especially

conspicuous on the base (Fig. 26a). This character is unusual in littorinids, but is also known in *Littoraria vespacea* Reid, *Peasiella isseli* (Semper in Issel) and *Mainwaringia leithii* (Smith), a diverse group not sharing close relationship.

Protoconch. Shells of *Bembicium* and *Risellopsis* are usually eroded, so that it is rare to find specimens with intact apices. Protoconchs have been examined in only one example of each of four species of *Bembicium* and two of *B. auratum*. In these

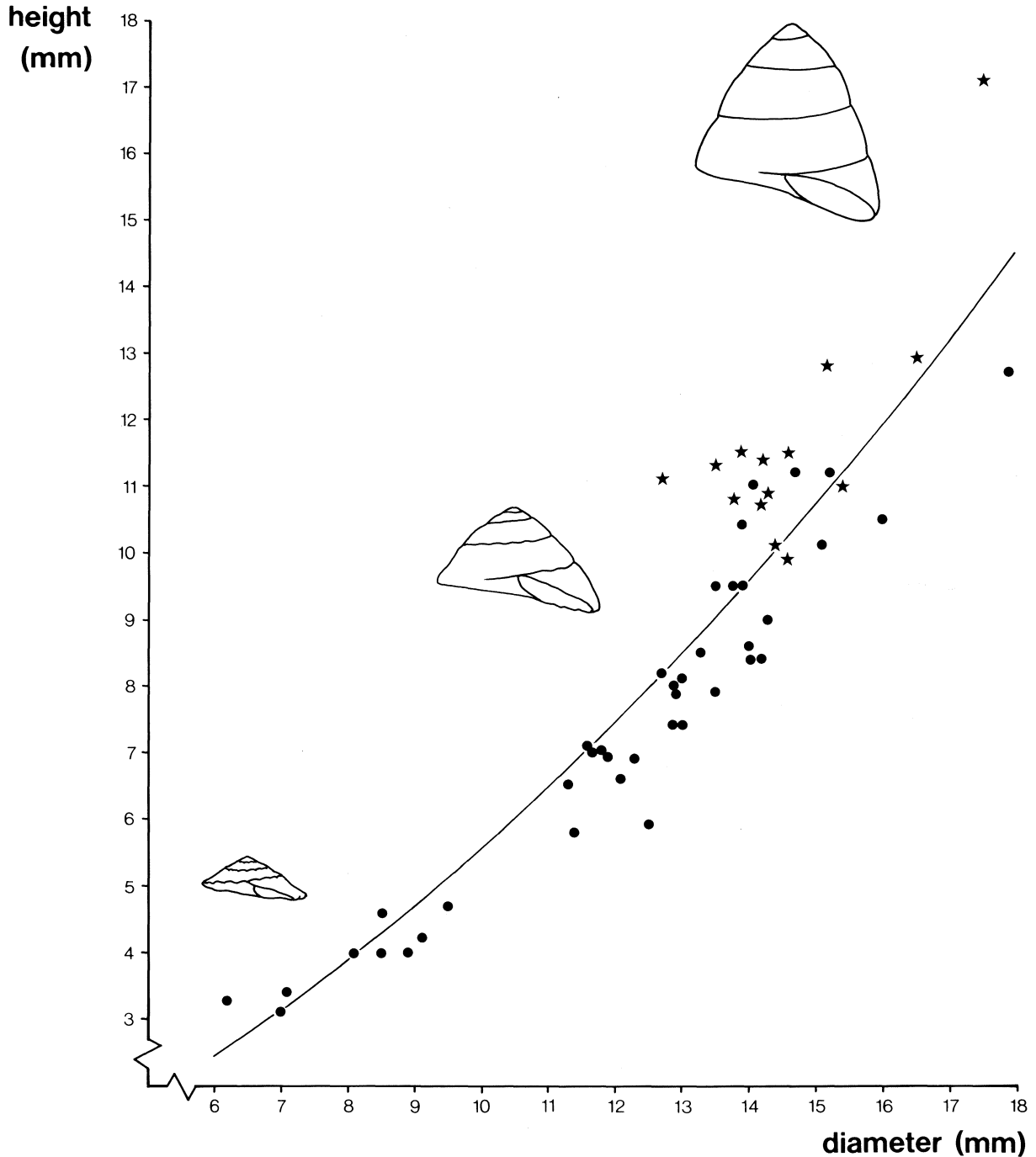


Fig.1. Allometry in shell growth of *Bembicium nanum* (Lamarck) from Honeymoon Beach, Jervis Bay, N.S.W. (AMS C144329). Fitted curve has the equation: height = 0.130 (diameter)^{1.63} ($r^2 = 0.90$; 95% confidence limits of exponent = 1.48–1.78). Solid circles indicate shells with a thin, growing edge to aperture; asterisks are adult shells.

specimens the protoconch is low, only slightly protruberant, of 1.25 to 1.5 whorls, and measuring 0.35 to 0.45 mm in diameter. Protoconch stages I and II (Jablonski & Lutz, 1980) cannot be distinguished, for the surface is smooth, but for traces of radial growth striae close to the terminal lip. The lip itself is no more than a strong growth line, not raised or ornamented; in *B. auratum* (Fig. 17d) it is indented by a curvature, and this is more conspicuous in *B. nanum* (Fig. 22d), while in *B. melanostoma*, *B. vittatum* (Fig. 11a) and *B. flavescens* (Fig. 14d) the edge of the lip and the growth striae behind it are almost straight.

It is well known that the type of larval development is reflected in the form of the protoconch. In littorinids with pelagic egg capsules and an estimated planktonic larval life of four to eight weeks, the protoconch is 0.25 to 0.45 mm in length, of 2 to 3.5 whorls, sculptured by spiral ribs or rows of tubercles, and terminated by a strong sinusigera rib (e.g. Struhsaker & Costlow, 1968; reviews by Bandel and Kadolsky, 1982, and Reid, 1986). In contrast, lecithotrophic species lacking a planktonic stage have a protoconch of less than 2 whorls, approximately 0.40 to 1.49 mm in diameter, with a straight lip lacking any trace of a sinusigera rib (Thorson, 1946; Bandel, 1975; Picken, 1979; Rosewater, 1982). The protoconchs of *Bembicium* species agree well with the available information on their life histories, as reviewed below. *B. nanum* and *B. auratum* develop in benthic egg masses and hatch as veligers (D.T. Anderson, 1961, 1962); the form of the protoconch suggests that the period of planktonic life may be short. *B. vittatum* is believed to lack a planktonic stage (H. Anderson, 1958), and the protoconchs of *B. melanostoma* and *B. flavescens* suggest that direct development may occur in these species also.

The protoconch of *Risellopsis varia* has not been seen, but veligers from the plankton with unsculptured shells of up to 1.5 whorls and 0.45 mm diameter, lacking a sinusigera notch, have been tentatively identified as belonging to this species (Pilkington, 1976).

Colour. Shell colouration in *Bembicium* is rather ill defined, both because shells are frequently eroded, and also because of the range of variation within species. In each species the palest specimens bear only a faint speckling of brown pigment on a white to cream ground colour, while the darkest show conspicuous axial stripes of dark brown to black, corresponding with either the ribs or folds of the axial sculpture. In all species spots may be present or absent on the base. The dark brown colour of the outer wall of the aperture, often in combination with an orange columella, is useful for defining the 'melanostoma' group (*B. melanostoma*, *B. vittatum*, *B. flavescens*). Apertural colouration in *B. auratum* is more variable, usually with a few broad black stripes at the margin of the outer lip, but commonly entirely

white in specimens from north Queensland. Only in *B. nanum* is shell colouration virtually diagnostic, the pattern of narrow black stripes on the dorsal surface, which forms four to ten short stripes inside the outer edge of the aperture, being distinctive. In *Risellopsis* the colour pattern is also primarily of radial stripes on the dorsal side, but in combination with more or less distinct spiral lines in the grooves of the spiral sculpture. In all species variation in colour appears to be continuous, and no discrete morphs can be recognised.

Operculum. The opercula of the family Littorinidae have been classified into four types (paucispiral types A and B, mesospiral, multispiral) and the occurrence of each reviewed by Bandel & Kadolsky (1982). Following this scheme, the opercula of *Bembicium* species are of the paucispiral type A. The coiling is most open in *B. nanum*, with an extremely acentric nucleus (Fig. 22f); no consistent differences occur in the remaining four species of the genus (Figs 14f, 17h). In *Risellopsis varia* the coiling is more tight and the nucleus more nearly central; this is the paucispiral type B (Fig. 26b). It may be noted that the genus *Peasiella*, similar in shell shape to *Bembicium*, has a multispiral operculum (Kesteven, 1903).

Bandel & Kadolsky (1982) suggested that tightly coiled opercula have evolved repeatedly amongst littorinids, from an originally paucispiral ancestral form. This was explained as an adaptation to life at high supratidal levels, where species develop a smaller and more circular aperture in order to minimise temperature stress and desiccation. Such an aperture is fitted more closely by a tightly coiled, circular operculum, and tight coiling also thickens the operculum. This suggestion is supported by *Bembicium* and *Risellopsis*, for the latter is reported to live at higher tidal levels, has a more circular aperture and a more tightly coiled operculum.

ANATOMICAL CHARACTERS

Head-foot. The appearance of the head is similar to that of other littorinids. In *Bembicium* species there is no striking colour pattern; pigmentation is a diffuse mottling on the sides of the foot, the head is darker, with fine lines of pigment across the snout and annular bands along the length of the yellowish tentacles (Fig. 2). In *Risellopsis* the head is also dark and the tentacles banded to their tips, but the front of the snout lacks pigment and there is a second white stripe across the head between the tentacles (Fig. 27e). Opercular tentacles, as seen for example in *Lacuna* and in some Eatoniellidae (Ponder, 1965, 1976) are absent.

The peculiar trochoidal shape of the shell of these two genera is reflected in the orientation of the head-foot. As expressed by Kesteven (1903), when compared with turbanate littorinids, the animal is 'twisted half round in its shell'. Fretter (1982) viewed

this as a displacement of the anterior end of the gill over the head, which normally lies to the left. In fact the arrangement of the pallial organs is no different from that of other littorinids, if the periphery of the shell and junction of the body whorl and penultimate whorl are taken as points of reference. Rather, the head and foot have been twisted 90° to the left in relation to both shell and mantle. The explanation is probably not to be found in the compression of the

left side of the mantle cavity consequent upon the change in shell shape, as was suggested by Fretter (1982). Instead, the orientation of the animal simply allows a greater area of contact between the foot and the substrate when the animal is partly retracted and the shell lies on its base. The columellar muscle retains the same origin on the columella as is found in turbinate littorinids; it has not descended to the shell base as stated by Kesteven (1903).

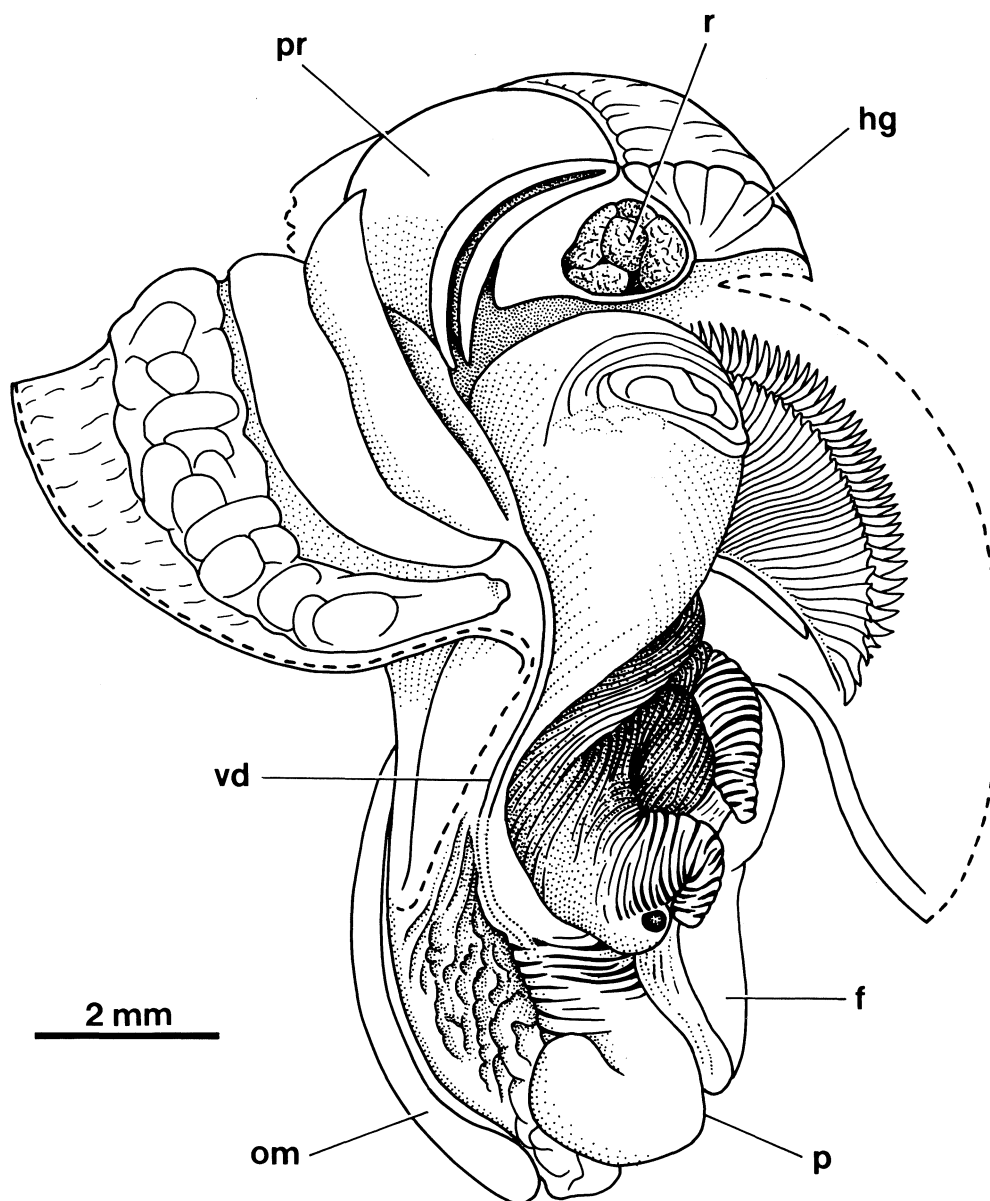


Fig.2. Male reproductive system of *Bembicium auratum* (Quoy & Gaimard), from Mallacoota, Vic. (AMS C144295). Prostate, rectum and hypobranchial gland have been sectioned, mantle cut along dotted lines and right side folded outwards. Abbreviations: f - foot; hg - hypobranchial gland; om - operculum; p - penis; pr - prostate; r - rectum; vd - anterior vas deferens.

Male reproductive tract. The plan of the male reproductive system of *Bembicium* and *Risellopsis* is typical for the family Littorinidae (Linke, 1933; Fretter & Graham, 1962; Reid, 1986). The testis overlies the digestive gland, and sperm collect in the coiled visceral vas deferens, which functions as a seminal vesicle and lies against the columella of the shell. The pallial vas deferens consists of a glandular prostate, leading to a duct or groove which carries sperm along the side of the head almost to the tip of the penis (Fig. 2). The lumen of the prostate is slit-like, open to the mantle cavity throughout its length. In *Risellopsis* the entire pallial vas deferens is an open groove, but in *Bembicium* the path of the sperm from the anterior end of the prostate, over the head and through the penis, is a closed duct. The open prostate and closed anterior vas deferens of *Bembicium* have previously been noted by Kesteven (1903), H. Anderson (1958) and Fretter (1982), while the histology of the testis, prostate and anterior vas deferens of *B. nanum* has been briefly described by Bedford (1965). The anatomy of *Risellopsis* has not previously been described.

The penis of *Bembicium* is situated just anterior to and beneath the right tentacle. When the animal is retracted into the shell, the penis is usually folded forward over the edge of the foot (Fig. 2), rather than back into the mantle cavity as in other littorinids. In general, the littorinid penis is differentiated into a wrinkled basal region, a smooth filament with abundant goblet cells (which conveys sperm into the bursa copulatrix of the female), and glandular tissue which produces an apparently adhesive mucus (Reid, 1986). In *Bembicium* the base is rather short and somewhat laterally compressed, with the ciliated sperm duct running through its ventral edge. The region corresponding to the filament is not clearly differentiated from the base except by lack of wrinkles, and in *B. vittatum* and *B. auratum* it is broader than the base and of a peculiar hammer-like or claw-like shape (Figs 12, 18). The filament is more slender in *B. melanostoma* and *B. flavescens* (Figs 8, 15a-h), and no more than a small protuberance in *B. nanum* (Fig. 15i-p). In all cases the opening of the penial sperm duct is subterminal, very markedly so in the four species with a large filamentous portion; in these the duct opens into a deep crease on the ventral surface. In *B. nanum* there is no such crease on the very small filament, but the opening is still a little behind the tip.

Although the filament of all but *B. nanum* appears to be opaque and swollen, histological sections show little differentiation between filament and base, and a lack of the subepithelial glands which are typical of other littorinids. Throughout the penis the epithelium is columnar, from 15 to 20 μm in thickness, increasing to 30 μm on the side of the base opposite to the sperm duct. The epithelial cells are possibly secretory, their bulbous distal ends staining purple in ABPAS and variously yellowish, orange or

faintly blue in Masson's trichrome. Only in *B. nanum* were goblet cells clearly visible in the epithelium, staining blue in ABPAS (indicating acidic mucins). Similar mucous cells were also scattered through the underlying connective and muscular tissue, but were not organised into glandular structures. Goblet cells are probably present in the other species also, but were poorly preserved in the specimens examined. Beneath the basement membrane of the epithelium the penis is packed with circular, longitudinal and oblique muscle fibres, with connective tissue fibres and blood spaces between. Fretter (1982) mentioned a 'semicircle of glands' in the base of the penis of *B. auratum*, but no such formation was observed in the present study.

The penis of *Risellopsis varia* is similar to that of *Bembicium* species in its position and orientation, and also in the secretory epithelium and lack of subepithelial glands. There is no clear division between the wrinkled base and smooth distal region which corresponds to the filament of other littorinids. Histologically, it can be seen that the columnar epithelium is thicker on the filament (28 to 36 μm) than on the base (8 to 19 μm), and possibly richer in goblet cells, although once again these were poorly preserved. On the edge of the base opposite to the sperm groove there is a small lobe (Fig. 27a-d), but this is not a glandular structure. The ciliated sperm groove terminates a little before the tip of the penis. At the tip a minute papilla is visible; here the epithelium is only 3 μm thick and the connective tissue layer and muscle fibres approach the surface. However, there is neither duct nor glandular tissue associated with the papilla.

Penes have not been accurately illustrated for any of the species by previous authors. Sketches were given by Kesteven (1903), Bedford (1965) and Muggeridge (1979). H. Anderson (1958) gave brief descriptions and noted that the penial shape of *B. nanum* differed from that of the other two species then recognised. Muggeridge (1979) found the proportions of the penis to be too variable for use as a taxonomic character in the genus *Bembicium*. In other littorinid groups it is now well known that the shape of the penis is a most important taxonomic character, often diagnostic of species, and this may be because penial shape is a character used for species recognition during copulation (review by Reid, 1986). In three cases penial characters can be used to separate pairs of species with almost identical shells (Sacchi & Rastelli, 1966; Murray, 1979; Reid, 1986).

In the present study the shape of the penis has been found to be a reliable character for the discrimination of the three species in the *Bembicium melanostoma* complex (*B. melanostoma* s. s., *B. vittatum*, *B. flavescens*), all with very similar shells. These species are also geographically isolated, but if penial shape is indeed a biological recognition character, the implication is that interbreeding could

not occur if their ranges were to overlap. The category of subspecies is therefore not appropriate. The similarity of penial shape is good evidence that the Queensland form of *B. auratum* is not specifically distinct from the typical form, despite recognisable differences in shell shape and colour.

It is true that penial shapes show some variation within species, as shown in the systematic accounts. This variability may be partly explained by different methods of relaxation before fixation, and possibly by differences in the state of maturity (although all specimens had mature testes). In some littorinids the penis is reduced in size or shed outside the breeding season, but in *B. auratum* and *B. nanum* Muggeridge (1979) found no change in the size of the penis once maturity was reached. Parasitism by trematodes may reduce penial size (Lysaght, 1941), but parasitised specimens were discarded in this study. Since the form of the penis is irregular, it would be difficult to quantify differences in shape. However, the differences between species are so striking that this is considered unnecessary.

The blunt form of the penis, swollen filament and absence of subepithelial glandular elements set *Bembicium* and *Risellopsis* apart from other littorinids, but do not provide any indication of relationships with other genera, at the present state of knowledge. It is not clear whether the open prostate is a plesiomorphic or apomorphic character amongst the Littorinidae. The open condition is more common, a closed prostate having been recorded only in *Cremanoconchus* (Linke, 1935) and *Littoraria* (Reid, 1986). However, amongst possible out-groups relevant to a discussion of littorinid phylogeny, the prostate is closed in *Pomatias* (Creek, 1951) and in *Lacuna* (Gallien & de Larambergue, 1938), but open in Eatoniellidae (Ponder, 1968). Similar doubt surrounds the status of the penial sperm groove. The closed condition of *Bembicium* occurs also in *Melarhaphe*, *Fossarilittorina*, *Peasiella*, some *Littoraria* species (all Reid, 1986), *Cremanoconchus* (Linke, 1935) and *Rufolacuna* (Ponder, 1976), while an open groove is found in other littorinid genera (Reid, 1986). The sperm groove is closed as a duct in *Pomatias* (Creek, 1951) and in *Lacuna* (Gallien & de Larambergue, 1938). The basal flap of *Risellopsis* is superficially similar to the penial glandular disc of the genera *Nodilittorina* and *Littoraria* (Reid, 1986), and the apical papilla is reminiscent of the mamilliform penial glands of *Littorina*, *Peasiella*, *Tectarius*, *Echininus*, *Nodilittorina* and *Mainwaringia* (Linke, 1933; Reid, 1986 and pers. obs.). Nevertheless, neither structure of *Risellopsis* is in fact glandular, and therefore they are probably not homologous with the appendages of other littorinids. An absence of penial glands, both mamilliform and disc-like, is recorded in *Cenchritis*, *Fossarilittorina*, *Melarhaphe* and rarely in *Nodilittorina*. In these cases the loss may be secondary, while in *Bembicium* it has been tentatively suggested that the absence is

plesiomorphic (Reid, 1986). No penial glands have been reported in *Pomatias* (Creek, 1951), but unspecialised subepithelial glandular cells are present in *Lacuna* (Gallien & de Larambergue, 1938; pers. obs.).

Sperm cells. In many littorinid genera the testis produces sperm of two types. In addition to the euspermatozoa (or 'typical sperm') there are rounded nurse cells, packed with yolk granules and sometimes rod-shaped inclusions (review by Reid, 1986). Nurse cells were not seen in the seminal vesicle of two living *Bembicium nanum* and four *B. auratum*, nor were they found in preserved specimens of these species or *Risellopsis varia*. However, Bedford (1965) described 'nurse cells with finely vacuolated cytoplasm and attached spermatids and spermatozoa' in the testicular tubules of *B. nanum*, and Muggeridge (1979) briefly mentioned nurse cells in *B. auratum*. It may be that nutritive cells similar to, or even homologous with, nurse cells are present during the development of euspermatozoa. Alternatively, these authors may have been mistaken, describing the artefactual agglutination of sperm which sometimes occurs in squashed preparations. Nurse cells of the type found in the seminal vesicle of other littorinids are absent in *Bembicium* and *Risellopsis*, and this may conceivably be a plesiomorphic character (Reid, 1986). It may also be mentioned that nurse cells are absent in *Lacuna pallidula* (Gallien & de Larambergue, 1938) and in *L. vincta* (pers. obs.). Further investigation of spermatogenesis is obviously required in *Bembicium* and *Risellopsis*. In *B. auratum* from Magnetic Island, Queensland, the eupyrene sperm were 220 to 240 μm in length, and 250 μm in *B. nanum* from Sydney.

Female reproductive tract. As in other littorinids, the female reproductive system consists of the ovary, overlying the digestive gland, and the oviduct, sequentially differentiated into gonadial, renal and pallial sections. The gonadial oviduct is thin walled, while the short renal portion has thick glandular walls, staining blue in MT and dark blue and purple in ABPAS. In species of *Bembicium* a short gonopericardial duct is present at the junction of the gonadial and renal sections of the oviduct. The functions of the pallial oviduct are concerned with reception and storage of sperm, fertilisation and the production of egg masses. In all littorinids the pallial oviduct is of a complex form, but the basic plan can be envisaged as a laterally flattened tube in the mantle wall, containing a dorsal groove for the passage of eggs and a ventral sperm groove. As the eggs pass anteriorly, they are first fertilised and then successively coated by albumen and other covering layers secreted by the glands of the pallial oviduct. The path of the egg groove is not straight, but is twisted into loops and spirals in a pattern characteristic for each genus in the family (see diagrammatic Fig. 6 in Reid, 1986). At the anterior

end, a ventral bursa receives sperm at copulation, and the ventral sperm groove leads posteriorly to the seminal receptacle, where sperm are stored. The structure of the pallial oviduct in the Littorinidae has recently been reviewed by Reid (1986). From the anterior opening of the pallial oviduct into the mantle cavity, a ciliated tract runs anteriorly to the ovipositor, an unpigmented raised area with a medial groove, on the right side of the head below the eye.

When a mature female *Bembicium* is removed from the shell, the pallial oviduct is conspicuously visible, occupying half a revolution on the uppermost surface of the animal (Fig. 3a). The dark red hypobranchial gland is closely applied to the mediodorsal side of the pallial oviduct, lying mostly below the peripheral keel of the shell, and the rectum lies against the medial surface. Most of the anterior and medial parts of the pallial oviduct are taken up by the greatly enlarged jelly gland, opaque whitish, cream or fawn in fresh and preserved material, and often with the internal septation visible externally. The posterolateral part of the pallial oviduct is comprised of the albumen gland, the anterior part of which is opaque cream or brown (the opaque albumen gland) while the posterior region is usually paler and more translucent (the translucent albumen gland). The spiral form of the albumen gland is clearly visible without dissection, but of the several previous authors who have described the reproductive system of *Bembicium*, only Kesteven (1903) has noted this feature. Careful dissection and serial sectioning are required to trace the ducts on the ventral side of the oviduct (Fig. 4).

The opening into the mantle cavity is about one quarter of the length of the pallial oviduct behind the anterior limit of the jelly gland (Fig. 4c), and lies on the medial side of a swollen chamber surrounded by a muscle layer up to 120 μm in thickness. The aperture is a small and inconspicuous slit (approximately 0.3 mm long) in all the specimens of *Bembicium* examined, and contrary to the observations of Fretter (1982), does not resemble the large slit-like opening seen in *Pomatias* (Creek, 1951), although it is possible that the aperture may be enlarged during oviposition. The large, muscular bursa copulatrix (muscle layer 60 to 170 μm thick) separates from the ventrolateral side of the anterior chamber of the oviduct almost adjacent to the aperture (Fig. 4, section 3). Sperm in the bursa were found to be orientated and attached to the epithelial lining, in contrast to the observation of Bedford (1965). Almost simultaneously, a narrow and inconspicuous duct 70 μm in diameter separates from the anterior chamber and runs posteriorly to the crescent-shaped seminal receptacle, which lies far back, adjacent to the renal oviduct and posterior to the bursa (Fig. 4a,c). An equally long duct, running parallel and dorsal to that to the seminal receptacle, carries the ova forwards from the renal oviduct to the anterior

chamber, where fertilisation probably occurs. This extension of the renal oviduct has a diameter of 150 to 300 μm (including a muscle coat four fibres in thickness), with a ciliated columnar epithelium staining blue in MT and magenta in ABPAS. It is distinguished from the true renal oviduct by its thinner, non-glandular walls and by its staining reactions, and is probably of pallial origin. Neither of the two previous detailed accounts of the reproductive system of *Bembicium* (H. Anderson, 1958; Bedford, 1965) have described this unusual feature of the anterior position of the meeting point of ova and sperm.

From the anterior chamber, fertilised ova pass posteriorly into the morphologically dorsal egg groove. This is initially surrounded by the opaque albumen gland, staining pale blue in MT and purple to blue in ABPAS (indicating mixed and acidic mucins). Posteriorly, the egg groove is twisted into a doubly wound spiral, of two and one half revolutions, the greater part of which is surrounded by the translucent albumen gland, staining colourless in MT and red to magenta (neutral mucins) in ABPAS. The final half revolution of the egg groove, and the straight section anterior to the spiral portion, run through the large jelly gland. The walls of the jelly gland are thrown into folds, to form incomplete septa across the long axis of the pallial oviduct. Anteriorly, the jelly gland is divided into inner and outer chambers (Fig. 4, section 2); the inner chamber (closest to the rectum) ends blindly posteriorly, but the two chambers communicate anteriorly. In MT the jelly gland stains colourless to pale blue, and in ABPAS mostly magenta (neutral mucins), but sometimes with purple or bluish areas. Since the glandular part of the pallial oviduct is a laterally flattened tube twisted into a spiral on the dorsal side only, the albumen and jelly glands have a common lumen, with interconnection in the axis of the spiral, as shown in the serial sections (Fig. 4, sections 6 and 7). Both albumen and jelly glands have a similar histological structure, consisting of very tall (80 to 360 μm), columnar cells with ciliated supporting cells in a glandular epithelium (Bedford, 1965). Throughout the pallial oviduct, but especially in the jelly gland, there are scattered, flask-shaped cells in the epithelia which contain granules staining red in MT and magenta in ABPAS. These have also been noted by Bedford (1965), and may be excretory amoebocytes (Linke, 1933).

The histology of the female reproductive system of *Bembicium nanum* has been described in detail by Bedford (1965). Some differences in terminology should be noted: the term 'renal oviduct' should be restricted to the short, thick-walled, swollen region between the gonadial and pallial sections; the 'vagina' is the muscular chamber opening to the mantle cavity. Both H. Anderson (1958) and Kesteven (1903) referred to the entire pallial oviduct as the 'uterus'. Contrary to the descriptions of H.

