CHAPTER 9: SYSTEMATIC DESCRIPTIONS

9.1 Key to shells

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

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

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

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

- Sutures impressed, spire whorls rounded 7

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

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

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

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

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

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

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

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

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

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

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

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

13 Columella white and wide 14

\- Columella purple, brown or narrow 16

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

9.2 Genus *Littoraria*

Littoraria Griffith & Pidgeon, 1834: 598 [type species by monotypy *Littorina pulchra* 'Gray' Sowerby, 1832 = *Turbo zebra* Donovan, 1825]

DIAGNOSIS. Shell sculpture of spiral ribs and grooves, nodulose sculpture lacking; shell pattern usually of short spiral dashes aligned to form axial stripes. Operculum thin, paucispiral. Penial glands absent; penial glandular disc present; penial sperm groove open or closed; prostate a closed tube. Sperm nurse cells present, usually with rod-shaped inclusions, sometimes flagellate. Egg groove of pallial oviduct runs through a single spiral loop of $2\frac{1}{2}$ to $9\frac{1}{2}$ whorls, incorporating both albumen and capsule glands, or albumen glands alone in ovoviviparous species. Egg capsules of oviparous species planktonic, biconvex, with a circumferential lamella, containing a single ovum. In ovoviviparous species capsule glands are absent and embryos are brooded in mantle cavity and spawned at veliger stage; one species is suspected to undergo direct development. Radula often 'hooded', with frontal plate anterior to cusps of rachidian tooth. Distribution largely tropical and subtropical; habitat usually mangroves, driftwood and saltmarshes, sometimes rocky shores; zonation supralittoral.

9.2.1 Subgenus *Littoraria*

DIAGNOSIS. Shell solid; varices absent; microsculpture, if present, is of spiral striae, often over whole surface; shell colouration may be somewhat variable but rarely polymorphic. Penial base bifurcate or simple; penial sperm groove open or closed. Sperm nurse cells not flagellate. Bursa copulatrix may open at anterior or posterior end of straight section of pallial oviduct; capsule glands present.

Development oviparous. Rachidian tooth of radula may or may not be hooded.

9.2.1.1 *Littoraria* (*Littoraria*) *vespacea* n. sp.

TYPES. *Holotype*: BMNH 198345, Santubong, Sarawak, Borneo. *Paratypes*: BMNH, USNM, AMS.

ETYMOLOGY. Latin: like a wasp, in reference to colour pattern of shell.

DIAGNOSIS. Shell: small; solid; spire low; whorls rounded; columella wide, very deeply excavated, excavated area brown; primary grooves 8; 23–35 flattened ribs on last whorl, with narrow grooves between; microsculpture of faint spiral striae on ribs; colour white to yellow with pattern of black dashes entirely aligned to form axial stripes, numbering 12–15 on last whorl. Animal: penis not bifurcate, filament large, constricted at base; oviparous.

SHELL. (Fig. 9.1). *Shape*. Height 10–25 mm. Teleoconch 5–6 whorls. Shell of moderate thickness, solid. Spire relatively low, outline slightly convex; whorls well rounded; sutures impressed. Peripheral keel absent. Adult lip slightly thickened, not flared. Varices absent. Columella wide, so deeply excavated that inner lip of aperture stands up sharply; pillar straight or slightly convex, strongly narrowed towards base. Sexual dimorphism: males smaller.

Dimensions: Table 9.1.

Sculpture (Fig. 9.2a,b). Protoconch not seen. All whorls of teleoconch sculptured with spiral grooves. Primary grooves 8(9), almost equidistant, posterior 3 ribs usually a little wider. Secondary sculpture develops on whorl 5; posterior rib usually

Fig. 9.1 *Littorarta* (*Littorarta*) *vespacea*: (a,b) paratype, ♀, Santubong, Sarawak (DGR); (c) ♀, Port Kelang, Malaysia (DGR); (d,e) holotype, ♂, Santubong, Sarawak (BMNH 198345); (f-i) paratypes, Santubong, Sarawak (DGR); (f,i) ♀; (g) ♀; (h) ♂.

