

Systematic Revision of the Recent Species of *Peasiella* Nevill, 1885 (Gastropoda: Littorinidae), with Notes on the Fossil Species

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ABSTRACT

Peasiella is a genus of the Littorinidae, whose members have minute, trochoidal shells, and are found on rocky shores in the Indo-Pacific region. Six Recent species are recognized herein, one of which is described as new. Shell characters are highly variable, but usually adequate for identification, and provide characters for a key. The reproductive anatomy, paraspermatic nurse cell, egg capsule, head-foot, and radula are described. Distribution maps are provided, and the species can be classified as oceanic, continental, or intermediate, according to their distribution and habitat. Within the subfamily Littorininae the phylogenetic relationships of *Peasiella* are uncertain. Fossils are known from France and New Zealand, the earliest from the Middle Eocene. Four fossil species are briefly described, but the account is probably not complete, because fossils may have been misclassified in other families.

INTRODUCTION

Living species of *Peasiella* are restricted to the Indo-Pacific region. Their shells are minute and trochoidal, quite unlike those of most other littorinids. Consequently, this is one of the most poorly known genera in the family Littorinidae. Nevill (1885) listed seven species, and Tryon (1887), in the first and hitherto only monograph, included eight species. In the present revision six Recent species are recognized, one of which is described as new.

Because of the trochoidal shell and multispiral operculum, it is not surprising that six of the 19 available names for Recent species were first described as members of the Trochidae (Gould, 1849; Adams, 1853; Reeve, 1862; Pease, 1868; Issel, 1869; Turton, 1932). Fossil species have been placed in the non-littorinid genera *Trochus*, *Pseudonina*, *Tornus*, and *Xenophora* (Deshayes, 1824; Morgan, 1915; Cossmann & Peyrot, 1917-19). The littorinid affinities of these shells were first noted by Dunker (1861), who described a species as a *Risella* Gray, 1842 (= *Bembicium* Philippi, 1846; see Reid, 1988). This classification was followed by most later authors, and indeed the name *Peasiella* was first proposed as a subgenus of *Risella* by Nevill (1885). Because the operculum of *Peasiella* is multispiral, while that of *Bembicium* is pauci-

spirally, Kesteven (1903) used it as a full genus, and removed it to the Modulidae, together with the littorinid genus *Echinella* Swainson, 1840 (= *Tectarius* Valenciennes, 1832; see Reid, 1989), which also has a multispiral operculum. The only other authors to indicate a relationship between *Peasiella* and *Tectarius* were Souverbie and Montrouzier (1879), who described a *Peasiella* species as an *Echinella*. *Peasiella* became widely accepted as a full genus through the work of Japanese authors (e.g., Habe, 1956, 1964, 1984; Oyama & Takemura, 1961; Yamamoto & Habe, 1962). Nevertheless, the superficial resemblances between shells of *Peasiella* and *Bembicium* continued to suggest a close relationship, and Rosewater (1970) considered that they should be placed together in a separate subfamily. The status and relationships of all the genera of the Littorinidae have recently been revised, using cladistic analysis of anatomical characters, and it has been shown that while *Bembicium* is a member of the Lacuninae, *Peasiella* belongs in the relatively derived Littorininae (Reid, 1989). However, the relationships of *Peasiella* with other littorinid genera remain uncertain.

An exhaustive survey of the fossil species is beyond the scope of this work, for the material is widely scattered in museum collections, and much of it is probably misclassified in other families.

Peasiella species are often common, but are inconspicuous, so that their ecology is poorly known. The available information is summarized below. Museum collections do provide some information about habitat preferences, and give a relatively complete picture of geographical distribution.

MATERIALS AND METHODS

This account is based on the collections of the following museums: British Museum (Natural History), London (BMNH); Muséum National d'Histoire Naturelle, Paris (MNHN); National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM); Academy of Natural Sciences of Philadelphia (ANSP); Museum of

Comparative Zoology, Harvard University (MCZ); Los Angeles County Museum of Natural History (LACM); Natal Museum, Pietermaritzburg (NM); National Science Museum, Tokyo (NSMT); Australian Museum, Sydney (AMS); Western Australian Museum, Perth (WAM); New Zealand Geological Survey, Lower Hutt (NZGS). Material has been collected personally (DGR, specimens in BMNH) in Australia, Hong Kong, and Hawaii. In addition, type specimens have been borrowed from the Zoological Survey of India, Calcutta (ZSI); Oxford University Museum (OUM); Museum für Naturkunde, East Berlin (ZMB) and Museo Civico di Storia Naturale 'Giacomo Doria', Genoa (MGD). All type specimens have been examined unless otherwise stated. Lectotypes have only been designated from syntypic series when only a part of the original series was made available for examination.

Shell height was measured parallel to the axis of coiling, and shell diameter perpendicular to this axis. The height/diameter ratio was calculated as an index of shell shape. The number of whorls of the teleoconch was counted from the sinusigera ridge terminating the protoconch, and the number of protoconch whorls counted as described by Reid (1988:94). The numbers of ribs and grooves given in parentheses are the rare extremes of the range.

The amount of preserved material available was not large, but 74 specimens were dissected, as listed in parentheses among the locality records, with the sex indicated. No specimens were found to contain parasitic trematodes. Serial histological sections were cut of three male and two female *P. roepstorffiana*, and one female each of *P. tantilla* and *P. lutulenta*. These were stained with either Masson's trichrome (MT) (Culling, 1963) or by the alcian blue-periodic acid-Schiff (ABPAS) technique for the histochemical differentiation of mucins (Mowry, 1956). Spermatozoa from the seminal vesicle were examined by light microscopy in four *P. roepstorffiana*, three *P. lutulenta* (in each case from whole animals fixed and stored in 10% formalin in seawater), one each of *P. tantilla* and *P. isseli*, and three *P. roepstorffiana* (in these three cases samples from living animals were fixed in 1% formalin in seawater, immediately before examination).

Radulae of 31 specimens were examined, from three to eight for each species. They were treated with boiling 50% potassium hydroxide solution for 15 minutes, rinsed, cleaned ultrasonically for ten seconds, and mounted flat for examination by scanning electron microscopy. Photographs were taken of top and side views, and from the anterior end at 45° to the horizontal; this last was adopted as the standard view for showing cusp shape.

All collections listed in the locality records were examined, and have been used to construct distribution maps.

GENERAL DESCRIPTION

The following descriptions of shell and anatomy of *Peasiella* are brief. A general, comparative account of all

the genera of the Littorinidae has been given elsewhere (Reid, 1989).

Shell and protoconch: Shells of *Peasiella* are small (less than 6.6 mm diameter) and almost always umbilicate. The shape is usually trochoidal (conical, with a keeled periphery), but can be rounded at the margin and depressed. The surface is usually sculptured by major spiral grooves and fine spiral microstriae (figure 16). Conspicuous features such as carinate spiral ribs and radial folds show considerable variability within species. The folds may produce undulations of the peripheral keel, or in extreme cases cause it to appear crenulated (scalloped). The high degree of intraspecific variation can be ascribed in part to large-scale geographical variation (see systematic section). In addition, the shells show allometric growth (the apical angle decreasing with size), and a small degree of sexual dimorphism (females being larger and slightly lower-spined than males). Nevertheless, all the six Recent species can be distinguished by their shells. The arrangement of ribs on the shell base is an especially useful character. *Peasiella isseli* and *P. infracostata* may both occasionally show small periostracal bristles on the ribs around the umbilicus (figure 15).

The shell color pattern is basically of spiral rows of dark spots, most prominent at the suture and periphery, which sometimes form oblique or even spiral lines. Again there is much intraspecific variation on a geographical scale, but color patterns are nevertheless useful for identification (figures 1–14).

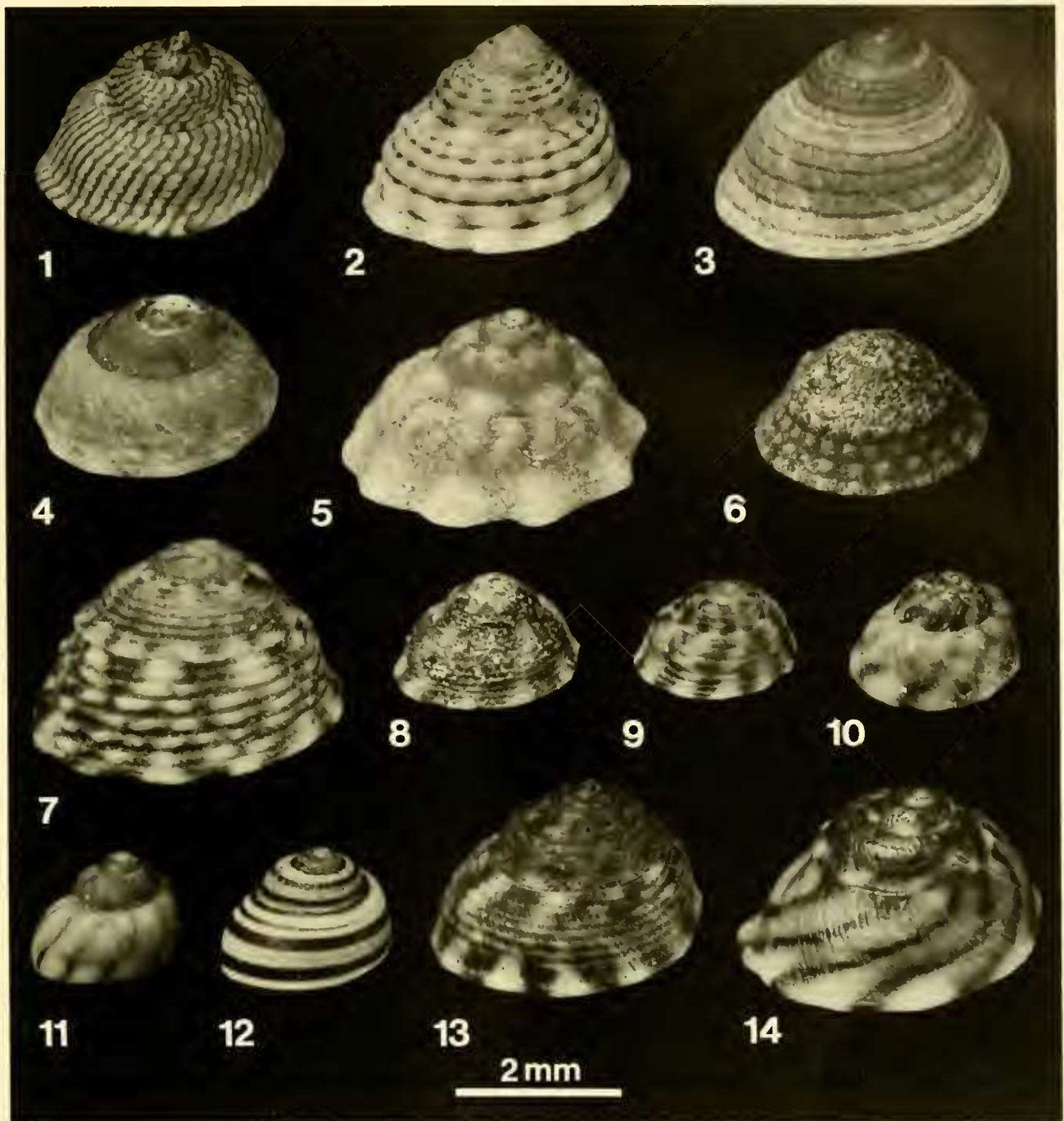
All the species show a small (0.21–0.28 mm diameter), sculptured protoconch, terminated by a sinusigera ridge, indicating planktotrophic development. The protoconch consists of 2.3 to 2.8 whorls, of which the last 1 to 1.5 are sculptured by four or five zigzag or almost straight spiral cords (figures 17, 18). It is only rarely preserved intact in adult shells.

Operculum: The operculum is round, corneous and multispiral, with five to seven revolutions (figure 19). This type is found elsewhere in the Littorinidae only in *Tectarius* (*Echininus*) Clench & Abbott, 1942.

Head-foot: Pigmentation of the head-foot is relatively pale, and frequently there are one to three black bands across the base of the snout. There may be one or two longitudinal black lines on the tentacles (figures 31–50). From the limited amount of preserved material available, it appears that the pigmentation pattern of the head may prove to be a useful taxonomic character in this genus.

There is no evidence of longitudinal division of the foot in preserved specimens, but this requires confirmation in living animals.

Male reproductive system: Both the prostate gland and the anterior vas deferens along the side of the head are open grooves, but the penial vas deferens is superficially closed (*i.e.*, the duct is not surrounded by muscle, but an epithelial connection to the surface remains). The penis is long and usually with a single mamilliform penial



Figures 1-14. Shells of *Peasiella* species, showing color patterns. 1. *P. tantilla*, Pupukea, Oahu, Hawaiian Is (BMNH). 2. *P. conoidalis*, New Caledonia (BMNH). 3. *P. roepstorffiana*, Orpheus I., Queensland (BMNH). 4, 5. *P. roepstorffiana*, Ping Chau, Hong Kong (BMNH). 6. *P. roepstorffiana*, Fiji (BMNH). 7. *P. lutulenta*, Barrow I., Western Australia (BMNH). 8. *P. lutulenta*, Hoi Sing Wan, Hong Kong (BMNH). 9. *P. lutulenta*, Rowes Bay, Townsville, Queensland (holotype, AMS C149052). 10. *P. infracostata*, Japan (BMNH). 11. *P. infracostata*, Karachi (BMNH). 12. *P. infracostata*, Cape Ferguson, Queensland (BMNH). 13. *P. isseli*, Suez (BMNH 82.8.7.316). 14. *P. isseli*, Grand Bay, Mauritius (possible syntype of *Risella isseli* var. *mauritianus* Viader, 1951; BMNH 1989004).

gland halfway along its length. Histological examination reveals an additional type of penial gland, a small patch of simple, subepithelial glands (not forming a glandular disk, see Reid, 1989), at the base of the mamilliform

gland. These two glandular types can be distinguished by their staining reactions. The secretion of the mamilliform gland stains red in MT and magenta in ABPAS, whereas that of the simple gland is colorless or pale blue

in MT and stains darker magenta in ABPAS. The secretion passes out through the hollow, raised papilla of the mamilliform gland, but in the simple gland the secretion passes in intercellular extensions through the overlying epithelium to the surface. Goblet cells (staining blue in ABPAS) are abundant in the penial filament (*i.e.*, distal to the mamilliform gland).

In general, penial shape is similar in all *Peasiella* species, and so is not a useful taxonomic character (figures 31–50). *Peasiella roepstorffiana* is unusual, because in parts of its range the mamilliform gland is absent. Penial shape is normally rather constant within littorinid species, and it is possible that two species may be involved here, as discussed in the systematic section.