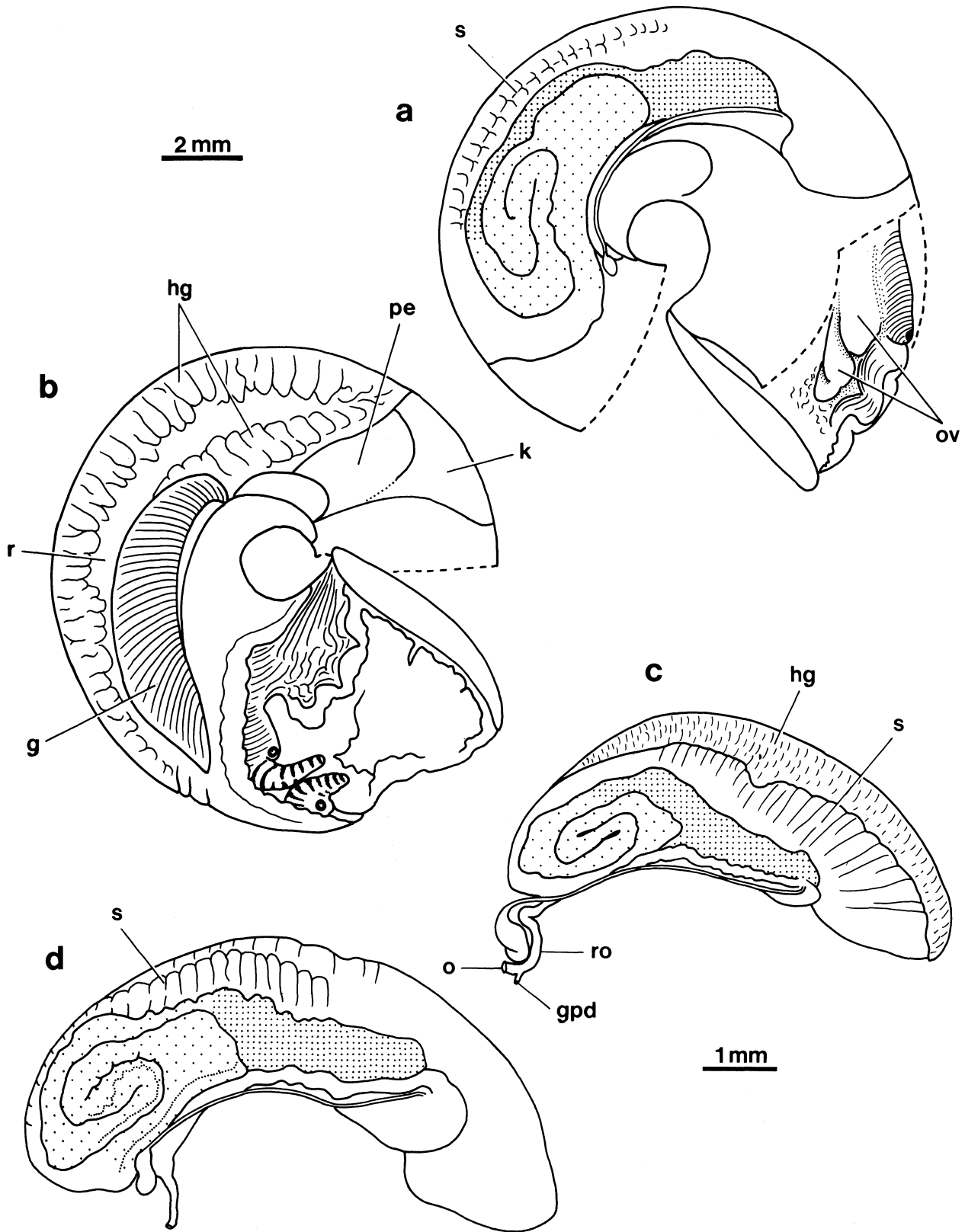


Fig.3. a,b *Bembicium melanostoma* (Gmelin), from Pittwater, Tas. (AMS C144402), female removed from shell; **a**, viewed from apex of shell, with part of mantle cut away to show ovipositor; **b**, viewed from base of shell; **c**, pallial oviduct of *Bembicium nanum* (Lamarck), from Nelson's Bay, Port Stephens, N.S.W. (AMS C144288); **d**, pallial oviduct of *Bembicium auratum* (Quoy & Gaimard), from North Keppel Island, Qld. (AMS C144367). Abbreviations: **g** - gill; **gpd** - gonopericardial duct; **hg** - hypobranchial gland; **k** - kidney; **o** - ovarian oviduct; **ov** - ovipositor; **pe** - pericardium; **r** - rectum; **ro** - renal oviduct; **s** - septa of jelly gland; dark stipple, opaque albumen gland; light stipple, translucent albumen gland.

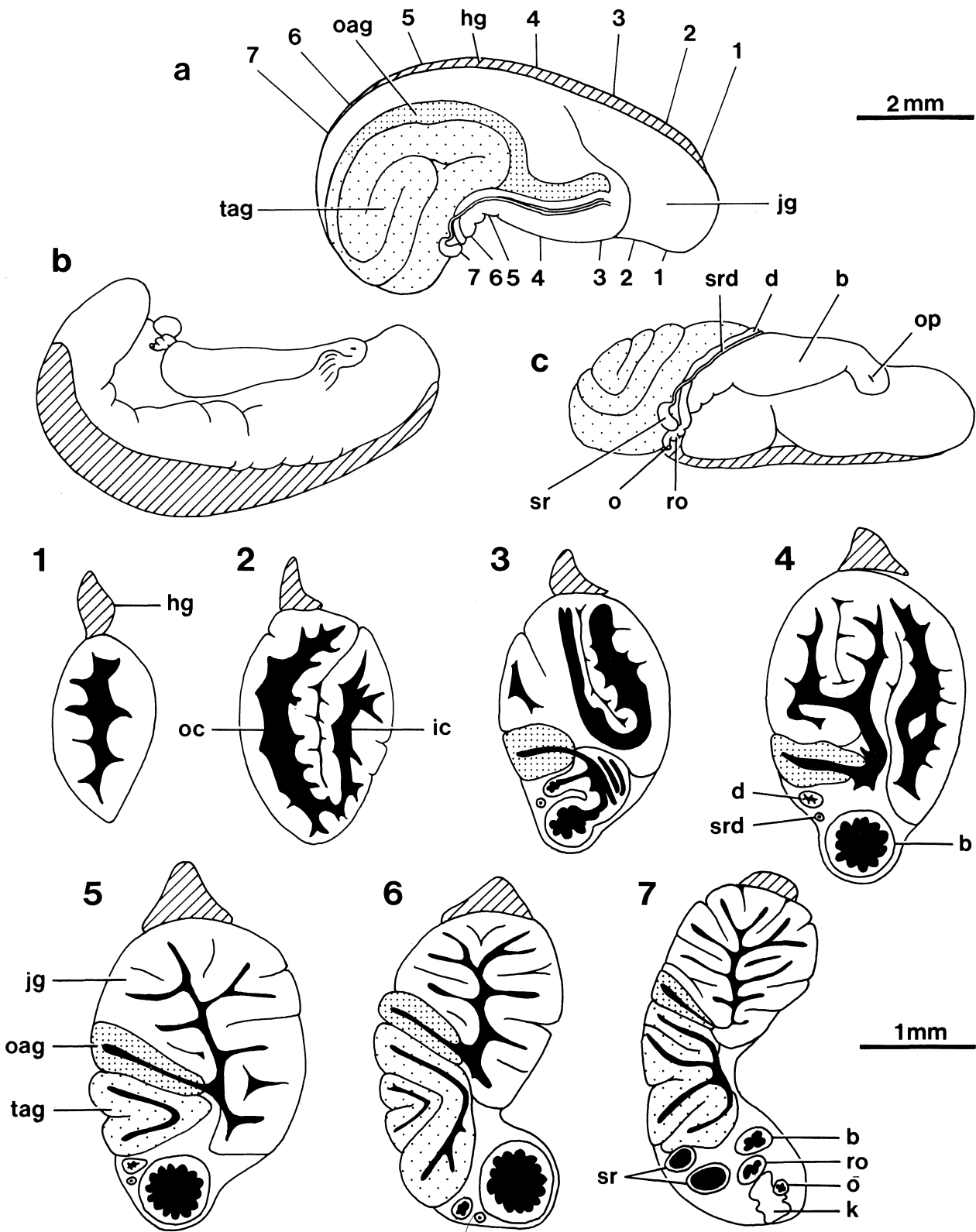


Fig.4. Pallial oviduct of *Bembicium auratum* (Quoy & Gaimard), from Magnetic Island, Qld (BMNH): **a**, lateral view; **b**, medial view; **c**, ventral view; 1-7, serial sections. Abbreviations: **b** - bursa; **d** - duct from renal oviduct to pallial oviduct; **hg** - hypobranchial gland (cross hatched); **ic** - inner chamber of jelly gland; **jg** - jelly gland; **k** - part of kidney; **o** - ovarian oviduct; **oag** - opaque albumen gland (dark stipple); **oc** - outer chamber of jelly gland; **op** - opening of muscular chamber of pallial oviduct into mantle cavity; **ro** - renal oviduct; **sr** - seminal receptacle; **srd** - duct to seminal receptacle; **tag** - translucent albumen gland (light stipple).

Anderson (1958) and Bedford (1965) there is no ventral sperm groove or channel in the lumen of the pallial oviduct, because sperm and ova meet anteriorly, in the muscular chamber.

No significant differences in the form of the pallial oviduct were observed amongst the five species of *Bembicium*. The appearance of the oviducal glands showed some variation with the degree of hydration of the tissue, being swollen and translucent in formalin, shrunken and opaque in 70% ethanol. Kesteven (1903) noted a reduction in the size of the reproductive system of *B. nanum* outside the breeding season, although Bedford (1965) found no change throughout the year.

The female reproductive system of *Risellopsis varia* is similar to that in the genus *Bembicium*. Externally, the pallial oviduct can be seen to consist of a swollen jelly gland and a posterior spiral albumen gland of two and one half revolutions (Fig. 5). There are, however, some notable differences. The renal oviduct runs directly into the opaque albumen gland (Fig. 5c), and the latter is contained entirely within the spiral portion of the pallial oviduct (Fig. 5a). Nevertheless, the duct of the seminal receptacle joins the oviduct in an anterior position, as in *Bembicium*. Presumably, sperm reach the unfertilised ova by means of the sperm groove, which is a ciliated ventral channel (Fig. 5, section 3) continuous with the lumen of the jelly gland, so that fertilisation can occur as the ova enter the opaque albumen gland from the renal oviduct. The duct to the seminal receptacle, and also the ventral channel and jelly gland, separate from the muscular anterior chamber anterior to the small opening of the pallial oviduct into the mantle cavity (Fig. 5, sections 1 and 2). As in *Bembicium* species, the jelly gland is divided into two chambers in the straight part of the pallial oviduct (Fig. 5, section 3), and these communicate anteriorly, while the inner chamber ends blindly posteriorly. In the single serially sectioned specimen of *R. varia* three regions of the jelly gland could be distinguished by their staining reactions using the ABPAS technique. The inner chamber stained dark magenta and purple, the outer chamber and its continuation into the spiral portion adjacent to the hypobranchial gland stained purple and blue, and the bulk of the jelly gland medial to the spiral albumen gland stained pale magenta. It may be noted that in unstained preserved specimens of *Bembicium* the part of the jelly gland corresponding to the outer chamber frequently appears more white and opaque than the rest, implying some differentiation within the gland, although this was not evident in the serial sections. As in *Bembicium*, the albumen gland of *R. varia* is differentiated into opaque and translucent parts. The spiral form of the pallial oviduct is rather more clear externally in *R. varia* than in *Bembicium* species, for in the former the ciliated grooves of the albumen gland and ventral channel contain black pigment.

The overall similarity of the pallial oviducts of *Bembicium* and *Risellopsis* confirms the close relationship between these genera, while comparison with other members of the family shows important differences. The anterior position of the opening of the duct to the seminal receptacle is not found in any other littorinids and is a possible synapomorphy of the two genera. Out-group comparison is a problem, because a seminal receptacle is absent in *Pomatias* (Creek, 1951) and *Lacuna* (Gallien & de Larambergue, 1938) and the homology of the posterior sperm sac of Eatoniellidae (Ponder, 1968) is uncertain. However, in the Rissoacea the seminal receptacle and its junction with the pallial oviduct are in a posterior position (e.g. Ponder, 1983, 1985). Assuming that the posterior position for the junction of renal oviduct and albumen gland, and of the duct to the seminal receptacle (as found in all other littorinids), are primitive, then *Risellopsis* represents an intermediate stage in the evolution of the condition seen in *Bembicium*. In *Risellopsis* the duct of the seminal receptacle has lengthened and its opening to the pallial oviduct has migrated anteriorly. This long duct was probably not achieved by closure of the sperm groove to form a duct, since both structures are present in *Risellopsis*. In this intermediate stage the route of the sperm would seem to be unnecessarily lengthened. Shortening of the route was achieved by bringing the junction of the renal oviduct with the albumen gland (the site of fertilisation) forwards. In the process the ventral sperm groove was eliminated, fertilised ova being passed directly into the anterior prolongation of the albumen gland.

The partial division of the jelly gland into two chambers is another unusual feature of *Bembicium* and *Risellopsis*, which may be synapomorphic. No such division is found in species of *Littorina* with enlarged jelly glands which produce a benthic gelatinous spawn (Linke, 1933; Hannaford Ellis, 1979; Fretter, 1980). Amongst possible out-groups, a similar arrangement occurs only in *Lacuna* (pers. obs.).

Histologically, the jelly glands of *Bembicium* and *Risellopsis* are similar to that described in *Littorina obtusata* (L.) by Linke (1933), consisting of a glandular epithelium of very tall columnar cells. However, in the other littorinid genera so far examined (including *Littorina*, Linke, 1933, Hannaford Ellis, 1979; *Littoraria*, Reid, 1986; *Peasiella*, *Nodilittorina*, *Mainwaringia*, all pers. obs.), the albumen and capsule glands are subepithelial, and the passage of the egg groove through them is lined by a non-secretory ciliated epithelium. In contrast, the albumen glands of *Bembicium* and *Risellopsis* are epithelial, of the same structure as the jelly gland. Despite this difference from the other littorinid genera listed above, the same differentiation of the albumen gland into opaque and translucent parts is seen in both groups.

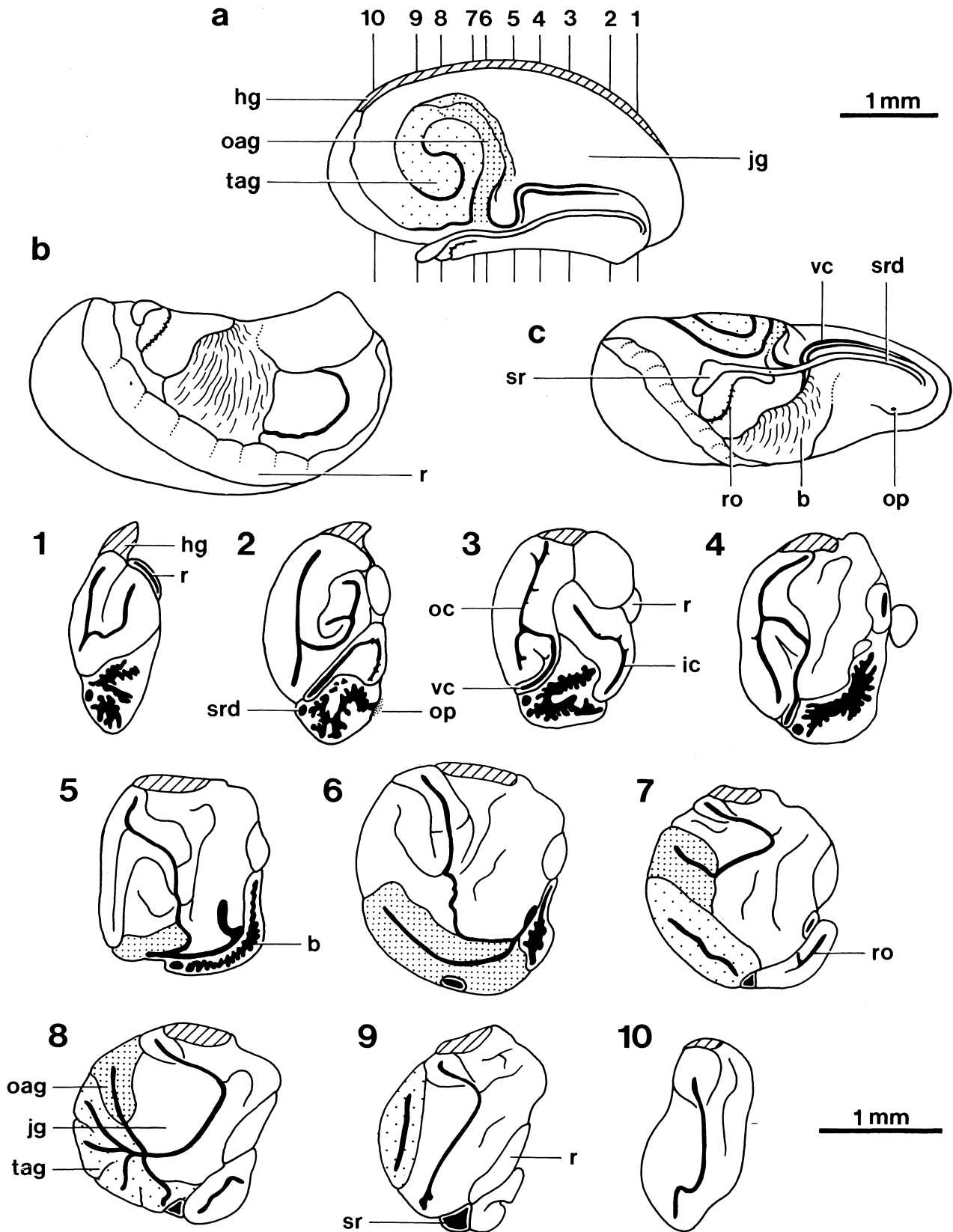


Fig.5. Pallial oviduct of *Risellopsis varia* (Hutton), from Ringaringa, Stewart Island, New Zealand (NMNZ 80806): **a**, lateral view; **b**, medial view; **c**, ventral view; 1-10, serial sections. Abbreviations: **b** - bursa; **hg** - hypobranchial gland (cross hatched); **ic** - inner chamber of jelly gland; **jg** - jelly gland; **oag** - opaque albumen gland (dark stipple); **oc** - outer chamber of jelly gland; **op** - opening of muscular chamber of pallial oviduct into mantle cavity; **r** - rectum; **ro** - renal oviduct; **sr** - seminal receptacle; **srd** - duct to seminal receptacle; **tag** - translucent albumen gland (light stipple); **vc** - ciliated ventral channel.

In all the possible out-groups, *Pomatias* (Creek, 1951), Eatoniellidae (Ponder, 1968) and *Lacuna* (pers. obs.) the glands of the pallial oviduct are epithelial, so this feature is likely to be plesiomorphic in *Bembicium* and *Risellopsis*.

The absence of capsule glands in *Bembicium* and *Risellopsis* is also noteworthy. Their distribution in other littorinids suggests that these glands produce the egg capsule and the jelly within it (Reid, 1986). The types of spawn in Littorinidae and their evolution are discussed in the following section. Here it may be pointed out that in *Littorina* species producing benthic gelatinous spawn an opaque capsule gland is present, although of small size (Hannaford Ellis, 1979; Fretter, 1980; Reid, 1986), suggesting that they have been derived from ancestors which produced pelagic capsules. In *Lacuna*, also producing a benthic gelatinous spawn, capsule glands are absent (pers. obs.). Taking *Lacuna* as an out-group, it is tentatively suggested that the absence of capsule glands in *Bembicium* and *Risellopsis* is plesiomorphic. It will be necessary to examine the oviducts of other littorinids with gelatinous spawn to test this hypothesis. The homologies of the so-called 'capsule gland' of *Pomatias* (Creek, 1951) and of the oviducal glands of Eatoniellidae (Ponder, 1968) are doubtful.

The suggestion that *Bembicium* species may be hermaphroditic was first made by Tenison-Woods (1877), although it is likely that he confused the prominent ovipositor of females with the penis of males (Kesteven, 1903). Abnormalities do occur, however. Muggeridge (1979) found some females of both *B. auratum* and *B. nanum* with vestigial penes, which she suggested may have been induced by alteration of the hormonal balance following recovery from parasitic infection (see Streiff & Le Breton, 1970). In the present study a single unparasitised male *B. auratum* was collected at North Harbour, Sydney, with a normal penis and prostate, but with a mixed gonad containing both eggs and sperm. True protandrous hermaphroditism has been found amongst the Littorinidae only in the genus *Mainwaringia* (Reid, in prep.).

Egg masses. The eggs of *Bembicium* are deposited in small ovoid or irregular gelatinous masses, attached in closely packed clusters to a hard substrate. The egg masses have been described in detail in three species. In *B. auratum* the individual gelatinous masses are bean-shaped, 2 to 3 by 1 to 1.5 mm, and each contains 60 to 100 eggs; these are deposited over an area of 3 to 5 cm² on the undersides of stones in rock pools, making a total of up to 12,500 eggs. Individual eggs range in diameter from 115 to 122 µm, and are each surrounded by albumen in a transparent, ovoid, egg envelope, measuring 215 to 234 by 240 to 272 µm (H. Anderson, 1958; D.T. Anderson, 1962; Muggeridge, 1979). The egg masses of *B. nanum* are oval, containing 100 to 200 creamy white eggs 100 µm in diameter, and each surrounded

by an ovoid, transparent envelope 200 to 220 by 190 to 210 µm; the spawn is attached to the rock in fissures or under weed, in the adult habitat (D.T. Anderson, 1961). Both these species hatch as veligers after ten to 12 days (D.T. Anderson, 1961, 1962).

The eggs of *B. vittatum* are larger, of an average diameter of 172 µm, contained in envelopes 404 by 460 µm, and are deposited in irregularly shaped masses each containing eight to 30 eggs (H. Anderson, 1958, as *B. melanostoma*). The larger eggs and greater supply of albumen is related to the probable lecithotrophic development of this species, which lacks a planktonic veliger stage (H. Anderson, 1958).

Pilkington (1974) has described the egg masses of *Risellopsis varia*. These are irregular in shape, each 5 to 6 mm in diameter, flat at first but becoming convex with development. Veligers hatch after 12 days in the laboratory. In a sample of egg masses preserved in alcohol from Stewart Island (NMNZ M80806, pers. obs.), the individual masses measured 2 to 3 mm in diameter and were closely attached to the rock and each other in clusters of 20 or more. Individual masses contained 250 to 500 eggs, measuring 103 to 119 µm in diameter, and enclosed in ovoid envelopes 122 to 178 by 144 to 189 µm.

Amongst other littorinids, production of benthic gelatinous spawn is relatively unusual, having been recorded in six species of *Littorina* (Kojima, 1958; Buckland-Nicks *et al.*, 1973; Fretter, 1980), two of *Laevilitorina* (Picken, 1979; Simpson & Harrington, 1985), two of *Laevilacunaria* (Picken, 1979), two of *Pellilitorina* (Picken, 1979) and one of *Macquariella* (Simpson and Harrington, 1985). This type of spawn is also known in at least two species of *Lacuna* (Thorson, 1946). In all these cases, except *Lacuna vincta* (as *L. divaricata* in Thorson, 1946), the planktonic stage is eliminated, and juveniles hatch directly from the egg mass. Amongst littorinids, the combination of benthic spawn and a planktonic veliger stage is known only in *Bembicium nanum*, *B. auratum*, *Risellopsis varia* and *Lacuna vincta*.

It has been suggested that a benthic gelatinous spawn is primitive in the Littorinidae and in *Lacuna* (Fretter, 1980). However, Reid (1986) argued that at least in *Littorina* the benthic spawn was derived from an ancestral state with pelagic capsules. In view of the absence of capsule glands in *Bembicium*, *Risellopsis* and *Lacuna*, as discussed above, the conflicting hypotheses could be resolved by the suggestion that a benthic spawn is plesiomorphic in these three genera, and secondarily derived in *Littorina*. All the littorinids with benthic spawn have in common a mainly cool temperate, arctic or antarctic distribution (although *B. auratum* extends to northern Queensland), conforming to a general tendency towards reduction or elimination of planktotrophic development in benthic marine animals inhabiting high latitudes (Thorson, 1950; Jablonski & Lutz, 1983). If viewed as an ecological

adaptation, it is possible that benthic egg masses may have appeared independently in several clades. Further information, especially on the anatomy and relationships of the four antarctic genera with benthic spawn listed above, will be required to resolve this problem.

Radula. The radulae of *Bembicium* and *Risellopsis* are of the normal taenioglossate type, with seven teeth in each row, a central rachidian tooth flanked by a lateral and an inner and an outer marginal on each side. In *Bembicium* the length of the central tooth is approximately 1.6 times its width, when the flat radula is viewed from above (e.g. Fig. 19). The central tooth bears one large anterior cusp, flanked by two smaller cusps which may be reduced to mere denticles. The thickened shaft of the central tooth is supported by lateral 'wings', and the posterior edge of the base is rounded or truncated, without projections. Each of the paired teeth in a row also bears one major cusp, closely similar in size and shape to that of the central tooth. In addition each lateral tooth bears one to two (rarely three) small inner cusps and one small outer cusp. The base of the lateral is broad, hollowed out into a deep groove in which lies the shaft of the inner marginal. The cusp pattern of the inner marginal is similar to that of the lateral, with two small inner cusps and one small outer cusp flanking the main cusp. The outer marginals bear only one to three small inner cusps, in addition to the main cusp, which is itself smaller than those of the outer teeth. Few figures of the radula of *Bembicium* have previously been published, all poorly drawn (Troschel, 1856–63; Gray, 1857; Woodward, 1866; Kesteven, 1903).

The radula of *Risellopsis* is basically similar to that of *Bembicium* (Fig. 26c,d; Hutton, 1882; Kesteven, 1902). The cusps of the rachidian tooth are relatively reduced in size, but an additional pair of denticles is present, the thickened shaft is narrowed, and the posterior edge of the base elaborated to give three rounded projections. The major cusps of the lateral and inner marginal teeth are not pointed or leaf-shaped as in *Bembicium*, but bluntly truncated. Cusp numbers and relative sizes on the paired teeth are similar to *Bembicium*; the lateral bears two to three small inner cusps, a major cusp and one to two small outer cusps; the inner marginal bears two small inner cusps, a major cusp and a small outer cusp; the outer marginal bears two inner cusps and a major cusp.

The radula of both genera fall within the morphological range of other members of the Littorinidae (e.g. Rosewater, 1970, 1972, 1980; Bandel, 1974; Ponder, 1976; Arnaud & Bandel, 1978; Bandel & Kadolsky, 1982). In particular the deep gutter or 'littorinid embayment' of the lateral tooth is characteristic of the family (Troschel, 1856–63; Rosewater, 1980; Bandel & Kadolsky, 1982). In comparison with other littorinids, the radula is of a rather unspecialised type, corresponding to the 'moderate' type of Rosewater (1980) and the group

exemplified by *Littorina littorea* of Bandel (1974). This type may not be primitive for the family as a whole; the ancestral condition may be represented by the type with a broad central tooth with at least five cusps, as found in the Eatoniellidae (Ponder & Yoo, 1978), in Lacuna (Troschel, 1856–63), and in some antarctic littorinids (Ponder, 1976; Arnaud & Bandel, 1978). Nevertheless, the radulae of *Bembicium* and *Risellopsis* clearly lack the extreme specialisations found in *Echininus* and some *Nodilittorina* species (Bandel & Kadolsky, 1982).

A striking feature of the radula of *Bembicium* is the lack of differentiation between teeth in a row, and the similarity of their cusp shapes. This similarity may be under developmental constraint; the form of the major cusps shows considerable variation within *Bembicium* species, but the cusps of all teeth in a row vary together in the same way (Fig. 19). Again in contrast to many other littorinids, the cusps of the teeth are not recurved posteriorly, but instead are deflected anteriorly, so that the angle between the cusp and the shaft of each tooth is 110° to 140°. The small number of cusps on the outer marginal teeth is also unusual in the family (Bandel, 1974).

Radular characters have been used to discriminate between species of littorinids (e.g. Bandel, 1974; Bandel & Kadolsky, 1982), but this practice has not been adequately validated by studies of intraspecific variability. Where intraspecific variation has been considered, it has been found to be rather high (Borkowski, 1975; Goodwin & Fish, 1977). In the Littorinidae, radular characters appear to be taxonomically useful only at the generic and subgeneric levels in most instances (Reid, 1986). In this study of *Bembicium*, ten specimens of *B. auratum* were examined, and showed an exceptionally high degree of variability in cusp shape within this species (Fig. 19). Variation was not a consequence of differences in orientation of the specimen or angle of the cusps. All radulae were taken from large adults, and there was no correlation with sex. Variation within a sample from a single locality was as great as that between widely separated localities, and no geographical trend was evident. A similar degree of variation was found in the four other species of the genus, although only five radulae of each were examined. This variability precluded the use of radular characters as taxonomic criteria in *Bembicium*. Four specimens of *Risellopsis varia* showed close similarity of cusp form.

Alimentary system, pallial complex and nervous system. The alimentary system of *Bembicium* and *Risellopsis* is similar to that of other littorinids (illustrated by Fretter & Graham, 1962; Reid, 1986). A pair of pale, thin-walled oesophageal pouches arise from the ventral side of the anterior oesophagus just posterior to the buccal mass; these pouches are not bi-lobed as in *Littoraria* (Reid, 1986). The mid-oesophagus is glandular and cream in colour, with the coiled radular sac closely attached to its upper

surface. One important, and probably apomorphic, feature of both genera is the position of the salivary glands, which lie entirely anterior to the nerve ring around the oesophagus (Fig. 6a). They are pinkish

red in colour, often fused together in the midline, and of large size (one to four times as large as the oesophageal pouches). Because of their large size, the salivary glands appear in a rather posterior position,

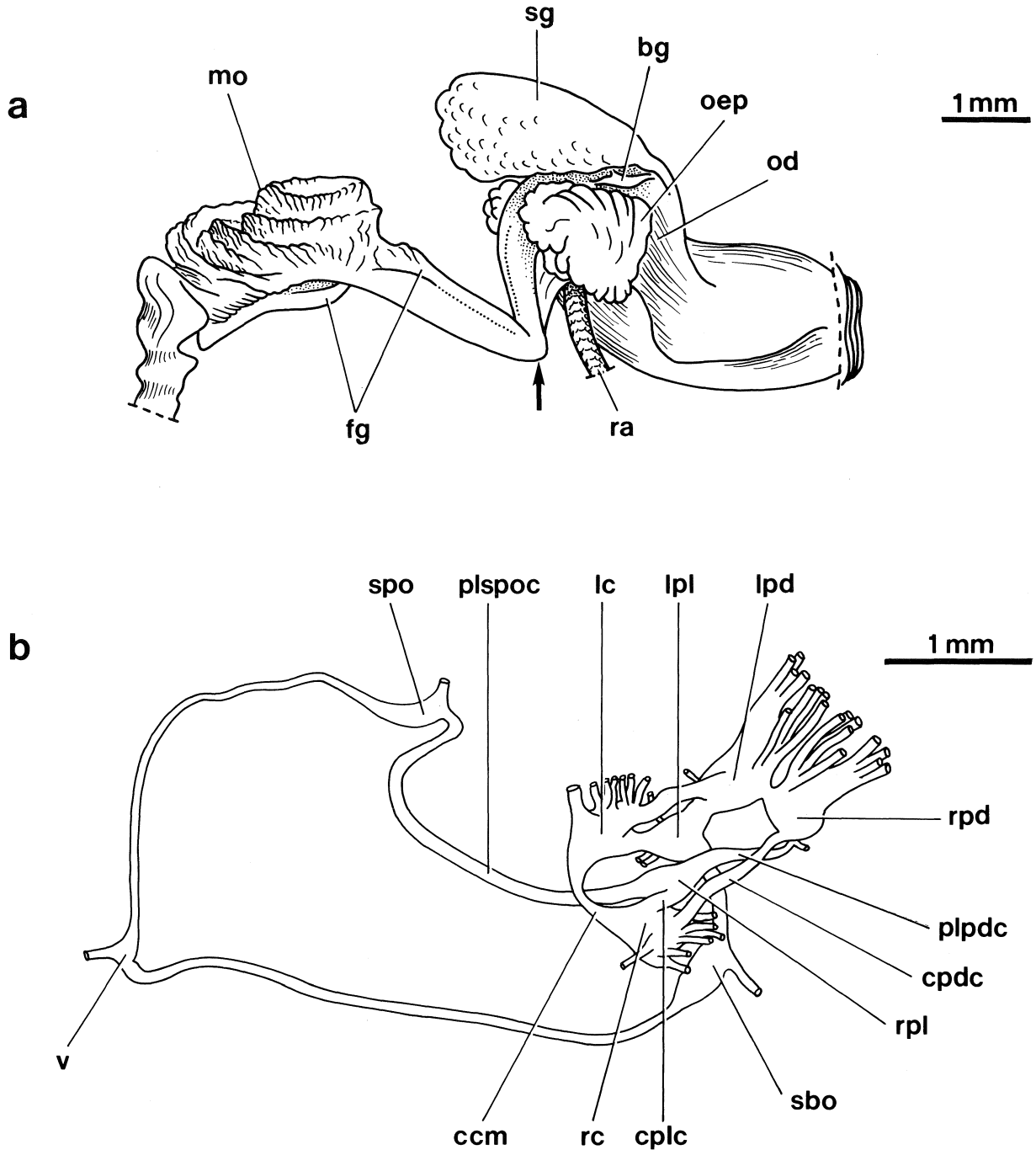


Fig.6. *Bembicium auratum* (Quoy & Gaimard), from Nelson's Bay, Port Stephens, N.S.W. (AMS C144288): **a**, foregut, with coil of radular sac removed from its position overlying mid-oesophagus (on which it has left an impression, an artefact of preservation); **b**, principal ganglia of nervous system. Abbreviations: **bg** - buccal ganglion; **ccm** - cerebral commissure; **cpdc** - cerebropedal connective; **cplc** - cerebropleural connective; **fg** - good groove; **lc** - left cerebral ganglion; **lpd** - left pedal ganglion; **lpl** - left pleural ganglion; **mo** - mid-oesophagus with imprint of radular sac; **od** - position of odontophore; **oep** - oesophageal pouch; **plpdc** - pleuropedal connective; **plspoc** - pleurosupraoesophageal connective; **ra** - radula; **rc** - right cerebral ganglion; **rpdc** - right pedal ganglion; **rpl** - right pleural ganglion; **sbo** - suboesophageal ganglion; **sg** - salivary gland; **spo** - supraoesophageal ganglion; **v** - visceral ganglion; arrow marks position of nerve ring around oesophagus.

partly overlying the radular sac, but neither ducts nor glandular material pass through the nerve ring. A narrow posterior extension of the glands, apparently along a blood vessel, is sometimes present, but terminates in front of the nerve ring. Amongst other littorinaceans, the salivary ducts pass through the nerve ring to posterior glands in *Littorina* (Fretter & Graham, 1962), *Nodilittorina* and *Cenchritis* (pers. obs.), either ducts or glands pass through in *Macquariella*, *Laevilittorina* and the Eatoniellidae (Ponder, 1983), and the glands are constricted into two parts by the nerve ring in *Littoraria* (Reid, 1986) and in *Lacuna* (pers. obs.). The salivary glands pass through the nerve ring in the majority of mesogastropods, and this state is presumably primitive (Ponder, 1983). The stomach of *Bembicium* is like that of other littorinids, although the U-shaped proximal region is shortened, and there is only a single opening of the ducts from the digestive gland, rather than three as in *Littorina* (Fretter & Graham, 1962) and *Littoraria* (Reid, 1986).