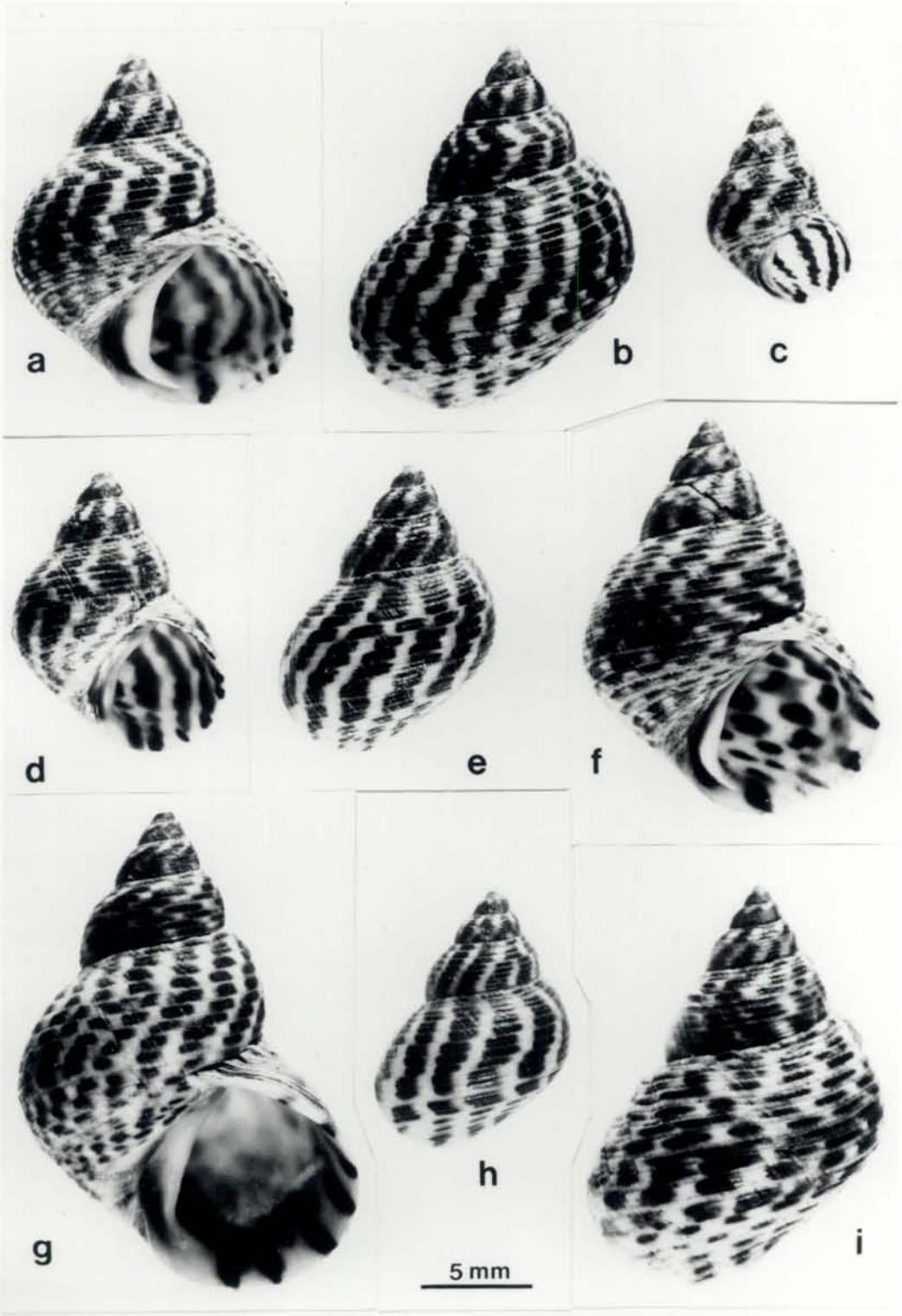
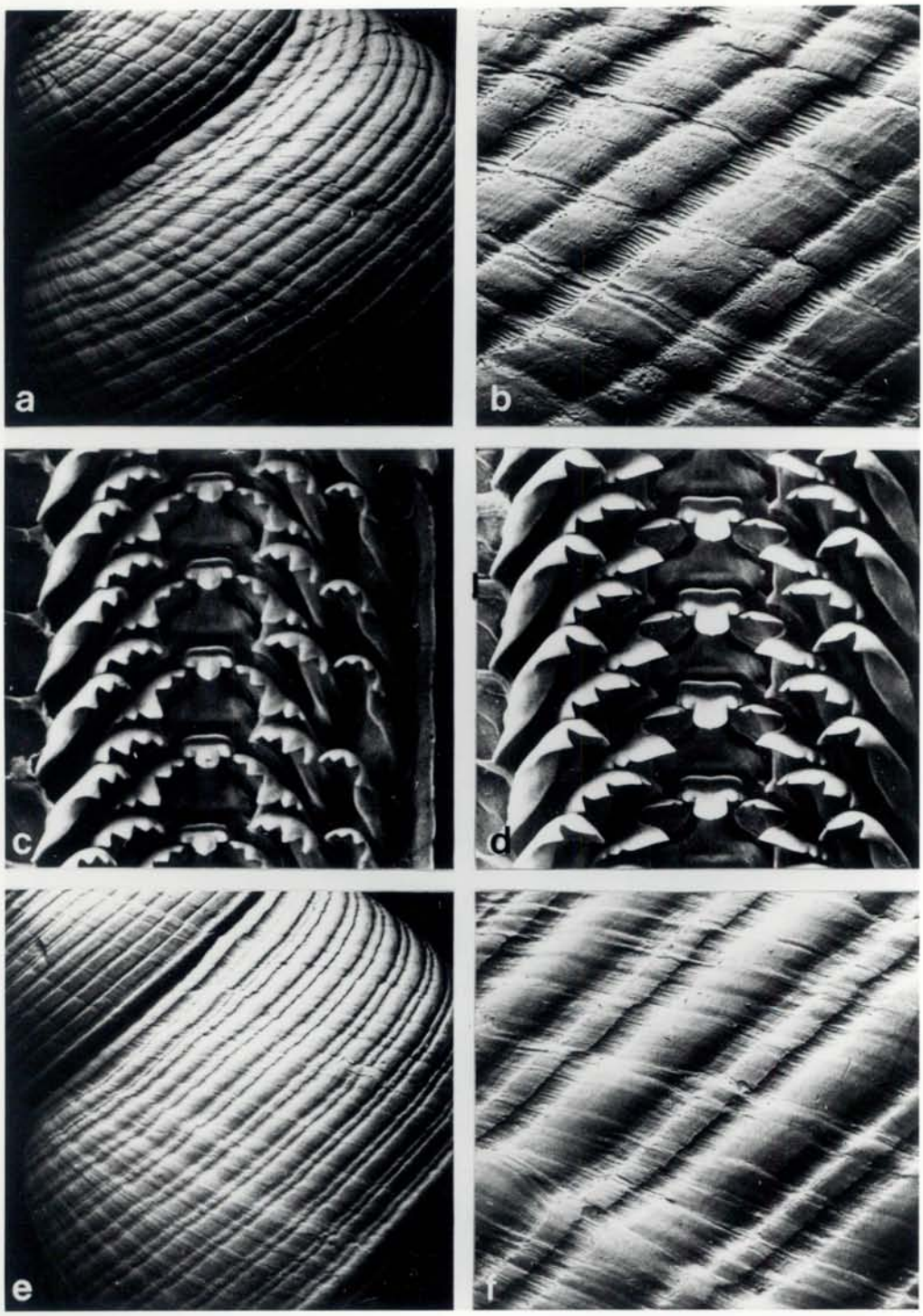

a
b
c
d
e
f
g
h
i
5 mm

Table 9.1 Dimensions of *Littoraria* (*Littoraria*) *vespacea*.