Spermatozoa: As in all members of the Littorininae, the spermatozoa in the seminal vesicle are dimorphic. The euspermatozoa are filiform and 36 to 50 μm in length. The paraspermatic nurse cells are irregularly rounded or oval and 11 to 23 μm in diameter. They are packed with conspicuous round granules (small and indistinct in *P. roepstorffiana*) and a nucleus is sometimes visible, but they lack rod-shaped inclusions (figures 51–56). In most other littorinines the euspermatozoa are attached in bunches to the nurse cells, to form spermatozeugmata, which may function to prevent premature dispersal of sperm from the largely open male pallial gonoduct (Reid, 1989). However, in the few *Peasiella* that have been examined, the euspermatozoa are not attached to the nurse cells and the two cell types are simply packed together in the seminal vesicle. This condition is also found in *Melarhaphé* Menke, 1828, which, like *Peasiella*, has a superficially closed penial duct. Whether the apparent absence of spermatozeugmata is primitive, or a secondary loss as a consequence of closure of the penial duct, is unknown. The former is more likely, because elsewhere in the Littorininae spermatozeugmata

can be found in genera with superficially closed penial ducts (*e.g.*, *Cenchritis* von Martens, 1900, some species of *Littoraria* Griffith & Pidgeon, 1834). As discussed in the systematic section, some specimens of *P. roepstorffiana* lack nurse cells in the seminal vesicle. Neither intraspecific nor intrageneric variation in the presence of nurse cells has been reported in any other littorinids.

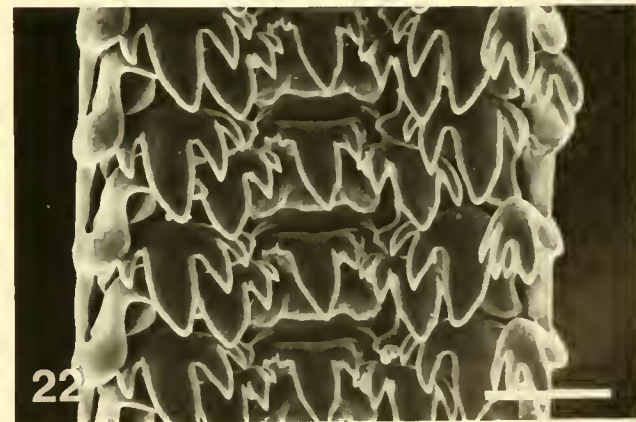
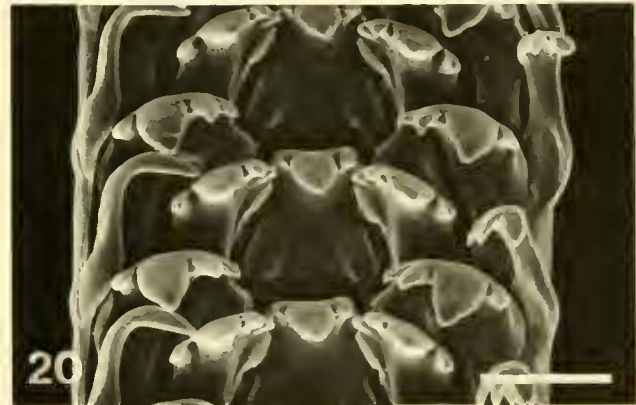
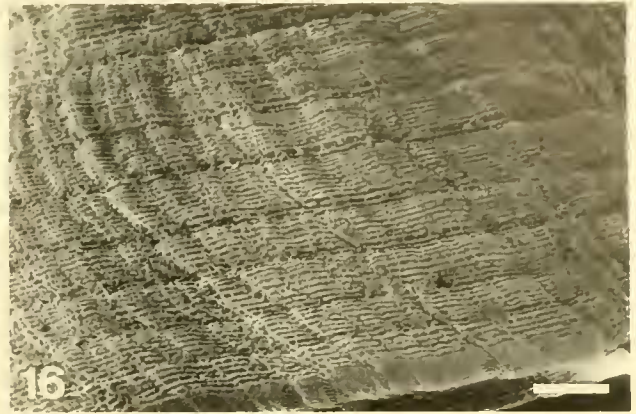
Female reproductive system: The general arrangement of the pallial oviduct is the same as in other oviparous members of the Littorininae, with the egg groove passing successively through opaque albumen gland (colorless in MT, magenta in ABPAS), translucent albumen gland (colorless in MT, blue or magenta-purple in ABPAS), opaque capsule gland (red in MT, pale purple in ABPAS), translucent capsule gland (blue in MT, dark purple and magenta in ABPAS), and small jelly gland (colorless in MT, magenta in ABPAS). Differentiation of these glands can sometimes be seen in the whole animal and in gross serial sections; the opaque capsule gland is especially prominent, visible as a chalky white or cream crescent on the lateral side of the pallial oviduct (figures 57–63, 65, 66). The spiral route of the egg groove (figures 58, 66), with a backward loop of albumen gland followed by a larger loop of capsule gland, is unique to the genus, and is the same in all six species.

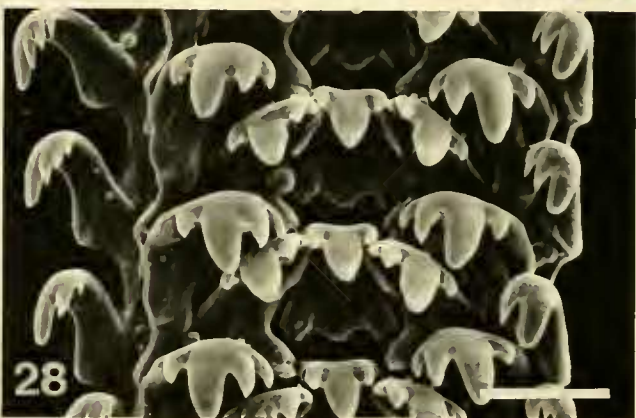
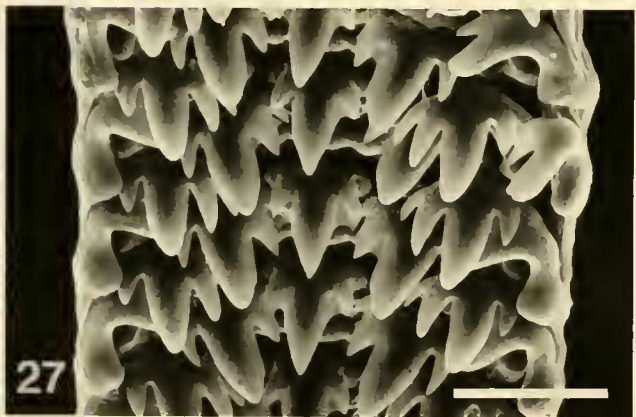
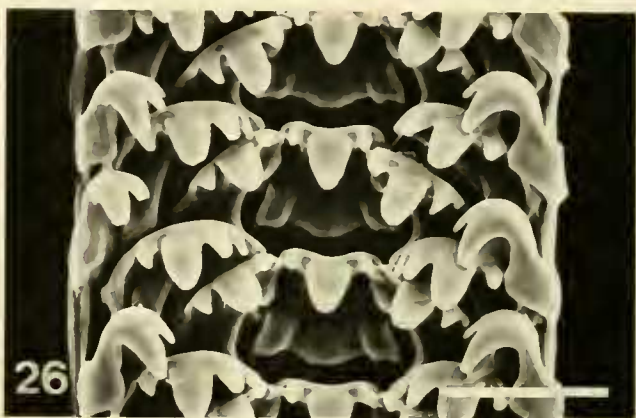
The histological structure of the glands of the pallial oviduct is unusual, in that there is not a clear separation between a non-glandular epithelial lining of the egg groove and the subepithelial glandular follicles beneath [as found in all other Littorininae except *Melarhaphé* (Reid, 1989)]. The posterior part of the jelly gland and all of the capsule gland clearly show subepithelial glandular tissue, but the albumen gland appears to be largely of epithelial structure. Probably the glandular cells are both epithelial and subepithelial throughout the pallial oviduct.

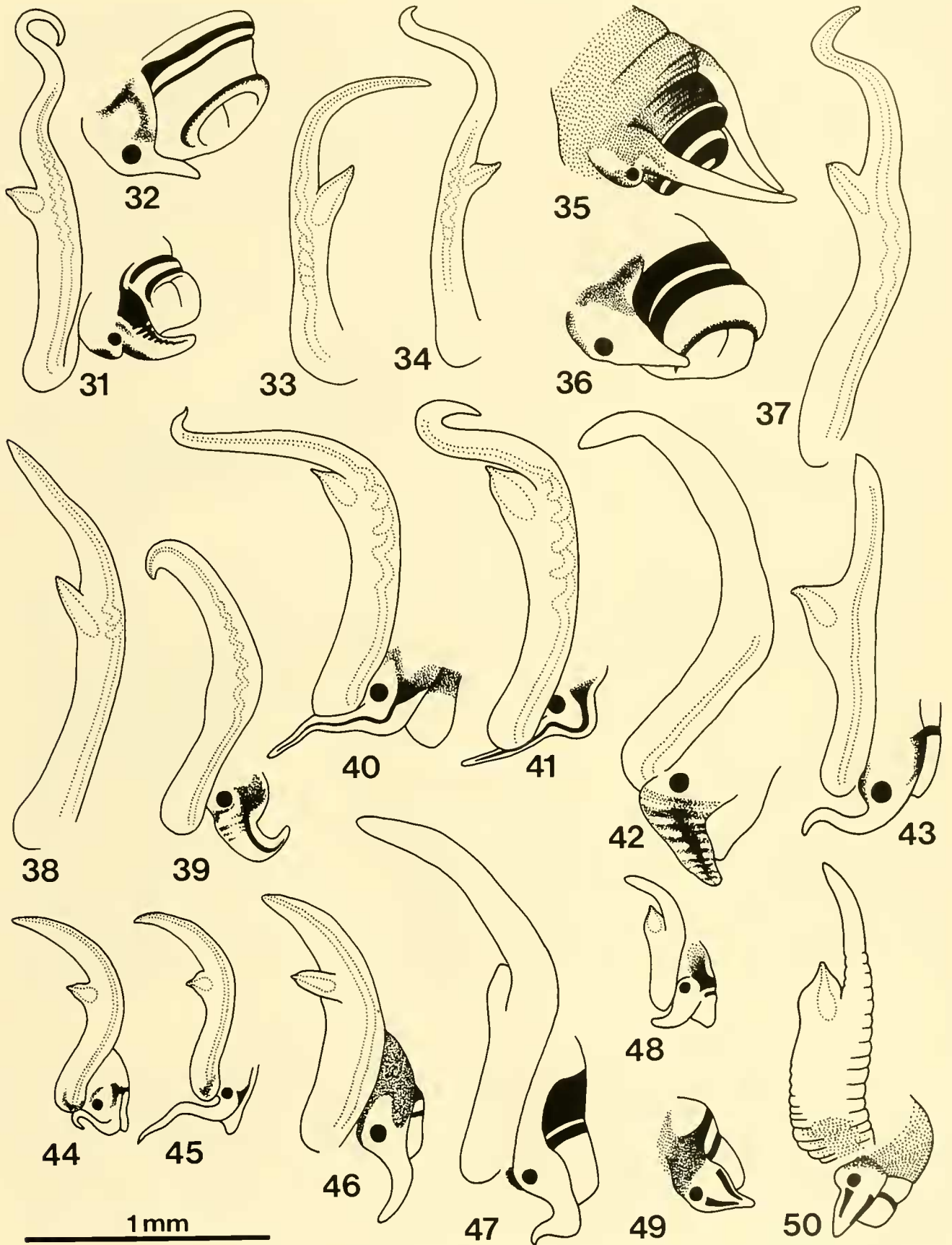
Figures 15–22. Sculptural details, protoconchs, operculum, and radula of *Peasiella* species. Scale bars 15–19 = 0.2 mm; 20–22 = 0.02 mm. **15.** *P. isseli*, detail of umbilicus showing periostracal bristles, Oman (BMNH). **16.** *P. conoidalis*, detail of sculpture on last whorl, Anaa, Tuamotu Is (BMNH). **17.** *P. roepstorffiana*, protoconch, Orpheus I., Queensland (BMNH). **18.** *P. conoidalis*, protoconch, Oneroa, Tuamotu Is (USNM 720753). **19.** *P. roepstorffiana*, operculum, Samar I., Philippines (NSMT 56716). **20–22.** *P. tantilla*, three views (flat, side and anterior from an angle of 45°) of a single radula, Coconut I., Oahu, Hawaiian Is (BMNH).

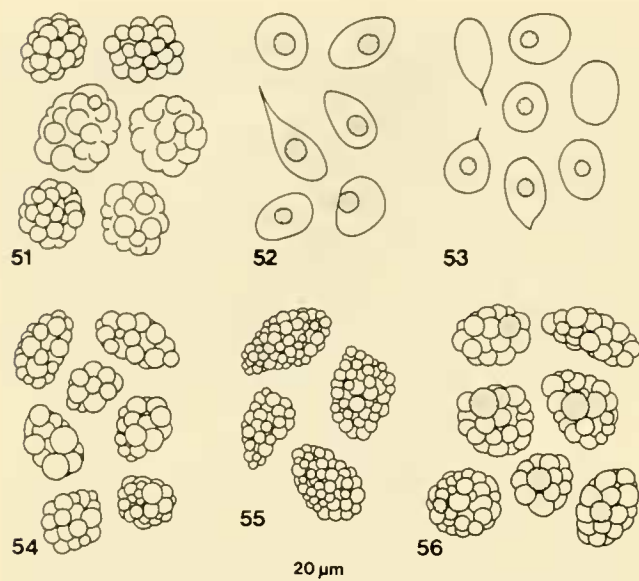
Figures 23–30. Radulae of *Peasiella* species. 23, 24, and 27 are anterior views from an angle of 45°; others are vertical views of flat radulae. Scale bars = 0.02 mm. **23.** *P. conoidalis*, Dumidu I., Male, Maldive Is (ANSP 305263). **24.** *P. conoidalis*, Anaa, Tuamotu Is (BMNH). **25.** *P. roepstorffiana*, Magnetic I., Queensland (BMNH). **26.** *P. roepstorffiana*, Ping Chau, Hong Kong (BMNH). **27.** *P. lutulenta*, Barrow I., Western Australia (WAM 2347-67). **28.** *P. isseli*, Mahé, Seychelles (BMNH). **29.** *P. infracostata*, Okinawa, Ryukyu Is (AMS C146902). **30.** *P. infracostata*, Capc Ferguson, Queensland (BMNH).

Figures 31–50. Heads and penes of *Peasiella* species. All or part of penial vas deferens and duct of mamilliform gland indicated by dotted lines when visible by transparency. All drawn from fixed material, except 34 and 50, drawn live and relaxed in 7.5% magnesium chloride solution. **31–36.** *P. tantilla*. **31, 32.** Coconut I., Oahu, Hawaiian Is (BMNH). **33–35.** Pupukeya, Oahu (BMNH). **36.** Kahuku, Oahu (AMS C144407). **37, 38.** *P. conoidalis*, Otepipi, Anaa, Tuamotu Is (BMNH). **39–42.** *P. roepstorffiana*. **39.** Ping Chau, Hong Kong (BMNH). **40, 41.** Picnic Bay, Magnetic I., Queensland (BMNH). **42.** Marine Biological Center, Phuket I., Thailand (BMNH). **43–46.** *P. lutulenta*. **43.** Shark Point, Barrow I., Western Australia (WAM 2347.67). **44, 45.** Rowes Bay, Townsville, Queensland (BMNH). **46.** Sai Kung, Hong Kong (BMNH). **47, 48.** *P. infracostata*. **47.** Kuchino, Shiznoka Pref., Japan (BMNH). **48.** Hoi Sing Wan, Tolo Channel, Hong Kong (BMNH). **49, 50.** *P. isseli*. **49.** Baie Ternay, Mahé, Seychelles (BMNH). **50.** Eilat, Israel (BMNH).