Of the structures of the pallial complex, the hypobranchial gland is particularly well developed in *Bembicium* and *Risellopsis*. It is dark red in colour, and may reach a width of 2.0 mm in large specimens of *B. auratum* and *B. nanum*.

The nervous system of *B. nanum* has been illustrated by Kesteven (1903, as *Risella melanostoma*), and that of *B. auratum* is shown in Fig. 6b. The arrangement is similar to that of *Littorina* (Bouvier, 1887; Fretter & Graham, 1962), although relative to the size of the ganglia, the connectives and commissures forming the ring around the oesophagus are condensed. As a measure of the degree of condensation of the supraoesophageal nerve tract, Davis *et al.* (1976) have defined the RPG ratio (length of the pleuro-supraoesophageal connective divided by the sum of the lengths of the supraoesophageal ganglion, pleuro-supraoesophageal connective and right pleural ganglion). The lengths of ganglia are difficult to measure precisely in *Bembicium*, but an RPG ratio for *B. auratum* (Fig. 6b) was approximately 0.76 and for *B. nanum* (from figure by Kesteven, 1903) 0.69, which are similar to the figures 0.72 and 0.84 measured by Davis *et al.* (1976) from published figures of *Littorina littorea*.

BIOLOGY AND ECOLOGY

Habitat, predation and competition. Since species of *Bembicium* are common in the littoral zone, there is a considerable amount of information available about various aspects of their ecology. Their occurrence is frequently mentioned in general accounts of intertidal zonation. *Bembicium melanostoma* is found in the eulittoral, or barnacle, zone on sheltered rocky shores and in lagoons (Guiler, 1952a,b) and also, in Victoria, amongst

mangroves (Macpherson & Gabriel, 1962). In an enclosed lagoon in southern Tasmania, Guiler (1951) recorded the species in a salt marsh, and found densities of up to 86/m² on sandy mud between the marsh and the *Zostera* belt. The closely related species *B. vittatum* occupies a similar range of habitats in South Australia (Womersley, 1956; H. Anderson, 1958; Womersley & Edmonds, 1958; all as *B. melanostoma*) and in Western Australia, where a density of 1.82/m² (biomass 1.26 g/m²) was recorded on sandflats in Oyster Harbour (Wells & Threlfall, 1980, as *B. auratum*). The third member of the *melanostoma* group, *B. flavescens*, has been reported from stones on flat muddy beaches on Lord Howe Island (Etheridge, 1889), and from the upper littoral on exposed rock platforms (museum records, AMS).

Throughout its wide geographical range, *B. auratum* occurs on the roots and trunks of mangroves, in estuaries and in sheltered rocky bays, and is only rarely found on rocky or coral substrates on the open coast (Stephenson *et al.*, 1931, as *B. melanostoma*; H. Anderson, 1958; Chalmer *et al.*, 1976; Roberts & Wells, 1980, both as *B. melanostomum* (sic); Branch & Branch, 1980). This species may be one of the dominant molluscs in mangroves and at the mouths of estuaries (Roberts & Wells, 1980). Densities of up to 200/m² have been recorded at Patonga, New South Wales (Branch & Branch, 1980). At this site *B. auratum* was absent from the low water mark of spring tides, and declined in numbers at higher levels. Although the snails were found grazing both on trunks and on the mud surface, they showed a preference for hard substrates and were most common on a belt of oysters.

Bembicium nanum is the only member of the genus which occurs on exposed rocky shores on mainland coasts, and even then is more frequent where wave action is reduced (Guiler, 1950, 1952b; H. Anderson, 1958; Bennett & Pope, 1960; Meyer & O'Gower, 1963; Underwood, 1975a). It is a dominant species of the upper eulittoral (barnacle or barnacle-limpet-mussel zone), and on rock platforms at Cape Banks, New South Wales, densities range from 19 to 205/m² (Meyer & O'Gower, 1963) or 70 to 160/m² (Underwood, 1975a, b). At this locality the distribution patterns have been analysed in detail. Underwood (1976a) found a homogeneous random dispersion with respect to patches of the encrusting alga *Peyssonelia* and shallow rock pools (although O'Gower & Meyer, 1971, reported reduced densities in pools), and a significantly aggregated dispersion on both bare rock and the alga (Underwood, 1976b). No seasonal changes in distribution were detected (Underwood, 1975b, 1976b).

The differences in the habitats of *Bembicium* species are such that syntopic occurrences are rare. Where mangroves occur on an ocean rock platform north of Sydney, *B. auratum* and *B. nanum* have been found together (Dakin, 1980: 248). These two

species also co-occur on the rocky shores of sheltered inlets, as in Port Stephens and Batemans Bay, New South Wales (AMS records), Port Jackson, New South Wales (pers. obs.) and Outer Harbour, Port Adelaide, South Australia (AMS records). In the mangroves of Western Port Bay, Victoria (pers. obs.) and on the sheltered rocky shores in southeastern Tasmania (TM records), *B. auratum* may be found together with *B. melanostoma*. Both *B. auratum* and *B. vittatum* occur in Oyster Harbour, southwestern Australia (Roberts & Wells, 1980; WAM records). *B. melanostoma* is occasionally found with *B. nanum* on rocky shores of moderate exposure in Port Phillip and Western Port Bays, Victoria (NMV records; pers. obs.) and in Tasmania (TM records). The segregation of *Bembicium* species is, however, normally so complete that they have been regarded as ecotypes of a single species (e.g. Guiler, 1952b). Differing tolerances of reduced salinity may partly account for the differences in habitats. In South Australia *B. nanum* and *B. vittatum* occur only in fully marine conditions, while *B. auratum* is found in estuaries and shows activity down to a 35% dilution of normal seawater (H. Anderson, 1958).

Differences in shell size within and between habitats have been noted by several authors. In *B. nanum*, larger individuals are found in positions exposed to stronger wave action, except under extreme exposure (Meyer & O'Gower, 1963; O'Gower & Meyer, 1965). On sandy or muddy flats in South Australia, shells of *B. vittatum* are smaller than on rocky shores (Womersley & Edmonds, 1958). A dwarf form of *B. auratum* occurs on high islands off the coast of northern Queensland. *B. nanum* shows a shore-level size gradient with juveniles in the upper parts of the range (Underwood, 1975a; Chilton & Bull, 1984), as is the case in many intertidal littorinids, of which juveniles are believed to inhabit the zone of minimal mortality (Vermeij, 1972). In contrast, Branch & Branch (1980) found juveniles of *B. auratum* in the lower part of the range, where survival may have been enhanced by the presence of a belt of oysters which provided a hard substrate, and where food levels were highest.

Little information is available on the predators of *Bembicium*. In New South Wales adult mortality is low (0.060 deaths/individual/month, Underwood, 1975a) and predation by crabs and large invertebrates is said to be insignificant (Underwood, 1978). On rocky shores in South Australia the crab *Ozius truncatus* is a predator of small snails and may be responsible for the maintenance of the observed shell size gradients (Chilton & Bull, 1984, 1986).

Bembicium nanum and *Nerita atramentosa* show significant segregation in their distributions on the shore, leading to the suggestion of interspecific competition between them (Underwood, 1976b). This has been confirmed by caging experiments, which also showed competitive effects from *Cellana*

tramoserica. The possibility of intraspecific competition for a limited supply of algal food has been demonstrated by caging *B. nanum* at two to four times the natural density, resulting in increased mortality and reduced flesh weight (Underwood, 1978). Similar caging experiments have shown intraspecific competition at densities greater than normal in *B. auratum*, and the correlation between chlorophyll levels in the substrate and natural snail density, together with depletion of chlorophyll in cages with high snail densities, suggest that food supply is the limiting resource (Branch & Branch, 1980).

There is relatively little information about the ecology of *Risellopsis varia* on New Zealand shores. It occurs in the upper eulittoral zone, in crevices amongst barnacles and *Modiolus* (Suter, 1913; Morton & Miller, 1968; Powell, 1979). The species attains a larger shell size in the southern parts of its range (Morton & Miller, 1968).

Reproduction, growth and population dynamics.

The reproductive seasons of *Bembicium* species show variation between localities, but in general the period of peak spawning is winter and spring. At Port Adelaide, South Australia, *B. auratum* produced egg masses in the laboratory from July to January (H. Anderson, 1958). At Middle Harbour, Sydney, egg masses of this species were found under stones in rock pools from August to December (D.T. Anderson, 1962). However, at Patonga, 50 km north of Sydney, a population spawned throughout the year, but with a peak in the numbers of mature gonads from April to September (Muggeridge, 1979). At some time during January to April each individual underwent a short period of total oocyte resorption, although this was asynchronous in the population as a whole. The males in this population contained sperm throughout the year, although in some individuals the testis, but not the penis, was reduced in size in January and February (Muggeridge, 1979). The breeding season of *B. vittatum* is not known, but egg masses have been recorded in the laboratory in October by H. Anderson (1958, as *B. melanostoma*), who suggested that the spawning period may have been earlier or shorter than in *B. auratum*.

Bembicium nanum has also been examined at several localities. At Harbord, north of Sydney, egg masses were found from October to April (D.T. Anderson, 1961), although Bedford (1965) reported continuous breeding in the vicinity of Sydney. A more detailed study by Underwood (1974) at Cape Banks, Botany Bay, demonstrated spawning from July to February, with reduction in size of the ovary from March to April or February to March. The testes were much reduced in size from March to May. At Balmoral, Port Jackson, Muggeridge (1979) recorded spawning by *B. nanum* from July to January, but without a synchronised rest period following spawning. The testes were enlarged for

most of the year, with some reduction from February to April, but the size of the penis was not reduced.

The breeding season of *Risellopsis varia* is not known, although veligers tentatively identified as this species have been recorded in plankton samples off Otago from January to April (Pilkington, 1976).

The factors controlling spawning in *Bembicium* species have not been investigated, although at least in *B. auratum* the onset of the major spawning period is associated with rising sea temperatures, and its cessation may be triggered by high summer temperatures (Muggeridge, 1979). The breeding cycles of both *B. auratum* and *B. nanum* show a correlation with the seasonal availability of phytoplankton as food for the veliger larvae (Underwood, 1974; Muggeridge, 1979).

As discussed above, *B. auratum*, *B. nanum* and *Risellopsis varia* hatch from benthic egg masses as planktonic veligers, while *B. vittatum* (H. Anderson, 1958, as *B. melanostoma*), and possibly also *B. melanostoma* and *B. flavescens*, are believed to lack a planktonic stage, undergoing direct development in the egg mass. The time from oviposition until hatching in *B. auratum* is ten days (Muggeridge, 1979, at 12 to 18°C; also D.T. Anderson, 1962), and in *B. nanum* 12 (D.T. Anderson, 1961) to 16 days (Bedford, 1966). The ultrastructure and cytochemistry of oogenesis and embryology of *B. nanum* have been described in detail by Bedford (1966). There is no information on the length of larval life; veligers of *B. auratum* have survived for 14 days in the laboratory (Muggeridge, 1979). D.T. Anderson (1961) kept veligers of *B. nanum* for four days, and described them as 'planktotrophic'. On the basis of the time lag between spawning and the appearance of 5 mm recruits in the size-frequency distribution of *B. nanum* on the shore, Underwood (1975a) suggested that this species might spend as long as one year in the plankton. This estimate was derived from the backward extrapolation of the constant rate of growth of juvenile cohorts. However, since the size of the protoconch of *B. nanum* indicates settlement at a diameter of 0.39 mm, the apparent lag period can be explained either by inadequate sampling of small juveniles or by rapid growth between settlement and appearance of 5 mm snails in the size-frequency histograms.

The shape of the protoconch of *Bembicium* species suggests a relatively short planktonic phase. In *B. auratum* this is supported by size measurements; the shell of the veliger 1.5 days before hatching, illustrated by D.T. Anderson (1962), measures 260 µm in diameter, which may be compared with a protoconch diameter, indicating size at settlement, of 350 µm. However, *B. nanum* appears to hatch at a smaller size; published figures of the veligers just before hatching show a shell size of 114 to 128 µm (Bedford, 1966) or 175 µm (D.T. Anderson, 1961), while the protoconch measures 390 µm. For comparison, the planktotrophic veliger of *Littorina*

scutulata grows from 160 µm at hatching to 300–360 µm at settlement in about three weeks (Buckland Nicks *et al.*, 1973). Newly hatched veligers of *Nodilittorina hawaiiensis* measure 110 to 120 µm and settle about 24 days later at a size of 250 µm (Struhsaker & Costlow, 1968, as *Littorina picta*, rearing temperature 25°C). Tropical *Littoraria* species grow from 100 to 140 µm at hatching to 320 to 415 µm at settlement, although the developmental time is not known (Reid, 1986). The size increment of *B. nanum* is similar to these, and the veliger presumably feeds in the plankton. By comparison, the veliger of *B. auratum* grows relatively little in the plankton and might even be non-planktotrophic. The relative size of the velum is, however, similar in *Bembicium* species (D.T. Anderson, 1961, 1962; Bedford, 1966) and in the planktotrophic *N. hawaiiensis* (Struhsaker & Costlow, 1968).

The suggestion of direct development in *B. vittatum* rests on the observation by H. Anderson (1958, as *B. melanostoma*) that embryos in the laboratory developed past the veliger stage, although they did not hatch from the egg capsules. Development of this species should be re-examined, and also in the closely related species *B. melanostoma* and *B. flavescens*.

Veligers of *Risellopsis varia* hatched from egg masses after 12 days at room temperature, with a shell 0.18 mm long (Pilkington, 1974). Similar veligers from plankton hauls off Otago measured 0.38 to 0.45 mm, but their identification was uncertain (Pilkington, 1976).

Bembicium auratum at Patonga, New South Wales, reached the maximum size of 16 to 19 mm shell diameter three years after settlement, at a mean growth rate of 0.58 mm per month (Muggeridge, 1979). Slow growth was also found by Branch & Branch (1980), who recorded increments in shell diameter of about 0.6 mm per month in juveniles at the same locality. Females showed slightly higher growth rates, maturing at a diameter of 12 mm, while males were mature at ten to 12 mm (Muggeridge, 1979). The population was dominated by adults, suggesting substantial juvenile mortality and high adult survival (Branch & Branch, 1980).

Analysis of polymodal size-frequency distribution has yielded a growth curve for *B. nanum* at Cape Banks. For the smallest cohort (I to 10 mm) growth in basal diameter was at a steady rate of 0.44 mm per month, reaching maturity at 11 mm. Instantaneous mortality rates were 0.233 deaths/individual/month for the juvenile cohort and 0.060 for adults, and longevity was estimated as four to eight years (Underwood, 1975a). Caging experiments at this locality demonstrated similar growth rates at three tidal levels, and showed that only near the upper limit of the vertical range was there insufficient food, or time for feeding, to permit maximal growth (Underwood, 1984).

Fossil Record

The generic name *Risella* was used by Cossmann (1915) for European fossils from as far back as the Triassic. However, his subgenus *Riselloidea* has been transferred to the archaeogastropod family *Amberleyidae* (Brookes Knight *et al.*, 1960) and his subgenus *Tanaliopsis* is regarded as a member of the *Thiaridae* (Kollmann, 1975). Two European Tertiary fossils have also been referred to *Risella* or *Bembicium*. These are *Trochus minutus* Deshayes (e.g. Cossmann, 1888, 1915; Glibert, 1962), and *Risella girondica* Benoist (Cossmann & Peyrot, 1919), both of which are members of the littorinid genus *Peasiella* (Reid, in prep.). *Tectarius rehderi* Ladd (Rosewater, 1972) bears a superficial resemblance to species of *Bembicium*, but is not a member of the genus (pers. obs. of type).

Fossil species of *Bembicium* are known only from New Zealand and Australia, and the earliest are of late Oligocene to early Miocene age. *B. priscum* Powell & Bartrum, described from the Otaian Stage (Lower Miocene) of New Zealand, probably occurs also in the Waitakian (basal Miocene) and the Lillburnian or Waiauian Stages (late Middle to early Upper Miocene). Also from the Otaian Stage are *B. discoideum* n. sp. and an unnamed species as yet known only from juveniles. A poorly preserved shell from the Altonian Stage (Lower Miocene) may represent an additional species. The only *Bembicium* known from the Tertiary of Australia is *B. altum* (Tate), which ranges from the Late Oligocene to Middle Miocene. As expected of intertidal molluscs found on hard substrates, fossils of *Bembicium* are rare.

Ludbrook (1984) has discussed the occurrence of the Recent *Bembicium* species in the Quaternary deposits of South Australia. Interestingly, although the genus is now extinct in New Zealand, it occurred there in the Pleistocene (Hutton, 1893; Suter, 1906, 1918; Speight, 1913; Finlay, 1923; Fleming, 1966). Previous authors have recorded these New Zealand fossils as *B. melanostoma*. However, without anatomical evidence even Recent shells of the *melanostoma* group can be difficult to distinguish. Four Pleistocene shells from the Castlecliffian Stage of the Wanganui area, New Zealand (NZGS) have been examined and all are rather worn (Fig. 24h). It can only be said that of the Recent species they most closely resemble the *melanostoma* group, and especially some specimens of *B. vittatum* from South Australia. *B. 'melanostoma'* has also been recorded from the Boat Cove Formation (Quaternary) of Raoul Island in the Kermadec Group (Marshall, 1981; specimen lost), to which the closest Recent occurrence is of *B. flavescens* at Norfolk Island.

Several Tertiary shells from New Zealand have been placed in the genus *Risellopsis*. These are *R. prisca* Powell and *Submargarita? tricincta* Marshall (Powell, 1935) and *R. gliscens* Marwick (1965). Maxwell (1969) has transferred the last to

Pterolabrella (Vitrinellidae), which seems appropriate for the others also (B. Marshall, pers. comm.; pers. obs.). The genus *Risellopsis* is represented only by the Recent species *R. varia*, of which there is but one known Pleistocene occurrence.

Biogeography

The genus *Bembicium* occurs only in mainland Australia, Tasmania and on Lord Howe and Norfolk Islands although, as discussed in the preceding section, there are fossil records from New Zealand and the Kermadec Islands. It is a typical and characteristic member of the endemic temperate molluscan fauna of the southern Australian region, and as such had its origin in the Australian - New Zealand element of the southeastern Australian Tertiary fauna (Darragh, 1985). Although the earliest fossils are from New Zealand, it is likely that the group originated in Australia, from which migration of most marine groups has proceeded eastwards (Knox, 1963).

On the basis of the distribution of intertidal organisms, seven biogeographical provinces have been recognised around the coast of the Australian mainland and Tasmania (Knox, 1963; Wilson & Gillett, 1971), although the boundaries between them are seldom sharply defined. Comparing the distributions of the *Bembicium* species with these biogeographical provinces, it can be seen that *B. melanostoma* is restricted to the cold temperate Maugean Province, being found only in Tasmania and on the mainland in Port Phillip and Western Port Bays. The western limit of the Maugean Province is at Robe, South Australia (Knox, 1963).

Bembicium nanum extends from Port Lincoln, South Australia, around the coasts of Victoria, Tasmania and New South Wales, having its northern limit at Yeppoon, Queensland (23°05'S). As noted by Underwood (1974), this is considerably north of the accepted boundary between the warm temperate Peronian and tropical Solanderian Provinces, at 25°S (Endean *et al.*, 1956). In contrast, the distribution of *B. auratum* includes that of *B. nanum*, and extends northward to Lizard Island (14°40'S). This species does, however, show geographical variation, with shells from northern Queensland being recognisably distinct from those from the more southerly parts of the range. Both northern and southern shell forms occur in Hervey Bay (25°S), with outlying northern forms (and intermediates) in Moreton Bay (27°S) and southern forms at One Tree Island (23°30'S). This agrees with the provincial boundary at 25°S and the northern affinities of Moreton Bay (Endean *et al.*, 1956). Records of *B. melanostoma* from Queensland (e.g. H. Anderson, 1958) are erroneous, and based on confusion with the northern form of *B. auratum*.

In southern Australia, the western limit of *B. nanum*, at Port Lincoln, is not a recognised biogeographical boundary. The most easterly record

of *B. vittatum*, at Port MacDonnell, is close to the boundary between the Flindersian and Maugean Provinces. In Western Australia, both *B. vittatum* and *B. auratum* reach their northern limit in the Houtman Abrolhos Islands (although the former is abundant, and the latter known from a single specimen and otherwise not further north than Perth). Wells (1980) found the sharpest change in the region of overlap between tropical and warm temperate molluscan faunas on the west coast to lie between Perth and the Houtman Abrolhos Islands.

Bembicium flavescens occurs only at Lord Howe and Norfolk Islands, as first noted by Etheridge (1889, as *Ricella* (sic) *plicatula*). Studying the chitons, Hedley & Basset Hull (1912) remarked on the similarity between the faunas of these islands, and the lack of relationship with Australia and New Zealand. However, Iredale (1914) considered that the biogeographical affinities of Lord Howe Island lay primarily with New Caledonia to the north, and that there was little similarity with Norfolk Island or the Kermadecs. This view was maintained by Iredale & Allen (1940), although they also pointed out the resemblances of the intertidal molluscs of Lord Howe, including *Bembicium*, to those of the Australian mainland. Knox (1963) classified Lord Howe and Norfolk Islands in separate biogeographical provinces, the Phillipian and Norfolkian respectively, although they had previously been joined in a single province (Dell, 1958).

The three species *B. melanostoma*, *B. vittatum* and *B. flavescens* are clearly very closely related and have in the past been considered synonymous (H. Anderson, 1958), since their shells may be of similar appearance. It is shown here that they are separable by their penial anatomy, and that their distributions do not overlap. *B. vittatum* may undergo direct development in benthic egg masses (H. Anderson, 1958, as *B. melanostoma*), and the protoconchs of *B. melanostoma* and *B. flavescens* suggest that they may have a similar development. The lack of a planktonic stage in all three species could explain their potential for isolation and allopatric speciation. It is surprising that *Bembicium* on Lord Howe and Norfolk Islands appear to be conspecific when separated by about 1000 kms of open ocean, but current patterns do not preclude circulation between the islands (see charts in Endean *et al.*, 1956) and might carry egg masses attached to floating debris. Populations of *B. melanostoma* exist on either side of Bass Strait, but there are no records of this species west of Port Phillip Bay, nor of *B. vittatum* east of Port MacDonnell in South Australia. The 400 km stretch of coastline between these points is one of exposed headlands and sandy beaches, which may be unsuitable for either species. No records of *Bembicium* species are available from the remote coast of the Great Australian Bight between Ceduna and Albany, explaining a gap in the distribution maps. It is

noteworthy that the lack of rocky substrates between Perth and Geraldton (Wells, 1980) has not prevented *B. vittatum* from reaching the Houtman Abrolhos Islands.

A number of authors have mistakenly recorded species of *Bembicium* in lists of Recent molluscs of New Zealand (Deshayes & Milne Edwards, 1843, as *Trochus melanostomus*; Dunker & Zelebor, 1866, and von Martens, 1873, both as *Risella kiellmannsegi*; Hutton, 1878, as *Risella aurata*; Hutton, 1880, as *R. melanostoma*). Unless the Pleistocene records of *Bembicium* in New Zealand and the Kermadecs were only chance spatfalls, it is possible that extinction was caused by periodic subantarctic temperatures during the Pleistocene (see Beu, 1966; Marshall, 1981). Present day sea temperatures in New Zealand (Garner & Ridgway, 1965) and the Kermadecs (Marshall, 1981) are no cooler than those prevailing in Tasmania (Knox, 1963), where *Bembicium* is abundant. Since the molluscan fauna of the Kermadec Islands shows only weak affinity with that of New Zealand (Dell, 1958), it is likely that *Bembicium* reached the islands from Australia, via Norfolk Island.

Risellopsis varia is found throughout New Zealand and the Chatham Islands (Suter, 1913; Powell, 1979).

Relationships Within The Littorinacea

In the preceding sections describing the morphology of *Bembicium* and *Risellopsis*, the attempt has been made to assess character states as plesiomorphic or apomorphic with respect to other littorinacean taxa. However, it will be apparent that the choice of outgroup on which to base such decisions is unclear, and that in some cases the choice alters the conclusion. A detailed account of the phylogeny of the Littorinidae, and the relationships with other littorinacean families, is in preparation, but here it is appropriate to review briefly the current ideas, in the light of new information about *Bembicium* and *Risellopsis*.

The anatomy of a number of littorinid genera, including *Littorina*, *Melarhappe*, *Cenchritis*, *Tectarius*, *Echininus*, *Nodilittorina* and *Littoraria*, is now fairly well known, as reviewed in the preceding sections and by Reid (1986). These 'typical' littorinids seem to form a natural group, united by the presence of sperm nurse cells, specialised penial glands or glandular discs, a generally open prostate, production of pelagic egg capsules, a complex spiral pallial oviduct with anterior bursa copulatrix and posterior seminal receptacle, and subepithelial albumen and capsule glands in the pallial oviduct, although some of these characters may be secondarily lost.

Unfortunately the anatomy of *Lacuna* and related genera is poorly known; only *L. pallidula* has been described in detail (Gallien & de Larambergue, 1938), although *L. vincta* is similar (pers. obs.).

Traditionally, these have been grouped as a separate family, the Lacunidae, on the basis of their umbilicate shells, low and subtidal habitat, pair of opercular tentacles, and radular characters. Ponder (1976) has pointed out that none of these characters is of significance at the family level, and has tentatively included the *Lacuna* group as a primitive subfamily of the Littorinidae. Other characters of this group which should be noted are the absence of sperm nurse cells, the presence of unspecialised subepithelial glands in the penis, the closure of the prostate, pallial vas deferens and penial sperm duct, the anterior bursa copulatrix, the absence of a seminal receptacle, the storage of sperm in the renal oviduct, the epithelial albumen glands in the multispiral pallial oviduct, and the absence of capsule glands. Several Antarctic genera, such as *Laevilitorina* and *Laevilacunaria*, appear to be intermediate between littorinids and lacunids in shell and radular characters (Ponder, 1976; Arnaud & Bandel, 1978), but almost nothing is known of their anatomy.

The affinities of the freshwater *Cremnoconchus* are doubtful. It is usually placed in the Littorinidae, although at least a separate subfamily may be desirable. Its anatomy has been described by Linke (1935), and characters include the absence of penial glands, the retraction of the penial filament, the closed prostate, pallial vas deferens and penial sperm duct, the anterior bursa copulatrix, the absence of a seminal receptacle, storage of sperm in the renal oviduct, and the multispiral pallial oviduct with capsule glands. It is not known whether sperm nurse cells are present.

Looking to more distantly related littorinaceans, the terrestrial Pomatiasidae (as represented by *Pomatias elegans*, described by Creek, 1951) show an absence of penial glands, a closed prostate, pallial vas deferens and penial sperm duct, no anterior bursa copulatrix, a widely open pallial oviduct, storage of sperm in the ovarian oviduct, opening of the renal oviduct into a posterior muscular chamber (possibly homologous with the seminal receptacle) and albumen and 'capsule' glands of the epithelial type.

The Eatoniellidae are believed to be primitive littorinaceans (Ponder, 1968; Ponder & Yoo, 1978) and are aphallate, with open pallial gonoducts in both sexes, no anterior bursa copulatrix, a posterior seminal receptacle for the storage of sperm and a pallial oviduct with epithelial glands.

The following tentative interpretation is suggested. With the Pomatiasidae and Eatoniellidae as outgroups, the family Littorinidae is defined by the synapomorphies of an anterior bursa copulatrix, closed pallial oviduct, and a spiral route of the egg groove within the pallial oviduct. There is no justification for separating the Bembiciidae as a separate family. From the available information *Bembicium* and *Risellopsis* together seem to form a distinct group within the Littorinidae, defined by the synapomorphies of the anterior salivary glands, the

anterior position of the junction of the duct of the seminal receptacle with the pallial oviduct, the longitudinal division of the jelly gland (shared with *Lacuna*) and shell shape (a convergence with *Peasiella*), and also by their Australasian distribution. This group could be recognised as a subfamily, to stand alongside Littorininae (synapomorphies of sperm nurse cells, mamilliform or disc-shaped penial glands, pelagic egg capsules, subepithelial albumen and capsule glands in pallial oviduct), and Lacuninae (loss of seminal receptacle, closed prostate). Confirmation or rejection of this scheme must await information on the anatomy of Antarctic littorinids, Arctic genera related to *Lacuna* and further details of *Cremnoconchus*. It is not at present possible to evaluate the relationships between these 'subfamilial' groups. Even from the brief descriptions given above, it will be seen that convergence of characters has occurred. The *Bembicium* group may appear to share characters with the Littorininae (seminal receptacle, open prostate), but these are synplesiomorphies.

Excluded Species

Brief accounts are given here of species which have been placed in the genera *Bembicium*, *Risella* or *Risellopsis* by previous authors, but which should now be excluded. Mesozoic fossils ascribed to *Risella* by Cossmann (1915) and Tertiary vitrinellids from New Zealand once placed in *Risellopsis*, have been discussed above.