Specimen	Locality	Sex	Primary grooves	H (mm)	B (mm)	LA (mm)	WA (mm)	C (mm)	PR	S	SH
L. vespacea holotype BMNH 198345	Santubong, Sarawak	♂	8	12.8	10.2	7.9	6.1	1.9	1.25	0.77	1.62
DGR	Santubong, Sarawak	♂	8	14.7	10.5	9.0	7.0	2.3	1.40	0.78	1.63
DGR	Santubong, Sarawak	♂	8	11.2	8.1	6.6	5.1	1.3	1.38	0.77	1.70
DGR	Santubong, Sarawak	♀	8	17.9	13.7	11.2	9.0	2.0	1.31	0.80	1.60
DGR	Santubong, Sarawak	♀	8	15.7	12.1	9.2	7.4	1.8	1.30	0.80	1.71
AMS C.131737	Sembawang Estuary, Singapore		8	23.8	17.9	13.2	11.4	3.0	1.33	0.86	1.80
DGR	10 km N. Port Kelang, Malaysia	♂	8	9.5	6.8	5.5	4.5	1.2	1.40	0.82	1.73
DGR	10 km N. Port Kelang, Malaysia	♀	8	8.7	6.9	5.5	4.5	1.2	1.26	0.82	1.58
DGR, mean of 10	Santubong, Sarawak	♂		10.52					1.332	0.800	1.657
standard error				0.62					0.013	0.007	0.014
DGR, mean of 10	Santubong, Sarawak	♀		14.43					1.337	0.801	1.700
standard error				0.76					0.007	0.009	0.025
statistic t or U				3.980					52.5	51	67
probability				0.001					0.883	0.970	0.218

Fig. 9.2 (a–c) *Littoraria* (*Littoraria*) *vespacea*, Santubong, Sarawak: (a) last whorl (×9); (b) detail (×38); (c) radula (×250). (d–f) *Littoraria* (*Littorinopsis*) *lutea*, Ubin I., Singapore: (d) radula (×200); (e) last whorl (×8); (f) detail (×33).


a
b
c
d
e
f

remains undivided, but the several ribs immediately below it become divided each by a narrow secondary groove, and later all other ribs may be thus divided at $\frac{1}{4}$–$\frac{1}{2}$ width. Tertiary sculpture and intercalated riblets may appear at end of whorl 6, on largest shells. Ribs total 23–35(40) on last whorl; all ribs remain flattened, but for the rounded posterior rib. Grooves narrow, less than $\frac{1}{5}$ rib width; secondary grooves impressed lines only. Microsculpture of faint spiral striae on ribs, sometimes absent; faint axial growth striae cover surface, stronger in primary grooves. Periostracum sometimes produced into small bristles on ribs.

Colour. Rather constant; ground colour whitish or cream yellow, with pattern of short black dashes on ribs. Dashes usually remain discrete, and are almost always entirely aligned to form axial or somewhat oblique stripes, numbering (9)12–15 on last whorl. Alignment may become less perfect in largest shells. On base, alignment is less pronounced; characteristically 2 or more secondary ribs in middle of base lack pigment, while the primary rib between shows normal black dashes. Exterior pattern visible within aperture, but clouded by white callus except at margins. Columella and parietal callus white, excavation of columella brown or dull purple.

ANIMAL. *Colour*. Pigmentation black; sides of foot darkly mottled; head black; tentacles black banded, broad unpigmented stripe each side of base, often meeting behind tentacle.

Penis (Fig. 9.3a–f). Length to 4.0 mm. Base simple, incorporating glandular disc. Filament large, tapering near tip, constricted at base. Sperm groove open. Base cream, ochraceous at base of glandular disc and of filament; glandular disc opaque cream; filament off white.

Sperm. Eupyrene sperm 279–303 μm. Nurse cells (Fig. 9.3g–i) 15–23 μm, oval to rounded; rods 1(2–3), small, central or asymmetrically placed, not projecting, oval or fusiform; yolk granules large.