Figures 51–56. Paraspermatic nurse cells of *Peasiella* species. All drawn from living material fixed in 1% solution of formalin in seawater. 51. *P. tantilla*, Pupukea, Oahu, Hawaiian Is. 52. 53. *P. roepstorffiana*, Picnic Bay, Magnetic I., Queensland. 54. 55. *P. lutulenta*, Sai Kung, Hong Kong. 56. *P. isseli*, Eilat, Israel.

Another unusual feature is that in three species (*P. tantilla*, *P. conoidalis*, *P. roepstorffiana*) the bursa copulatrix is rudimentary or absent. In the remaining three species (*P. infracostata*, *P. isseli*, *P. lutulenta*) the bursa is large and anterior in position (figure 65). Situated at the back of the spiral part of the pallial oviduct, the seminal receptacle is constricted into two parts, an anterior coiled part and a posterior bulb, both of which store sperm (figures 58, 66). This condition has not been noted in other littorinids.

Egg capsule and development: The egg capsule has been described only for *P. infracostata*. It was first illustrated by Tokioka (1950) (figure 64) as 'Littorina-capsula habei', and subsequently identified by Habe (1956, as *P. roepstorffiana*). The pelagic capsule is 150–200 µm in diameter and contains a single egg 70 µm in diameter. It is of the 'cupola' type, of basically hemispherical shape with the domed surface sculptured by five concentric rings. The capsule has also been illustrated by Amio (1963); this less detailed drawing shows a pill-

box shaped capsule with a circumferential flange. All littorinids with pelagic egg capsules undergo planktonic development, and this type of development is confirmed by the shape and size of the protoconch of *Peasiella* [see Reid (1989) for a review].

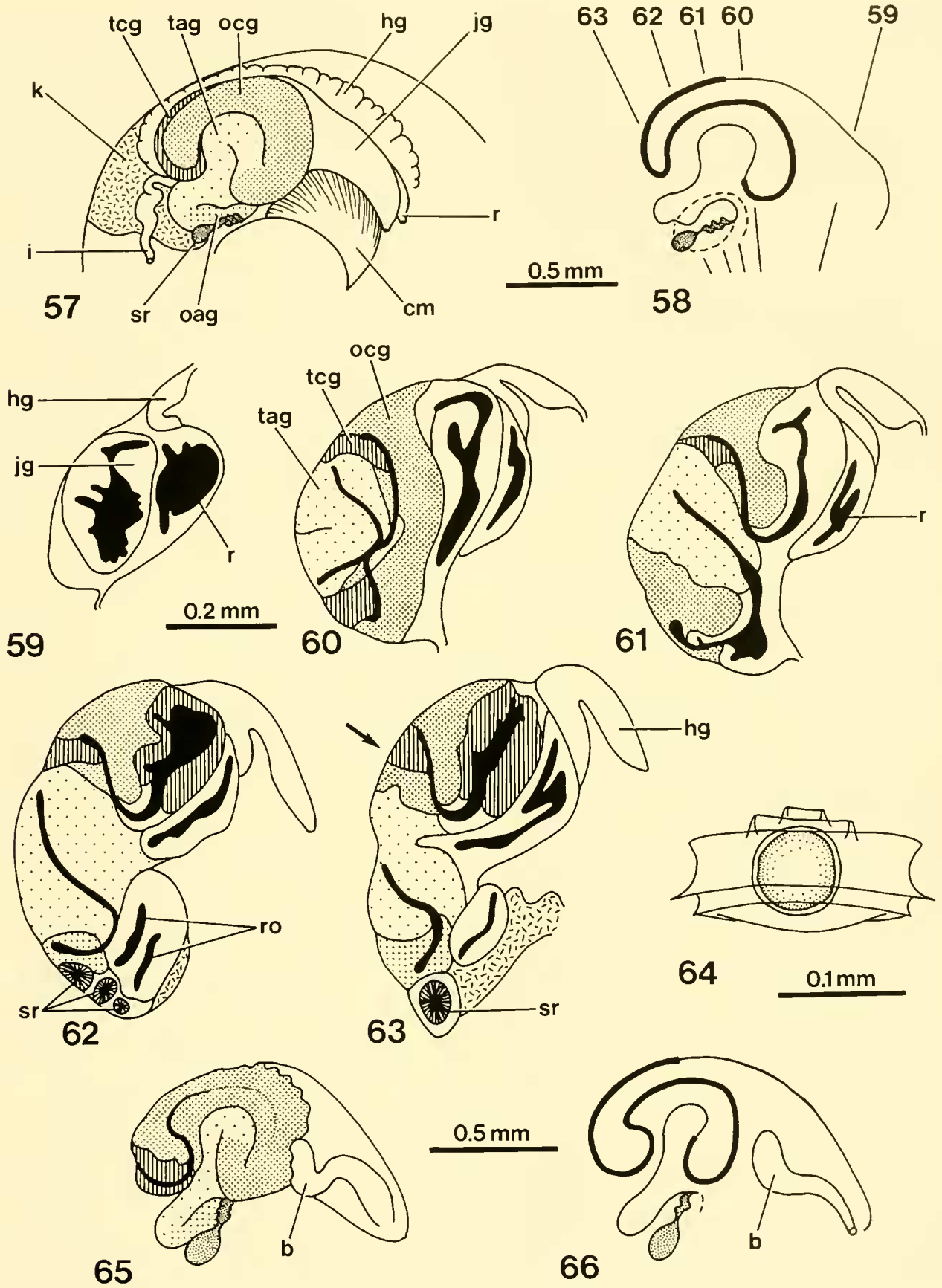
Radula: Characters of the radula are relatively constant within the genus (figures 20–30), and, with one exception, do not provide useful taxonomic characters. The central tooth varies from rectangular to almost square in the group (length/width at mid-point = 1.05–1.57), but does not show consistent intraspecific differences. There are two prominent basal projections and three tooth cusps (sometimes with two extra denticles). All the radular cusps are moderately long, and are pointed or rounded. The cusp patterns of the lateral and inner marginal teeth are similar to each other, and there are four cusps on each. The outer marginal tooth has three cusps in most species (but five to six in *P. infracostata*) and there is no outer projection on the base.

Alimentary system: The ducts of the salivary glands pass through the nerve ring around the anterior esophagus, and there is glandular material both anterior and posterior to the ring.

ECOLOGY

Little is known about the ecology of *Peasiella* species. The available information about their habitats is summarized in the systematic section. All species are apparently predominantly intertidal, occurring most commonly in the mid- to upper eulittoral zone on hard substrates, often in the empty shells of barnacles. They do, however, occur to lower levels on the shore than the littorinids with which they are sympatric, and there are reports of sublittoral occurrences. They can be found on various substrates, including limestone, granite and volcanic rocks, beach rock, coral rubble and mangrove trunks, and occur in a range of conditions of exposure to wave action. Ohgaki (1985) reported that an unidentified *Peasiella* species (probably including both *P. roepstorffiana* and *P. lutulenta*) occurred only on sheltered shores in Hong Kong. As discussed below, distribution records suggest a marked preference by each species for either continental coasts, promontories and high islands, or atolls. *Peasiella* species are usually common where they occur. In Japan, *P. infracostata* reached a density of 5 per 12.5

Figures 57–66. Female reproductive tract and egg capsule of *Peasiella* species. Abbreviations: b, bursa; cm, columellar muscle; hg, hypobranchial gland; i, intestine; jg, jelly gland in straight section of pallial oviduct; k, kidney; oag, opaque albumen gland; ocg, opaque capsule gland; r, rectum; ro, renal oviduct; sr, seminal receptacle; tag, translucent albumen gland; tcg, translucent capsule gland. 57–63. *P. roepstorffiana*, Picnic Bay, Magnetic I., Queensland (BMNH). 57. Pallial oviduct *in situ*, from right side of body whorl, showing relation to surrounding organs. 58. Diagram of spiral route of egg groove in figure 57, showing orientation of sections in figures 59–63 (solid line, egg groove; thickened line, portion of egg groove through capsule gland; dashed line, renal oviduct). 59–63. Sections through pallial oviduct in figure 57 (arrow in figure 63 indicates orientation from which figure 57 is viewed). 64. Egg capsule of *P. infracostata*, Ago and Tanabe Bays, Japan (after Tokioka, 1950). 65. 66. *P. lutulenta*, Sai Kung, Hong Kong (BMNH). 65. Entire pallial oviduct. 66. Diagram of spiral route of egg groove in figure 65 (conventions as in figure 58).



cm² on a moderately exposed shore at Amakusa (Mori *et al.*, 1985; Tanaka *et al.*, 1985), while Habe (1958) recorded up to 4,200 per 25 cm² at Tanabe Bay. Taylor (1976) noted that the muricoidean gastropod *Drupella cariosa* included *Peasiella* in its diet.

The spawning season of *P. infracostata* in Japan is from May to September (Kojima, 1960; Amio, 1963; Hirai, 1963; Ohgaki, 1981). The heat resistance of this species has been measured by Fraenkel (1966).

FOSSIL RECORD

Cenozoic fossils of *Peasiella* are not uncommon in France, and at least one species, *P. reyti*, may have lived in a sheltered, perhaps muddy, environment. The oldest are of Middle Eocene age, the youngest from the Upper Miocene. In addition, there is a single specimen known from the Upper Oligocene of New Zealand. Among the material that has been examined, four species have been distinguished, and are described in the systematic section. Two of these have rather long histories, *P. reyti* of about 25 My, *P. roepstorffiana* (if the solitary fossil is correctly determined) of 30 My.

BIOGEOGRAPHY

The Recent species of *Peasiella* are restricted to the Indo-Pacific region and this, together with the European fossil occurrences, suggests an originally Tethyan distribution. Most of the species are exclusively tropical, but *P. infracostata* reaches a latitude of 33°S in South Africa and 41°N in Japan.

There is a close correspondence between geographical distribution and the environment in which the species occur. *Peasiella lutulenta* inhabits sheltered and somewhat muddy sites, and is found only on continental coasts. *Peasiella roepstorffiana* and *P. isseli* occur in cleaner water, on promontories and high islands, and therefore extend from the continental margins to high oceanic islands in the Pacific and Indian Oceans respectively. *Peasiella tantilla* also belongs in this ecological group, and is endemic to the Hawaiian Islands. *Peasiella infracostata* appears to be intermediate between these two groups; it does not tolerate such turbid conditions as *P. lutulenta*, and occurs on both continental coasts and high islands, but does not extend far into oceanic areas. Only *P. conoidalis* is common on atolls, and has a wide, but disjunct, distribution in the central Pacific and central Indian Oceans. A similar situation occurs in the littorinid genus *Littoraria* and in some other gastropods, in which species within a genus can be classified as 'oceanic' or 'continental' (Reid, 1986), but the species of *Peasiella* suggest a spectrum from one extreme to the other. There is some overlap between *Peasiella* species in these categories of habitat and distribution, and the highest diversity is found in South East Asia and the western Pacific, where *P. roepstorffiana*, *P. lutulenta* and *P. infracostata* occur together on certain continental shores (e.g., Queensland and Hong Kong).

PHYLOGENETIC RELATIONSHIPS OF PEASIELLA

In a recent cladistic analysis of all subgenera of the Littorinidae, it was shown that *Peasiella* is a member of the relatively derived subfamily Littorininae, based on the synapomorphies of paraspermatic nurse cells, capsule gland and egg capsules (Reid, 1989). The superficial resemblance of the shell to that of *Bembicium* (a member of the primitive Lacuninae) is therefore a case of convergence. Within the Littorininae, the affinities of *Peasiella* remain uncertain. The trochoidal shell shape and multispiral operculum are synapomorphies with *Tectarius*. However, these may be convergent, in view of the lack of longitudinal division of the foot, the superficially closed penial duct, absence of rods in the paraspermatic nurse cells, and double spiral loop of the pallial oviduct, which are found in *Peasiella* but not in *Tectarius*. There are no important synapomorphies with *Cenchritis* or with *Mainwaringia* Nevill, 1885, two other littorinine genera with uncertain relationships (Reid, 1989). One possible interpretation is that the four characters listed above are plesiomorphic, as they are believed to be in *Melarhappe* (the most primitive member of the Littorininae). If so, *Peasiella* may be the sister-taxon of all the remaining littorinine genera (excepting *Melarhappe*). This suggestion is supported by the histology of the glands of the pallial oviduct (which is intermediate between the epithelial state of *Melarhappe* and the subepithelial state of other littorinines) and by the absence of spermatozeugmata in *Peasiella* and *Melarhappe* (if this absence is indeed a plesiomorphic character). Clearly further characters are required to test this hypothesis.

Within the genus *Peasiella* the three species *P. tantilla*, *P. conoidalis* and *P. roepstorffiana* share the character state of a vestigial or absent bursa copulatrix. Presence of the bursa is a plesiomorphic character of the Littorinidae, so its absence in these three species is apomorphic. Some similarities in shell shape and color pattern are also shared by this group, which may be a monophyletic one.

SPECIES EXCLUDED FROM PEASIELLA

Confusion with the genus *Bembicium* (= *Risella*) has been discussed in the introduction, and the species of *Bembicium* have recently been revised by Reid (1988). The following species have in the past been assigned to *Peasiella*, but are now excluded:

Fossarus caledonicus Crosse, 1874

Classified as *Risella* (*Peasiella*) by Tryon (1887), this species is a member of the Omphalotropinae (Assimineaidae, Truncatelloidea) (W. F. Ponder, personal communication; Reid, 1988).

Tectarius luteus Gould, 1861

Grouped with *Peasiella* species by Smith (1884), this is

a *Plesiotrochus* (Cerithioidea) (Yen, 1944; see figure of holotype in Johnson, 1964).

Peasiella roosevelti
Bartsch & Rehder, 1939

Described from the Galapagos Islands, this is a synonym of *Nodilittorina porcata* (Philippi, 1846).

Trochus risella Benoist, 1874
(= *Risella girondica* Benoist, 1874),
Xenophora rhytida Cossmann, 1899

These were erroneously listed as members of *Peasiella* by Reid (1988), and are discussed below.

SYSTEMATIC DESCRIPTIONS

DIAGNOSIS OF GENUS *PEASIELLA*

Peasiella Nevill, 1885

Risella (*Peasiella*) Nevill, 1885:159 [type by original designation *Trochus tantillus* Gould, 1849].

Teleroconch small (up to 6.6 mm diameter); usually trochoidal and umbilicate, up to 5 whorls. Protoconch 0.21–0.28 mm diameter, 2.3–2.8 whorls, terminated by sinu-sigera ridge. Operculum round, corneous, multispiral. Mesopodial sole not longitudinally divided. Male reproductive system: prostate and anterior vas deferens open; penial vas deferens superficially closed; penis long, not bifurcate, some simple subepithelial glandular cells present and usually a single mamilliform penial gland. Parametric nurse cells lacking rods and not forming spermatozeugmata. Female reproductive system: bursa present or absent; egg groove coiled in 2 spiral loops, each of half a whorl; glands of pallial oviduct at least partly subepithelial; capsule gland present. Spawn of pelagic, cupola-type capsules containing single eggs; development planktotrophic. Radula: rachidian tooth rectangular to almost square, 3 main cusps; 4 cusps on lateral and inner marginal; outer marginal lacking basal projection, 3–6 cusps. Salivary glands constricted by nerve ring around oesophagus.