Genus *Peasiella* Nevill, 1885

Shells of the littorinid genus *Peasiella* bear a close resemblance to those of *Bembicium* and *Risellopsis*. They are trochoidal and umbilicate, sculptured with spiral grooves, sometimes also with axial folds and peripheral crenulations, occasionally with periostracal hairs, and reach a maximum diameter of 6.6 mm. Well preserved shells can be distinguished from *Bembicium* by the form of the protoconch, which is 0.23 to 0.27 mm in diameter, of 2.0 to 2.2 whorls, sculptured by four wavy spiral ridges, and terminated by a marked sinusigera notch. The operculum is multispiral, unlike that of either *Bembicium* or *Risellopsis*. Anatomically, *Peasiella* is clearly separated by the vermiform penis, usually with a single penial gland, the form of the pallial oviduct (capsule glands are present, the bursa copulatrix vestigial or absent) and production of pelagic egg capsules. It is believed to be related to such typical littorinid genera as *Nodilittorina*, *Tectarius*, *Echininus* and *Cenchritis* (Reid, 1986). The genus *Peasiella* is widely distributed in the Indo-Pacific region, occupying crevices on rocks and mangroves, high in the intertidal zone.

Peasiella has in the past been considered a subgenus of *Risella* (e.g. Nevill, 1885; Tryon, 1887). Although given generic status by Thiele (1929) and

Wenz (1938), confusion still arises and the genus *Bembicium* is still sometimes used for the members of *Peasiella* (e.g. Glibert, 1962; Cernohorsky, 1978). A systematic account of *Peasiella* is in preparation, but meanwhile the available names for Recent species of the genus may be listed: *Margarita angulata* A. Adams, 1853; *Risella balteata* Preston, 1908; *Risella isseli* var. *carinata* Pallary, 1926; *Trochus conoidalis* Pease, 1868; *Trochus diminutivus* Reeve, 1862; *Cyclostrema fuscopiperata* Turton, 1932; *Echinella gaidei* Montrouzier, 1879; *Risella infracostata* Issel, 1869; *Risella isseli* Semper in Issel, 1869; *Risella isseli* var. *mauritanica* Viader, 1951; *Risella templiana* var. *nigrofasciata* Nevill, 1885; *Risella parvula* Dunker, 1861; *Risella roepstorffiana* Nevill, 1885; *Trochus sismondae* Issel, 1869; *Risella templiana* var. *subimbricata* Nevill, 1885; *Risella tantillus* var. *subinfracostata* Nevill, 1885; *Trochus tantillus* Gould, 1849; *Risella templiana* Nevill, 1885; *Risella isseli* var. *undata* Pallary, 1926. The names of the Tertiary species of *Peasiella* include the following: *Xenophora bouryi* Cossman, 1888; *Risella girondica* Benoist, 1874; *Trochus minutus* Deshayes, 1824; *Tornus orthezensis* Cossmann & Peyrot, 1915; *Xenophora pontileviensis* Morgan, 1915; *Pseudonina reyti* Cossmann & Peyrot, 1917; *Xenophora rhythida* Cossmann, 1900.

Risellopsis mutabilis May, 1909

The shell is superficially similar to that of *Risellopsis varia*, although with a more expanded last whorl and a groove outlining the umbilicus. The interior is greyish and does not appear nacreous, and the external colouration is purple black with two to three large, irregular white blotches at the shoulder

and suture of the final whorl in the largest shells (4 mm). The operculum is round and multispiral, the radula rhipidoglossate, and there are traces of epipodial tentacles (pers. obs., NMV F52213). The species is therefore a member of the Trochidae, and the genus *Fossarus* A. Adams & Angas, 1864 seems appropriate (A. Warén, pers. comm.).

Fossarus caledonicus Crosse, 1874

Although described as a *Fossarus*, this species has subsequently been placed in *Peasiella*, as a subgenus of *Risella* (Tryon, 1887; Kesteven, 1902). The shell bears superficial resemblance to *Peasiella* (see Crosse, 1875), but shows curious fine axial wrinkles, no spiral sculpture, a single strong basal rib, and a protoconch which suggests direct development. The operculum is round and multispiral. The radula is short and taenioglossate, with elongate, multicusped teeth. This species is believed to be a member of the Omphalotropinae (Assimineidae, Rissoacea) (W.F. Ponder, pers. comm.).

SYSTEMATIC DESCRIPTIONS

The range of intraspecific variation in shell characters in *Bembicium* is such that identification of unlocalised dry shells can be difficult or impossible. The following key therefore also makes use of anatomical characters and geographical distribution. For easier comparison, Table 1 lists the conchological characters of Recent *Bembicium* species. The key includes a short diagnosis of *Peasiella*, the range of which overlaps that of *Bembicium* in Queensland, and shells of which can easily be confused with juvenile *Bembicium*.

Table 1. Summary of shell characters of Recent *Bembicium* species.

Species	Radial folds, last whorl	Primary grooves, whorls 3-4	Total grooves, last whorl	Ridges on base, whorls 3-4	Ridges on base, last whorl	Columella colour	Aperture colour	Mean height/diameter ratio (\pm 95% confidence limits)
<i>B. melanostoma</i>	13-20	5	5-7	5-6	5-9	orange; (brown)	brown	0.855 \pm 0.020
<i>B. vittatum</i>	16-20 (12-25)	5-6	5-7(8)	5-6	7-9 (5-10)	orange, cream	brown, orange-brown	0.776 \pm 0.028
<i>B. flavescens</i>	14-23	5-6	5-7(9)	6-9	6-9	orange, (pink-brown)	brown	0.802 \pm 0.031
<i>B. auratum</i>	11-17 (9-21)	6-7	7-11 (6-12)	5	7-11	white, pale brown	cream or brown callus, usually 1-4 brown stripes at margin	0.965 \pm 0.024
<i>B. nanum</i>	15-20	4-5	7-9	3-4	4-7	white, pale orange	white, 4-10 brown stripes at margin, cream or brown callus	0.798 \pm 0.028

Parentheses indicate extremes of range.

Key to Recent species of *Bembicium* and *Risellopsis*

1. Shell small (< 6.6 mm diameter); protoconch 2.0–2.2 whorls, sculptured by 4 wavy spiral ridges; operculum multispiral; penis vermiform, usually with a single mamilliform penial gland; pallial oviduct lacks bursa copulatrix, capsule glands present. *Peasiella*
 — Shell up to 28 mm diameter; protoconch 1.25–1.5 whorls, smooth; operculum paucispiral; penis broad, lacking penial glands; pallial oviduct with bursa copulatrix, capsule glands absent. 2
2. Shell < 8.3 mm diameter; 0–3 spiral ribs above peripheral keel, 4 on base; periostracum produced into bristles on ribs of well-preserved specimens; operculum paucispiral type B; New Zealand. *Risellopsis varia*
 — Shell up to 28 mm diameter; 4–11 grooves above peripheral keel, 3–11 ridges on base; operculum paucispiral type A; Australia. (*Bembicium*) 3
3. 5–7 (rarely 9) spiral grooves above peripheral keel on last whorl; columella usually orange; aperture dark brown within. 4
 — 7–12 spiral grooves above peripheral keel on last whorl; columella usually white, cream or brown; aperture cream or brown within, usually with black or brown and white stripes at margin. 5
4. 6–9 ridges on base of juveniles of 3–4 whorls; no umbilicus even in juveniles; apex sometimes blunt; penis Fig. 15a–h; Lord Howe and Norfolk Is. *B. flavescens*
 — 5–6 ridges on base of juveniles of 3–4 whorls; umbilicus in juveniles only; penis Fig. 8; Tasmania and Victoria. *B. melanostoma*
 — 5–6 ridges on base of juveniles of 3–4 whorls; umbilicus may persist in adult shells; penis Fig. 12; South and Western Australia. *B. vittatum*
5. 6–7 primary grooves on early whorls, 7–12 on last whorl; 7–11 ridges on base of last whorl; exterior often with dark nodules at periphery; penis Fig. 18. *B. auratum*
 — 4–5 primary grooves on early whorls, 7–9 on last whorl; 4–7 ridges on base of last whorl; exterior with 18–38 oblique black lines, of which 4–10 are visible within margin of aperture; penis Fig. 15i–p. *B. nanum*

Genus *Bembicium* Philippi, 1846

Risella Gray, 1842: 60 [type species by subsequent designation (Gray, 1847) *Trochus melanostoma* Gmelin]. Here regarded as a *nomen oblitum*.

Bembicium Philippi, 1846: 130 [type species by subsequent designation (Herrmannsen, 1846) *Trochus melanostomus* (sic) Gmelin].

Diagnosis. Shell trochoidal, periphery usually keeled, base rather flat; small umbilicus in juveniles, usually closed in adults; within aperture of adults a thickened ridge present below peripheral keel. Protoconch smooth, 1.25–1.5 whorls, 0.35–0.40 mm diameter, sinusigera rib weak or absent. Teleoconch sculptured by spiral grooves and axial folds. Operculum paucispiral type A. Gonochoristic. Prostate an open groove; anterior vas deferens over head and through penis a closed tube; penis simple, opening of sperm duct subterminal, subepithelial glands absent. Sperm of one type only, nurse cells absent in seminal vesicle. Pallial oviduct comprises a single proximal spiral of albumen gland, and an

enlarged distal jelly gland, the latter divided into inner and outer chambers, capsule glands absent; opening into mantle cavity small and subterminal; 2 long separate ducts connect posterior seminal receptacle and renal oviduct to pallial oviduct, close to opening of the latter into mantle cavity; anterior bursa copulatrix. Benthic gelatinous egg masses; development either direct or planktotrophic. Radula littorinoid, each tooth bearing single major cusp and 2–3 smaller cusps, major cusps closely similar in size and shape in each tooth row, but variable within species. Salivary glands anterior to nerve ring around oesophagus.

Bembicium melanostoma (Gmelin, 1791)

Figs 3a,b, 7–9, 11e,f

Trochus in fauce nigerrimus Chemnitz, 1781: 29, pl. 161, figs 1526a,b*.

Trochus melanostoma Gmelin, 1791: 3581 [refers to Chemnitz, 1781: pl. 161, figs 1526a,b; neotype (H. Anderson, 1958: 554) SAM D14590, Furneaux Island

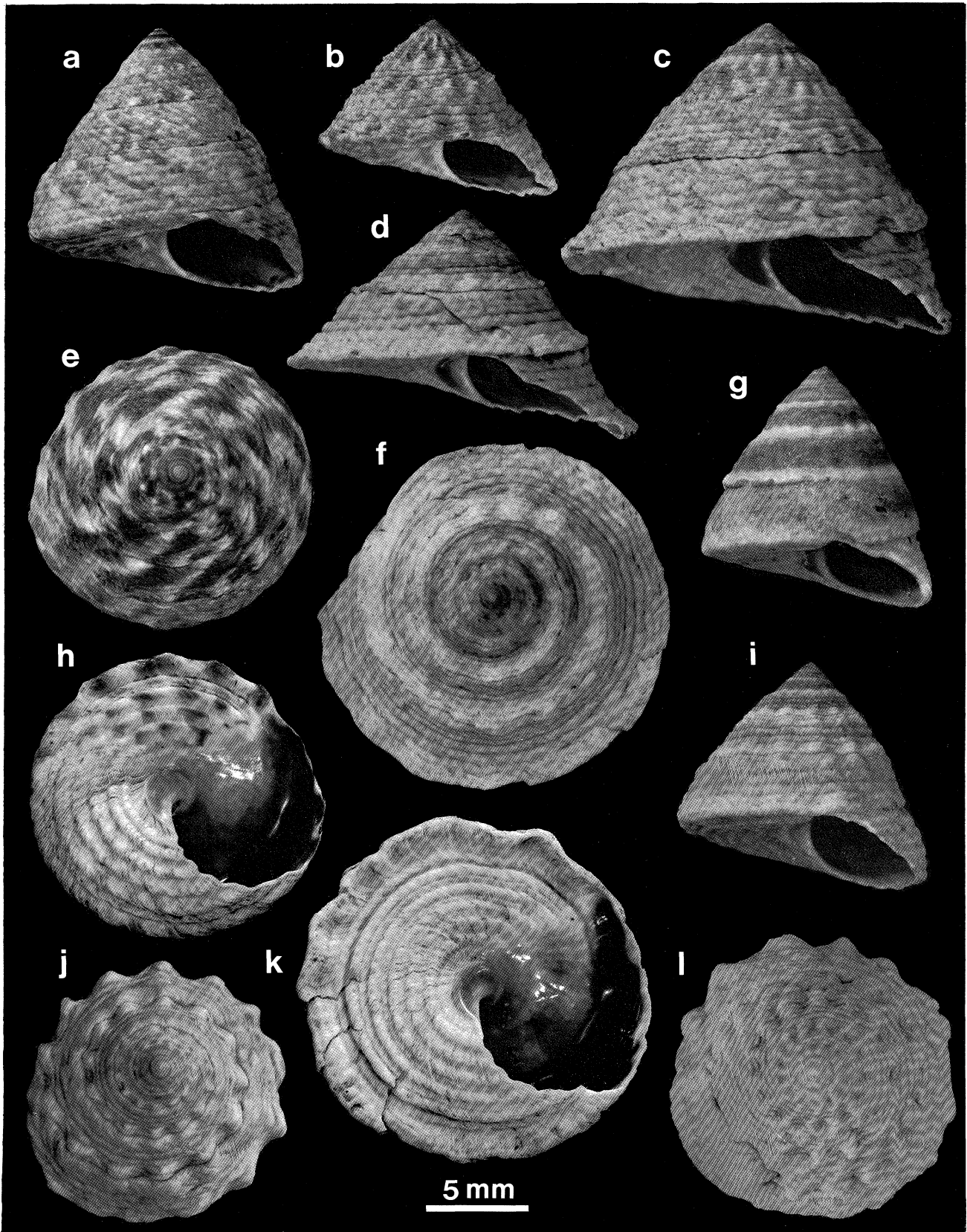


Fig.7. *Bembicium melanostoma* (Gmelin): a, Coal River estuary, south-east Tas. (TME14479); b, Western Port Bay, Vic. (AMS C81871); c,d,f,k (3 views), Duck Bay, Smithton, Tas. (TM E14255); e,h (2 views), Cardinia Creek, Western Port Bay, Vic. (BMNH); g,i, Welcome River, Tas. (TM E15138); j, Crayfish Creek, Tas. (TM E5823); l, whitened to show sculpture, Western Port Bay, Vic. (AMS C81871).

- Group, Bass Strait, Australia].—Dillwyn, 1817: 797 *; Deshayes & Milne Edwards, 1843: 157–158 *.
- Bembicium melanostomum* (sic).—Philippi, 1846: 130 [in part]; Kershaw, 1955: 307; MacPherson & Gabriel, 1962: 90.
- Bembicium melanostoma*.—May, 1921: 48 [in part]; May, 1923: pl. 22, fig. 20; Wenz, 1938: 523, fig. 1380 *; MacPherson & Chapple, 1951: 118; H. Anderson, 1958: 553–558, pl. 2, figs 1, 2c [in part]; Ludbrook, 1984: 70, figs 20f–h, pl. 10j.
- Risella melanostoma*.—Gray, 1847: 150 *; Philippi, 1853: 8, pl. 1, figs 21, 22 [in part]; Adams & Adams, 1858: pl. 33, figs 5a–c*; Crosse, 1864: 229–233, pl. 11, fig. 1; Angas, 1865: 172 [in part]; Smith, 1884: 61–62 [in part]*; Tryon, 1887: 262–263, pl. 49, figs 20, 21, pl. 50, figs 30, 31 [in part]; Pritchard & Gatliff, 1902: 92–94 [in part].
- Littorina melanostoma*.—Tenison-Woods, 1879: 61–65 [in part].
- Trochus luteus* Quoy & Gaimard, 1834: 271–273, pl. 62, figs 8–11 [lectotype MNHNP, 15.2 x 15.8 mm, Port Western [Western Port Bay, Victoria, Australia] here restricted].
- Bembicium luteum*.—Philippi, 1846: 132 [in part]*.
- Risella lutea*.—Philippi, 1853: 4, pl. 1, figs 1, 2 [in part]*; Chenu, 1859: 302, fig. 2126*; Crosse, 1864: 237–239*; Fischer, 1879: 463, pl. 38, figs 2, 2a, 2b [in part]; Smith, 1884: 61–62 [in part]*.
- Trochus melanostoma* Reeve, 1842a: 185 [possible syntypes BMNH 1986074, 'coast of New Holland', here restricted to Tasmania].—Reeve, 1842b: 166, pl. 218, fig. 16.
- Bembicium lividum* Philippi, 1846: 131 [lectotype Philippi, 1853: pl. 1, fig. 27, New Holland]*.
- Risella livida*.—Philippi, 1853: 10, pl. 1, figs 27, 28*; Crosse, 1864: 240–241*.
- Trochus (Bembicium) squamiferus*.—Gould, 1852: 192, pl. 14, figs 227, 227a [not 'Koch' Philippi, 1844]*.
- Risella aurata*.—Tenison-Woods, 1877 [in part, not Quoy & Gaimard, 1934].
- Bembicium planum*.—Kershaw, 1955: 307 [not Philippi, 1846].

* references without adequate locality data may refer to either or both *B. melanostoma* and *B. vittatum*.

Nomenclature. The synonymy is complicated by the closely similar, and often indistinguishable, shells of *B. melanostoma* and *B. vittatum*. Published figures and most dry shells can only be identified with certainty when accompanied by locality data, since the two species are allopatric.

In his description of *Trochus melanostoma*, Gmelin refers to figures by Chemnitz (1781) of a shell collected by Cook in the 'South Seas'. The figures are poor, but the status of the species has been fixed by H. Anderson (1958), who designated as neotype a specimen from the Furneaux Island Group.

Quoy & Gaimard (1834) described *Trochus luteus*, and mentioned two localities in their text, Port du Roi-Georges (King George Sound, W.A.) and Port Western (Western Port Bay, Victoria). There are two syntypic lots in the MNHNP; one is labelled 'P.R.G.' (probably Port du Roi-Georges). The other,

unlocalised, includes the figured specimen (Quoy & Gaimard, 1834, pl. 62, fig. 8) which was also illustrated by H. Anderson (1958, pl. 2, fig. 2e). The shells in this lot resemble others from Western Port Bay more closely than the more depressed shells of *B. vittatum* from King George Sound. By designation of the figured specimen as lectotype, and restriction of the type locality to Port-Western, *Trochus luteus* is established as a synonym of *B. melanostoma*.

Reeve (1842a,b), apparently unaware of Gmelin's earlier use of the name, described *Trochus melanostoma* from 'New Holland'. Possible syntypes have been selected from the Cuming Collection in the BMNH, which resemble Reeve's figure. An original label accompanying the lot states the locality as Tasmania, and the type locality is fixed accordingly.

It should be noted that since '*melanostoma*' was used as a noun in apposition by Gmelin, the ending remains unchanged in combination with the generic name *Bembicium*.

Shell. (Fig. 7) DIMENSIONS. Adult size range 6.5–25 mm diameter; mean height/diameter ratio 0.855 (st. dev.=0.103, range 0.624–1.104, n=100 from 58 localities).

SHAPE. Teleoconch 5.5–7 whorls; shell of moderate thickness. Outline approximately equilaterally conical; sides lightly convex; base flat to slightly concave. Periphery strongly keeled, sometimes sharply flanged, but may become a little rounded on last whorl; sutures indistinct, unless preceding whorl is flanged. Small umbilicus in juvenile shells, becoming closed during fourth whorl. Ridge below peripheral keel in aperture is poorly developed.

SCULPTURE. Protoconch smooth, 0.40 mm diameter, 1.5 whorls, terminated by a growth line with no evidence of a sinusigera notch. First whorl of teleoconch marked by spiral striae and growth lines. On second whorl, 5 primary spiral grooves appear above periphery, 1–2 times the width of the rounded ribs between them; also on second whorl, radial folds appear, numbering 12–16 per whorl, and stretching from suture to periphery. Microsculpture of fine spiral threads, covering entire surface. Persistence of radial folds on subsequent whorls is variable; most commonly they become restricted to periphery, numbering 13–20 per whorl, and then obsolete on last 1–2 whorls, but sometimes persist, strongly crenulating periphery of last whorl, or may be absent after whorl 3. Spiral ribs and grooves persist, grooves are narrow and number 5–7 above periphery on last whorl, ribs a little narrower towards periphery. On larger whorls, microsculpture becomes oblique relative to spiral grooves, but remains perpendicular to the closely-spaced growth lines. On juvenile shells of 3–4 whorls, base is marked by 5–6 narrow spiral ridges, of which outermost is most prominent; a single additional ridge appears outside the prominent ridge, and single ridges in some inner

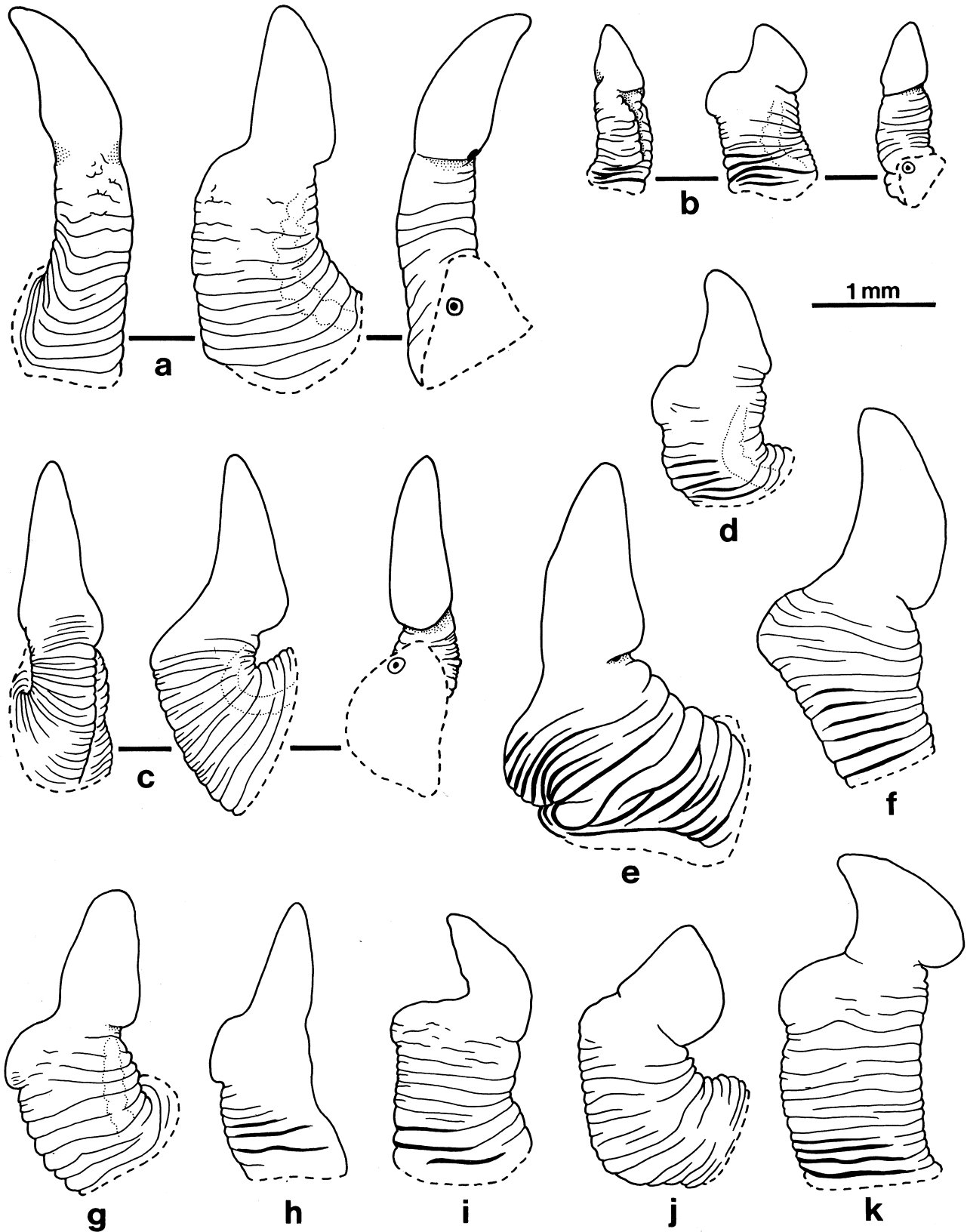


Fig.8. Penes of *Bembicium melanostoma* (Gmelin): a,c, Pittwater, 12 miles east-north-east Cambridge, Tas. (AMS C144404); b, Sidmouth, West Tamar River, Tas. (AMS C144332); d, Cremorne, Frederick Henry Bay, Tas. (AMS C144370); e, Eaglehawk Bay, Norfolk Bay, Tas. (AMS C144315); f, Brighton, Vic. (NMV F52230); g, Reidle Bay, Maria Island, Tas. (AMS C144403); h, Oyster Cove, Tas. (TME E12523); i, Simpson's Bay, Bruni Island, Tas. (TME E4860); j, Cat Bay, Phillip Island, Vic. (NMV F52207); k, Summerlands, Phillip Island, Vic. (NMV F5576); a,b,c, each show dorsal, lateral and ventral views (relative to orientation of head), all others are lateral views.

grooves, giving 5–9 subequal rounded ridges on base of last whorl; grooves between are 0.5–1 times rib width, marked by spiral microsculpture and close radial growth lines.

COLOUR. Shell cream to blue grey, peripheral folds or flange usually conspicuously paler; surface usually faintly flecked with darker grey, or occasionally with a dark purple brown pattern of irregular stripes and blotches. Eroded shells are black brown with a peripheral white stripe. Base commonly cream and unmarked, but sometimes with grey or brown flecks and spots on ribs. Columella almost always orange, sometimes orange brown or brown. Within aperture, area from suture to periphery is dark brown; base cream, parietal callus area cream to pale orange.

Animal. PENIS (Fig. 8). Filament $\frac{1}{3}$ – $\frac{1}{2}$ length of penis, laterally flattened, often elongate and curved away from opening of sperm duct, tip rounded; base lightly or not at all pigmented.

PALLIAL OVIDUCT (Fig. 3a).

RADULA (Fig. 11e,f). Length to 40 mm; relative length 1.93–2.67.

Distribution. **HABITAT.** Intertidal sand and mud flats in sheltered inlets; salt marshes and sometimes mangroves; eulittoral of sheltered rocky shores.

RANGE. (Fig. 9). Tasmania, Western Port and Port Phillip Bays, Victoria.

RECORDS. Victoria: Swan Bay (AMS, USNM); Portarlington (NMV); Williamstown (NMV,

USNM); Quail Island (NMV); Cardinia Creek, Western Port Bay (DGR); Cat Bay, Phillip Island (NMV); Palana, Flinders Island (TM); Tasmania: West Point, Marrawah (TM); Welcome River (TM); Duck Bay, Smithton (TM); Batman Bridge, Tamar River estuary (AMS); Sidmouth, West Tamar River (AMS); Mussel Roe Bay (TM); Cape Barren Island (TM); Coles Bay (TM); north side Reidle Bay, Maria Island (AMS); Pittwater, 12 miles east-north-east Cambridge (AMS); Eaglehawk Bay, south-east Norfolk Bay (AMS); Oyster Cove (TM); Simpsons Bay, Brunni Island (TM)

Remarks. The three species in the *melanostoma* group, *B. melanostoma*, *B. vittatum* and *B. flavescens*, are closely related. Shell characters which distinguish the group from the remaining two Recent species of *Bembicium* include the five to seven (sometimes up to nine) distinct spiral grooves above the periphery on the last whorl, five to nine ridges on the base of small shells of three to four whorls, and the colouration of the aperture, with a dark brown interior and orange columella. Although the combination of these features is characteristic, no single one is diagnostic (Table 1). Within the *melanostoma* group, *B. flavescens* can usually be distinguished by its smaller size, often blunt apex and lack of an umbilicus even in juveniles. The shells of *B. melanostoma* and *B. vittatum* are often inseparable, although a very small umbilicus is often

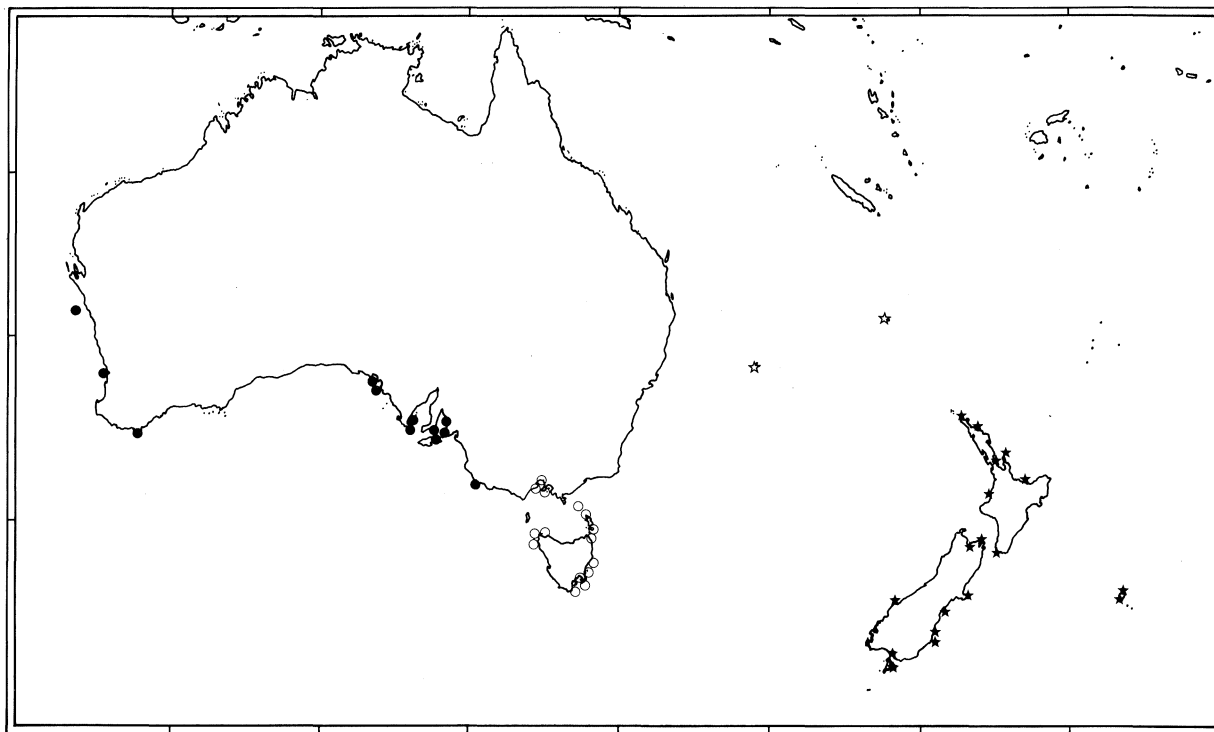


Fig. 9. Distribution of *Bembicium vittatum* Philippi (closed circles), *B. melanostoma* (Gmelin) (open circles), *B. flavescens* (Philippi) (open asterisks) and *Risellopsis varia* (Hutton) (closed asterisks).

present in adult shells of *B. vittatum*, but not in *B. melanostoma*. Also, the rather small, thin-shelled form of *B. vittatum* with a rounded periphery, found in sheltered bays in South Australia (described by Crosse as *Risella bruni*, e.g. Fig. 10j,k), is unique to this species.

The separation of the allopatric species *B. melanostoma*, *B. vittatum* and *B. flavescens* is based on consistent differences in penial shape. Since this may imply reproductive isolation, they are considered to be full species, rather than geographical subspecies, despite the close similarity of their shells. An electrophoretic analysis of isoenzymes would be desirable to test this conclusion. The 400 km stretch of coastline between the westernmost limit of *B. melanostoma* (Port Phillip Bay) and the easternmost limit of *B. melanostoma* (Port MacDonnell) is possibly too exposed for survival of either species. However, material of *Bembicium* species from this area in museums is limited and examination of this region for possible sympatric or intermediate populations would be desirable.