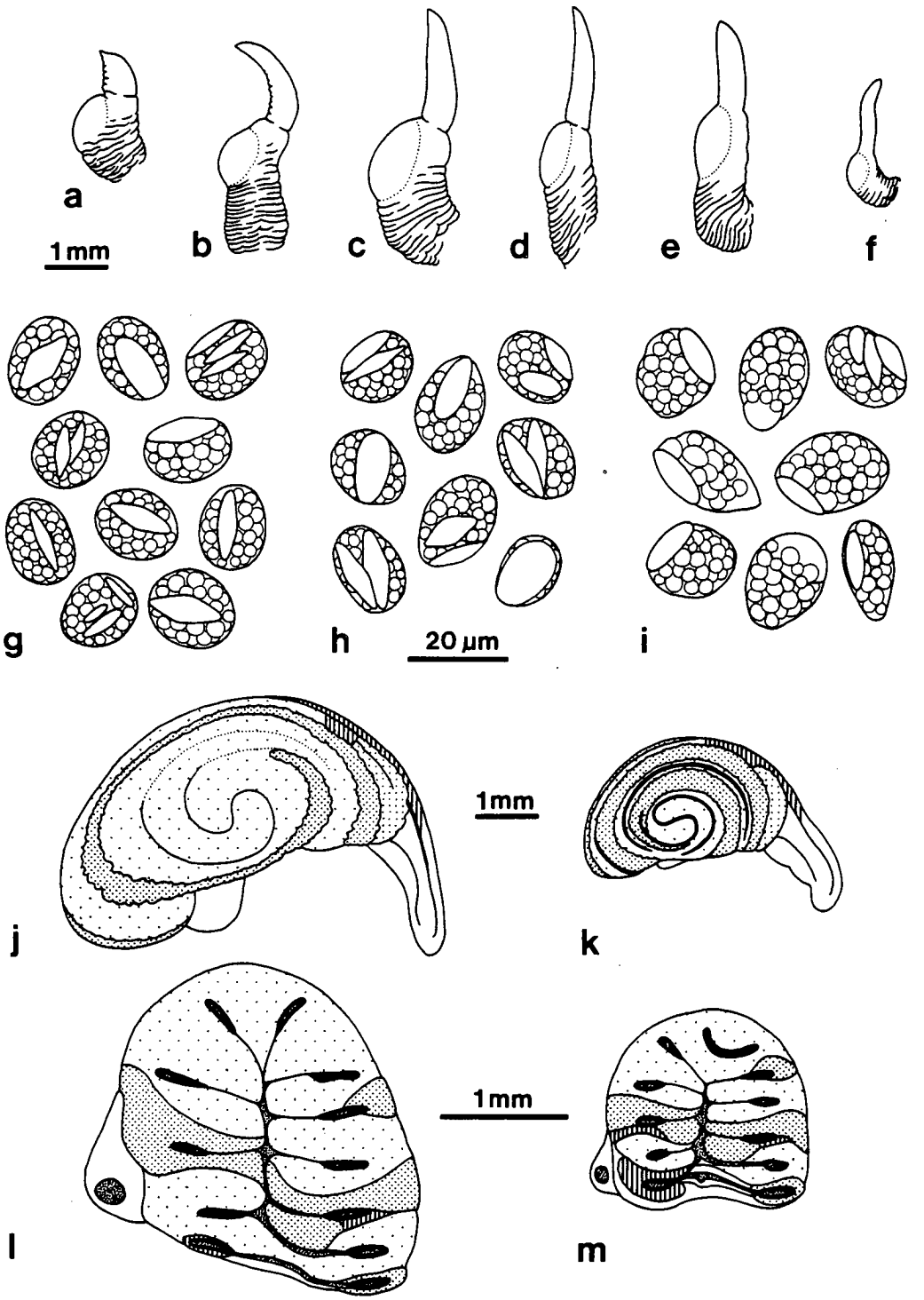


Fig. 9.3 *Littoraria* (*Littoraria*) *vespacea*: (a) penis, contracted; (b-f) penes, relaxed; (a-e) Santubong, Sarawak; (f) Port Kelang, Malaysia; (g-i) sperm nurse cells; (g,h) Port Kelang, Malaysia; (i) Santubong, Sarawak; (j-m) pallial oviducts, with transverse sections, Santubong, Sarawak.

Pallial oviduct (Fig. 9.3j-m). Length to 6.0 mm. Spiral section to 5.5 mm diam., $6\frac{1}{2}$ whorls; opaque albumen gland $\frac{1}{3}$ whorl, white; translucent albumen gland white; opaque capsule gland $1\frac{1}{2}$–2 whorls, pale pink or cream; translucent capsule gland red brown; spiral distinct externally; egg groove darkly pigmented. Straight section to 1.9 mm, grey to pale brown, brownish translucent capsule gland visible posteriorly; no terminal papilla. Bursa to 1.4 mm, anterior. Development assumed oviparous.

Radula (Fig. 9.2c). Length to 19 mm; relative length 1.14–1.50. Saw-toothed type; central rachidian cusp square, edge slightly pointed; cusps of paired teeth almost equilaterally triangular; lateral with no gap anterior to main cusp.

Pallial complex. Hypobranchial gland 0.5–1.0 mm wide, lemon yellow when fresh, grey brown when preserved.

DISTRIBUTION. *Habitat*. On trunks in *Avicennia* and *Sonneratia* fringes, 0.8–1.9 m above ground; on roots in *Rhizophora* and *Bruguiera* forests, 0.3–0.8 m above ground; extending as far as landward zone; also in crevices on wooden pilings. A continental species.

Range (Fig. 9.4). West coast of peninsular Malaysia, Singapore, Sarawak and southern Vietnam.

Records. MALAYSIA: PENINSULA: Batu Maung, Penang (DGR); 10 km N. of Port Kelang (DGR); Kuala Selangor (USNM, ANSP); SARAWAK: Santubong (DGR); SINGAPORE: Jelutong, Ubin I. (DGR); Sembawang Estuary (AMS); Kranji (BMNH, ANSP); VIETNAM: Vung Tau (ANSP).

REMARKS. This species may have been hitherto overlooked as a result of its resemblance to *L. articulata*, *L. strigata* and *L. intermedia*. In addition, the distribution of *L. vespacea* is restricted and specimens are rare in museum collections. Despite the close similarity of the shell to *L.* (*Palustorina*) *articulata* and *L.* (*P.*)