KEY TO RECENT SPECIES OF *PEASIELLA*

The following key employs only shell characters, and because these are variable one species appears twice. The only anatomical characters useful for identification are the lack of the bursa copulatrix in *P. tantilla*, *P. conoidalis* and *P. roepstorffiana*, and the presence of 5–6 cusps on the outer marginal tooth of *P. infracostata*. The distribution maps may also assist with identification.

1. Shell color pattern of 45–55 oblique axial lines on body whorl *P. tantilla*
- Shell color pattern otherwise 2
2. Dorsal surface smooth or with fine spiral microstriae only 3

- Dorsal surface with fine spiral microstriae, major spiral grooves, and sometimes radial folds and carina at shoulder 4
- 3. Base with 4–5 spiral ribs, extending to edge of umbilicus; dorsal color pattern of 7–13 brown spots at periphery, often joined to suture by oblique lines, or of 2–7 brown spiral lines *P. infracostata*
- Base with 1–6 spiral ribs, on outermost ½–¾ of basal radius only; dorsal color yellow or orange, sometimes with darker tessellation, or single spiral brown band, or 9–12 peripheral spots only *P. roepstorffiana*
- 4. Base of columella thickened and angled; basal sculpture of 1–3 ribs near periphery, separated by a gap from up to 3 smaller ribs around umbilicus *P. lutulenta*
- Base of columella not thickened or angled 5
- 5. Outline equilaterally conical or taller (height/diameter ratio > 0.87); often with radial folds and crenulated margin; base with 5–8 ribs from periphery to umbilicus; color white or cream, sometimes with faint brown dots in spiral grooves *P. conoidalis*
- Outline more depressed 6
- 6. Base with 1–6 spiral ribs, on outermost ½–¾ of basal radius only; no shoulder carina; periphery sometimes crenulated *P. roepstorffiana*
- Base with 3–8 spiral ribs, becoming finer and more closely spaced towards umbilicus; usually angled or carinate at shoulder; periphery not crenulated *P. isseli*

RECENT SPECIES OF *PEASIELLA*

Peasiella tantilla (Gould, 1849)
(figures 1, 20–22, 31–36, 51, 67–73, 81)

Trochus tantillus Gould, 1849:118 [holotype USNM 5615: 34 paratypes MCZ 169392, not seen; Sandwich Is (= Hawaiian Is)].—Gould, 1852:184–185, 503, pl. 13, figs. 215, 215a, b.

Risella tantilla.—Martens & Langkavel, 1871:41; Smith, 1876: 552.

Risella (*Peasiella*) *tantillus*.—Nevill, 1885:159.

Risella (*Peasiella*) *tantilla*.—Tryon, 1887:263, pl. 50, figs. 32–34.

Peasiella tantillus.—Kesteven, 1903:633, fig. 1 (radula, operculum).

Peasiella tantilla.—Kay, 1979:74, fig. 24A.

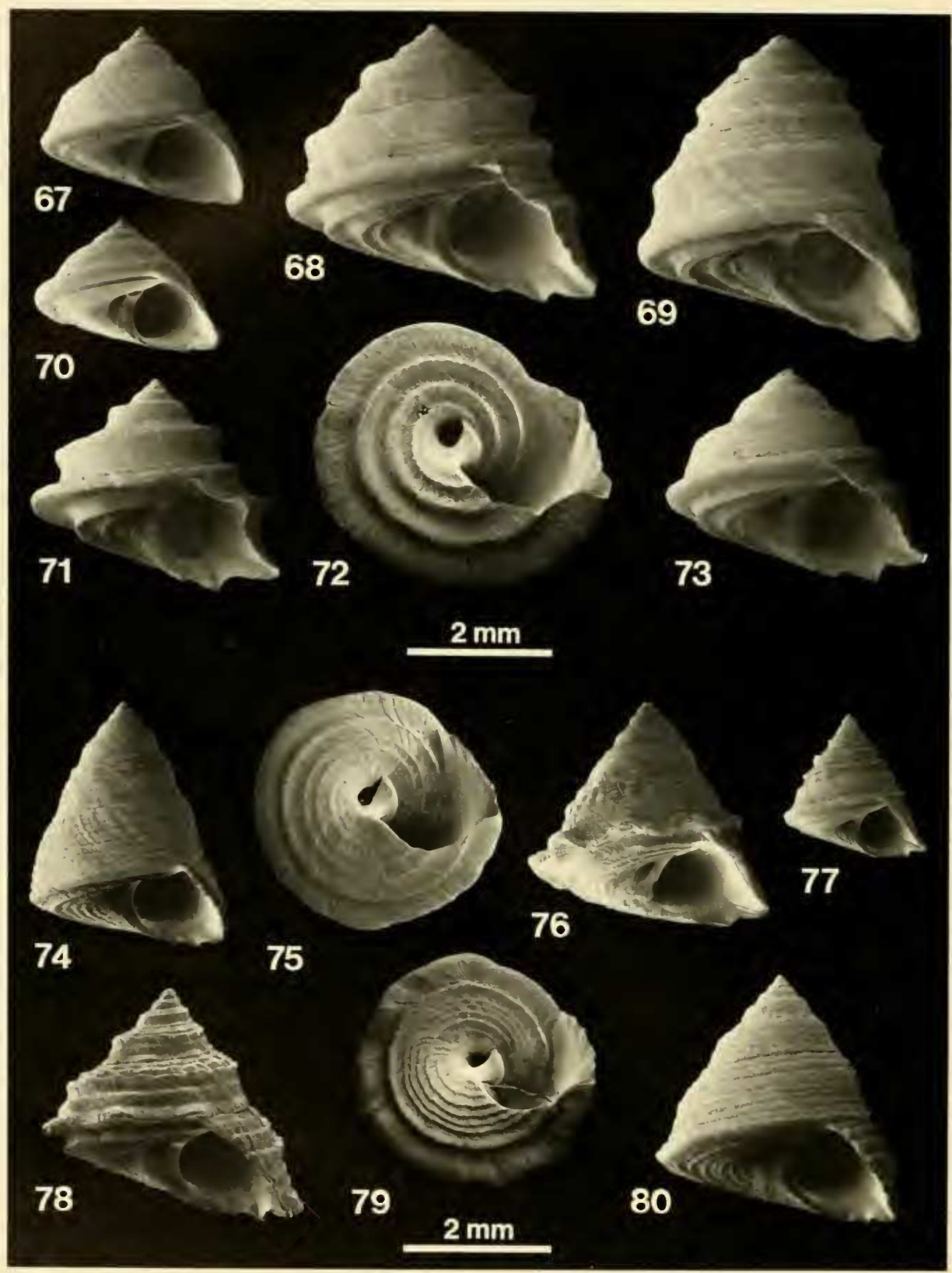
Bembicium tantillum.—Cernohorsky, 1978:43–44, pl. 11, fig. 5.

Margarita angulata A. Adams, 1853:190 [type not found; Sandwich Is].

Risella parvula Dunker, 1861:42–43 [5 syntypes ZMB; Sandwich Is].

Trochus diminutivus Reeve, 1862: pl. 11, sp. 57 [type not found; Oahu Is (Hawaiian Is)].

Shell (figures 1, 67–73): *Dimensions:* Adult size range 3.3–6.6 mm diameter, mean height/diameter ratio 0.877 (95% confidence limits \pm 0.034, range 0.744–1.093, n = 30 from 13 localities).



Shape: Teleoconch 3–5 whorls. Outline equilaterally conical or taller; sides convex; sometimes turreted by carinate rib on shoulder; base flat. Peripheral keel with strong rib; margin not undulating or crenulated; suture indistinct or only slightly impressed. Umbilicus small or closed. Columellar pillar gently concave and rounded at base.

Sculpture: Protoconch 0.24 mm diameter, 2.8 whorls. Teleoconch whorls with 5–10 spiral grooves above periphery, usually rather indistinct; single prominent rib at shoulder in carinate forms. Microsculpture of fine spiral striae over whole surface. Base with (1)2–4 spiral ribs, strong in carinate forms, outermost rib strongest, becoming weaker and more closely spaced towards umbilicus.

Color: Shell whitish, golden yellow or red brown. Pattern of oblique axial lines of red brown or black, 45–55 at periphery of last whorl, but pattern sometimes faint; spiral grooves sometimes darker, giving tessellated pattern. Base white to red brown, alternating white and red brown spots on ribs. Columella whitish, red brown at base. Aperture cream to red brown, exterior pattern showing through.

Animal: *Head-foot* (figures 31, 32, 35, 36): 2–3 black bands across snout; tentacles unpigmented or with 2 longitudinal black lines; sides of foot black or mottled.

Penis (figures 31, 33, 34): Single penial gland; filament slender.

Paraspermatic nurse cells (figure 51): Irregularly rounded, packed with round granules.

Pallial oviduct: Bursa vestigial or absent.

Radula (figures 20–22): Outer marginal with 3 cusps.

Distribution: *Habitat:* Crevices and pools on exposed and sheltered rocky shores, usually in upper eulittoral and supralittoral zones (Kay, 1979; personal observation), also in shallow subtidal zone on corraline algae (S. Kool, personal communication).

Range (figure 81): Hawaiian Is.

Records: Oahu: Waialee (MCZ); Kahuku (AMS, 1♂, 1♀); Coconut I., Kaneohe Bay (DGR, 1♂, 2♀); Kuilima (DGR); Pupukea (BMNH, 3♂, 1♀); Diamond Head (USNM); Maui: Honokowai (USNM); Kauai: Kealia (USNM); Hawaii: Honaunau, Kona (USNM); Hilo (USNM); Laupahoehoe Point (USNM); Punaluu Black Sand Beach (USNM).

Remarks: This is the largest member of the genus, easily distinguished by its color, pattern, commonly carinate

sculpture and few, strong basal ribs. It is a common species, endemic to the Hawaiian Islands.

Peasiella conoidalis (Pease, 1868)

(figures 2, 16, 18, 23, 24, 37, 38, 74–80, 81)

Trochus conoidalis Pease, 1868:287, pl. 24, fig. 8 [4 syntypes ANSP 18868; Paumotu (= Tuamotu Is); figure 76].

Risella (*Peasiella*) *conoidalis*.—Nevill, 1885:160; Tryon, 1887:263, pl. 50, fig. 38; Couturier, 1907:161; Dautzenberg & Bouge, 1933:359.

Risella conoidalis.—Hedley, 1899:424

Risella tantilla.—Smith, 1876:552 [in part, not Gould, 1849].

Echinella gaidei Montrouzier in Souverbie & Montrouzier, 1879:26–29, pl. 3, figs. 3, 3a, b [17 syntypes MNHNP; Lifou, Loyalty Is; figure 78].

Risella (*Peasiella*) *gaidei*.—Tryon, 1887:263, pl. 50, figs. 35–37.

Peasiella gaidei.—Oyama & Takemura, 1961: *Peasiella* and *Littorinopsis* pl., figs. 4–6; Higo, 1973:46; Habe, 1984:11, fig. 2.

Shell (figures 2, 16, 18, 74–80): *Dimensions:* Adult size range 1.9–5.1 mm diameter; mean height/diameter ratio 1.029 (95% confidence limits \pm 0.045, range 0.773–1.333, $n = 42$ from 22 localities).

Shape: Teleoconch 3–6 whorls. Outline equilaterally conical or taller; sides lightly convex; whorls sometimes shouldered; base flat to slightly convex. Periphery strongly keeled, sometimes with straight, undulating, or crenulated flange; suture indistinct except in strongly sculptured and shouldered shells. Umbilicus usually small, sometimes closed in small shells. Columellar pillar gently concave and rounded at base.

Sculpture: Protoconch 0.21–0.22 mm diameter, 2.8 whorls. Teleoconch whorls with (4)6–8 strong, equidistant grooves above periphery, occasionally increasing to 12 on last whorl; short radial plications sometimes present at suture, giving 3 subsutural ribs a beaded appearance; third rib below suture occasionally enlarged, making whorls shouldered. Periphery sometimes with 9–15 short axial folds, crenulating margin. Microsculpture of fine spiral striae over whole surface. Base with (4)5–8 spiral ribs, outermost largest; finer and more closely spaced towards umbilicus.

Color: Shell white, cream or orange yellow; pattern usually indistinct, but spiral grooves sometimes darker or marked by brown dots, and periphery occasionally with orange or brown marks corresponding with axial

Figures 67–73. *Peasiella tantilla*. **67, 70.** Pupukea, Oahu, Hawaiian Is (BMNH). **68, 69.** Mokuoloe I., Oahu (USNM 346450). **71–73.** Keaukaha, Hilo, Hawaii (USNM 339423). **Figures 74–80.** *P. conoidalis*. **74, 79.** Otepipi, Anaa, Tuamotu Is (BMNH). **75, 80.** Takume, Tuamotu Is (USNM 723721). **76.** Syntype of *Trochus conoidalis* Pease, 1868, Tuamotu Is (ANSP 18868). **77.** Mataira I., Raroia, Tuamotu Is (USNM 698654). **78.** Syntype of *Echinella gaidei* Montrouzier in Souverbie & Montrouzier, 1879, Lifou, Loyalty Is (MNIINP).



Figure 81. Distributions of *Peasiella tantilla* (asterisks) and *P. conoidalis* (dots).

fold. Base unmarked. Aperture and columella orange yellow.

Animal: *Head-foot:* Unpigmented.

Penis (figures 37, 38): Single penial gland; filament slender.

Pallial oviduct: Bursa apparently absent.

Radula (figures 23, 24): Outer marginal with 3 cusps.

Distribution: *Habitat:* Atolls and oceanic islands. On and under coral rubble or under thin layer of sand, on intertidal reef flats (Viader, 1951; J. Trondle, personal communication); on limestone in high intertidal zone (G. J. Vermeij, personal communication); on beachrock in barnacle zone (J. D. Taylor, personal communication).

Range (figure 81): Maldive Is, Seychelles, southern and western Pacific, from southern Japan to Queensland, Marshall and Tuamotu Is.

Records: Seychelles: Aldabra Atoll (BMNH); Maldive Is: Dunidu I., North Male (ANSP); Fadiffolu (ANSP); Chagos Arch.: Diego Garcia (Viader, 1951); Japan: Yakushima (NSMT); Oku, Okinawa, Ryukyu Is (LACM); Taiwan: Yeh-Liu (ANSP); Philippines: Binanga Port, Luzon (USNM); Corregidor I., Luzon (ANSP); 10 km N of Calavag, Palawan (D. Kadolsky Colln); Mariana Is: Tagachan Point, Guam (G. J. Vermeij Colln); Caroline Is: Ponape (AMS); Marshall Is: Engebi I., Eniwetok (USNM); Bikini (USNM); Busch I., Rongelap (USNM); Enybor I., Jaluit (USNM); Gilbert Is: Tarawa (AMS); Ellice Is: Funafuti (AMS); Australia: Queensland: Lizard I. (ANSP); Papua New Guinea: Rabaul, New Britain (AMS); Bougainville Strait (AMS); Milne Bay (AMS); Solomon Is: NW Sta Isabel I. (LACM); Lauosi I., Malaita I. (AMS);

New Hebrides: Malakula I. (AMS); Efate I. (LACM); Loyalty Is: Lifou (AMS, MNHNP); New Caledonia: Pannie (Hedley, 1899); Fiji: Deuba (AMS); Samoa: Swains I. (USNM); Line Is: Palmyra (USNM); Society Is: Moorea (LACM); Tahiti (BMNH); Tuamotu Is: Makatéa (USNM); Rangiroa (USNM); Manihi (LACM); Anaa (BMNH, 3♂, 3♀); Marutéa du Sud (AMS); Takume (USNM); Oneroa (USNM); Amanu (USNM).