Bembicium melanostoma has been recorded as a Pleistocene fossil in New Zealand, but the available specimens are worn (e.g. Fig. 24h) and, in the absence of anatomical information, cannot be assigned with certainty to any of the three species of the *melanostoma* group.

***Bembicium vittatum* Philippi, 1846**

Figs 9, 10, 11a–d, 12

Bembicium vittatum Philippi, 1846: 131 [lectotype Philippi, 1853: pl. 1, fig. 25; Adelaide, New Holland].—Cotton & Godfrey, 1938: 10.

Risella vittata.—Philippi, 1853: 9, pl. 1, figs 25, 26; Crosse, 1864: 241–242.

Risella fimbriata Philippi, 1851: 32 [no locality].—Philippi, 1853: 5–6, pl. 1, figs 9, 10 [lectotype fig. 9].

Risella bruni Crosse, 1864: 239–240, pl. 11, fig. 3 [syntypes BMNH 1870.10.26.152; Spencer Gulf, South Australia].—Angas, 1865: 173; Smith, 1884: 61.

Bembicium bruni.—Cotton & Godfrey, 1938: 10.

Risella lutea.—Fischer, 1879: 463 [in part, not Quoy & Gaimard, 1834].

Risella melanostoma.—Angas, 1865: 172 [in part, not Gmelin, 1791]; Tryon, 1887: 262–263, pl. 49, figs 15, 26–29 [in part, not Gmelin, 1791]; Pritchard & Gatliff, 1902: 92–94 [in part, not Gmelin, 1791]; Verco, 1908: 8 [not Gmelin, 1791].

Littorina melanostoma.—Tenison-Woods, 1879: 61–65 [in part, not Gmelin, 1791].

Bembicium melanostoma.—Hedley, 1916: 187 [not Gmelin, 1791]; H. Anderson, 1958: 553–558, pl. 1 fig. 2 (egg masses), pls 3–5 [a–c in part, not Gmelin, 1791].

Risella aurata.—Tenison-Woods, 1877 [in part, not Quoy & Gaimard, 1834].

Bembicium auratum.—Wells, 1980: 240 [not Quoy & Gaimard, 1834]; Wells & Bryce, 1986: pl. 10, no. 114 [not Quoy & Gaimard, 1834].

Note: refer also to synonymy of *B. melanostoma*.

Nomenclature. *Bembicium vittatum* and *B. melanostoma* cannot be reliably separated using shell characters alone; however, their geographical ranges are not known to overlap, and since Philippi gave the type locality 'Adelaide' for his species, the name *vittatum* can be associated with the western species of the *melanostoma* complex.

Philippi (1851) gave no locality for *Risella fimbriata*. This species is tentatively included in the synonymy of *B. vittatum* on the basis of the author's description of an open umbilicus, a feature which has not been seen in adult shells of *B. melanostoma*.

The shells described by Crosse (1864) as *Risella bruni* belong to a dwarf form of this species with rounded periphery and depressed outline, found in sheltered gulfs in South Australia.

Shell. (Fig. 10). DIMENSIONS. Adult size range 5.5–20 mm diameter; mean height/diameter ratio 0.776 (st. dev.=0.126, range 0.584–1.099, n=77 from 41 localities).

SHAPE. Teleoconch 5–7.5 whorls; shell of moderate thickness. Outline varies from low to equilaterally conical; sides lightly convex; base flat. Periphery strongly keeled, sometimes sharply flanged, but commonly becoming a little rounded on last whorl; sutures indistinct if whorls are flat, but clear in shells with slightly rounded whorls and in those with a prominent, undulating, peripheral flange. Small umbilicus present in juvenile shells, which often persists in adults. Ridge below peripheral keel within aperture is poorly developed.

SCULPTURE (Fig. 11a,b). Protoconch smooth, 0.37–0.45 mm diameter, 1.5 whorls, terminated by a growth line with no evidence of a sinusigera notch. First whorl of teleoconch marked by spiral striae and growth lines. On second and third whorls, 5–6 primary spiral grooves appear above periphery, approximately equal to width of the rounded ribs between them; also on third whorl, radial folds appear, numbering 11–17 per whorl, and stretching from suture to periphery. Microsculpture of fine spiral threads, covering entire surface. Persistence of radial folds on subsequent whorls variable; may remain prominent, numbering 16–20 (extremes of range 12–25) on last whorl, most well developed at periphery (especially shells from Houtman Abrolhos Islands), or more commonly become obsolete on last 1–3 whorls. Spiral ribs and grooves persist, grooves narrow, number 5–7 (rarely 8) above periphery on last whorl, ribs a little narrower towards periphery. On larger whorls, microsculpture becomes oblique relative to spiral grooves, but remains perpendicular to closely spaced growth lines. On juvenile shells of 3–4 whorls, base sculptured by 5–6 narrow spiral ridges, of which outermost most prominent; single ridges develop in some inner grooves to give 7–9 (extremes of range 5–10) subequal, rounded ridges on base of last whorl; grooves between are 1–3 times rib width, marked by spiral microsculpture and close

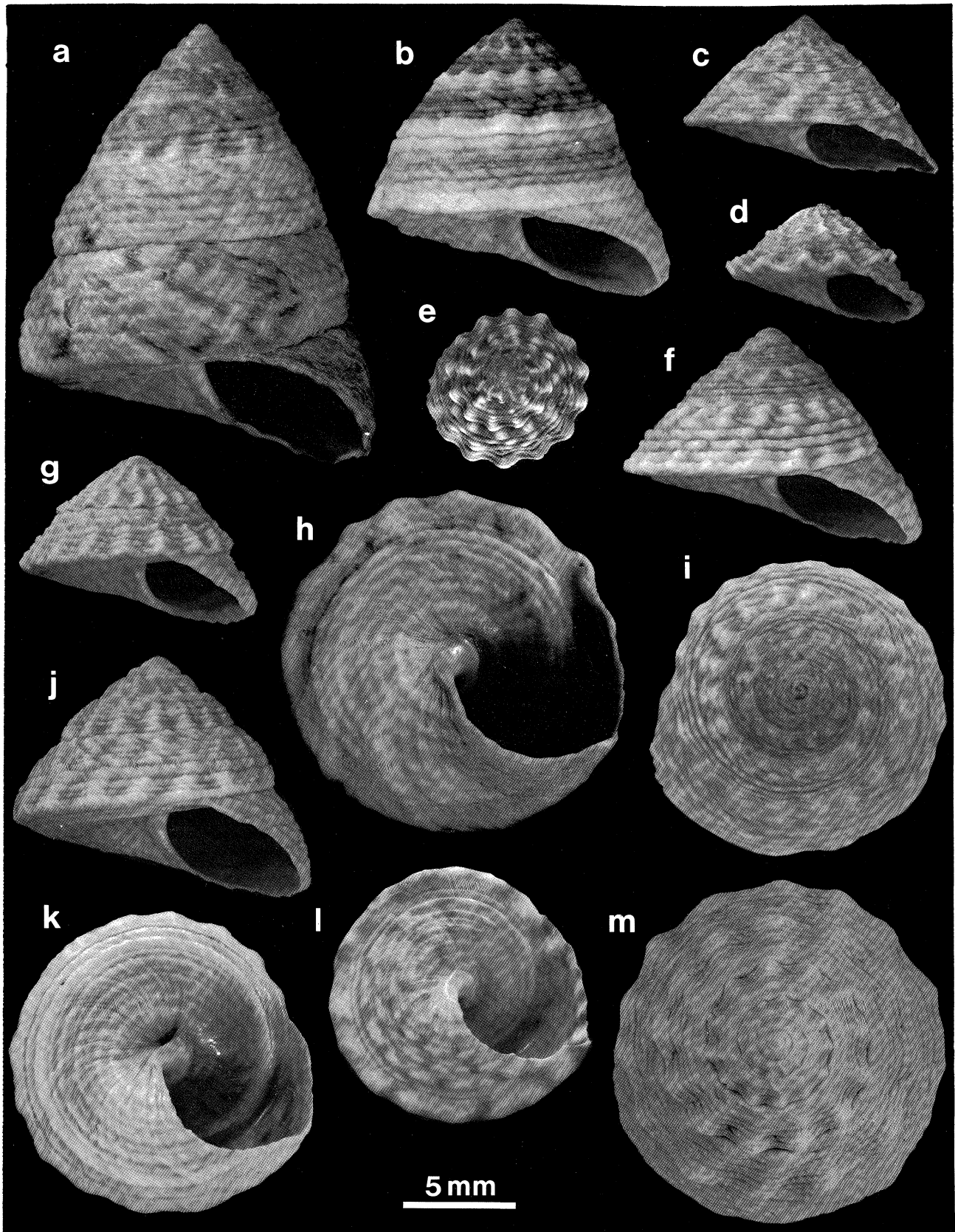


Fig. 10. *Bembicium vittatum* Philippi: **a**, Port Lincoln, S.A. (SAM D17473); **b,h**, St Kilda, Adelaide, S.A. (AMS); **c,l** (2 views), Salt Creek Bay, Yorke Peninsula, S.A. (SAM D17472); **d**, Mangrove Island, Abrolhos Islands, W.A. (WAM 421-85); **e**, Lusby Island, Sir Joseph Banks Group, S.A. (SAM D17474); **f,i** (2 views), **j,k** (2 views), Streaky Bay, S.A. (AMS C144305); **g**, Mangrove Island, Abrolhos Islands, W.A. (WAM N/1625); **m**, whitened to show sculpture, St Kilda, Adelaide, S.A. (AMS).

radial growth lines; ridges near umbilicus may be nodulose.

COLOUR. Shell cream to lilac grey, sometimes paler at suture or periphery; surface flecked and mottled with darker grey, occasionally with dark brown to black radial stripes in sculptural folds. Base may be unmarked or may bear brown flecks and spots on ribs. Columella orange or cream. Within aperture, area from suture to periphery is darkest, orange brown to dark brown; base cream; parietal callus area cream to pale orange.

Animal. PENIS (Fig. 12). Filament $\frac{1}{2}$ length of penis or greater, swollen, claw-shaped, pointed, with deep crease beside opening of sperm duct; base unpigmented or slightly so.

RADULA (Fig. 11c,d). Length to 35 mm; relative length 1.68–2.60.

Distribution. HABITAT. Intertidal sand and mud flats in sheltered inlets; salt marshes and mangroves; eulittoral of sheltered rocky shores.

RANGE (Fig. 9). From Port MacDonnell, South Australia, westward to Houtman Abrolhos Islands, Western Australia.

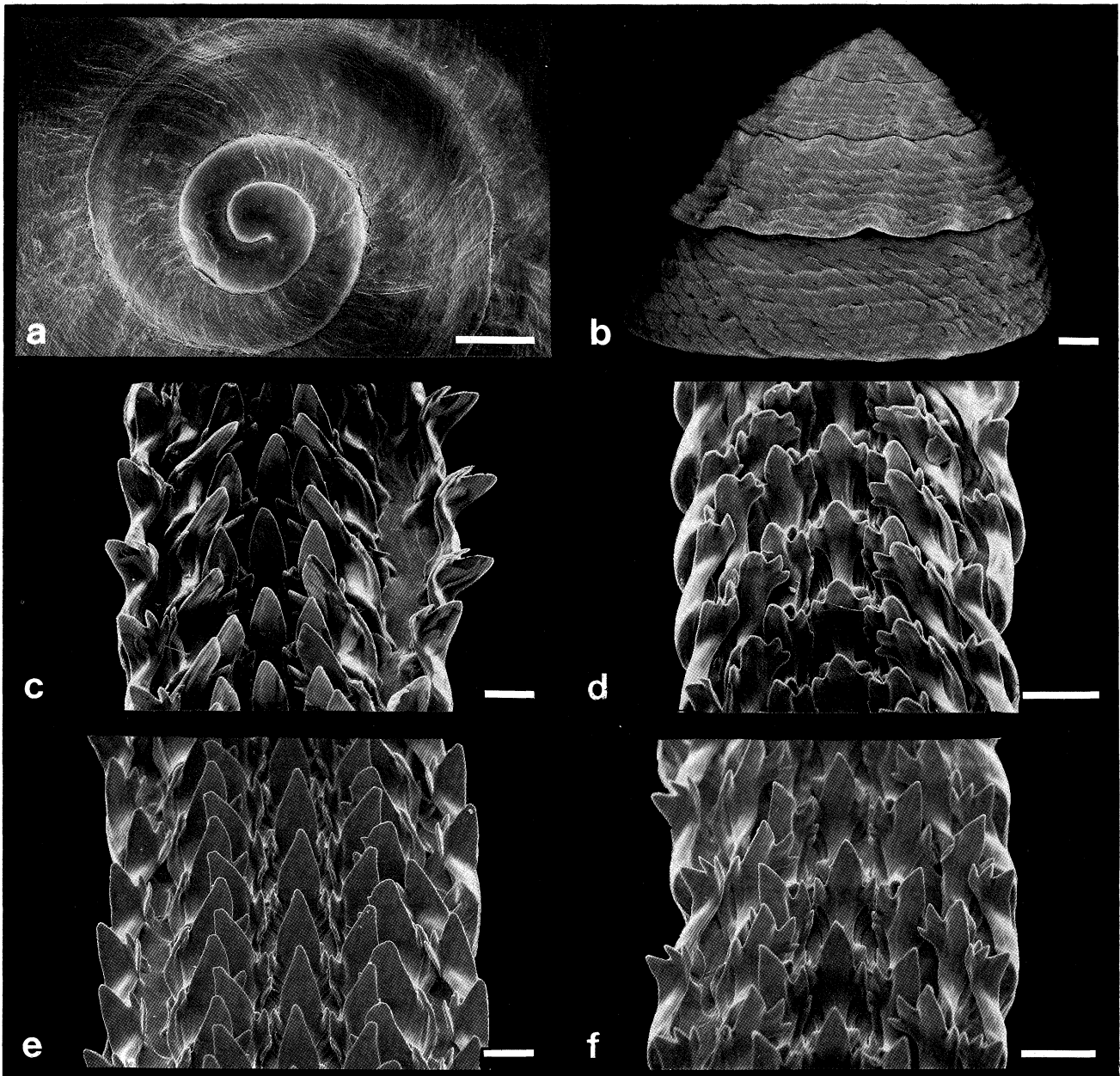


Fig. 11. *Bembicium vittatum* Philippi and *B. melanostoma* (Gmelin): **a,b** (2 views), *B. vittatum*, St Kilda, Adelaide, S.A. (AMS) (Bar a = 200 μ m, bar b = 1 mm); **c**, *B. vittatum* radula, Oyster Harbour, Albany, W.A. (AMS C144304); **d**, *B. vittatum* radula, Streaky Bay, S.A. (AMS C144305); **e**, *B. melanostoma* radula, Pittwater, 12 miles east-north-east Cambridge, Tas. (AMS C144402); **f**, *B. melanostoma* radula, Reidle Bay, Maria Island, Tas. (AMS C144403) (bar c–f = 50 μ m).

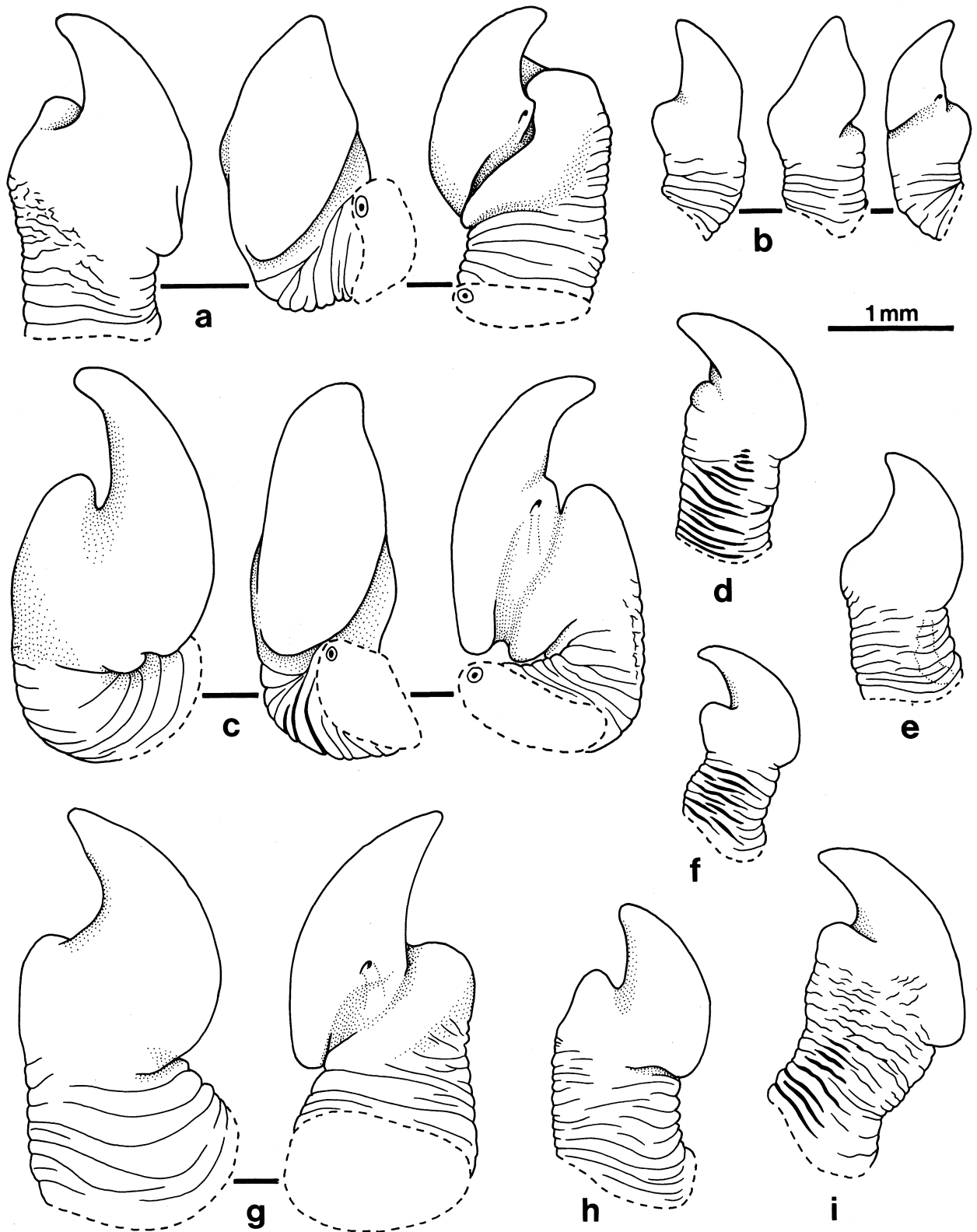


Fig.12. Penes of *Bembicium vittatum* Philippi: **a,c**, Streaky Bay, S.A. (AMS C144305); **b**, Kalgan River, Albany, W.A. (AMS C144321); **d**, MacDonnell Bay, S.A. (AMS C144377); **e,g**, Oyster Harbour, Albany, W.A. (AMS C144304); **f**, Bay of Shoals, Kangaroo Island, S.A. (AMS C144375); **h**, Little Rat Island, Houtman Abrolhos Islands, W.A. (AMS); **i**, Pelican Lagoon, Kangaroo Island, S.A. (AMS C144378); **a,b,c**, each show lateral, ventral and medial views (relative to orientation of head), **g**, lateral and medial views, all others are lateral views.

RECORDS. South Australia: MacDonnell Bay (AMS); Port Willunga (SAM); St Kilda, Adelaide (AMS); Edithburg (AMS); Pelican Lagoon, American River, Kangaroo Island (AMS, SAM); Tumbly Bay (AMS); Lusby Island (AMS); Port Lincoln (AMS, SAM); Streaky Bay (AMS); Thevenard, near Ceduna (AMS); Western Australia: Oyster Harbour, Albany (AMS, WAM, BMNH); Penguin Island (WAM); Little Rat Island, Houtman Abrolhos Islands (AMS); Wooded Island, Houtman Abrolhos Islands (AMS, WAM).

Remarks. See remarks on *B. melanostoma*.

***Bembicium flavescens* (Philippi, 1851)**

Figs 9, 13, 14, 15a–h

Risella flavescens Philippi, 1851: 39 [Norfolk Island].—

Philippi, 1853: 7, pl. 1, figs 17, 18 [lectotype fig. 18].

Risella plicatula Philippi, 1851: 39–40 [Norfolk Island].—

Philippi, 1853: 9, pl. 1, figs 23, 24 [lectotype fig. 23].

Risella (sic) *plicatula*.—Etheridge, 1889: 24, 29.

Risella melanostoma.—Smith, 1884: 61–62 [in part, not Gmelin, 1791]; Tryon, 1887: 262–263, pl. 49, figs 22–25 [in part, not Gmelin, 1791].

Bembicium melanostoma.—H. Anderson, 1958: 553–558 [in part, not Gmelin, 1791].

Nomenclature. Like other species in the genus, *Bembicium flavescens* is variable in sculpture, and Philippi's species *Risella plicatula* is simply a strongly sculptured form. Both *R. flavescens* and *R. plicatula* were said by Philippi (1851) to have been seen in the collection of Hanley. However, neither is present amongst the material of Hanley in the Leeds City Museum (A. Norris, pers. comm.) and therefore the figures subsequently published by Philippi (1853) have been designated as lectotypes.

Shell. (Fig. 13). DIMENSIONS. Adult size range 4.5–16 mm, mean height/diameter ratio 0.802 (st. dev.=0.086, range 0.641–1.031, n=31 from 12 localities).

SHAPE. Teleoconch 4.5–6.5 whorls; shell moderately solid. Outline approximately equilaterally conical, apex sometimes blunt, sides lightly convex, base flat. Periphery strongly keeled, often crenulated by radial folds; sutures distinct if preceding whorl has crenulated periphery, giving turreted outline to spire. No umbilicus, even in juveniles of only 3 whorls. Within aperture, ridge below peripheral keel inconspicuous even in adults.

SCULPTURE (Fig. 14a–e). Protoconch smooth, 0.40 mm diameter, 1.5 whorls, terminated by growth line with no evidence of sinusigera notch. First whorl of teleoconch marked by growth lines and spiral striae of microsculpture. On second whorl, 5–6 wide primary spiral grooves appear above periphery, 1–3 times width of irregularly rounded ribs between them; grooves contain microsculpture of fine spiral threads; also on second whorl 13–17 radial folds appear, stretching from suture to periphery. On later whorls spiral grooves increase to 5–7 (rarely up to 9),

becoming narrower than the ribs between; ribs are rendered beaded or minutely nodulose by radial growth lines, and persist to last whorl. Microsculpture spreads over ribs as well as grooves, becoming somewhat oblique relative to spiral ribs. Radial folds increase to 14–23 per whorl, most prominent at periphery; folds may become obsolete on last 1–2 whorls, or may persist strongly. Although prominent, peripheral keel seldom conspicuously flanged even in juvenile shells. On juvenile shells of 3–4 whorls, base convex and marked by 6–9 fine spiral ridges, of which only outermost but one is prominent; on later whorls ridges become subequal and rounded, separated by shallow grooves approximately equal to rib width; grooves crossed by closely spaced growth lines and indistinct spiral microsculpture.

COLOUR. Upper half of each whorl blue grey, lower half white or cream; gaps between radial folds grey to dark brown or purple black, sometimes forming irregular radial stripes and blotches. Base white to cream, marked by scattered purple-brown spots on ribs, or irregular radial flames. Columella and parietal callus salmon orange to pinkish brown; aperture dark brown except for part below peripheral keel which is white.

Animal. PENIS (Fig. 15a–h). Filament $\frac{1}{2}$ – $\frac{1}{3}$ length of penis, laterally compressed, blade-shaped; side of base away from sperm duct produced into a finely wrinkled flange, base unpigmented.

RADULA (Fig. 14g,h). Length to 28 mm; relative length 2.19–3.05.

Distribution. HABITAT. Mid to upper eulittoral rock platforms; stones on muddy beach (Etheridge, 1889).

RANGE (Fig. 9). Lord Howe Island, Norfolk Island.

RECORDS. Lord Howe Island: Ned's Beach (AMS); Signal Point (AMS); Old Gulch (AMS); Norfolk Island: Point Hunter Reserve (AMS); Cascade (AMS); Anson Bay (AMS).

Remarks. See remarks on *B. melanostoma*.

It may seem surprising that *B. flavescens* occurs on both Lord Howe and Norfolk Island, separated by about 1000 km, especially if, as is possible, the species has direct development. The two populations are anatomically and conchologically indistinguishable, however. Electrophoretic studies could be carried out to determine the degree of genetic difference between the populations.

***Bembicium auratum* (Quoy & Gaimard, 1834)**

Figs 2, 3d, 4, 16–20

Trochus auratus Quoy & Gaimard, 1834: 276–277, pl. 62, figs 15–19 [lectotype MNHNP 21.3 x 25.1 mm; Entrecasteaux Channel, Van Diemen's Island [Tasmania]].

Risella aurata.—Crosse, 1864: 233–234; Angas, 1865: 173; Tenison-Woods, 1877 [in part]; Fischer, 1879: 462–463, pl. 34, figs 2, 2a.

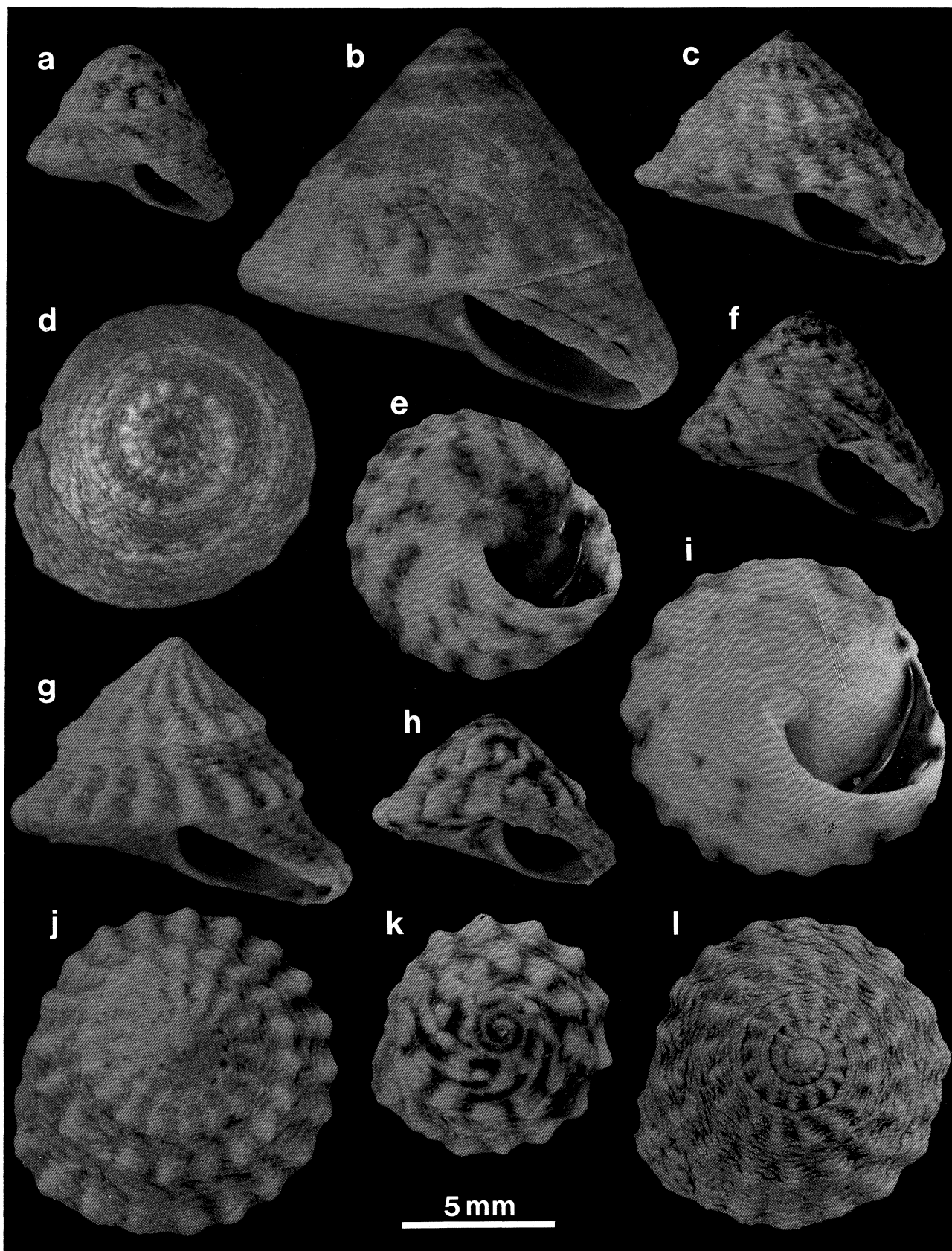


Fig.13. *Bembicium flavescens* (Philippi): a,c,e,f (2 views), h,k (2 views), Signal Point, Lord Howe Island (AMS C144350); b,g,j (2 views), Ned's Beach, Lord Howe Island (AMS C144404); d, Cascade, Norfolk Island (AMS C144354); i, Point Hunter Reserve, Norfolk Island (AMS C144401); l, whitened to show sculpture, Signal Point, Lord Howe Island (AMS C144350).

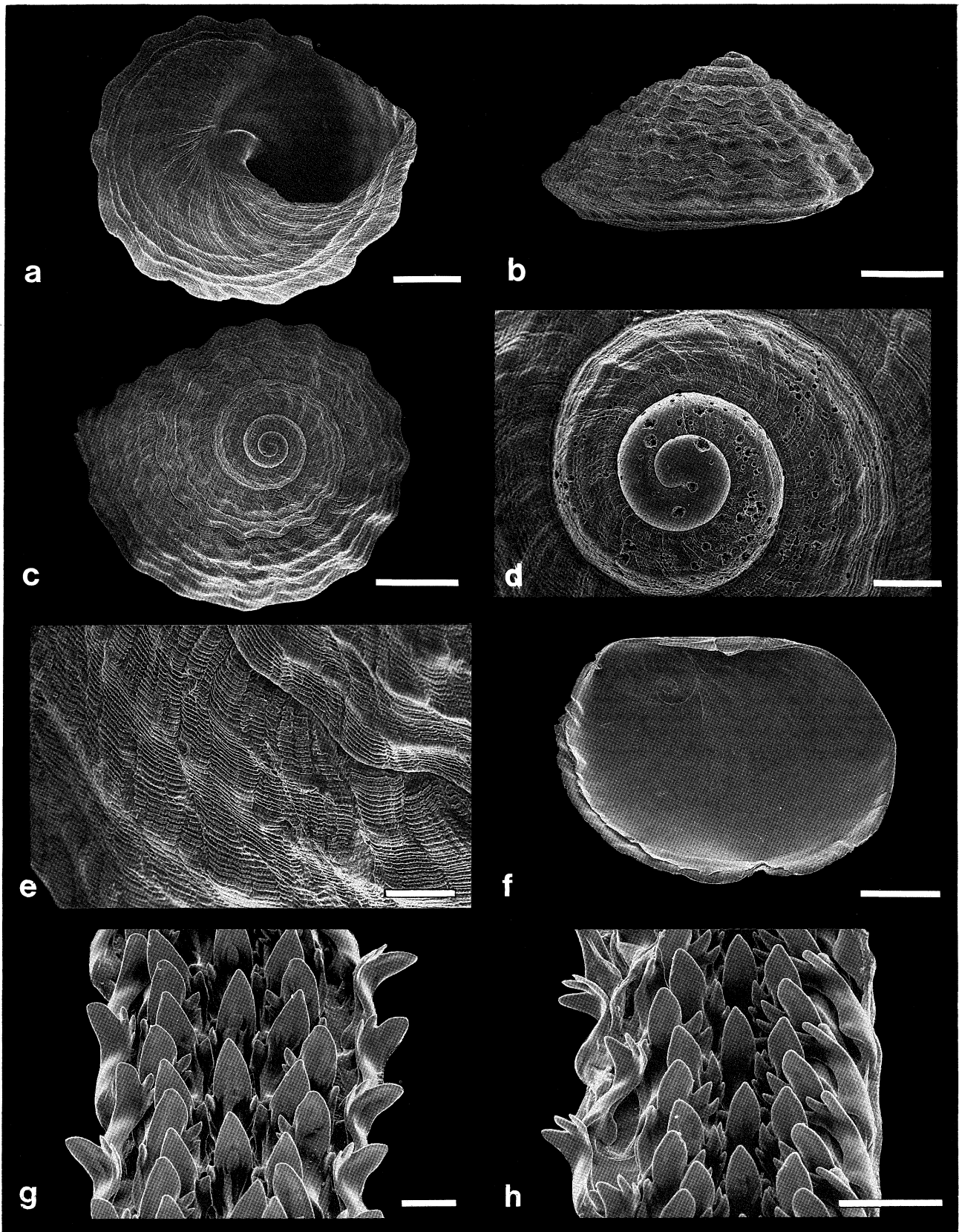


Fig.14. *Bembicium flavescens* (Philippi): **a,b-e** (4 views), juveniles, Signal Point, Lord Howe Island (AMS C144350) (bars a-c = 1 mm, bars d,e = 200 μ m); **f**, operculum, Ned's Beach, Lord Howe Island (AMS C144404) (bar = 1 mm); **g**, radula, Point Hunter Reserve, Norfolk Island (AMS C144401); **h**, radula, Signal Point, Lord Howe Island (AMS C144350) (bars g,h = 50 μ m).