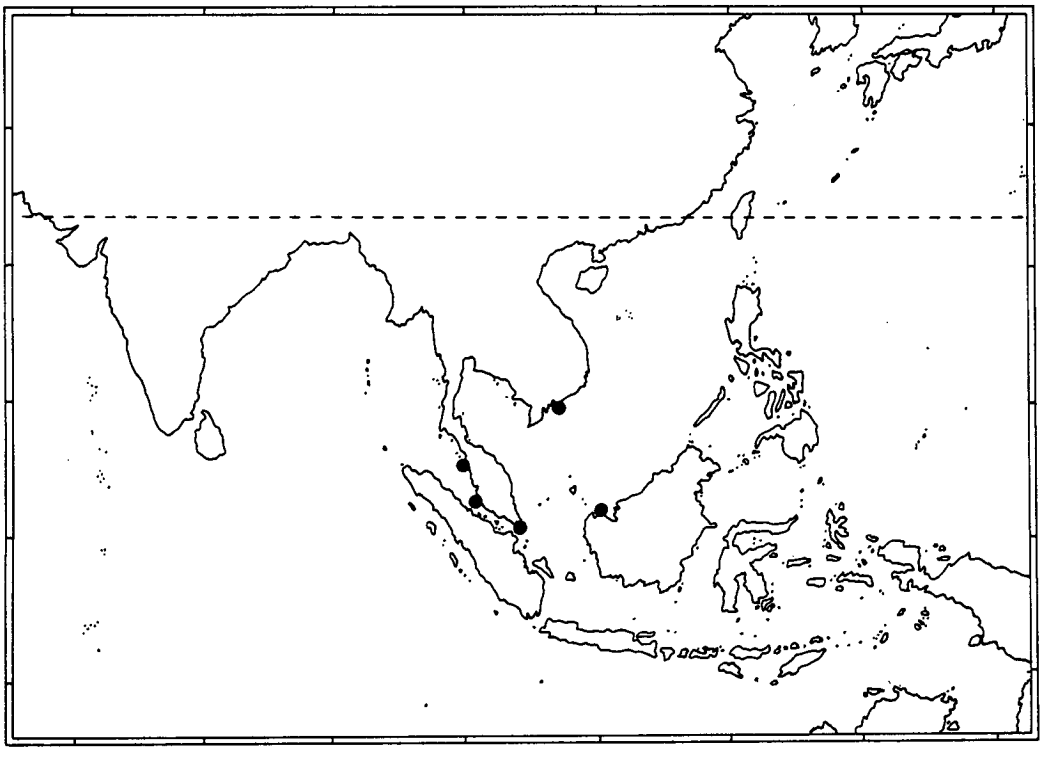


Fig. 9.4 Distribution of *Littoraria* (*Littoraria*) *vespacea*.

strigata, the anterior position of the bursa copulatrix and non-flagellate nurse cells preclude placement of *L. vespacea* in the same subgenus. Since the oviduct is of the oviparous type, the species is assigned to the subgenus *Littoraria*. *L. vespacea* does not appear to be closely related to any of the other Indo-Pacific species of the genus. The Eastern Pacific species *L. zebra*, *L. fasciata* and *L. varia* also show an oviduct of the oviparous type, with a bursa in the anterior position, as does the western Atlantic *L. irrorata*. It is interesting to note a resemblance of the shell of *L. vespacea* to those of young *L. zebra* and *L. fasciata*, in which the columella is also very deeply excavated and the microsculpture and colour pattern are similar, while the penis is reminiscent of that of *L. fasciata*.

The habitat of *L. vespacea* broadly overlaps that of *L. articulata* and *L. strigata*, but it does not occur in such large numbers and its distribution extends through the *Rhizophora* and *Bruguiera* zones to the outer edge of the landward fringe.

SIMILAR SPECIES. *L. vespacea* is clearly separated from *L. articulata* and *L. strigata* by the form of the penis, the non-flagellate sperm nurse cells, the anterior bursa copulatrix and the more numerous whorls of the pallial oviduct. The shells are similar, but those of *L. vespacea* are usually distinguished by their more inflated whorls, very deeply excavated columella and more numerous axial series of dark dashes in a more regular arrangement. *L. intermedia* should not be confused with *L. vespacea*, for in the former the spire is taller, the ground colour of the shell is grey or brown, the columella purple, the penis is bifurcate and the oviduct of the ovoviviparous type.

9.2.2 Subgenus *Lamellilittorina*

Littorina (*Lamellilittorina*) Tryon, 1887: 230 [type species by subsequent designation (Wenz, 1938) *Littorina albicans* Metcalfe, 1852]

DIAGNOSIS. As for the only known member, *L. albicans*.

9.2.2.1 *Littoraria* (*Lamellilittorina*) *albicans* (Metcalfe, 1852)

Littorina albicans Metcalfe, 1852: 73 [Borneo; lectotype (Rosewater, 1970) BMNH 1968355]; Reeve, 1857: *Littorina* pl. 9, figs 44a,b; Nevill, 1885: 150–151