Remarks: This widely distributed species is distinguished from *P. tantilla* by its pale color, finer and more numerous basal ribs, and frequently crenulated margin. The tall outline, basal sculpture of fine ribs extending right to the umbilicus, and the dorsal color pattern, separate it from *P. roepstorffiana*.

Peasiella roepstorffiana

(Nevill, 1885)

(figures 3–6, 17, 19, 25, 26, 39–42, 52, 53, 57–63, 82–89, 96)

?*Risella* (*Peasiella*) *tantillus* var. *parvula*.—Nevill, 1885:159 [not Dunker, 1861].

Risella (*Peasiella*) *roepstorffiana* Nevill, 1885:161 [1 syntype seen, here designated lectotype, ZSI 1916; Andaman Is; figure 89; 5 possible syntypes BMNH 1989005; S. Andaman].—Tryon, 1887:264, pl. 50, fig. 43.

Risella (*Peasiella*) *templiana* Nevill, 1885:161 [1 syntype seen, here designated lectotype, ZSI 1913; Andaman Is; figure 83].

Risella (*Peasiella*) *templiana* var. *nigrofasciata* Nevill, 1885:161–162 [1 syntype seen, here designated lectotype, 4.8 × 3.2 mm, ZSI M17732/3; Andaman Is].

Risella (*Peasiella*) *templiana* var. *subimbricata* Nevill, 1885:162 [1 syntype seen, here designated lectotype, ZSI 4.8 × 4.1 mm; Andaman Is].

Risella balteata Preston, 1905:197, pl. 14, fig. 13 [2 syntypes BMNH 1908.7.2.68-69; Andaman Is].
 ?*Risella tantilla*.—Hedley, 1910:355 [not Gould, 1849].
Peasiella sp. Morton & Morton, 1983:62, figs. 5.3, 5.8.

Shell (figures 3-6, 17, 82-89): *Dimensions:* Adult size range 1.6-5.0 mm diameter; mean height/diameter ratio 0.757 (95% confidence limits ± 0.022 , range 0.556-1.000, $n = 101$ from 55 localities).

Shape: Teleoconch 3.5-5 whorls. Outline varying from rather depressed to equilaterally conical; sides convex or rarely almost straight; whorls usually gently rounded; base flat to slightly convex. Peripheral keel strongly angled, usually a sharp flange, margin usually straight, sometimes undulating or crenulated; suture slightly impressed or indistinct. Umbilicus open. Columellar pillar straight to slightly concave, rounded or slightly angled at base.

Sculpture: Protoconch 0.23 mm diameter, 2.3 whorls. Teleoconch whorls with (3)4-8 approximately equidistant spiral grooves above periphery, sometimes increasing to up to 13 on last whorl, sometimes obsolete. Short, fine, radial plications occasionally developed at suture. Sometimes 9-12 radial folds at periphery of last whorl, producing undulating or crenulated margin. Microsculpture of fine spiral striae over whole surface. Base with (1)3-5(6) approximately equidistant spiral ribs, either innermost or outermost strongest; innermost $\frac{1}{3}$ - $\frac{1}{2}$ of basal radius usually lacking spiral ribs, but rarely showing 1-2 small ribs.

Color: Shell cream, golden yellow or pinkish orange, sometimes with faint tessellated pattern over whole dorsal surface; spiral grooves sometimes brown; peripheral flange occasionally brown, either continuous or broken into spots corresponding with marginal crenulations. Shells occasionally with dark spiral band on lower half or middle of whorls. Base usually unpatterned; underside of peripheral flange sometimes brown or spotted. Interior of aperture golden yellow, exterior pattern showing through; columella yellow to purple brown. Distinctive red brown, tessellated color pattern occurring in Fiji, Samoa, southeastern Papua New Guinea and Philippines (figure 6): red brown and white spots on ribs, 11-24 at periphery of last whorl, making oblique tessellated pattern over whole surface, sometimes darkest on lower half of whorls; base and columella red brown; tessellations showing through in pale band within aperture.

Animal: *Head-foot (figures 39-42):* Black band across base of snout, single longitudinal black line on tentacles; head sometimes entirely unpigmented; foot with faint black speckling or unpigmented.

Penis (figures 39-42): Single penial gland in specimens from Queensland, but this is absent in those from Malaya, Thailand, and Hong Kong.

Paraspermatic nurse cells (figures 52, 53): Rounded to irregularly oval, sometimes with produced tip; finely

granular contents with indistinct nucleus; nurse cells absent in specimens from Hong Kong.

Pallial oviduct (figures 57-63): Bursa absent.

Radula (figures 25, 26): Outer marginal with 3(4) cusps.

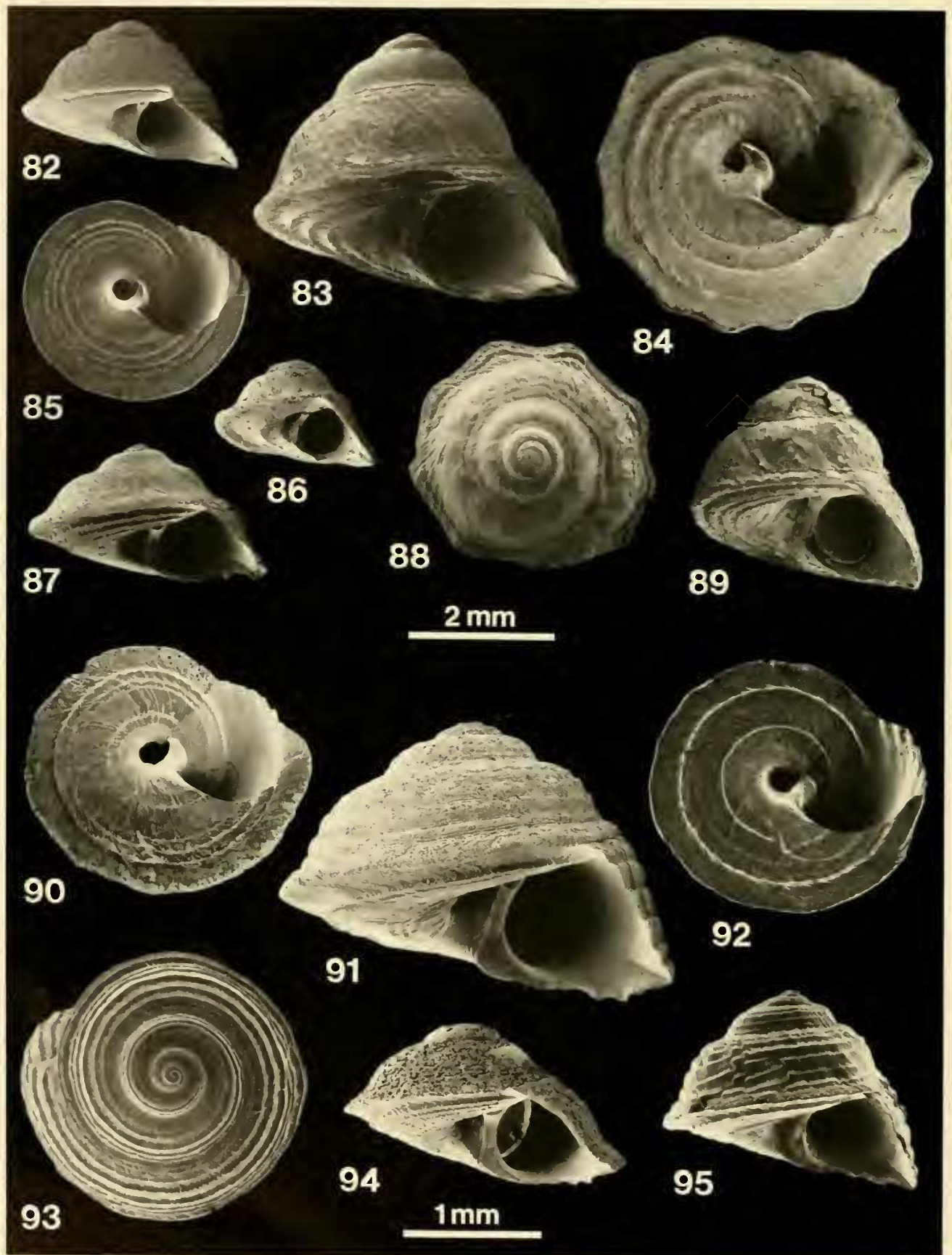
Distribution: *Habitat:* Islets and promontories on continental coasts; oceanic high islands. High eulittoral zone, on granite and volcanic rock, amongst and above barnacles and oysters. Rare or absent in turbid bays.

Range (figure 96): Central Indo-Pacific, from eastern Bay of Bengal to Hong Kong, Philippines, Palau, Queensland, Fiji and Samoa.

Records: Burma: Arakan (BMNH, USNM); Andaman Is (BMNH); Thailand: Marine Biological Center, Phuket I. (BMNH, 2♂, 1♀); Surin Beach, Phuket I. (BMNH, 1♂); Ko Tao (USNM); Pattaya (J. Le Renard Colln); Malaysia: Langkawi Is (USNM); Port Dickson (ANSP, 1♂); Mersing (BMNH); Vietnam: Baie d'Along (BMNH); Isle de la Table (MNHNP); Hong Kong: Ping Chau, Mirs Bay (BMNH, 3♂, 1♀); Hoi Ha, Mirs Bay (BMNH); Hoi Sing Wan, Tolo Channel (BMNH, 1♂); Lamma I. (AMS, 1♂); Sai Kung (DGR, 3♂, 1♀); Philippines: Binanga Port, Luzon (USNM); Scott's I., Lingayen Gulf, Luzon (LACM); Maricaban I., Luzon (USNM); Samar I. (NSMT); Zamboanga, Mindanao (NSMT); 10 km N of Calavag, Palawan (D. Kadolsky Colln); Caroline Is: Arakapesan, Palau (G. J. Vermeij Colln); Papua New Guinea: Nimoa, Louisiade Arch. (AMS); Milne Bay (AMS); Port Moresby (AMS); Queensland: Somerset (AMS); Lizard I. (AMS); Cooktown (AMS); Low Isles (AMS); Green I. (AMS); Dunk I. (ANSP); Orpheus I. (DGR); Picnic Bay, Magnetic I. (DGR, 5♂, 2♀); Gladstone (AMS); Fiji (BMNH, MCZ, MNHNP, ANSP, USNM); Nadi Bay, Viti Levu (AMS); Samoa: Pago Pago Harbor, Tutuila I. (LACM, AMS).

Remarks: This is a highly variable species, with a distinctive red brown, tessellated color form in the eastern and northeastern part of its range, and a more marked tendency towards marginal crenulation in the northern part. Nevertheless, considerable variation in shape and color also occurs within local populations, and recognition of geographical subspecies appears unnecessary. The unsculptured area around the umbilicus, and common golden yellow color with lines or tessellations, are the most useful diagnostic characters.

Of greater significance is the apparent geographical variation in anatomical characters. The amount of material available for dissection was limited, but the 12 males examined from Hong Kong, Malaya, and Thailand all lacked the mamilliform penial gland, while this was present in the 5 from Queensland. In addition, paraspermatic nurse cells were absent in 4 specimens from Hong Kong, but present in 3 from Queensland. Both nurse cells and the mamilliform gland are uniformly present in other *Peasiella* species. The lack of nurse cells could be simply a developmental abnormality or seasonal variation (although neither has been recorded elsewhere in the family). Penial shape is usually rather constant in



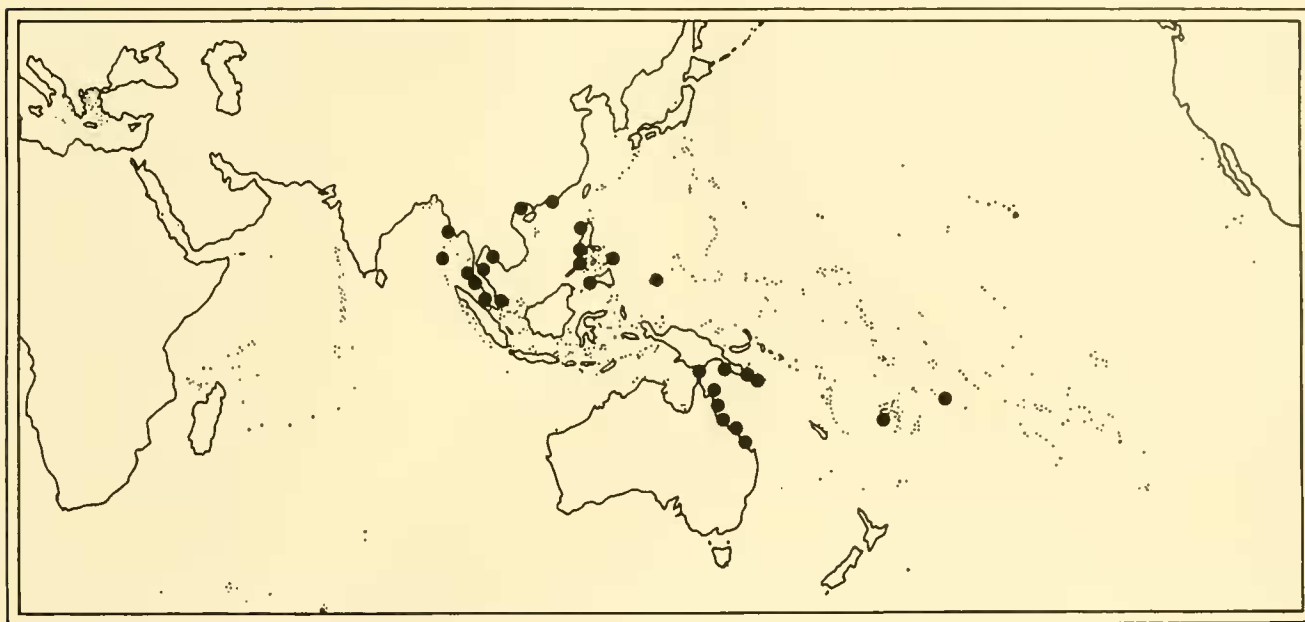


Figure 96. Distribution of *Peasiella roepstorffiana*.

littorinid species, and may differentiate between closely related species, leading to the idea that it serves the function of species recognition (*e.g.*, Reid, 1986). The geographical variation in penis shape in *P. roepstorffiana* could therefore be evidence that two species are involved. However, the number of mamilliform glands does show intraspecific variation, especially in littorinids with many such glands (Reid, 1989). In species of *Nodilittorina* (which normally have a single gland), abnormal animals can be found with two or none. A male *P. infracostata* has been found without a mamilliform gland. For this reason, and because of the absence of any consistently correlated shell characters by which two species could be distinguished in the *P. roepstorffiana* group, a single nominal species is retained here until further information is available.