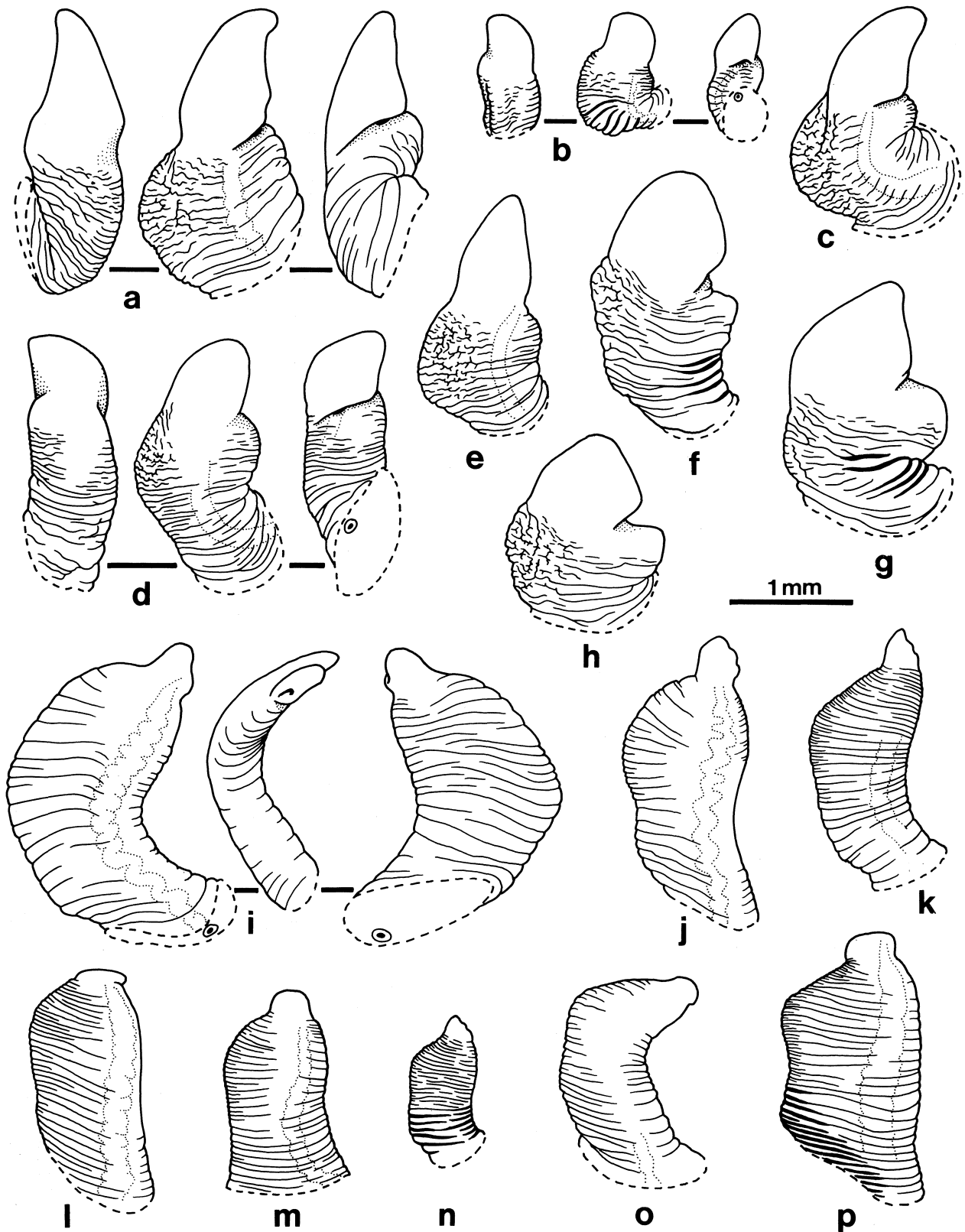


Fig. 15. a-h, penes of *Bembicium flavescens* (Philippi): a, Lord Howe Island (AMS C144294); b, Signal Point, Lord Howe Island (AMS C144350); c,d,e, Ned's Beach, Lord Howe Island (AMS C144404); f,g,h, Point Hunter Reserve, Norfolk Island (AMS C144401); i-p, penes of *Bembicium nanum* (Lamarck): i,j, Flinders, Vic. (AMS C144314); k,m, Nelson's Bay, Port Stephens, N.S.W. (AMS C144288); l, Yeppoon, Qld. (AMS C144338); n, Devonport, Tas. (AMS C144418); o, Normanville, S.A. (AMS); p, Pirates Bay, Eaglehawk Neck, Tas. (AMS C144334); a,b,d, each show dorsal, lateral and ventral views (relative to orientation of head), i, lateral, ventral and medial views, all others are lateral views.

- Bembicium auratum*.—MacPherson & Chapple, 1951: 118; H. Anderson, 1958: 560–565, fig. 1 (pallial oviduct), pl. 1, fig. 1 (vas deferens), fig. 3 (egg masses), pl. 2, figs a,b, pls 3–5 g, h; Dakin, 1960: 248, pl. 61, fig. 5; D.T. Anderson, 1962: 62–63, figs 1–6 (larval development); MacPherson & Gabriel, 1962: 89–90, fig. 118; Wilson & Gillett, 1971: 30, pl. 11, figs 13, 13a; Fretter, 1982 (anatomy); Ludbrook, 1984: 70, figs 20c–e.
- Littorina imbricata* Gray, 1839: 141 [lectotype BMNH 1968366, 16.4 x 17.9 mm; no locality].
- Bembicium imbricatum*.—Philippi, 1846: 132–133; Cotton & Godfrey, 1938: 10.
- Risella imbricata*.—Philippi, 1853: 4–5, pl. 1, figs 4, 5; Troschel, 1856–63: 137, pl. 11, fig. 8 (radula); Crosse, 1864: 242–243; Smith, 1884: 61–62; Nevill, 1885: 158.
- Trochus cicatricosus* 'Jonas' Philippi, 1843: 66, *Trochus* pl. 2, fig. 2 [type lost; New Holland].
- Bembicium melanostoma*.—Philippi, 1846: 130 [in part, not Gmelin, 1791]; Hedley, 1918: M51 [not Gmelin, 1791]; May, 1921: 48 [in part, not Gmelin, 1791]; H. Anderson, 1958: 553–558 [in part, not Gmelin, 1791]; Wells, 1980: 240 [not Gmelin, 1791]; Wells & Bryce, 1986: pl. 10, no. 112 [not Gmelin, 1791].
- Risella melanostoma*.—Philippi, 1853: 8 [in part, not Gmelin, 1791]; Chenu, 1859: 302, fig. 2127 [not Gmelin, 1791]; Tryon, 1887: 262–263, pl. 49, figs 3–9 [in part, not Gmelin, 1791]; Pritchard & Gatliff, 1902: 92–94 [in part, not Gmelin, 1791]; Hedley, 1910: 355 [not Gmelin, 1791].
- Littorina melanostoma*.—Tenison-Woods, 1879: 61–65 [in part, not Gmelin, 1791].
- Bembicium luteum*.—Philippi, 1846: 132 [in part, not Quoy & Gaimard, 1834].
- Risella lutea*.—Philippi, 1853: 4 [in part, not Quoy & Gaimard, 1834]; Adams & Adams, 1858: pl. 33, fig. 5 [not Quoy & Gaimard, 1834]; Angas, 1867: 209 [not Quoy & Gaimard, 1834]; Smith, 1884: 61–62 [in part, not Quoy & Gaimard, 1834]; Nevill, 1885: 159 [in part, not Quoy & Gaimard, 1834].
- Risella kielmannsegi* Zelebor in Dunker & Zelebor, 1866: 913 [type not seen; 'New Zealand' in error, probably Botany Bay, New South Wales, H. Anderson, 1958: 562] —Frauenfeld, 1867: 9, pl. 1, figs 11 a–e.
- Bembicium kielmannsegi*.—Iredale, 1936: 289; Allan, 1950: 81, fig. 19, no. 5; Dakin, 1953: 248, pl. 61, fig. 5; Iredale & McMichael, 1962: 39.
- Bembicium nodulosum* Musgrave, 1929: 344 [*lapsus*, Iredale, 1936: 289].—Iredale, 1931: 208–209.

Nomenclature. The tall spire and nodulose sculpture make this species readily recognisable, so that published figures can usually be identified.

Risella kielmannsegi was described from New Zealand, but as pointed out by H. Anderson (1958) the Novara Expedition also called at Botany Bay, and this is the likely origin of the specimens. Suter (1906, 1913) suggested that *R. kielmannsegi* was based on young *Astraea sulcata*, but Frauenfeld's excellent figures leave no doubt that the species is *Bembicium auratum*.

Shell. (Fig. 16) DIMENSIONS. Adult size range 5–28 mm diameter; mean height/diameter ratio 0.965 (st. dev. = 0.120, range 0.639–1.483, n = 100 from 36 localities).

SHAPE. Teleoconch 6.5–8 whorls; apical whorls commonly eroded; shell thick. Outline approximately equilaterally conical or taller; sides straight to lightly convex; base flat to slightly convex. Periphery strongly keeled in juveniles, becoming somewhat rounded on last whorl and bearing strong, blunt nodules. In shells from north Queensland keel marked by strong undulating flange throughout. Sutures indistinct, unless preceding whorl flanged. Small umbilicus in juvenile shells, becoming closed after third whorl. Within aperture of adults thickened ridge present below peripheral keel.

SCULPTURE. (Fig. 17a–g). Protoconch smooth, 0.35 mm diameter, 1.25 whorls, terminated by growth line with slight sinusigera notch. First whorl of teleoconch marked by faint spiral striae and growth lines. Beginning on second whorl, and more clearly by third, 6–7 primary grooves appear above periphery, equal in width to beaded ribs between them. Microsculpture of fine spiral threads at first distinct only in grooves, but after whorl 3 over whole surface. During second whorl radial folds appear, numbering 11–15 per whorl, stretching from suture to periphery, but prominence and persistence of radial folds variable. Typically folds remain prominent near suture and especially towards periphery of all succeeding whorls, numbering 11–17 per whorl (extremes of range 9–21). In some shells (especially those from north Queensland), radial folds become almost obsolete after whorl 3, remaining only as indistinct undulations of peripheral flange. Spiral sculpture persists, of 7–11 (extremes of range 6–12) narrow grooves on last whorl; ribs appear beaded or minutely scaly where crossed by radial growth lines. On last whorl microsculpture becomes oblique relative to spiral ribs. On juvenile shells of 3–4 whorls, base marked by 5 sharp spiral ridges, of which outermost is most prominent; further ridges soon appear, giving a total of 7–11 subequal grooves on base of last whorl, separated by grooves similar in width. Closely spaced radial growth lines and spiral microsculpture cover base.

COLOUR. Shell from entirely cream to brown. Juveniles either entirely brown, or with brown colour between radial folds. In adults brown colour forms broad, irregular, axial stripes corresponding to the radial folds, becoming more prominent in eroded shells. Shells from north Queensland may lack brown colour. Base with irregular dashes and spots of brown on spiral ridges. Columella white to pale brown. Aperture commonly cream with black pattern near margin, corresponding to stripes of exterior, becoming obscured by cream or dark brown callus within; aperture may, however, be entirely cream (especially in shells from north Queensland) or blackish brown.

Animal. (Fig. 2). PENIS (Fig. 18). Filament approximately half length of penis, swollen, irregularly hammer-shaped, tip usually rounded,

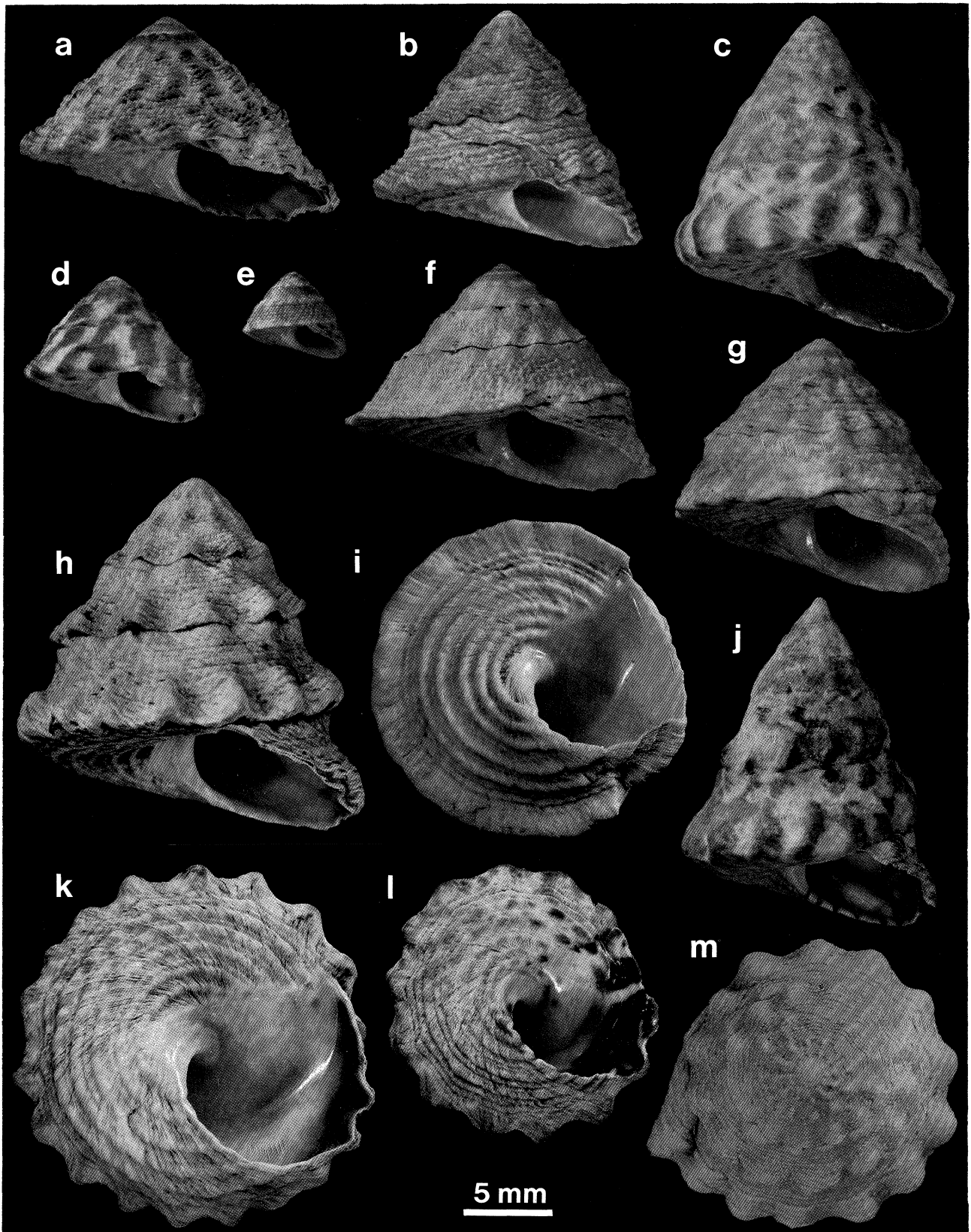


Fig.16. *Bembicium auratum* (Quoy & Gaimard): **a**, Point Perpetua, Sarina Beach, Qld (AMS C144373); **b**, Eurimbula Creek, south of Bustard Head, Qld (AMS C144286); **c**, Oyster Harbour, Albany, W.A. (AMS C144304); **d**, North Keppel Island, Qld (AMS C144367); **e**, Shute Island, Whitsunday Islands, Qld (BMNH); **f,i** (2 views), Proserpine River estuary, Wilson, Qld (AMS C144335); **g**, Campwin, south of Mackay, Qld (BMNH); **h,k** (2 views), Western Port Bay, Vic. (AMS C144357); **j,l**, Nelson's Bay, Port Stephens, N.S.W. (AMS C144288); **m**, whitened to show sculpture, Western Port Bay, Vic. (AMS C144357).

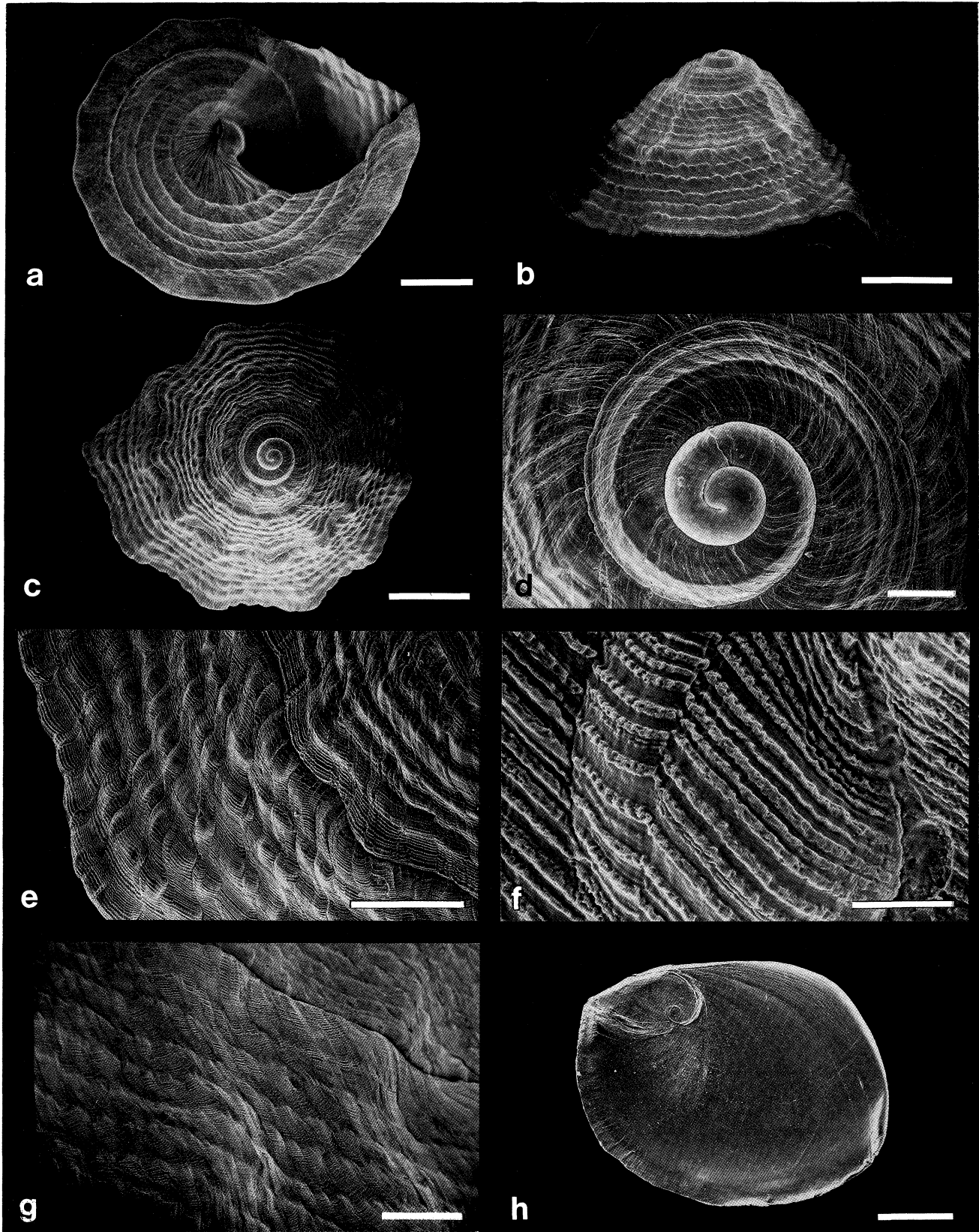


Fig.17. *Bembicium auratum* (Quoy & Gaimard): **a**, juvenile, Iluka, N.S.W. (AMS C144387) (bar = 500 µm); **b-f** (5 views), juvenile, Urangan, Qld (AMS C144275) (bars b,c = 1 mm; bar d = 200 µm; bar e = 500 µm; bar f = 50 µm); **g**, sculpture of last whorl, Stradbroke Island, Qld (AMS C144347) (bar = 1 mm); **h**, operculum, Bateman's Bay, N.S.W. (AMS C144364) (bar = 1 mm).

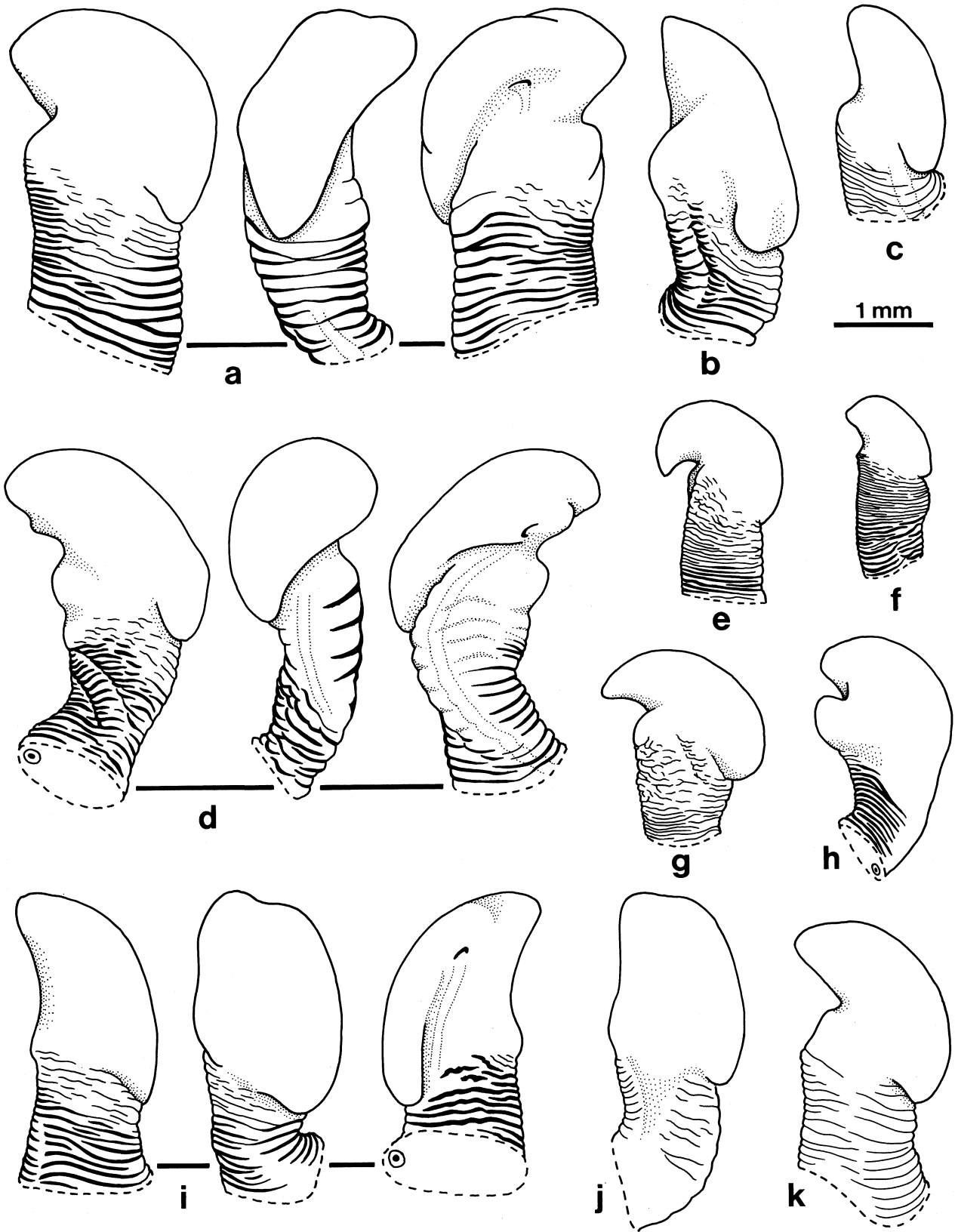


Fig. 18. Penes of *Bembicium auratum* (Quoy & Gaimard): **a,d**, Nelson's Bay, Port Stephens, N.S.W. (AMS C144288); **b,i**, Bateman's Bay, N.S.W. (AMS C144364); **c**, North Keppel Island, Qld (AMS C144367); **e,f,g**, Magnetic Island, Qld (BMNH); **h**, Corinella, Western Port Bay, Vic. (NMV F52210); **j,k**, Proserpine River, Wilson, Qld (AMS C144335); **a,d,i**, each show lateral, ventral and medial views (relative to orientation of head), all others are lateral views.

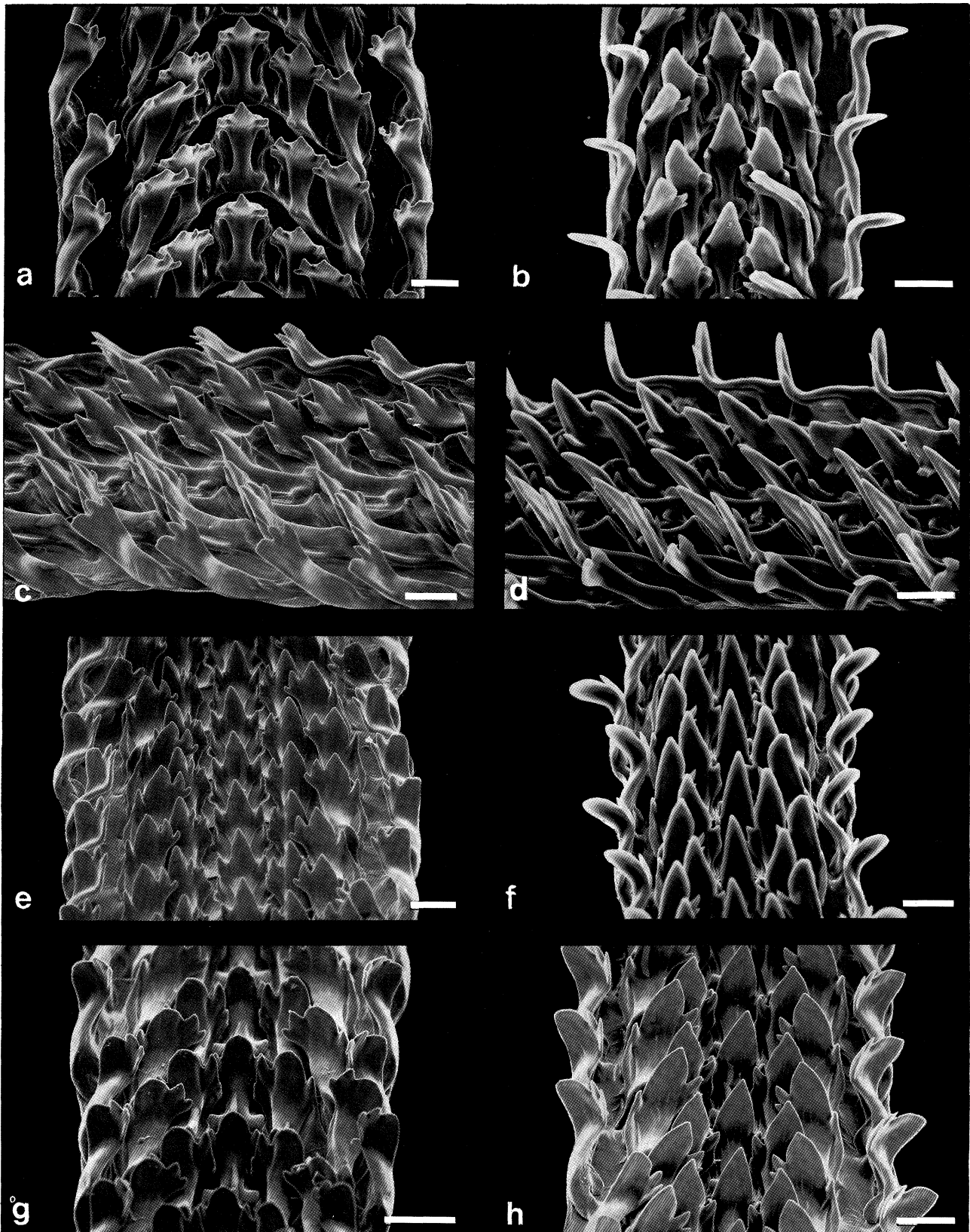


Fig.19. *Bembicium auratum* (Quoy & Gaimard) radulae: **a,c,e** (3 views), Nelson's Bay, Port Stephens, N.S.W. (AMS C144288); **b,d,f** (3 views), Sidmouth, West Tamar River, Tas. (AMS C144332); **g**, Magnetic Island, Qld (BMNH); **h**, Minim Cove, Swan River estuary, W.A. (AMS C144325) (bars a-h = 50 μ m).

sometimes hooked; base usually with black pigment.

PALLIAL OVIDUCT (Figs 3d, 4).

RADULA (Fig. 19). Length to 42 mm; relative length 1.98–2.66.

Distribution. HABITAT. Roots and trunks of mangroves, in estuaries and inlets; sometimes on sheltered rocky shores.

RANGE (Fig. 20). From Lizard Island, Queensland, south around the Australian coastline, including Tasmania, to Perth, Western Australia (also one specimen from Houtman Abrolhos Islands).