Litorina albicans – Weinkauff, 1882: 81–82, pl. 11, figs 2,3

Littorina (*Lamellilittorina*) *albicans* – Tryon, 1887: 253, pl. 46, figs 25,26

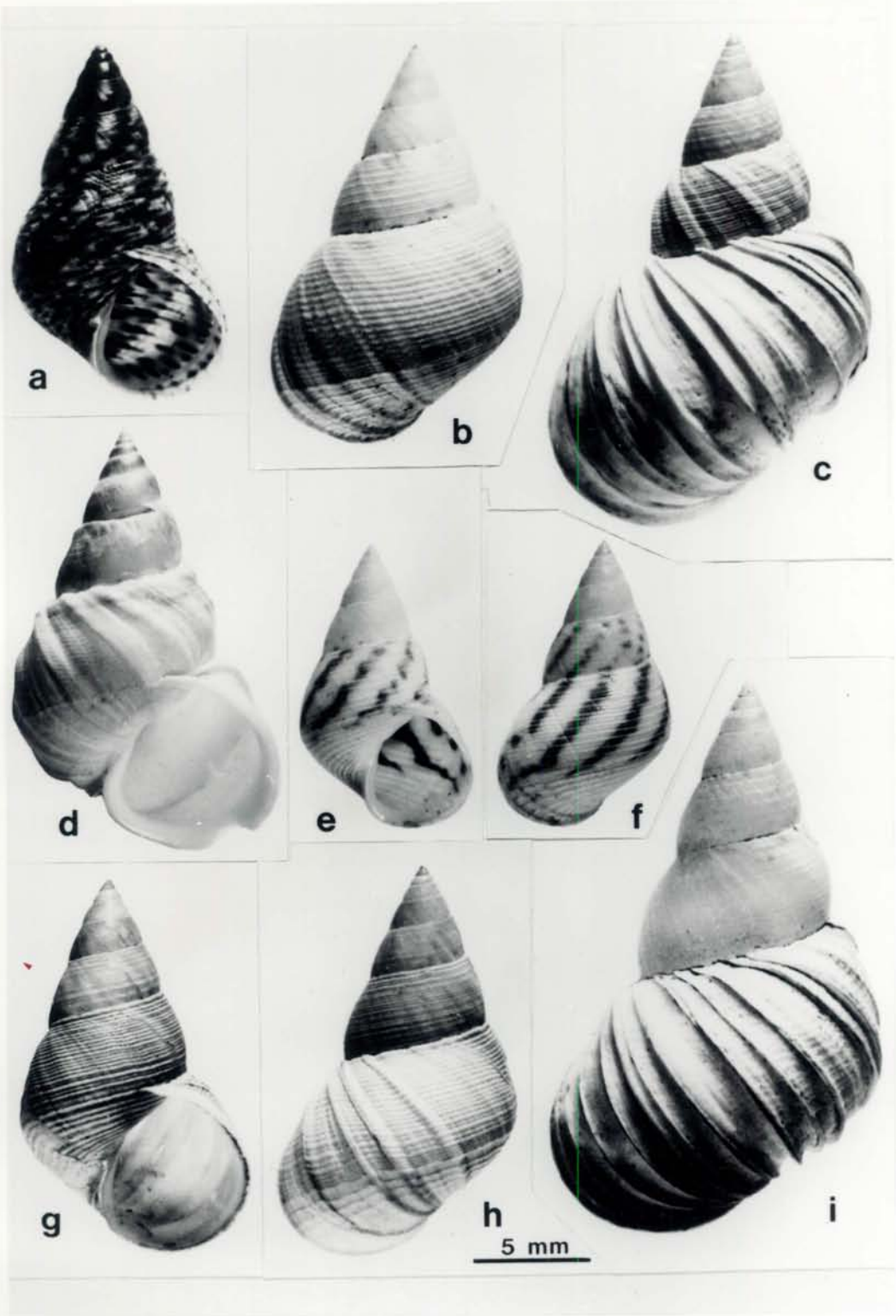
Littorina (*Littorinopsis*) *albicans* – von Martens, 1897: 199

Littorina (*Littorinopsis*) *scabra scabra* – Rosewater, 1970: 456–461, pl. 352, figs 5,31 [in part; not Linnaeus, 1758]

DIAGNOSIS. Shell: thin; spire flat sided, last 2 whorls rounded; lip thickened and flared; varices frequent, 0–20; columella rather narrow, only slightly excavated; protoconch large, broadly conical, 5 whorls; primary grooves 20–23; ribs on body whorl numbering over 100, flattened; microsculpture of deep axial lines in primary grooves; colour polymorphic, yellow, pink or brown when young, sometimes with 9–12 narrow oblique stripes on last whorl, but adult shells usually faded entirely to white or lilac. Animal: penis bifurcate, small, filament extremely small; oviparous.

SHELL (Fig. 9.5). *Shape*. Height 12–24 mm. Teleoconch 5.5–6.5 whorls. Shell thin, delicate, translucent. Spire outline: slightly convex,

Fig. 9.5 *Littoraria* (*Lamellilittorina*) *albicans*: (a–c) Santubong, Sarawak (DGR); (a) ♀; (b) ♀; (c) ♂; (d) lectotype of *Littorina albicans* Metcalfe, Borneo (BMNH 1968355); (e–i) Santubong, Sarawak (DGR); (e,f) ♀; (g,h) ♂; (i) ♀.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5 mm

whorls 1-2 rounded, 3-5 rather flat with indistinct sutures, 5-6 rounded with impressed sutures. Peripheral keel slight in young shells, becoming obsolete on whorl 6. Adult lip thickened and flared; varices 0-20, typically numerous on last whorl. Columella rather narrow, flat or shallowly excavated; pillar almost straight. Sexual dimorphism: slight, males smaller, relatively lower spire and larger aperture.

Dimensions: Table 9.2.