A single fossil from the Upper Oligocene of New Zealand may be referable to this species (see below).

Peasiella lutulenta new species
(figures 7–9, 27, 43–46, 54, 55,
65, 66, 90–95, 97)

Bembicium sp. Wells & Slack-Smith, 1981:269.

Peasiella lutulenta n. sp. Etymology: Latin *lutulenta*, muddy, in reference to habitat of species. Types: holotype AMS C149052, Kissing Point, Rowes Bay, Townsville, Queens-

land (figure 9); 10 paratypes AMS C149053, 16 paratypes BMNH 1988138.

Shell (figures 7–9, 90–95): *Dimensions:* Adult size range 1.7–3.8 mm diameter; mean height/diameter ratio 0.716 (95% confidence limits ± 0.031 , range 0.500–0.909, $n = 36$ from 26 localities).

Shape: Teleoconch 2.5–4 whorls. Outline varying from rather flattened to almost equilaterally conical; sides convex; base flat to slightly convex. Peripheral keel with strong flange, margin not usually undulating or crenulated; suture slightly impressed. Umbilicus open. Columellar pillar straight, with thickened angle at base, forming margin of umbilicus.

Sculpture: Protoconch 0.24–0.27 mm diameter, 2.4 whorls. Teleoconch whorls with (4)5–7(9) strong, approximately equidistant spiral grooves above periphery. Microsculpture of fine spiral striae over whole surface. Peripheral keel usually entire, rarely with 9–11 slight crenulations. Base with 2–6 spiral ribs, outermost 1–3 ribs most prominent, usually separated from smaller ribs around umbilicus by marked gap.

Color: Shell cream to pale horn color; 7–16 brown to black spots at periphery, usually also at suture, the two series connected by fainter irregular axial stripes; occasionally axial stripes complete and conspicuous. Periph-

Figures 82–89. *Peasiella roepstorffiana*. 82, 85. Orpheus I., Queensland (BMNH). 83. Lectotype of *Risella templiana* Nevill, 1885, Andaman Is (ZSI 1913). 84. Hong Kong (BMNH). 86. Viti Is (Fiji) (BMNH). 87, 88. Ping Chau, Hong Kong (BMNH). 89. Lectotype of *Risella roepstorffiana* Nevill, 1885, Andaman Is (ZSI 1916). Figures 90–95. *P. lutulenta*. 90, 94. Hoi Sing Wan, Hong Kong (BMNH). 91. Shark Point, Barrow I., Western Australia (BMNH). 92, 93, 95. Cockle Bay, Magnetic I., Queensland (BMNH).

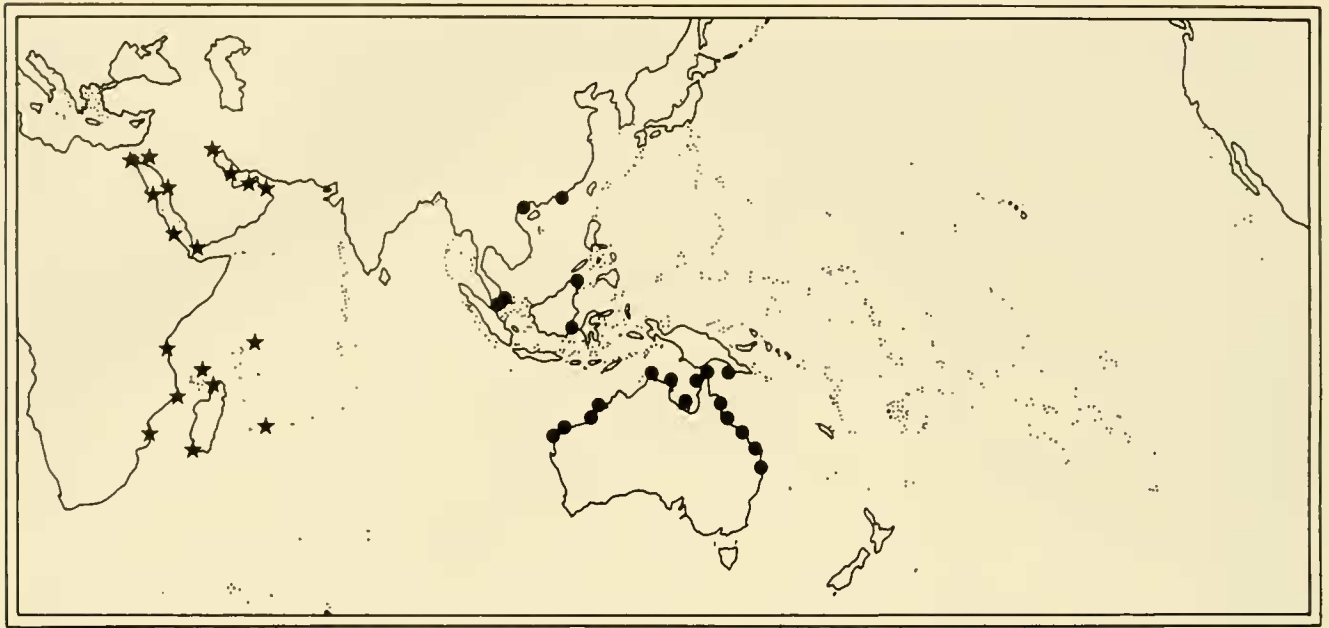


Figure 97. Distributions of *Peasiella isseli* (asterisks) and *P. lutulenta* (dots).

eral spots usually showing through at periphery of base. Columellar pillar whitish, red brown at base. Interior of aperture cream, exterior pattern showing through.

Animal: *Head-foot* (figures 43–46): 0–2 black bands across base of snout; black pigment above and below eye, but tentacles unpigmented; foot unpigmented or black mottled.

Penis (figures 43–46): Single penial gland.

Paraspermatic nurse cells (figures 54, 55): Irregularly oval, packed with round granules.

Pallial oviduct (figures 65, 66): Large anterior bursa present.

Radula (figure 27): Outer marginal with 3 cusps.

Distribution: *Habitat:* Sheltered, often muddy, continental shores. On rocks and outer fringes of mangrove forests, frequently in empty barnacles.

Range (figure 97): Central Indo-Pacific, including Hong Kong, Malaysia, Borneo, and northern Australia.

Records: Hong Kong: Hoi Sing Wan, Tolo Channel (BMNH, 2♂, 2♀); Hoi Ha, Mirs Bay (BMNH); Sai Kung (DGR, 3♂, 3♀); Vietnam: Isle de la Table (MNHNP, MCZ, ANSP); Baie d'Along (BMNH); Malaysia: Mersing (BMNH, 1♀; AMS); Tanjong Tuan (AMS); Port Dickson (ANSP, 1♂); Borneo: Sandakan (USNM); Balikpapan (AMS); Papua New Guinea: Eli Beach, Port Moresby (AMS); Australia: Western Australia: Beagle I., Onslow (AMS); Shark Point, Barrow I. (WAM, 2♂, 1♀); Dampier (AMS); Port Hedland (AMS); La Grange Bay (ANSP); Turtle I., King Sound (AMS); Northern Territory: East Point, Darwin (AMS); Maningrida (AMS); Gove Penin.

(DGR); Queensland: Sweers I., Wellesley Is (AMS); Ma-poon (AMS); Wednesday I. (AMS); Somerset (AMS); Port Douglas (AMS); Bingil Bay (AMS); Dunk I. (ANSP); Cockle Bay, Magnetic I. (DGR); Rowes Bay, Townsville (DGR, 2♂, 1♀); Bowen (AMS); Island Head Creek, N of Yeppoon (AMS); Gladstone (AMS); Facing I. (AMS); Point Vernon, Hervey Bay (AMS); Moreton Bay (AMS).

Remarks: The thickened columellar base is diagnostic of this species. Other useful characters include the basal sculpture and usually coarse, dark color pattern on the dorsal side (which separate it from *P. roepstorffiana*), the coarse dorsal sculpture (separating it from *P. infracostata*) and the lack of a shoulder keel (separating it from many individuals of *P. isseli*).

Late Pleistocene fossils have been found in Shark Bay, Western Australia (G. W. Kendrick, WAM), but the closest Recent specimens are from Onslow, 500 km to the north.

Peasiella isseli
(Semper in Issel, 1869)
(figures 13–15, 28, 49,
50, 56, 97–105)

Trochus sp. Audouin, 1826:42.

Risella isseli Semper in Issel, 1869:194, 347 [refers to Savigny, 1817: pl. 5, figs. 35.1, 35.2; lectotype here designated MNHNP 1.5 × 1.4 mm, figured by Bouchet & Danrigal, 1982: fig. 65; figures 101, 103 herein; Suez].—Pallary, 1926: 84, pl. 5, figs. 35.1, 35.2.

Risella (Peasiella) isseli.—Nevill, 1885:160–161; Tryon, 1887: 263, pl. 50, figs. 39, 40.

Risella isseli var. *carinata* Pallary, 1926:84–85, pl. 5, fig. 36 [reproduced from Savigny, 1817: 1 syntype seen, MNHNP 1.5 × 1.3 mm; Suez].

Risella isseli var. *undata* Pallary, 1926:84, pl. 5, fig. 35.3 [reproduced from Savigny, 1817; type not found; Suez].

Risella isseli var. *maurittiana* Viader, 1951:149, pl. 3, figs. 10, 11 [2 syntypes in Mauritius Institute, not seen; Cannonier's Point and Grand Bay, Mauritius; 3 possible syntypes BMNH 1989004, figure 14].

Trochus sismondae Issel, 1869:225–226, pl. 2, fig. 13 [holotype MGD 4.0 × 4.1 mm; Suez].

Shell (figures 13–15, 98–105): *Dimensions:* Adult size range 1.9–5.6 mm diameter; mean height/diameter ratio 0.758 (95% confidence limits \pm 0.044, range 0.545–1.077, $n = 45$ from 26 localities).

Shape: Teleoconch 2.5–3.5 whorls. Outline varying from depressed to almost equilaterally conical; sides convex, sometimes with strong shoulder carina; base convex. Periphery strongly keeled, sometimes with strong rib or flange; margin usually entire, rarely slightly crenulated; suture slightly impressed. Umbilicus small. Columellar pillar concave, slightly angled at base.

Sculpture: Protoconch 0.26–0.28 mm diameter, 2.3–2.5 whorls. Teleoconch whorls with (6)7–9(12) equidistant or irregularly spaced spiral grooves above periphery, occasionally obsolete; shoulder rib sometimes enlarged or carinate. Microsculpture of fine spiral striae over whole surface. Rarely, periphery and shoulder with 7–12 radial folds, forming slight marginal crenulations. Base with (3)4–6(8) spiral ribs, outermost largest, finer and more closely spaced towards umbilicus; ribs around umbilicus sometimes bearing periostracal bristles.

Color: Shell cream, tan, spire sometimes pink or lilac, or entire shell dark brown or black. Pattern sometimes absent. Patterned shells with (6)8–16 dark brown spots at periphery, sometimes connected to sutural spots by oblique brown lines; others with faint marbled pattern over entire shell; base usually unpatterned. Columella white to brown; aperture cream to brown.

Animal: *Head-foot (figures 49, 50):* Two black lines across base of snout, two longitudinal black lines on tentacles; sides of foot blackish.

Penis (figure 50): Single penial gland.

Paraspermatic nurse cells (figure 56): Round or oval, packed with round granules.

Pallial oviduct: Large anterior bursa present.

Radula (figure 28): Outer marginal with 3–4 cusps.

Distribution: *Habitat:* Continental coasts and oceanic high islands, only rarely on atolls. Upper eu littoral zone of rocky shores.

Range (figure 97): Western Indian Ocean, including Persian Gulf and Red Sea, south to Moçambique and Madagascar.

Records: Egypt: Suez (BMNH); Israel: Eilat (BMNH, 1♂, 2♀; USNM, ANSP); Sudan: Dongonab Bay (BMNH); Port Sudan (ANSP); Ethiopia: Massawa (BMNH, NM);

Dehui I., Dahlak Is (BMNH); Saudi Arabia: Jeddah (USNM); Yemen: Aden (BMNH); Oman: Bandar Khayrhan (BMNH); Persian Gulf: Abu Dhabi (BMNH); Qatar (BMNH); Kuwait (BMNH); Tanzania: Zanzibar (BMNH); Moçambique: Moçambique I. (NM); Benguera I., Bazaruto Arch. (NM); Madagascar: Nossi Bé (USNM, ANSP); Tuléar (MNHNP); Mauritius: Grand Bay (BMNH); Seychelles: Baie Ternay, Mahé I. (BMNH, USNM); Northwest Bay, Mahé I. (ANSP, 5♀); Aldabra Atoll (BMNH).

Remarks: This is another species with very variable shell characters. The shoulder is often keeled, but the species is separated from similarly shouldered shells of *P. tantilla* and *P. conoidalis* by the color pattern, a generally more depressed outline and often by the basal sculpture. Specimens without a shoulder keel are separated from *P. lutulenta* by their narrower columellar base, and from most specimens of *P. roepstorffiana* by the basal sculpture. Distinction from *P. infracostata* is discussed below.

Peasiella infracostata

(Issel, 1869)

(figures 10–12, 29, 30, 47, 48, 64, 106–112)

Trochus sp. Audouin, 1826:42.

Risella infracostata Issel, 1869:195–196 [refers to Savigny, 1817: pl. 5, fig. 40; lectotype, here designated, MNHNP 1.5 × 1.2 mm, figured by Bouchet & Danrigal, 1982: fig. 64; Suez; figure 109 herein].—Pallary, 1926:86, pl. 5, fig. 40; Dautzenberg, 1929:496.

Risella (Peasiella) infracostata.—Nevill, 1885:160; Tryon, 1887: 264, pl. 50, figs. 41, 42.

Risella (Peasiella) tantillus var. *subinfracostata* Nevill, 1885: 160 [1 syntype seen, here designated lectotype, ZSI, 2.3 × 2.2 mm; Nicobar Is].