RECORDS. Queensland: Lizard Island (N; AMS); north of Cooktown (N; AMS); Low Isles (N; AMS); Missionary Bay, Hinchinbrook Island (N; DGR); Cockle Bay, Magnetic Island (N; DGR); Bowen (N; AMS); Lindeman Island (N; AMS); Hamilton Island (N; AMS); Shute Island, Shute Harbour (N; DGR); Brampton Island (N; AMS); Sarina (N; DGR, AMS); North Keppel Island (N; AMS); One Tree Island, Capricorn Group (S; AMS); Colleseum Inlet, south of Gladstone (N; AMS); Eurimbula Creek, south of Bustard Head (N; AMS); Burnett Heads (S; BMNH); Pialba (S; AMS); Gatekers Bay, Hervey Bay (N;

AMS); Wathumba Creek estuary, Fraser Island (N; AMS); Tin Can Bay, north-east of Gympie (N; AMS); between Dunwich and Myora, Stradbroke Island (I; AMS, USNM); Goat Island, Moreton Bay (N; AMS); New South Wales: Brunswick Heads (S; AMS); Woolli (S; AMS); Nelson's Bay, Port Stephens (S; AMS); Lane Cove River (S; AMS); Kurnell (S; BMNH, USNM); Batemans Bay (S; DGR, AMS); Victoria: Mallacoota (S; AMS, NMV); Lakes Entrance (S; NMV); Corinella, Western Port Bay (S; NMV); Williamstown (S; NMV); Moysse River estuary, Port Fairy (S; AMS); Tasmania: Northeast River, Flinders Island (S; TM); Prosser River estuary (S; TM); Eaglehawk Bay, south-east Norfolk Bay (S; AMS); Saltwater River (S; TM); Petcheys Bay, Huon (S; TM); Schooner Cove, Port Davey (S; TM); Black River estuary (S; TM); Forth River (S; TM); South Australia: Largs North Beach, 19 km north of Adelaide (S; AMS); Patawalonga Creek (S; SAM); Port Noarlunga estuary (S; SAM); Western Australia: Oyster Harbour, Albany (S; BMNH, AMS, WAM); Kalgan River (S; AMS, WAM); Bunbury (S; AMS, WAM, USNM); Swan River estuary (S; AMS, WAM); Woodmans Point (S; WAM); Pelsart Group,

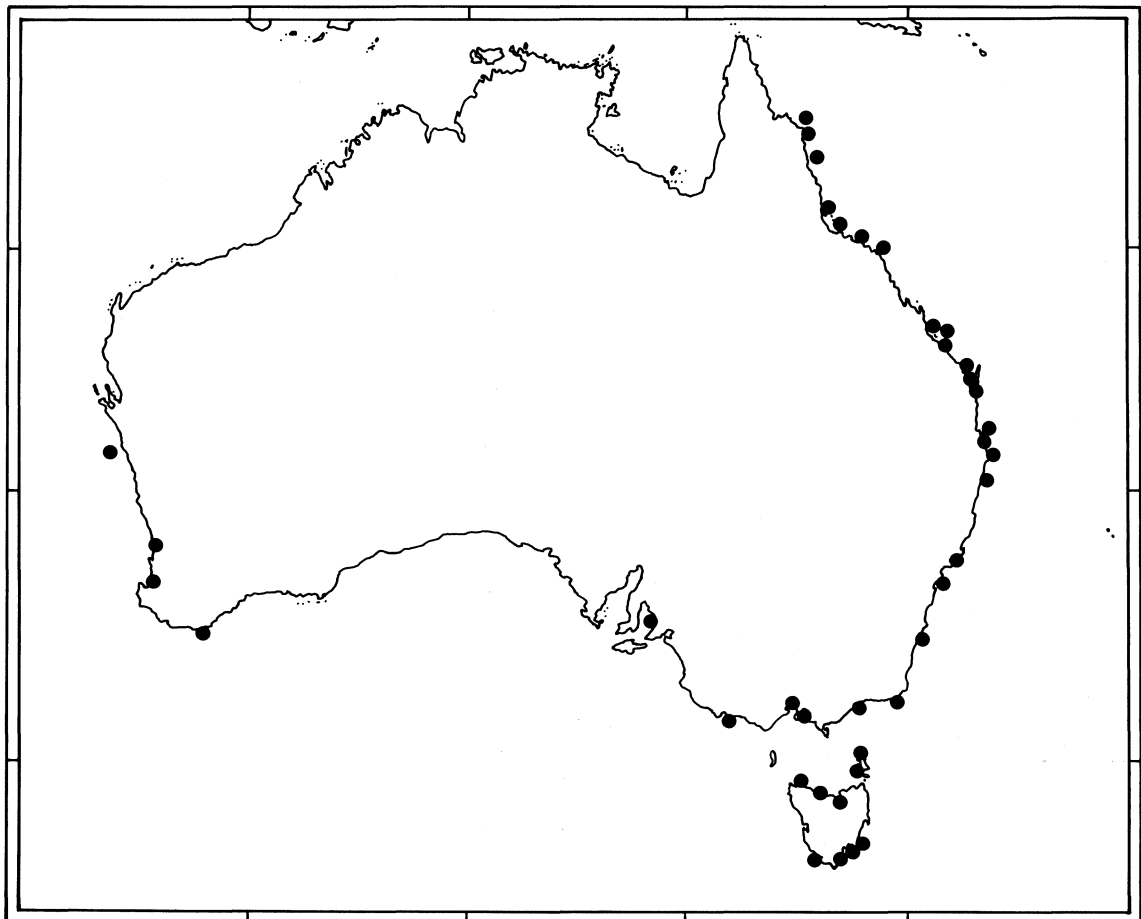


Fig. 20. Distribution of *Bembicium auratum* (Quoy & Gaimard).

Houtman Abrolhos Islands (S; WAM). Note: N, northern form; S, southern form; I, range of intermediates from N to S.

Remarks. The typical southern form of this species (Fig. 16c,h,j-m), occurring in southern Queensland and south and westwards around the coastline to the Houtman Abrolhos Islands, is easily distinguished from other members of the genus by its relatively tall spire, coarsely nodulose periphery (the nodules often black in eroded shells), and more numerous grooves above the periphery of the last whorl (seven to 11). In northern Queensland the form of the shell is different (Fig. 16a,b,d-g,i); the spire is lower, the periphery strongly keeled, the radial folds or nodules become obsolete on the last one to three whorls, and the aperture usually lacks black colour (as may the exterior of the shell also). For the present, these two forms are regarded as conspecific, since no consistent differences in penial or radular morphology could be detected, and in addition intermediate shells occur where the distributions of the two forms overlap. Genetic analysis of isoenzyme frequencies could well be used to examine the degree of similarity between northern and southern forms.

The detailed distribution of the two shell forms is interesting (see list of records above). The typical southern form is recorded as far north as Hervey Bay (25°S) and One Tree Island in the Capricorn Group (23°30'S), while the northern form is also found in Hervey Bay, and at Tin Can Bay (26°S) and Goat Island, Moreton Bay (27°S). A range of shell types, including northern, southern and intermediate shells, occurs in samples from Stradbroke Island (27°S), and also in a lot labelled 'Point Curtis' (AMS: probably = Port Curtis, 24°S). This pattern of distribution corresponds with the biogeographical boundary at 25°S and the northern affinities of Moreton Bay (Endean *et al.*, 1956a), and could be explained either by a direct ecophenotypic effect of temperature on shell form, or by the existence of geographical subspecies with different physiological tolerances and limited interbreeding in the zone of overlap.

A further aspect of variation in *Bembicium auratum* concerns the presence of dwarf populations of the northern form on offshore islands (Fig. 16d,e). Maximum adult sizes ranged from 6.7 to 11.9 mm in shell diameter in seven collections from islands north of 21°S (Lizard Island, Low Isles, Shute Island, Hamilton Island, Lindeman Island, Brampton Island, Goat Island), which may be compared with a range of 13.3 to 19.3 mm at eight mainland sites in the same region. Specimens from the large continental islands with turbid water and well-developed mangrove forests attained sizes in the same range as mainland shells (Hinchinbrook Island, 14.5 mm; Magnetic Island, 17.3 mm). A single shell from Hook Island (AMS) did not fit this pattern, measuring 17.6 mm in diameter. No preserved material of the dwarf forms was available for

comparison with mainland samples, but shell form was similar. It has been noted that the narrow mangrove fringes of small islands with clear water off the Queensland coast support assemblages of *Littoraria* species which differ from those in turbid, continental localities (Reid, 1986).

Bembicium nanum (Lamarck, 1822)

Figs 3c, 15i-p, 21-23

- Trochus nanus* Lamarck, 1822: 30 [9 syntypes, MHNG 1096/15, photograph of one seen; seas of New Holland].—Quoy & Gaimard, 1834: 273-274, pl. 62, figs 5-7; Delessert, 1841: pl. 36, figs 3 a-c; Deshayes & Milne Edwards, 1843: 150.
- Bembicium nanum*.—Philippi, 1846: 131-132; May, 1921: 48; May, 1923: pl. 22, fig. 21; Cotton & Godfrey, 1938: 10; MacPherson & Chapple, 1951: 118; Dakin, 1953, 1960: 247-248, pl. 61, fig. 7; Kershaw, 1955: 307; H. Anderson, 1958: 558-560, pls 3-5 d-f; D.T. Anderson, 1961 (development); MacPherson & Gabriel, 1962: 89, fig. 117; Bedford, 1965 (reproductive anatomy); Bedford, 1966 (oogenesis, embryology); Fretter, 1982: fig. 1 (anatomy); Ludbrook, 1984: 70, fig. 20i, pl. 11.
- Risella nana*.—Philippi, 1853: 6-7, pl. 1, figs 13-16; Chenu, 1859: 302, fig. 2125; Crosse, 1864: 234-236; Angas, 1867: 209; Smith, 1884: 61-62; Nevill, 1885: 159; Verco, 1908: 8.
- Trochus acuminatus* Wood, 1828: 16, pl. 5, *Trochus* fig. 6 [type not in BMNH; S. Sea].
- Trochus planus* Quoy & Gaimard, 1834: 274-275, pl. 62, figs 13, 14 [types lost (P. Bouchet, pers. comm.), lectotype pl. 62, fig. 14; East Passage, Port-Western, Bass Strait [Western Port Bay, Victoria]; not Gmelin, 1791].
- Bembicium planum*.—Philippi, 1846: 131; Cotton & Godfrey, 1938: 10; MacPherson & Chapple, 1951: 118.
- Risella plana*.—Philippi, 1853: 5, pl. 1, figs 6, 7; Crosse, 1864: 236-237, pl. 11, fig. 2; Angas, 1865: 173; Angas, 1867: 209; Nevill, 1885: 158; Verco, 1908: 8.
- Littorina australis* Gray, 1839: 141 [lectotype BMNH 1968365, 21.7 x 17.4 mm, one of 2 paralectotypes is probably *B. vittatum*; New Holland; not Gray, 1826, see Rosewater, 1970: 487].
- Bembicium pictum* Philippi, 1846: 132 [lectotype Philippi, 1853: pl. 1, fig. 11; Vandiemensland [Tasmania]].
- Risella picta*.—Philippi, 1853: 6, pl. 1, figs 11, 12.
- Risella grisea* Philippi, 1851: 31-32 [no locality].—Philippi, 1853: 8, pl. 1, figs 19, 20 [lectotype fig. 19].
- Risella crassa* Dunker, 1861: 42 [lectotype ZMB 19.4 x 15.5 mm; Sydney].
- Risella aurata*.—Tenison-Woods, 1877 [in part, not Quoy & Gaimard, 1834].
- Littorina melanostoma*.—Tenison-Woods, 1879: 61-65 [in part, not Gmelin, 1791].
- Risella melanostoma*.—Tryon, 1887: 262-263, pl. 49, figs 99, 10-14, 16-19 [in part, not Gmelin, 1791]; Pritchard & Gatliff, 1902: 92-94 [in part, not Gmelin, 1791]; Kesteven, 1903: 623-631, pl. 30, figs 1-13 (anatomy) [not Gmelin, 1791].
- Bembicium melanostoma*.—May, 1921: 48 [in part, not Gmelin, 1791]; Musgrave, 1929: 344 [not Gmelin, 1791]; Iredale, 1931: 208-209 [not Gmelin, 1791]; Allan, 1950: 80-81, fig. 19, no. 4 [not Gmelin, 1791];

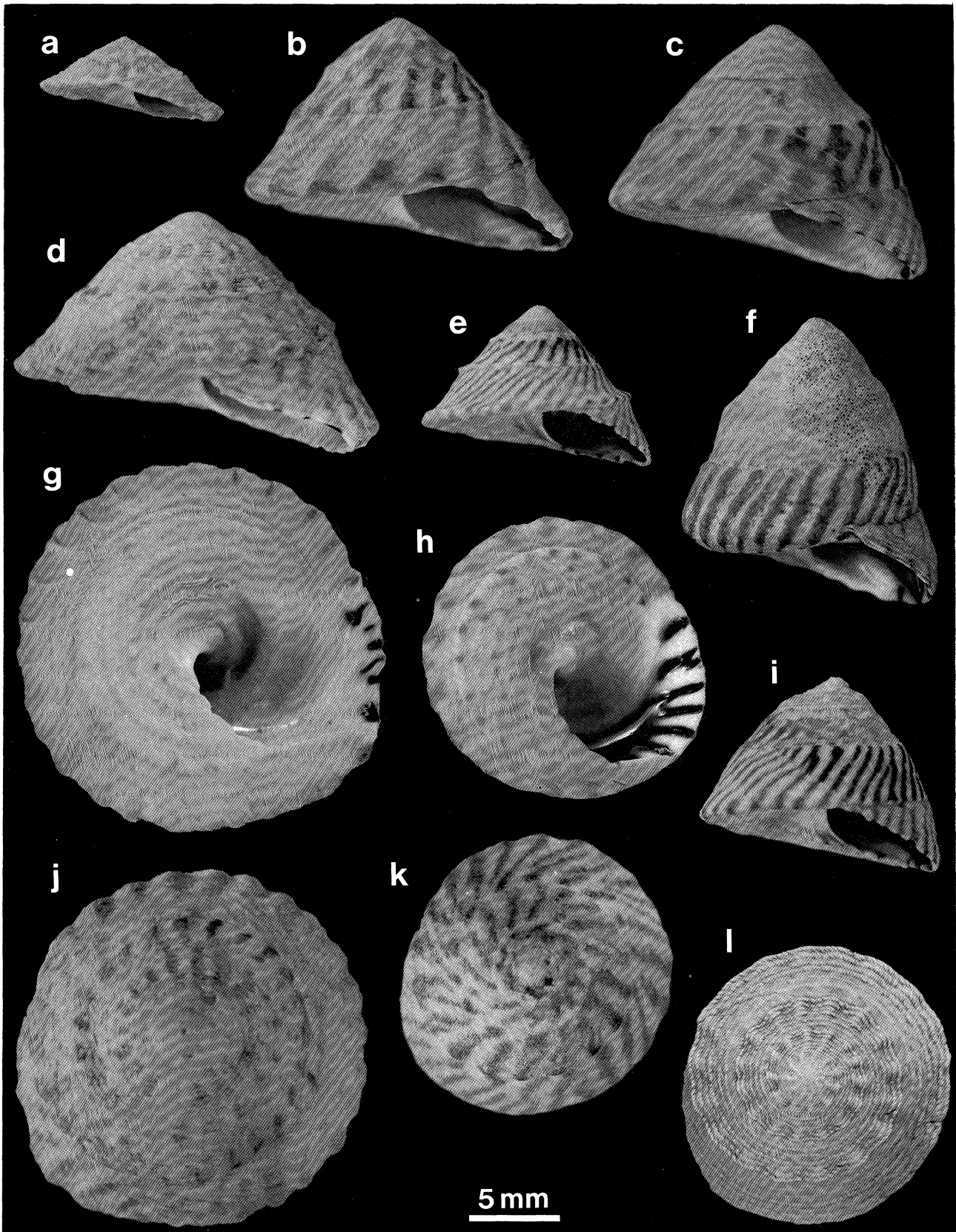


Fig.21. *Bembicium nanum* (Lamarck): **a**, juvenile, Normanville, S.A. (AMS); **b**, Honeymoon Beach, Jervis Bay, N.S.W. (AMS C144329); **c**, Charlesworth Bay, Coffs Harbour, N.S.W. (AMS C144327); **d,g,j** (3 views), Normanville, S.A. (AMS); **e,i**, Tomahawk Island, north-east Tas. (AMS C144287); **f**, Stony Point, Western Port Bay, Vic. (BMNH); **h,k** (2 views), Whisky Bay, Wilson's Promontory, Vic. (AMS C144399); **l**, whitened to show sculpture, Alexandra Headland, Qld (BMNH).

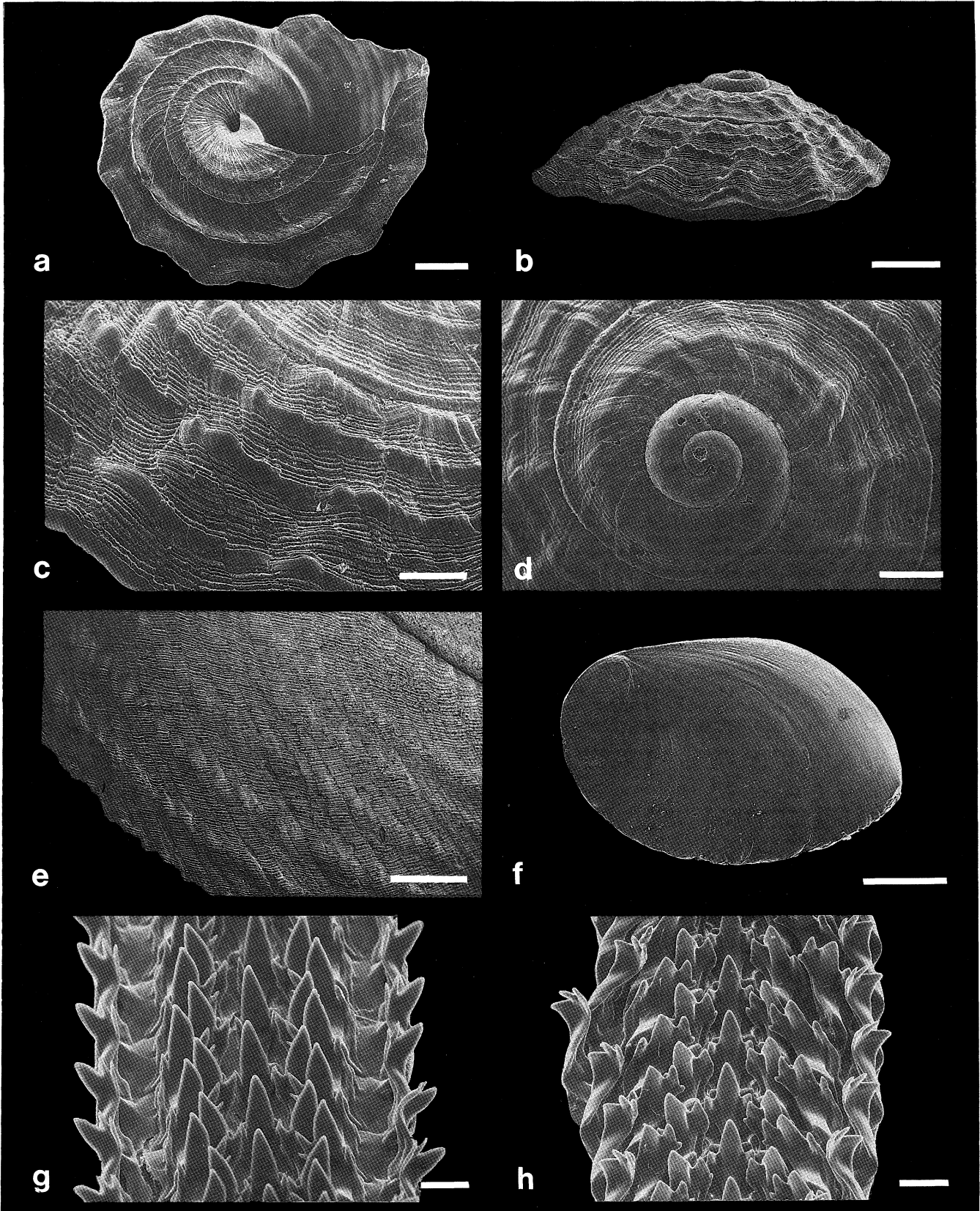


Fig.22. *Bembicium nanum* (Lamarck): **a,b-d** (3 views), juveniles, Iluka, N.S.W. (AMS C144387) (bars a,b = 500 μ m; bars c,d = 200 μ m); **e**, Point Hastings, Murwillumbah, N.S.W. (AMS C144323) (bar = 1 mm); **f**, operculum, Tomahawk Island, Tas. (AMS C144287) (bar = 1 mm); **g**, radula, Flinders, Vic (AMS C144314); **h**, radula, Nelson's Bay, Port Stephens, N.S.W. (AMS C144288) (bars g,h = 50 μ m).

Iredale & McMichael, 1962: 39 [in part, not Gmelin, 1791].

Nomenclature. The distinctively striped exterior and apertural margin leave no doubt as to the identification of *Trochus acuminatus* Wood, *Trochus planus* Quoy & Gaimard, *Bembicium pictum* Philippi and *Risella grisea* Philippi, although all are represented only by figures. *Littorina australis* Gray, 1839 is a primary homonym of a species published by the same author in 1826; the latter is now placed in the genus *Nodilittorina* (Rosewater, 1970). Examination of the types of *Risella crassa* Dunker showed this species to be synonymous with *B. nanum*, and not with 'Queensland specimens classified as *B. melanostoma*' (= *B. auratum*) as suggested by H. Anderson (1958). The marked allometry exhibited by this species (Fig. 1) led to the identification of flattened juveniles (Fig. 21a) as *planus* Quoy & Gaimard by many authors.

Shell. (Fig. 21). **DIMENSIONS.** Adult size range 10–25 mm diameter; mean height/diameter ratio 0.798 (st. dev.=0.135, range 0.488–1.473, n=100 from 56 localities).

SHAPE. Teleoconch 5.5–7 whorls; spire commonly severely eroded; shell thick. Outline low to equilaterally conical; sides lightly convex, base flat. Periphery strongly keeled, sometimes conspicuously flanged; sutures usually indistinct, but well marked if preceding whorl flanged. Small umbilicus in juvenile shells, becoming closed during third whorl. Within aperture a thickened ridge becomes prominent below peripheral keel in adult shells.

SCULPTURE. (Fig. 22a–e). Protoconch smooth, 0.39 mm diameter, 1.25–1.5 whorls, terminated by inconspicuous sinusigera ridge. First whorl of teleoconch marked by faint spiral striae and growth lines. On second whorl 4–5 wide primary spiral grooves appear above periphery, 1–2 times width of the irregularly rounded or nodulose ribs between them; grooves contain microsculpture of sharp spiral threads; also on second whorl 13–15 radial folds appear, stretching from suture to sharply flanged periphery. On subsequent whorls spiral grooves increase to 7–9, separated by ribs which are made beaded or even minutely lamellose by radial growth lines. Microsculpture spreads over ribs as well as

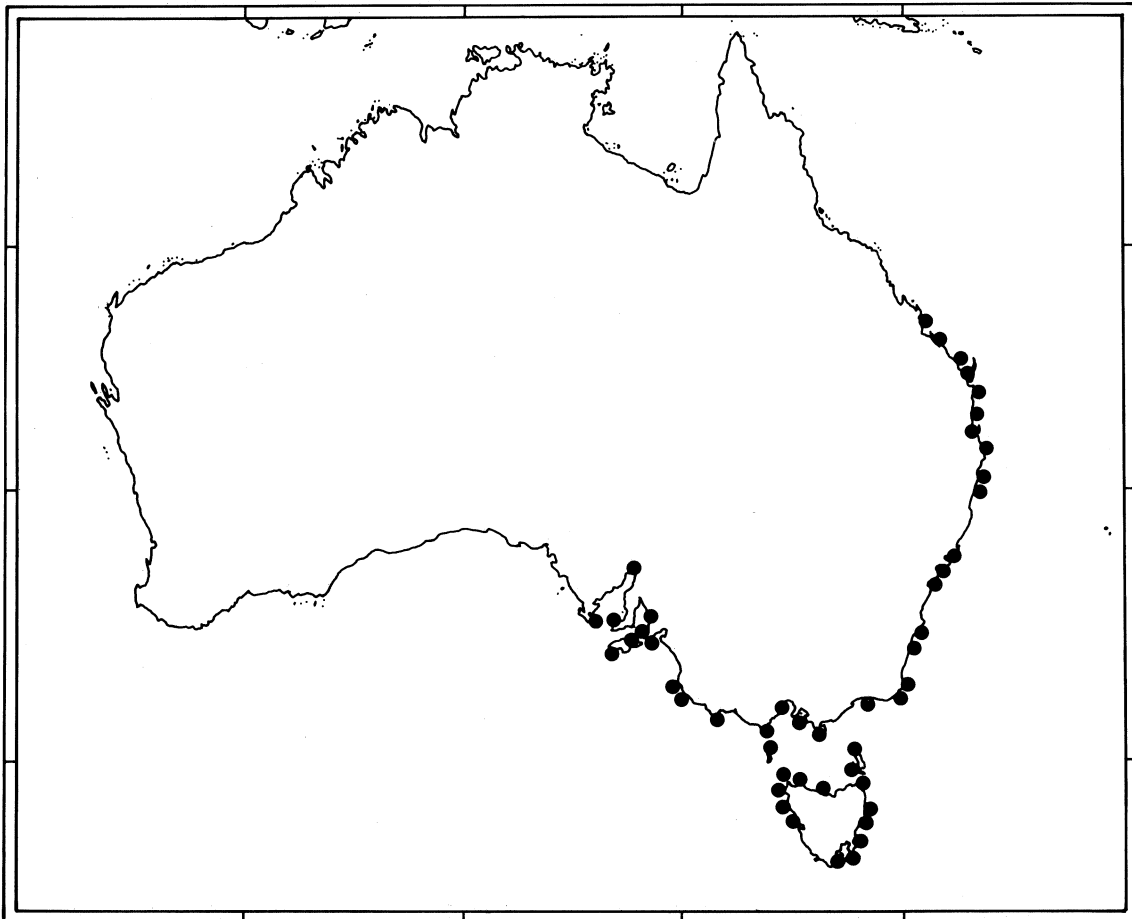


Fig.23. Distribution of *Bembicium nanum* (Lamarck).

grooves, becoming progressively more oblique in relation to spiral ribs, but remaining perpendicular to apertural margin. Radial folds increase to 15–20 per whorl, most prominent at periphery, but usually become obsolete on last 1–2 whorls. Spiral ribs become obsolete on last whorl, leaving surface smooth to the eye, sculptured only by oblique, irregular, but closely spaced, growth lines and fine, sharp, microsculptural threads perpendicular to the growth lines. Since shells are commonly severely eroded, with only last whorl relatively undamaged, radial and spiral sculpture of juvenile shell is only visible in small individuals or in those from sheltered habitats. On early whorls peripheral keel is marked by a strong flange, thrown into undulations by the radial folds on the upper surface. On juvenile shells of 2–3 whorls base is marked by 3 sharp spiral ridges, of which outermost is most prominent. On whorl 4 a fourth ridge appears between outer 2, and these 4 remain prominent on succeeding whorls. The flat grooves between are 2–4 times ridge width, marked by fine, closely spaced growth lines and faint spiral microsculpture; one additional riblet may be interpolated between outer 2 ridges on base of final whorl, and 2 more between outer ridge and peripheral keel.

COLOUR. Shell white, cream or pale yellow; on first 4–5 whorls keel and radial folds remain pale, spaces between grey to purple brown. Dark colour becomes restricted to radial folds; last two whorls marked by oblique black or purple brown lines, which tend to bifurcate towards periphery; dark lines number 18–38 at periphery of last whorl; striped pattern sometimes more diffuse. Base pale, with sparse dark spots on ridges. Columella white, cream, or pale salmon orange. Apertural margin white, conspicuously marked by 4–10 black or brown stripes corresponding to outer colour pattern; callus within aperture, on outer wall, dark brown or cream; base of aperture pale.

Animal. PENIS (Fig. 15i–p). Filament very small, no more than a rounded papilla on the wrinkled base.

PALLIAL OVIDUCT (Fig. 3c).

RADULA (Fig. 22g, h). Length to 48 mm; relative length 2.31–2.95.

Distribution. HABITAT. Upper eulittoral of moderately exposed rocky shores.

RANGE (Fig. 23). From Yeppoon, Queensland, south around the Australian coastline, including Tasmania, to Port Lincoln, South Australia (possibly further westwards, since few collections have been made from the Great Australian Bight).

RECORDS. Queensland: Yeppoon (AMS); Facing Island (AMS); Port Curtis (AMS); Burnett River mouth (AMS); Hervey Bay (AMS); Noosa Heads (AMS); Mooloolaba (AMS); Point Lookout, Stradbroke Island (AMS, USNM); New South Wales: Point Hastings, east of Murwillumbah (AMS); Iluka Bluff (AMS); Coffs Harbour (AMS); Nelson's Bay,

Port Stephens (AMS); Collaroy (AMS, USNM); North Harbour, Sydney (DGR); Jervis Bay (AMS); Batemans Bay (AMS); Merimbula (AMS); Victoria: Mallacoota (AMS); Wingan Inlet (NMV); Cape Conran (NMV); Whisky Bay, Wilson's Promontory (AMS); Cat Bay, Phillip Island (NMV); Flinders (AMS); Moonlight Head, Otways (NMV); Point Danger, Portland Bay (NMV); Tasmania: Palana, Flinders Island (TM); Eddystone (TM); Swansea, Great Oyster Bay (AMS); Pirates Bay, Eaglehawk Neck (AMS); Simpsons Bay, Bruni Island (TM); Trial Harbour (TM); Green Point, Marrawah (TM); Hunter Island (TM); King Island (TM); South Australia: Beachport (AMS); Robe (SAM); Victor Harbour (AMS); Second Valley (SAM); 2 miles south of Normanville (AMS); Blanche Point, north of Aldinga (AMS); Glenelg (SAM); Redbank, Nepean Bay, Kangaroo Island (AMS); Vivonne Bay, Kangaroo Island (AMS); Corny Point (AMS, USNM); Port Augusta (AMS); Port Lincoln (SAM).

Remarks. This species is the most easily recognised in the genus, characterised by a depressed and sharply keeled outline, three to four strong ribs on the base of juveniles (which remain the most prominent on the adult shell), and the colour pattern of oblique black stripes, also visible at the edge of the apertural lip. One geographical form can be recognised; in St Vincent and Spencer's Gulfs and on Kargaroo Island, South Australia, some collections are of unusually large shells with strongly flanged, crenulated margins, in which the typical striped pattern is diffuse or almost absent (Fig. 21d,g,j). Typical examples occur in the same geographical range, however, and no anatomical or radular differences between the two forms could be detected.

Bembicium altum (Tate, 1894)

Fig. 24b

Risella alta Tate, 1894: 184, pl. 11, fig. 4 [holotype SAM T240; Spring Creek and Muddy Creek [Victoria], 'Eocene' ['Spring Creek' refers to Jan Juc Formation at Torquay, Janjukian Stage, late Oligocene to early Miocene; 'Muddy Creek' refers to Muddy Creek Formation at Clifton Bank, Muddy Creek, Balcombian Stage, Middle Miocene; both localities Darragh, 1985: 101–104 and pers. comm.]].

Bembicium altum.—Darragh, 1970: 153.

Shell. (Fig. 24b). DIMENSIONS. Holotype diameter 6.4 mm, height 6.0 mm; 6 worn paratypes approximately 4 mm diameter; height/diameter ratio of holotype 0.94.

SHAPE. Teleoconch approximately 5 whorls. Outline equilaterally conical, sides straight; last 2 whorls slightly concave, earlier whorls bear nodules at shoulder; base flat. Periphery strongly keeled, sutures indistinct. Umbilicus closed.