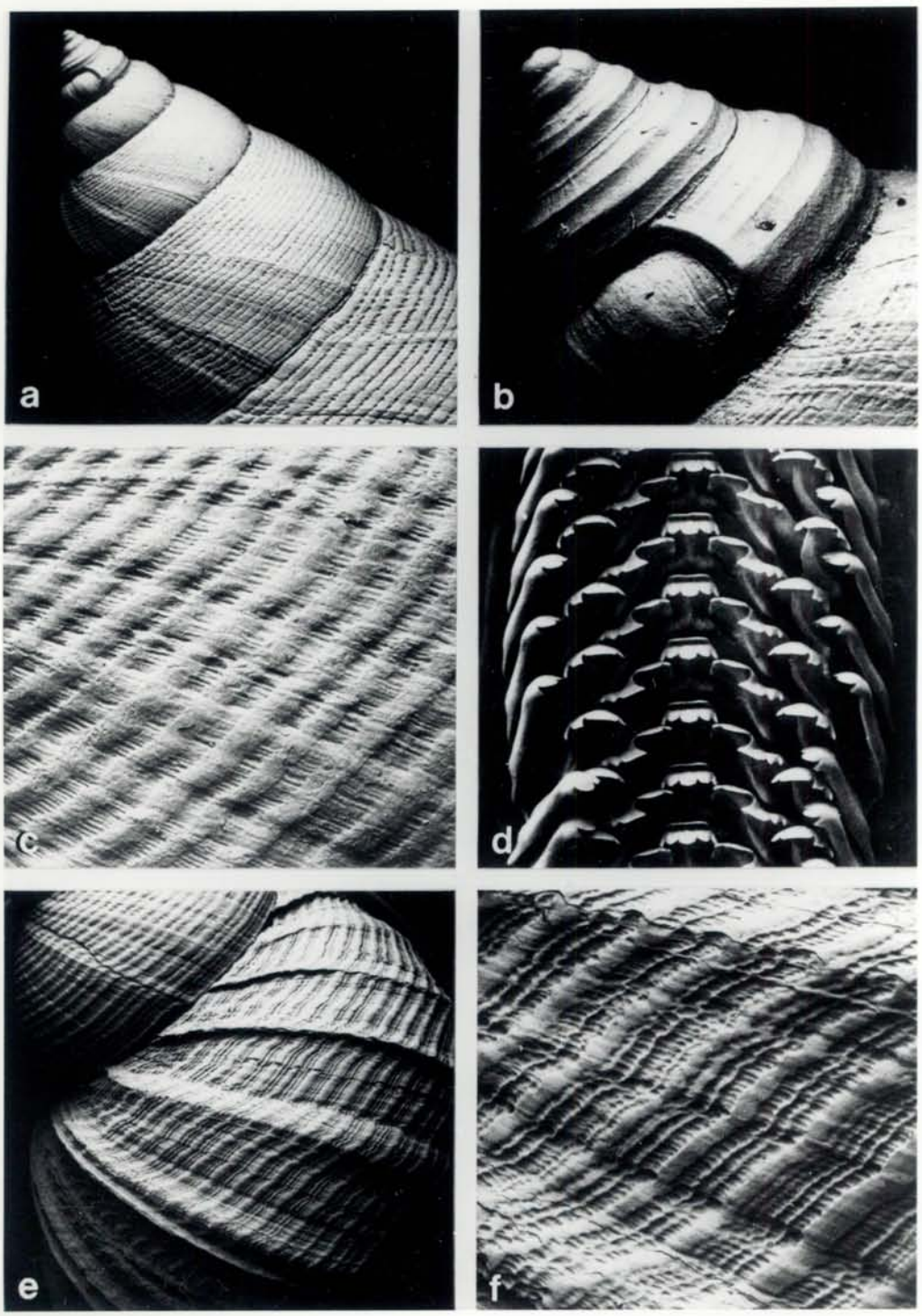
Sculpture (Fig. 9.6a-c,e,f). Protoconch large, 610-660 μm in length, of 5 whorls, broadly conical. First half whorl of teleoconch smooth. Primary grooves (17)20-23(26), equally spaced. Grooves $\frac{1}{3}$-1 rib width just before secondary sculpture begins. Secondary sculpture may form after a major varix on last whorl, by intercalation of 1-5 riblets between each pair of primary ribs. Secondary riblets at first narrow, but towards end of last whorl all ribs are subequal, remaining low and flattened, and numbering over 100. Spiral sculpture becomes irregular and less distinct where it is crossed by numerous varices and growth lines. Microsculpture of faint axial growth striae over whole surface, developed into deep, regular axial lines in primary grooves; on whorls 4-5 the primary grooves are narrow and therefore appear punctate; spiral microsculpture absent.

Colour. Polymorphic; yellow shells with faint pattern are most frequent, brown or pink shells not uncommon. Ground colour lemon yellow, cream, pale brown or orange pink, darkest towards apex. Alternate primary ribs often opaque white on penultimate whorl, all opaque by last whorl. Pattern of dark brown or lilac dashes on ribs, sometimes densely scattered over entire shell without conspicuous axial alignment; but usually first 4 whorls lack dark pigment, while last 2 are patterned with narrow, oblique stripes from suture to periphery, numbering 9-12 per whorl; pattern absent after first major varix. Yellow and pink shells fade to pure white with age, while in those which have been predominantly brown the dark pigment

Table 9.2 Dimensions of *Littoraria (Lamellilittorina) albicans*.

Specimen	Locality	Sex	Primary grooves	H (mm)	B (mm)	LA (mm)	WA (mm)	C (mm)	PR	S	SH
Littorina albicans lectotype, BMNH 1968355	Borneo		25	18.7	12.0	10.1	7.9	1.1	1.56	0.78	1.85
DGR	Santubong, Sarawak	♂	26	21.1	13.7	12.3	9.5	1.8	1.54	0.77	1.72
DGR	Santubong, Sarawak	♂	22	12.2	7.8	6.7	5.1	0.9	1.56	0.76	1.82
DGR	Santubong, Sarawak	♀	21	24.0	14.5	12.2	9.6	1.8	1.66	0.79	1.97
DGR	Santubong, Sarawak	♀	20	14.4	9.0	7.5	5.5	0.8	1.60	0.73	1.92
DGR, mean of 10	Santubong, Sarawak	♂		14.01					1.577	0.768	1.840
standard error				0.84					0.020	0.009	0.022
DGR, mean of 10	Santubong, Sarawak	♀		17.16					1.624	0.770	1.909
standard error				1.02					0.026	0.009	0.017
statistic t or U				2.390					65	63	83
probability				0.028					0.280	0.352	0.012

Fig. 9.6 *Littoraria* (*Lamellilittorina*) *albicans*, Santubong, Sarawak: (a) spire (×20); (b) protoconch (×90); (c) detail of penultimate whorl (×30); (d) radula (×190); (e) last whorl (×7); (f) detail (×27).


a
b
c
d
e
f

on the spire whorls fades to lilac and the body whorl and varices to white. Exterior pattern clearly visible within aperture of small translucent shells; aperture white in large individuals. Columella white; sometimes red brown in small pink or brown shells.

ANIMAL. *Colour*. Pigmentation pale to dark grey, correlated with shell colour, never unpigmented even in white shells; sides of foot faintly to darkly mottled; head darkest, red buccal mass clearly visible; tentacles red, with little dark pigment, no white stripes at either side of base, only groove between tentacle base and snout lacks pigment. Outer surface of mantle lemon yellow.