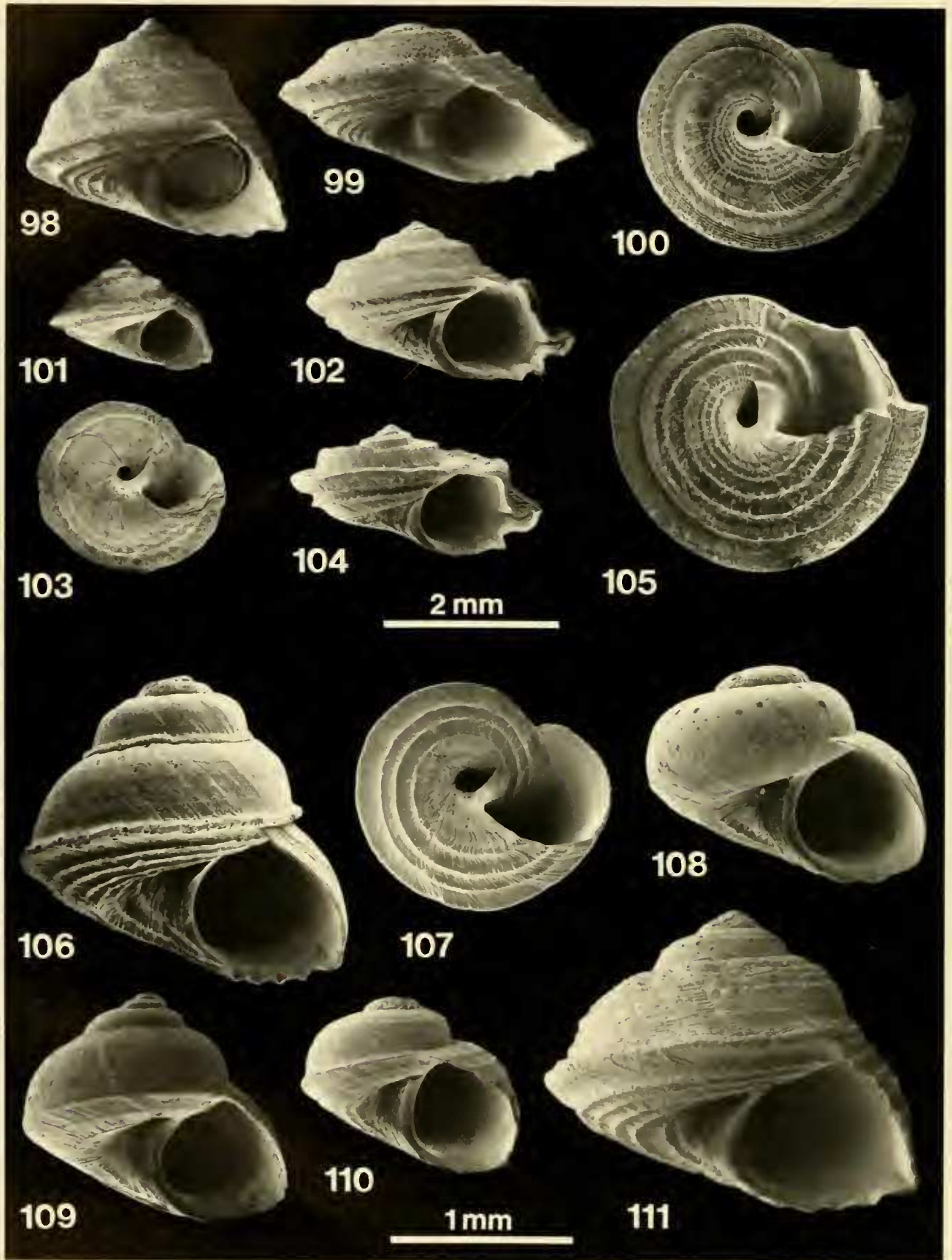
Cyclostrema fuscopiperata Turton, 1932:198–199, pl. 51, fig. 1379 [2 syntypes, OUM; Port Alfred, South Africa].

Peasiella roepstorffiana.—Habe, 1956: fig. A (egg capsule); Oyama & Takemura, 1961: *Peasiella* and *Littorinopsis* pl., figs. 1–3; Yamamoto & Habe, 1962:16, pl. 3, figs. 3, 4, 34, 35; Amio, 1963:303, figs. 22a,b (egg capsule); Habe, 1964:28, pl. 9, fig. 23; Higo, 1973:46; Habe, 1984:11, fig. 1 [all not Nevill, 1885].

'*Littorina-capsula habeii*' Tokioka, 1950: fig. 6.1 (egg capsule).

Shell (figures 10–12, 106–111): *Dimensions:* Adult size range 1.1–3.5 mm diameter; mean height/diameter ratio 0.846 (95% confidence limits \pm 0.022, range 0.600–1.120, $n = 79$ from 39 localities).

Shape: Teleoconch 2.5–4 whorls. Shell thin and translucent, or solid. Outline varying from almost equilaterally conical with rounded whorls to depressed globular or almost flat with inflated whorls; in Japan, whorls flat; base flat to convex. Periphery either uniformly rounded, or with weak or strong rib, or (in Japan) with strong flange; margin usually entire, rarely slightly crenulated; suture usually impressed. Umbilicus open, sometimes very small. Columellar pillar straight to uniformly rounded, curved and not thickened at base. Aperture occasionally somewhat patulous.



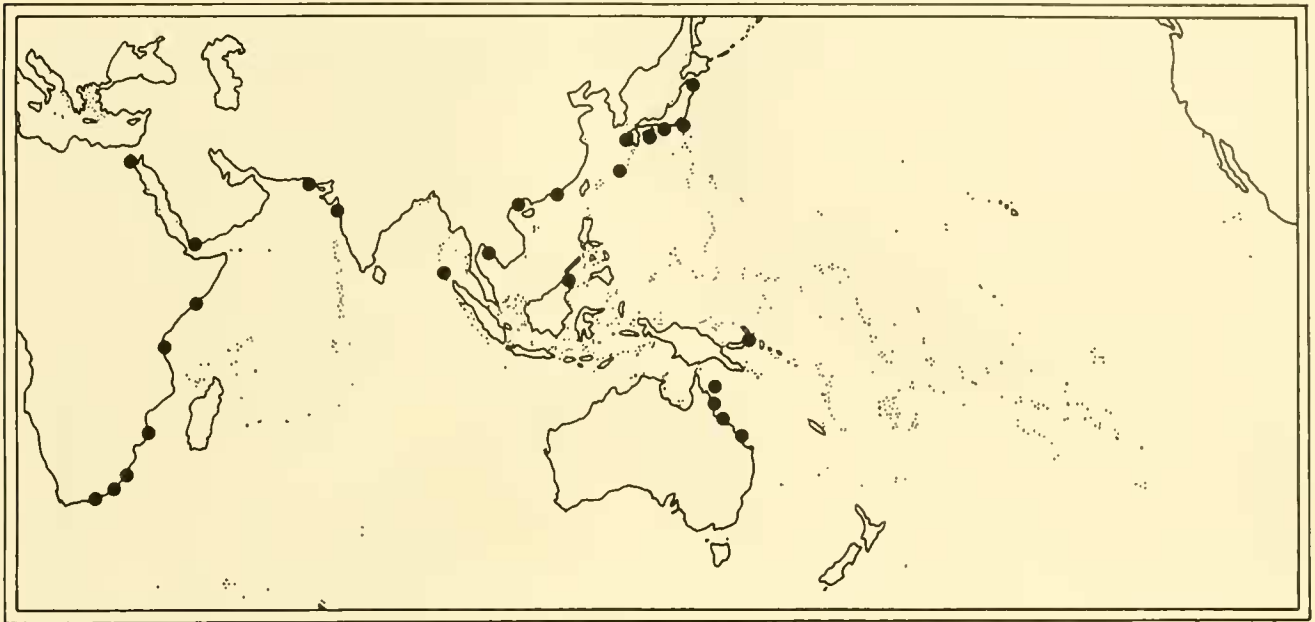


Figure 112. Distribution of *Peasiella infracostata*.

Sculpture: Protoconch not seen, apex usually eroded. Teleoconch whorls commonly smooth above periphery; spiral microstriae sometimes present and (in Japan) 7–10(11) equidistant spiral grooves. Base with (2)4–5 approximately equidistant spiral ribs, becoming a little stronger towards periphery. Basal and peripheral ribs sometimes bearing small periostracal bristles.

Color: Shell white to horn color; spire sometimes dark grey, black or purple brown. Shells from Indian Ocean (figure 11): suture and periphery with alternating brown and opaque white spots (9–13 brown spots at periphery of last whorl); sutural and peripheral spots sometimes connected by oblique brown lines; spiral brown line sometimes placed just above suture on spire whorls; base unmarked or with peripheral brown line. Shells from Pacific Ocean (figure 12): 2–7 brown or black spiral lines or dashes above periphery, with or without brown spots at suture and periphery; 3–4 lines in grooves of base. Shells from Japan (figure 10): black, eroded spire; periphery of last whorl paler, with 7–10 smudged brown spots, sometimes forming oblique stripes or continuous band; base with 7–10 brown spots or band in outermost groove and brown band around umbilicus. Aperture cream with exterior pattern showing through; columella white to purple.

Animal: *Head-foot* (figures 47, 48): Head with 2 black bands across base of snout, posterior one broad; tentacles

usually unpigmented, sometimes black pigment above and below eye or single longitudinal black line; sides of foot black, grey or unpigmented.

Penis (figures 47, 48): Single penial gland present, occasionally absent.

Pallial oviduct: Large anterior bursa present.

Egg capsule (figure 64): Cupola type, with 5 concentric rings.

Radula (figures 29, 30): Outer marginal with 5–6 slender cusps.

Distribution: *Habitat:* Usually on continental coasts, sometimes on high islands. On sheltered and moderately exposed shores, from mean high water of spring tides to below mid-tide level, in crevices and empty barnacles, especially on sheltered sides of rocks (Mori *et al.*, 1985).

Range (figure 112): Margins of Indian Ocean, from South Africa to Red Sea, margins of western Pacific Ocean, from Japan to Queensland.

Records: Egypt: Suez (MNHNP); Yemen: Aden (BMNH); Somalia: Mogadiscio (ANSP); Tanzania: Zanzibar (BMNH); Moçambique: Benguera I., Bazaruto Arch. (NM); South Africa: Mapelane, Zululand (NM); Um-dhloti, Natal (NM); Mbotyi, Pondoland (NM); East London (NM); Port Alfred (OUM); Pakistan: Karachi (BMNH,

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Figures 98–105. *Peasiella isseli*. 98. Suez (BMNH 88.10.14). 99. Baie Ternay, Mahé, Seychelles (BMNH). 100. 102. 104. 105. Bandar Khayrhan, Oman (BMNH). 101, 103. Lectotype of *Risella isseli* Semper in Issel, 1869, Suez (MNHNP). **Figures 106–111.** *P. infracostata*. 106–108. Karachi, Pakistan (BMNH). 109. Lectotype of *Risella infracostata* Issel, 1869, Suez (MNHNP). 110. Pattaya, Thailand (J. Le Renard Colln LR99012). 111. Zanpa Point, Okinawa, Ryukyu Is (AMS C146702).

2♂; 7 km WNW Bulegi Point, Sind Prov. (LACM); India: Mada I., Bombay (ANSP); Nicobar Is (ZSI); Thailand: Pattaya (J. Le Renard Colln); Borneo: Berhala Channel, Sandakan (USNM); Bak-Bak, Kudat (USNM); Vietnam: Isle de la Table, Tonkin (MNHN); Hong Kong: Hoi Sing Wan, Tolo Channel (BMNH, 1♂); Lok Wo Sha, Tolo Channel (BMNH); Ping Chau, Mirs Bay (BMNH); Hoi Ha, Mirs Bay (BMNH, 2♀); Japan: Zanpa Point, Okinawa, Ryukyu Is (AMS 1♀; USNM, NSMT); Kyushu: Tomioka, Kumamoto Pref. (NSMT); Nagasaki (USNM); Shikoku: Tatsukushi, Kochi Pref. (NSMT, USNM); Honshu: Tanabe Bay, Wakayama Pref. (USNM); Kuchino, Shiznoka Pref. (BMNH, 4♂); Arasaki, Kanagawa Pref. (NSMT, USNM); Kominato, Aomori Pref. (LACM, ANSP); Asamushi, Aomori Pref. (NSMT, USNM); Papua New Guinea: Duke of York I., Rabaul, New Britain (AMS); Australia: Queensland: SW Lizard I. (LACM); Port Douglas (AMS); Green I. (AMS); Halfmoon Bay (AMS); Ellis Beach (AMS); Turtle Bay, Cape Ferguson (BMNH); Facing I., Port Curtis (AMS).

Remarks: This species is the most variable in the genus in its shell form and coloration, with recognizable forms in several areas of its wide geographical range. Shells from the Indian Ocean, South East Asia and Queensland are globular, with inflated whorls lacking grooves or microstriae above the round or slightly angled periphery (figures 106–110), and quite unlike any other members of the genus. The difference between the oblique or spotted color pattern of shells from the Indian Ocean (figure 11) and the spiral lines of shells from the southwestern Pacific (figure 12) is rather consistent. However, it is probably of minor importance, since shells from the Indian Ocean may show a spiral line on the spire, and on the body whorl the oblique lines may become almost perpendicular to the apertural lip. In addition, shells from the Pacific may develop sutural and peripheral spots like those in shells from the Indian Ocean.

Shells from Japan are very different, distinguished by conical shape, peripheral flange, frequent presence of microstriae and grooves above the periphery, and color pattern of a blackish spire and peripheral spots (figures 10, 111). They are, however, connected to the typical form of the species by intermediates from China and Thailand (figure 110), which show the typical globular shape and lined pattern, but with spiral grooves and peripheral keel as seen in Japanese shells. Specimens from Okinawa are especially variable, ranging from smooth to strongly grooved, keeled to globular, and with black or lined spire whorls. Keeled and faintly grooved shells of *P. infracostata* do occasionally occur in the Indian Ocean (figure 106). The basal sculpture is similar in all parts of the range. Radulae have been examined in single specimens from Karachi and Cape Ferguson, Queensland, and in two specimens each from Kuchino and Tomioka, Japan; all show the 5–6 sharp cusps on the outer marginal teeth, which are diagnostic of this species (figures 29, 30).

The Japanese form of *P. infracostata* resembles those shells of *P. isseli* without a shoulder keel. Both species

can show a similar color pattern of oblique brown lines. Some collections of juvenile specimens from southern Africa (here doubtfully assigned to *P. infracostata*) contain keeled, shouldered, grooved shells which resemble *P. isseli*. Nevertheless, these two species are considered to be distinct, for the following reasons. Typical forms of both species are present in mixed samples from Zanzibar (BMNH), Aden (BMNH) and the Bazaruto Archipelago (NM). Locality records suggest that *P. infracostata* is a continental species (at least over most of its range in the Indian Ocean), while *P. isseli* is somewhat more oceanic, extending to islands in the western Indian Ocean. *P. infracostata* has not been reliably recorded from the Persian Gulf or Red Sea (the type locality, Suez, is therefore doubtful), where *P. isseli* occurs commonly. In areas where both species occur there are consistent differences in shell shape. In adult *P. infracostata* there is no shoulder keel, grooves are usually absent above the periphery, there are no more than 5 basal ribs, and the periphery is usually rounded. In *P. isseli* the shoulder is frequently keeled, grooves are present above the periphery, basal ribs may number more than 5, and the periphery is sharply keeled. Shell color patterns also differ: in *P. infracostata* the spire whorls often bear a spiral brown line, or may be entirely black; in *P. isseli* both patterns are rare. The most important anatomical difference is the presence of 5–6 narrow cusps on the outer marginal teeth of *P. infracostata* (3–4 in *P. isseli*). A possible difference in coloration of the tentacles requires confirmation in additional specimens.

FOSSIL SPECIES OF *PEASIELLA*

Peasiella minuta (Deshayes, 1824)
(figures 113–115)

Trochus minutus Deshayes, 1824:239–240, pl. 29, figs. 15–18 (Atlas, 1837) [type not seen; Valmondois].—Deshayes, 1864:956.