SCULPTURE. 3–5 broad grooves above peripheral keel, separated by slightly nodular, rounded ribs. Radial sculpture consists of 11–16 short folds or

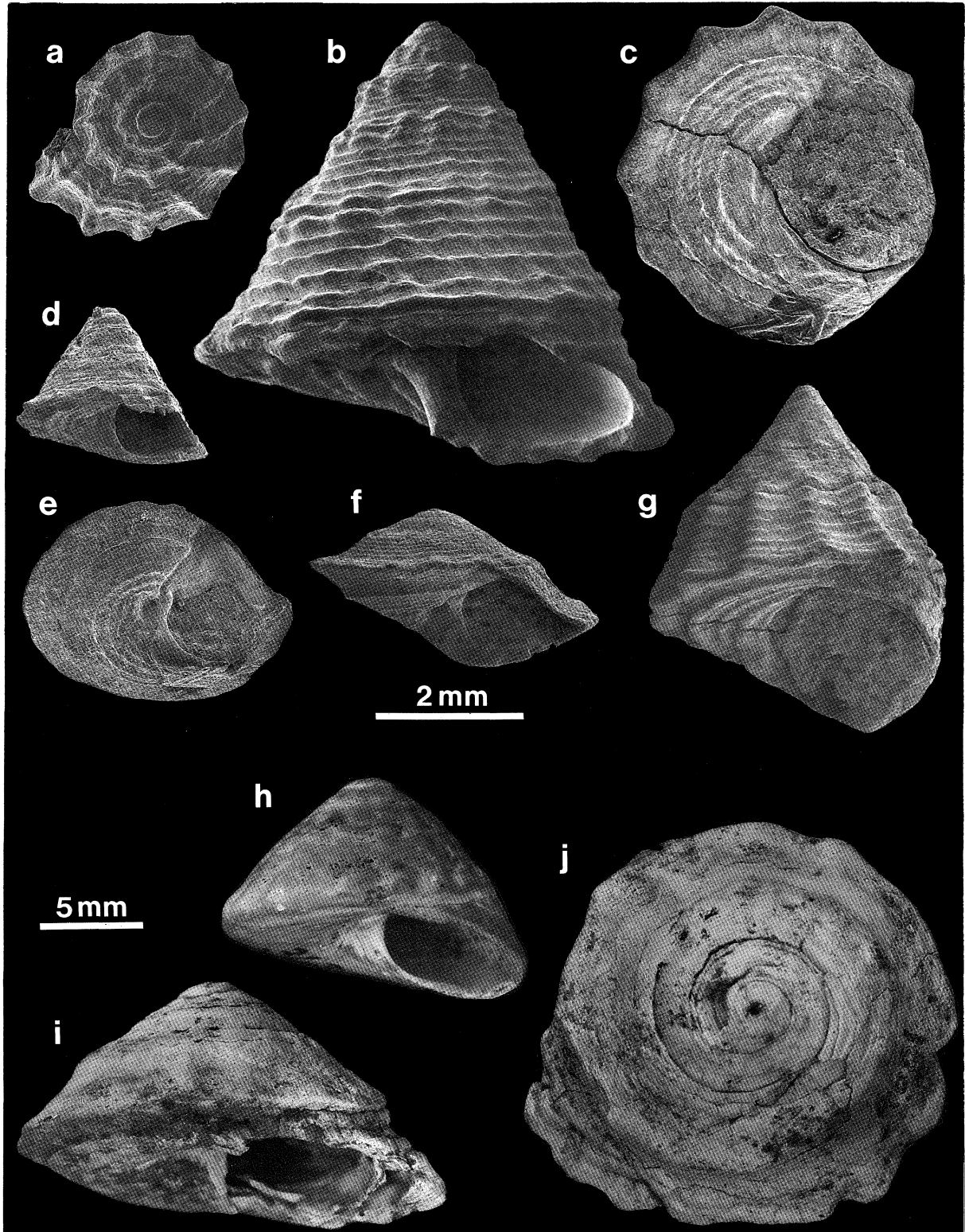


Fig. 24. Fossil *Bembicium* species: **a**, *Bembicium* sp., Pinehill Stream, Waimamaku Valley, Northland, New Zealand, Otaian Stage, Lower Miocene (NZGS TM6663); **b**, *B. altum* (Tate), holotype, 'Spring Creek and Muddy Creek', Vic., Late Oligocene to Middle Miocene (SAM T240); **c,g** (2 views), *B. priscum* Powell & Bartrum, holotype, Oneroa, Waiheke Island, New Zealand, Otaian Stage, Lower Miocene (Geol. Dept., Auckland Univ. G5535); **d**, *B. priscum*, Mataura R., 2.2 km east of Brydone, Southland, New Zealand, Waitakian Stage, basal Miocene (NZGS TM6674); **e,f** (2 views), *B. discoideum* n. sp., holotype, Pinehill Stream, Waimamaku Valley, Northland, New Zealand, Otaian Stage, Lower Miocene (NZGS TM6665); **h**, *B. 'melanostoma* group', Rangitikei River, Manawatu, New Zealand, Castlecliffian, Pleistocene (NZGS TM6661); **i,j** (2 views), *Bembicium* sp., Thomas River, Castle Hill Basin, Canterbury, New Zealand, Altonian Stage, Lower Miocene (NZGS TM6662).

nodules at suture of early whorls, becoming obsolete on last 2 whorls. In smaller specimens, peripheral keel bears about 13 slightly upturned, blunt nodules, which crenulate the margin, but crenulations are weak and irregular on largest shell. Base with 3 strong ribs in smaller specimens; base of holotype with 4 strong ribs and 2 threads in outermost groove.

Distribution. The localities given by Tate (1894) are of late Oligocene to Middle Miocene age (see above). In addition to the type collection in SAM, two specimens from Spring Creek are present in NMV (not seen; T. Darragh, pers. comm.).

Remarks. The low number of grooves above the periphery and of ridges on the base, and the prominent shoulder nodules on early whorls are distinguishing features of this species.

***Bembicium priscum* Powell & Bartrum, 1929**

Fig. 24c,d,g

Bembicium priscum Powell & Bartrum, 1929: 414, figs 7, 8 [holotype Geology Dept., Auckland Univ. G5535, 2 paratypes G5536-7; Oneroa, Waiheke Island, New Zealand, 'Hutchinsonian Stage, Upper Oligocene' [Cape Rodney Formation, north-west end of Oneroa Beach, Waiheke Island, Auckland, Otaian Stage, Lower Miocene; J.A. Grant-Mackie, pers. comm.]].—Fleming, 1966: 42.

Shell. (Fig. 24c,g,d). **DIMENSIONS.** Holotype diameter 3.8 mm, height 4.5 mm; height/diameter ratio 1.18.

SHAPE. Teleoconch approximately 5 whorls. Outline onion-shaped, at first concave, convex at last whorl; sides of early whorls straight, last 2 whorls concave, final ¼ whorl becoming convex; base flat, becoming convex. Periphery at first strongly flanged, becoming rounded at end of last whorl; sutures slightly impressed. Umbilicus closed.

SCULPTURE. Six grooves above peripheral keel, separated by rounded ribs approximately equal to groove width. Strong radial sculpture of 12 folds per whorl, from suture to periphery, aligned on succeeding whorls; folds crenulate the margin, but become obsolete just behind apertural lip. Base with 4 ribs, and a single thread in each of 2 outer grooves.

Distribution. **RANGE AND AGE.** Known from 3 collections, widely scattered in New Zealand: in Auckland, Hawke's Bay and Southland; basal Miocene to early Upper Miocene.

RECORDS. New Zealand: Cape Rodney Formation, north-west end Oneroa Beach, Waiheke Island, Auckland (NZ fossil record no. R10/f9001), Otaian Stage, Lower Miocene (Geol. Dept., Auckland Univ.); conglomerate, 1.6 km up Tutaematua Stream, Nuhaka, Wairoa district, Hawke's Bay (X19/f7499, NZGS loc. no. GS 1517), Lillburnian or Waiauian Stage, late Middle to early Upper Miocene (NZGS); west bank Maitua River, 2.2 kms east of Brydone, 7.2 kms downstream from

Maitua Bridge, near Gore, Southland (F46/f8492, GS 3600), Waitakian Stage, basal Miocene (NZGS).

Remarks. The above description is based on the type collection, and the onion shape and rounded last part of the final whorl, without radial folds, seem distinctive. The second collection listed above is a single poorly preserved shell with broken spire, but agrees with the holotype in other characters.

The third collection is doubtfully referable to *B. priscum*, comprising 27 specimens all less than 3 mm in diameter, of which only one (Fig. 24d) is well preserved. All are approximately equilaterally conical in outline, with straight sides, four to five basal ridges and six to eight grooves above the strong peripheral keel, which bears 12 to 13 pointed crenulations which are not continued as radial folds above the periphery. The umbilicus is open in the smallest specimens. The shape and sculpture are similar to the early whorls of *B. priscum*, except that no radial folds are present, but this feature is variable in Recent species. One specimen shows slight rounding of the last whorl, as in *B. priscum*.

***Bembicium discoideum* n. sp.**

Fig. 24e,f

Type material. HOLOTYPE NZGS TM 6665, 8 PARATYPES NZGS 6666-73, Pinehill Stream, near waterfall 200 m up from road, Waimamaku Valley, south of Hokianga Harbour, Northland, New Zealand (N.Z. fossil record no. O6/f40, NZGS loc. no. GS 12601), Otaian Stage, Lower Miocene.

Etymology. Greek, disc-like.

Shell. (Fig. 24e,f). **DIMENSIONS.** Shell size range 1.2-4.0 mm diameter; mean height/diameter ratio 0.578 (st. dev.=0.040, range 0.517-0.632, n=9, from type locality).

SHAPE. Teleoconch approximately 3-3.5 whorls; shell solid. Spire depressed, sides almost straight; base convex. Periphery bears strong, slightly upturned flange, at approximately half total shell height. Last whorl concave above periphery. Sutures indistinct. Small, open umbilicus. Columella thickened and angled at base.

SCULPTURE. Protoconch smooth, low, approximately 0.3 mm diameter and 1.25 whorls, no sinusigera ridge preserved. Teleoconch sculptured by 6-8 equally spaced spiral grooves above periphery. Margin with slight radial folds, producing 12-17 slight crenulations of the peripheral flange. On whorl 3 base has 3 spiral ribs, outermost the strongest, innermost being margin of umbilicus; number of ribs increases to 5-6, outermost remaining strongest; 3-5 spiral threads develop between strongest rib and periphery.

Distribution. **RANGE AND AGE.** Only known from 2 localities in the vicinity of Hokianga Harbour, Northland, New Zealand, from the Otaian Stage of the Lower Miocene (A.G. Beu, pers. comm.).

RECORDS. New Zealand: type locality (see above); blue-grey siltstone with thin shelly lenses, road cutting on north side of Otueka Hill, road to Mitimiti, north shore Hokianga Harbour, Northland (O5/f21, GS 12600) (NZGS).

Remarks. Despite small size, the holotype appears to be a mature specimen, shown by the delimitation of the parietal area of the aperture, which suggests an interruption to growth. The species is more depressed than any other *Bembicium*, and the base more convex. In addition, the open umbilicus is unusual, and the flange or 'lip' at the base of the columella is unique.

The second collection listed above is of a single specimen, of globular shape, with a rounded final whorl. The first two and one half whorls are as in the type collection, and the peculiar shape of the last whorl appears to be the result of damage during growth. It should, however, be noted that in *B. priscum* the last whorl does become rounded, giving the shell a globular shape.

Fossil *Bembicium* spp. indet.

A single specimen from the New Zealand Altonian Stage, Lower Miocene (Fig. 24i,j, NZGS TM6662, north bank of Thomas River, 400 m upstream from junction with Porter River, Castle Hill Basin, Canterbury, upper muddy beds, N.Z. fossil record no. K34/f9511, NZGS loc. no. GS 4681) is too poorly preserved for description, but is reminiscent of *Bembicium nanum* in outline. There are traces of four grooves above the periphery just behind the apertural lip, too few for *B. nanum*.

Two apparently juvenile specimens (Fig. 24a) were present with the type collection of *B. discoideum* (NZGS TM6663-4) from the Otaian Stage of the Lower Miocene. These measure 2.9 and 2.4 mm in diameter (height/diameter ratios 2.23, 2.0), with six grooves above the crenulated periphery, 12 strong radial folds, and are similar to juveniles of *B. nanum*. The base bears about five ridges, of which the outermost is strongest, and the umbilicus is rather wide, which are points of difference from *B. nanum*.

The occurrence of *Bembicium* aff. *melanostoma* in the Pleistocene of New Zealand has been discussed (Fig. 24h).

Genus *Risellopsis* Kesteven, 1902

Risellopsis Kesteven, 1902: 319-320 [type species by original designation *Fossarina varia* (Hutton) [i.e. *Adeorbis varius* Hutton]; not *Risellopsis* Cossmann, 1908, renamed *Riselloidea* Cossmann, 1909].

Diagnosis. As for the only known species, *R. varia*. Shell depressed trochoidal, periphery keeled or rounded, base convex, umbilicus open. Teleoconch sculptured by spiral ribs, 0-3 above peripheral keel, 4 on base. Periostracum produced into bristles on spiral ribs. Operculum paucispiral type B.

Gonochoristic. Prostate and anterior vas deferens both open grooves, open penial sperm groove; penis simple, small non-glandular lobe on ventral edge of base, opening of sperm groove almost terminal, minute papilla at filament tip, subepithelial glands absent. Pallial oviduct comprises single proximal spiral of albumen gland, and enlarged distal jelly gland, the latter divided into inner and outer chambers capsule glands absent; opening to mantle cavity small and subterminal; posterior seminal receptacle joined to pallial oviduct by long duct opening just anterior to opening of pallial oviduct to mantle cavity; renal oviduct joins albumen gland posteriorly; anterior bursa copulatrix. Benthic gelatinous egg masses; development planktotrophic. Radula littorinoid; main cusp of rachidian tooth somewhat reduced; main cusp on each lateral and inner marginal tooth bluntly truncated. Salivary glands anterior to nerve ring around oesophagus.

Risellopsis varia (Hutton, 1873)

Figs 5, 25-27

Adeorbis varius Hutton, 1873: 35 [lectotype NMNZ M160, paratype M1822; Stewart's Island; Chatham Islands].

Risella (?) varia.—Hutton, 1878: 27.

Fossarina varius.—Hutton, 1880: 79; Hutton, 1882: 164.

Risellopsis varia.—Kesteven, 1902: 320-321, fig. 29 (radula, operculum), figs 30-32; Suter, 1913: 191-192, pl. 35, fig. 13; Odhner, 1924: 21; Finlay, 1928: 241; Powell, 1937: 67, pl. 9, fig. 11; Fleming, 1966: 42; Morton & Miller, 1968: 80, 353, figs 23, 77; Pilkington, 1974: 411-413, fig. 1 (egg masses, veligers); Pilkington, 1976: 338, fig. 1a-c (veligers); Powell, 1979: 88-89, fig. 13, no. 7.

Risellopsis varia var. *carinata* Kesteven, 1902: 321-322, figs 33-35 [holotype AMS C11422; New Zealand].—Suter, 1913: 192, pl. 35, fig. 14; Bucknill, 1924: 38, pl. 6, figs 21, 21a; Finlay, 1928: 241.

Nomenclature. The development of the spiral ribs at and above the periphery is variable, and *R. varia* var. *carinata* is simply a strongly sculptured form of this species.

Shell. (Fig. 25). DIMENSIONS. Shell size range 3.1-8.3 mm diameter; mean height/diameter ratio 0.671 (st. dev.=0.079, range 0.500-0.860, n=42, from 23 localities).

SHAPE. Teleoconch approximately 3.5-5 whorls; apical whorls commonly eroded; shell solid. Spire low; whorls rounded or shouldered; base convex. Periphery usually bears a strong rib or keel, but is more uniformly rounded in shells with weak sculpture; sutures impressed. Small, open umbilicus, sometimes partly covered by inner lip of aperture. Inner margin of aperture uniformly rounded.

SCULPTURE. (Fig. 26a). Protoconch not seen. Teleoconch whorls sculptured by spiral ribs, of which strongest is that at periphery, which is

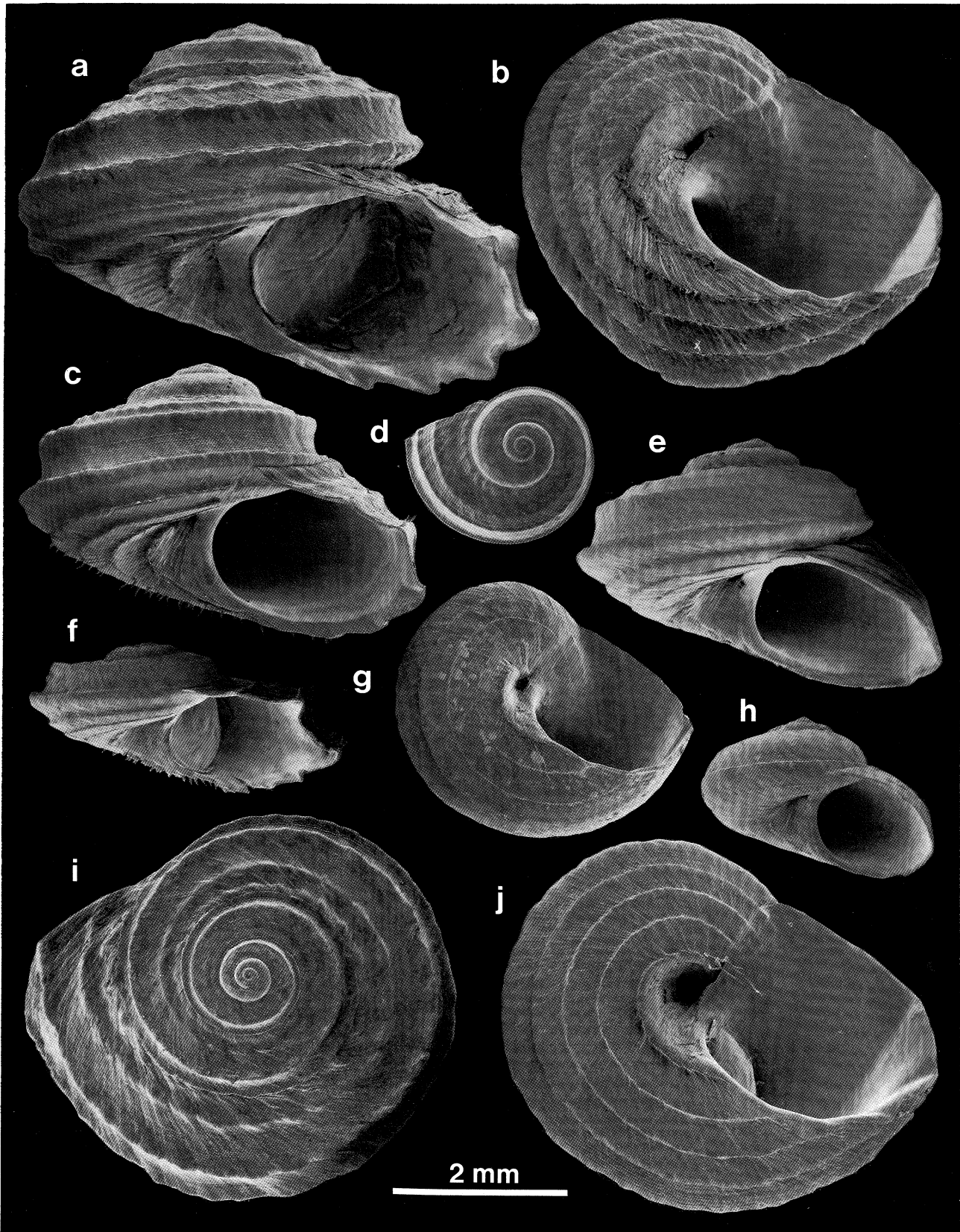


Fig.25. *Risellopsis varia* (Hutton): **a**, Sumner, New Zealand (BMNH); **b**, Portobello, Otago Harbour, N.Z. (NMNZ M16553); **c,e**, Ringaringa, Stewart Island, N.Z. (NMNZ M19595); **d**, Kapo Wairua, N.Z. (NMNZ M59386); **f**, Titirangi Bay, Marlborough Sounds, N.Z. (NMNZ M40667); **g,h**, Marakopa, Kawhia, N.Z. (NMNZ M18796); **i,j**, Karaka Bay, Cook Strait, N.Z. (NMNZ M2412).

usually developed as a carina; in addition, a rib or carina usually present on shoulder, a smaller rib towards suture; in the most strongly sculptured shells a third dorsal rib may appear at suture, rarely these three may be nodular or beaded. Microsculpture consists of fine spiral striae between ribs, and fine radial growth lines. Base sculptured by 4 equidistant spiral ribs (excluding peripheral keel), becoming weaker towards centre; innermost rib outlines umbilicus. In well preserved shells periostracum produced into row of bristles on each spiral rib; bristles most obvious on base, where they reach 0.2 mm in length.

COLOUR. Shell cream to horn colour; pattern of irregular brown blotches which extend from suture to shoulder (or periphery), numbering 6–8 (rarely 4) on last whorl; 2 continuous brown spiral lines, 1 on each side of shoulder rib, which is itself usually pale but sometimes brown; sometimes third brown line nearer suture. Base pale brown, lighter at periphery; umbilicus cream. Aperture cream, brown exterior pattern showing through, dorsal side of aperture often brown; columella white.

Animal. HEAD (Fig. 27e).

PENIS (Fig. 27a–d). No clear division between wrinkled base and smooth distal filament; blunt,

with minute terminal papilla; open sperm groove, terminating a little before the tip; small non-glandular lobe protrudes from dorsal side of base.

PALLIAL OVIDUCT (Fig. 5).

RADULA (Fig. 26c,d). Length to 11 mm; relative length 1.15–1.94.

Distribution. HABITAT. Upper eulittoral of rocky shores, in crevices amongst barnacles and *Modiolus*.

RANGE (Fig. 9). Throughout New Zealand, including Stewart Island and Chatham Islands.

RECORDS. New Zealand: North Island: Kapo Wairua, Spirits Bay (NMNZ); Whangaroa Harbour (AIM); Tryphena, Great Barrier Island (AIM); Takapuna (BMNH, USNM); Otarawairere Bay, Ohope (NMNZ); Marakopa, Kawhia (NMNZ); Karaka Bay (NMNZ); South Island: Titirangi Bay, Marlborough Sounds (AMS, NMNZ); Fossil Point, North Nelson (NMNZ); Sumner (BMNH, USNM); Caroline Bay, Timaru (USNM); Hampden (USNM); Portobello, Otago Harbour (NMNZ); Riverton (AIM); Open Bay Islands (NMNZ); Stewart Island: Ringaringa (USNM, NMNZ); Thule, Paterson Inlet (AIM); Chatham Islands: Red Bluff (NMNZ); Waitangi (AIM); Wharekouri (USNM).

Remarks. This species is variable in shell

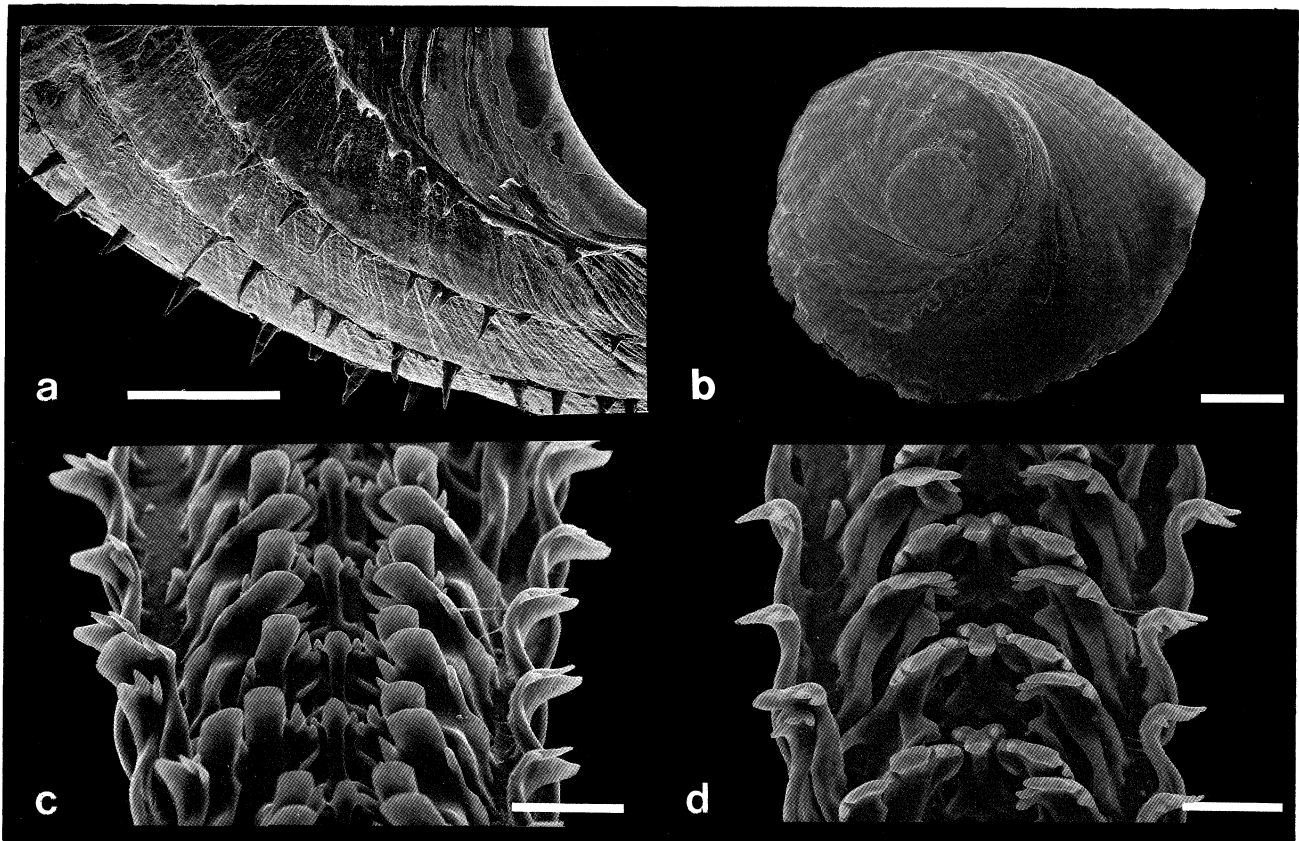


Fig. 26. *Risellopsis varia* (Hutton): **a**, periostracal bristles on base, Ringaringa, Stewart Island, New Zealand (NMNZ M19595) (bar = 500 μ m); **b**, operculum, Ringaringa, Stewart Island, N.Z. (NMNZ M80806) (bar = 500 μ m); **c,d** (2 views), radula, Ringaringa, Stewart Island, N.Z. (NMNZ M80806) (bar = 50 μ m).

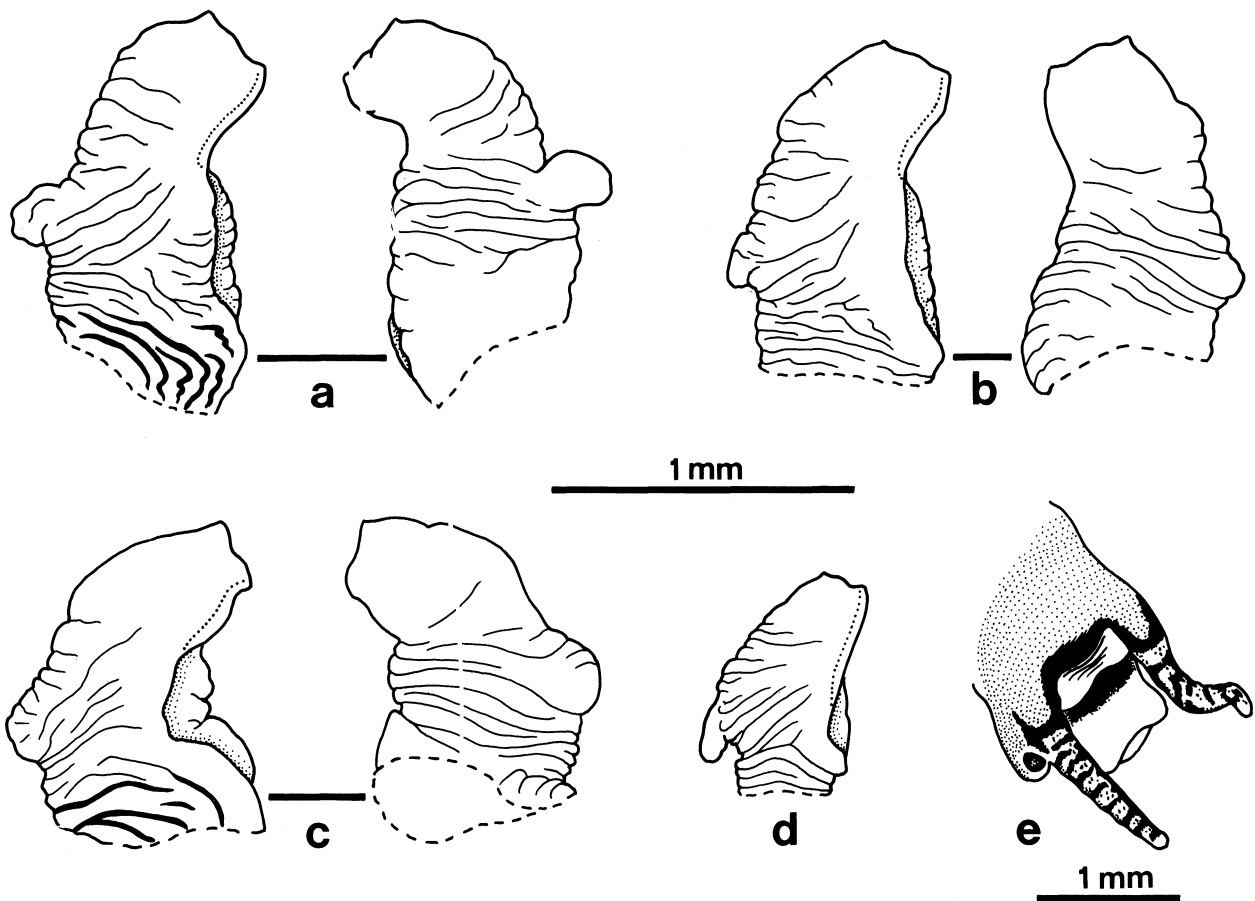


Fig. 27. *Risellopsis varia* (Hutton): a–d, penes; a–c, Ringaringa, Stewart Island, New Zealand (NMNZ M80806), lateral and medial views (relative to orientation of head); d, Titirangi Bay, Marlborough Sounds, N.Z. (AMS C144417), lateral view; e, head, Ringaringa, Stewart Island, N.Z. (NMNZ M80806).

sculpture, some specimens being almost smooth (Fig. 25h) while others are strongly carinate (Fig. 25a,c,f). As noted by Finlay (1928), gradations between these extremes are frequent and there is no apparent pattern of geographical variation in shell sculpture. The shape of the shell (especially of depressed forms, Fig. 25f) shows remarkable convergence with species of *Peasiella* (e.g. *P. isseli* (Semper in Issel)), which occupy a similar habitat in the tropical Indo-Pacific. The similarities with *P. isseli* extend to the presence of bristles on the periostracum, a feature rare in littorinids. One geographical trend which may be noted is that shells attain larger size in the south (Morton & Miller, 1968: 80). The maximum size of specimens seen from North Island was 5.8 mm in diameter, from South Island 7.1 mm, and from the Chatham Islands 8.3 mm.

A single Pleistocene fossil of *R. varia* is present in the NZGS (Brunswick marine sand member of Brunswick Formation, Mt. Jowett, Wanganui, N.Z. fossil record no. R22/f7416, NZGS loc. no. GS 4151; age: Terangian local stage of Hawera Series; late oxygen isotope stage 9 of Shackleton & Opdyke; A.G. Beu, pers. comm.).

Other fossils from New Zealand which have been classified as *Risellopsis* should be transferred to the Vitrinellidae.

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