Risella minuta.—Cossmann, 1888:257–258; Cossmann, 1899:325, pl. 23, fig. 24; Cossmann & Pissarro, 1907–1913: pl. 17, fig. 108.1; Cossmann, 1915:74, pl. 3, figs. 27–29.

Bembicium minutum.—Glibert, 1962:24.

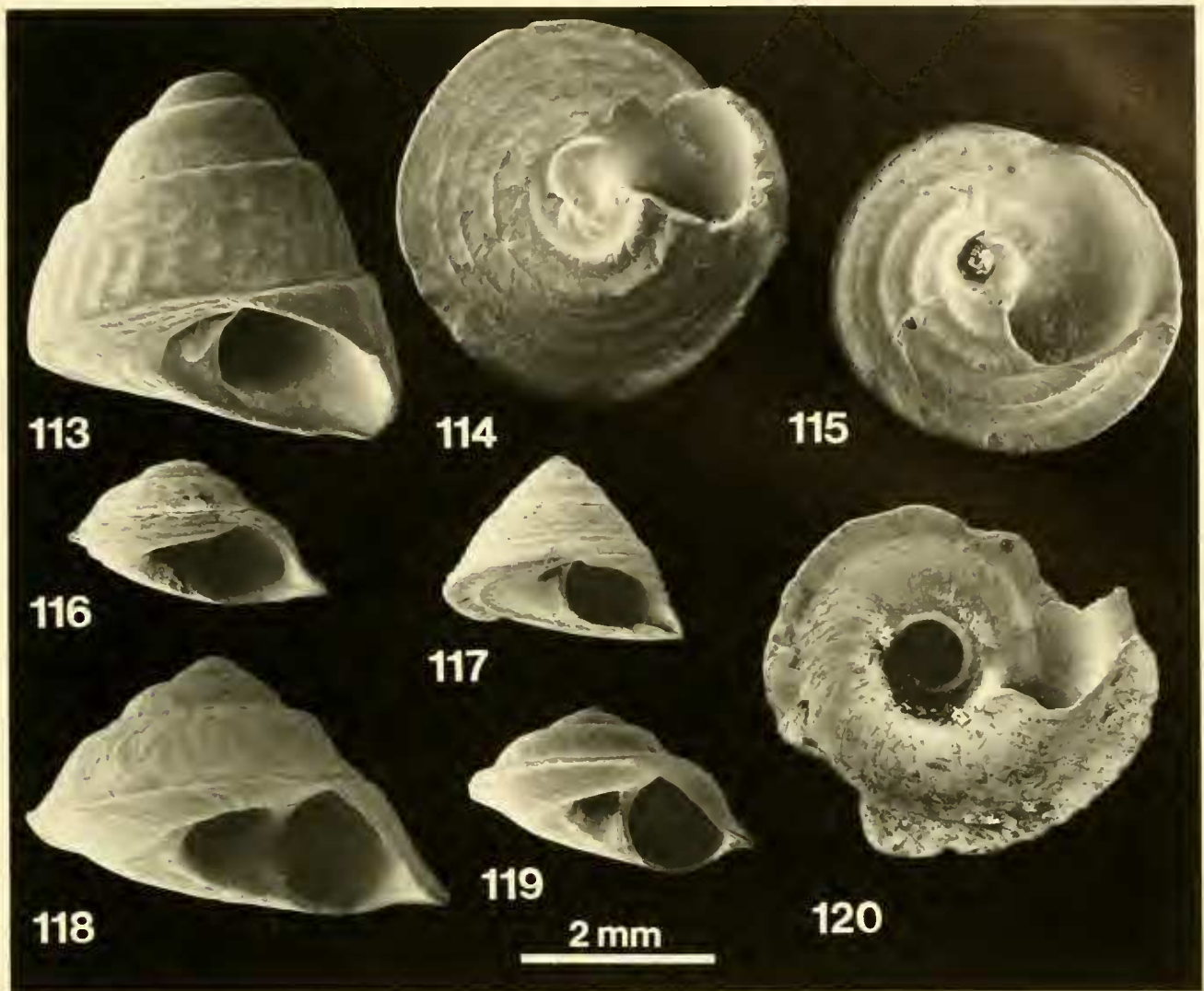
?*Xenophora bouryi* Cossmann, 1888:189, pl. 7, figs. 36–38 [type not seen; Neauphlette, Paris Basin, Eocene].

Shell (figures 113–115): *Dimensions:* Adult size range 3.1–6.6 mm diameter; mean height/diameter ratio 0.810 (95% confidence limits ± 0.074 , range 0.545–1.048, $n = 17$ from 6 localities).

Shape: Outline equilaterally conical or lower; periphery sharply angled or keeled, slight flange in juveniles; margins not crenulated; suture slightly impressed. Umbilicus becoming closed in larger shells.

Sculpture: Teleoconch whorls with 6–9(13) spiral grooves above periphery; sometimes with up to 30 oblique radial folds on last whorl. Base with 2–6(10) ribs, innermost outlining umbilicus, inner 2 often most prominent.

Distribution: *Range:* Paris Basin (Upper Eocene) and Loire (Middle Eocene) of France.



Figures 113–120. Fossil species of *Peasiella*. 113–115. *P. minuta*. 113, 114. L'Écaillette, Monneville, Paris Basin, Marinesian (J. Le Renard Colln LR99004). 115. Ronquerolles, Paris Basin, Auversian (J. Le Renard Colln LR99002). 116. *P. pontileviensis*, Ferrière-Larçon, Loire, Middle Miocene (MNHNP). 117. *P. aff. roepstorffiana*, Shell Gully, Chatton, Southland, New Zealand, Duntroonian (NZGS 9806). 118–120. *P. reyti*. 118, 120. Le Bois-Gouët, Loire Atlantique, Biarritzian (J. Le Renard Colln LR99010). 119. B7LSaubotte, Noaillan, Aquitanian (MNHNP).

Records: France: Paris Basin: Le Ruel, Bartonian (MNHNP); Le Ruel, Marinesian; Le Quoniam, Marinesian; L'Écaillette, Monneville, Marinesian; Ronquerolles, Auversian; Baron, Auversian; Barisseuse, Auversian; Méry-sur-Oise, Auversian; Loire: Saint-Lubin-de-la-Haye, Lutetian (all J. Le Renard Colln).

Remarks: This relatively common species shows variation in the development of the peripheral flange, closure of the umbilicus, and number of basal ribs. The combination of conical shape, marked spiral grooves above the periphery, and strong basal ribs extending to the umbilicus, is diagnostic.

The identity of *Xenophora bouryi* is uncertain; the description of radial costules and 3 basal ribs, and apparent lack of a thickened columellar base, resemble *P.*

minuta. However, the depressed shape, sinuous marginal flange and apertural form are different, and, taken together, suggest that it may not be a *Peasiella*.

Peasiella reyti
(Cossmann & Peyrot, 1917)
(figures 118–120)

Trochus thorinus.—Benoist, 1874b:316 [not Grateloup, 1832, *vide* Cossmann & Peyrot, 1917:63].

Pseudonina reyti Cossmann & Peyrot, 1917:363–365, text fig. 30, pl. 6, figs. 45–48 [type not seen: Mérignac, Aquitaine; Aquitanian].

Peasiella girondica.—Lozouet, 1986:229 [not *Risella girondica* Benoist, 1874].

Shell (figures 118–120): *Dimensions:* Adult size range 2.3–5.3 mm diameter; mean height/diameter ratio 0.627 (95% confidence limits \pm 0.065, range 0.459–0.756, $n = 9$ from 3 localities).

Shape: Spire relatively low; whorls convex at shoulder, concave towards periphery; suture impressed; base convex, becoming concave around umbilicus. Peripheral keel bearing strong flange, rarely slightly undulating. Umbilicus large (up to 0.3 of basal diameter). Columellar pillar uniformly rounded, thin.

Sculpture: Protoconch 0.30–0.36 mm diameter, 2 to approximately 3 whorls, terminated by sinusigera notch, but sculpture not preserved on specimens examined. Teleoconch whorls usually rather smooth, with growth lines and indistinct spiral microstriae only; sometimes coarser striations forming 11–14 indistinct grooves above periphery; radial sculpture absent, or coarsely rugose at shoulder, sometimes with 6–14 indistinct radial plications producing undulations of marginal flange. Edge of umbilicus a thickened rib, usually outlined by broad, shallow groove; rest of base almost smooth, but with radial growth lines (strongly developed near umbilicus), sometimes up to 10 faint spiral striae.

Color: Sometimes traces of a series of color spots at suture and periphery.

Distribution: *Habitat:* Near Montpellier this species occurred in an assemblage including barnacles, oysters, and the potamidid gastropods *Mesohalina*, *Potamides*, and *Terebralia*, together with driftwood, in a marl free of sand grains, suggesting a sheltered, muddy, possibly slightly brackish, intertidal, or lagoonal environment (D. Kadolsky, personal communication).

Range: Loire (Middle Eocene), Adour (Middle and Upper Oligocene), Languedoc (Upper Oligocene), and Aquitaine (Lower Miocene) of France.

Records: France: Le Bois-Gouët, Loire Atlantique, Biarritzian (J. Le Renard Colln); Gaas, Adour Basin, Middle Oligocene (MNHNP); Peyrère, Adour Basin, Chattian, Upper Oligocene (Lozouet, 1986); La Paillade, near Montpellier, latest Chattian (D. Kadolsky Colln); La Saubotte, Noaillan, Aquitanian (MNHNP).

Remarks: The nomenclature of this species is complex. It was incorrectly listed as *Trochus thorinus* Grateloup by Benoist (1874b), according to Cossmann and Peyrot (1917), who had examined both the Grateloup and Benoist Collections. The original description (Grateloup, 1832) and figure (Grateloup, 1847) of *Trochus thorinus* were both poor, but Cossmann and Peyrot (1917:280–282) examined the holotype and assigned the species (as a synonym of *Trochus biangulatus* Eichwald) to the genus *Gibbula* (Trochidae); furthermore, their figure bears no resemblance to *Peasiella*. The identity of *Trochus helicinus* Grateloup, 1832 (not Gmelin; renamed *subhelicinus* d'Orbigny, 1852) is uncertain; in the absence of type material in the Grateloup Collection, Cossmann and

Peyrot (1917) suggested that it was a synonym of *Trochus thorinus*.

From the original description (Benoist, 1874a) it is clear that *Trochus risella* (renamed *Risella girondica* by Benoist, 1874b) is not a *Peasiella*; it was described as 15 mm in diameter, imperforate, with concave whorls and tubercular sculpture. *Xenophora rhytida*, described and figured by Cossmann (1899), bears a superficial resemblance to a *Peasiella*, but the scalloped or spiked margin, projecting at the suture, the dorsal sculpture of 3 faint cords, and the narrow umbilicus, are all unlike the present species, and suggest that it may not be a littorinid.

The specimens examined during the present study bear a close resemblance to the original description and figures of *Pseudonina reyti* by Cossmann and Peyrot (1917), with the exception that the umbilicus is wider in the former, but this character is somewhat variable in living *Peasiella* species.

This species has a long stratigraphic range, from the Middle Eocene to the Lower Miocene, but from the material examined there seems no reason for subdivision. It is compared with *P. pontileviensis* below. In habitat, *P. reyti* may have resembled the Recent *P. lutulenta*.

Peasiella pontileviensis
(Morgan, 1915)
(figure 116)

Xenophora ? (*Haliphaebus*) *pontileviensis* Morgan, 1915:231–232, figs. 14a–d [type not seen; Vallon de Charenton, Pont-Levoy, Falunian].

Circulus pontileviensis.—Glibert, 1949:71, pl. 5, fig. 1.
Tornus orthezensis Cossmann & Peyrot, 1918:27–28, pl. 7, figs. 39–41 [type not seen; Orthez, Aquitaine, Helvetian].

Circulus orthezensis.—Glibert, 1949:71.

Risella girondica.—Cossmann & Peyrot, 1919:437–438, pl. 17, figs. 47, 48, 58 [not Benoist, 1874].

Shell (figure 116): *Dimensions:* 3.1–3.7 mm diameter; height/diameter ratio 0.548–0.568 ($n = 3$, from 1 locality).

Shape: Depressed; whorls lightly rounded; base convex. Strong flange at periphery, sometimes slightly undulating. Moderate umbilicus. Columellar pillar thickened and angled at base.

Sculpture: Spire whorls of teleoconch smooth; 6–8 spiral grooves and fine microstriae above periphery on last whorl; no radial sculpture. Margin of umbilicus thickened, but not outlined by a groove; 3–4 ribs on outer half radius of base.

Color: Two specimens have 7 brown spots at suture and 12–20 smaller spots at periphery of penultimate whorl, but little color on last whorl. A similar pattern covers the last 2 whorls in fig. 14d of Morgan (1915).

Distribution: *Range:* Loire (Middle Miocene) and Aquitaine (Lower and Upper Miocene) of France.

Records: France: La Brède, Aquitaine, Aquitanian (Cossmann & Peyrot, 1919); Orthez, Aquitaine, Helve-

tian (Cossmann & Peyrot, 1918); Ferrière-Larçon, Loire, Middle Miocene (MNHNP; Glibert, 1949).

Remarks: This species is similar to *P. reyti*, but appears to differ consistently in the presence of coarser spiral grooves above the periphery on the last whorl (grooves are absent or finer and more numerous in *P. reyti*), in the markedly thickened columellar base and in the presence of ribs on the outer part of the base. Elsewhere in the genus a thickened columellar base is found only in the Recent species *P. lutulenta*, from which *P. pontilevicensis* differs in its smooth spire whorls and presence of ribs on the outer part of the base only.

The three specimens examined showed 3 or 4 ribs on the base; in the original description there were said to be 2 (Morgan, 1915), and in *Tornus orthezensis* 5 (Cossmann & Peyrot, 1918). This range of variation is comparable to that of Recent species such as *P. roepstorffiana*. *Tornus orthezensis* was said to lack spiral sculpture on the dorsal surface (Cossmann & Peyrot, 1918), yet as noted by Glibert (1949) the accompanying figure of the holotype apparently shows faint spiral grooves.

This species appears to be generally rare; the authors quoted in the synonymy (with the exception of Morgan, 1915) recorded a total of only 9 specimens. However, Morgan (1915) recorded it as abundant at the type locality.

Peasiella aff. *roepstorffiana*
(Nevill, 1885)
(figure 117)

Shell (figure 117): *Dimensions:* 3.0 mm diameter; height/diameter ratio 0.767 ($n = 1$).

Shape: Outline slightly convex; whorls almost flat-sided; base slightly concave. Periphery sharply keeled, edge straight; suture indistinct. Umbilicus almost closed. Columellar pillar narrow, concave, rounded at base.

Sculpture: 6 strong, equidistant, spiral grooves above periphery. No radial sculpture. Single strong rib on outer part of base, with trace of another just within.

Distribution: *Record:* Shell Gully, Chatton, Okapua Valley, near Gore, Southland, New Zealand, Duntroonian, Upper Oligocene (NZGS).

Remarks: This single specimen from the Upper Oligocene of New Zealand falls just within the range of variation of the Recent species *P. roepstorffiana*. However, the single strong basal rib and very narrow umbilicus are atypical of that species, and until more specimens are available, identification is tentative.

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