Penis (Fig. 9.7a–d). Rather small, to 3.1 mm. Base bifurcate; limb bearing glandular disc short. Filament very small, tip mucronate. Sperm groove open. Base and filament off white; glandular disc cream.

Sperm. Eupyrene sperm 152–170 μm. Nurse cells (Fig. 9.7e–g) 14–22 μm; oval, pyriform (with eupyrene sperm attached at blunt end) or rounded; rods often apparently absent, seldom clearly visible, but if so then single, parallel sided, blunt to rounded, sometimes projecting to form papillose tip; yolk granules closely packed, indistinct, polygonal, often elongate or lozenge shaped.

Pallial oviduct (Fig. 9.7h–k). Length to 6.4 mm. Spiral section to 2.9 mm diam., $6\frac{1}{2}$ whorls; opaque albumen gland $\frac{1}{3}$ whorl, white; translucent albumen gland pale fawn; opaque capsule gland $1\frac{1}{2}$–2 whorls, cream; translucent capsule gland red brown; spiral distinct externally; egg groove darkly pigmented. Straight section to 2.5 mm, fawn, reddish translucent capsule gland visible posteriorly; no terminal papilla. Bursa long, to 2.4 mm, anterior. Development assumed oviparous.

Radula (Fig. 9.6d). Length to 12 mm; relative length 0.54–0.79. Chisel-toothed type; cusps of rachidian of equal length, central one slightly wider; cusps of paired teeth obliquely triangular; lateral

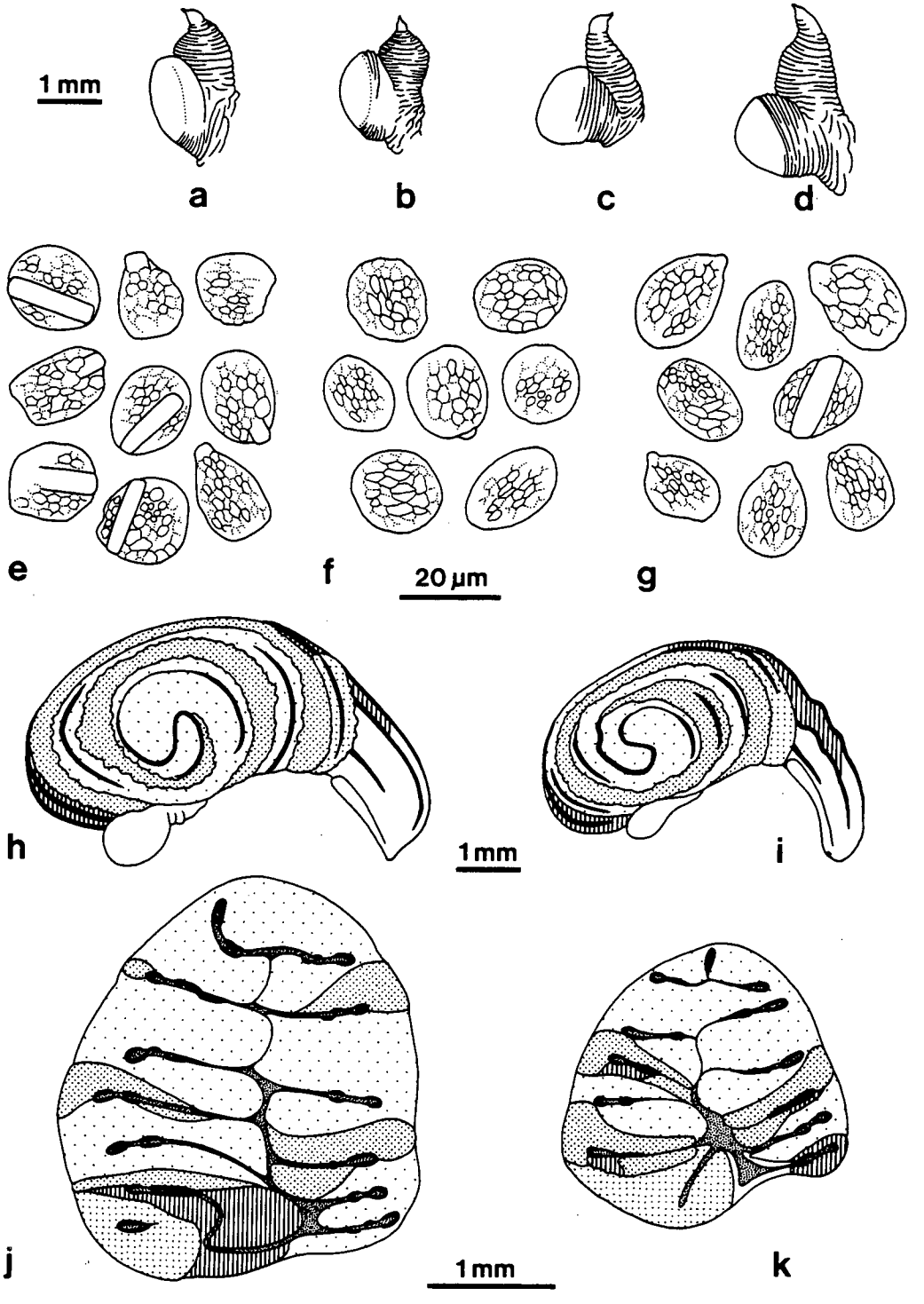


Fig. 9.7 *Littoraria* (*Lamellilitorina*) *albicans*, Santubong, Sarawak: (a-d) penes, relaxed; (e-g) sperm nurse cells; (h-k) pallial oviducts, with transverse sections.

with gap anterior to main cusp.

DISTRIBUTION. *Habitat.* Leaves of *Avicennia* from near seaward edge to landward fringe, 0.5–3.5 m above ground; scarce on *Sonneratia* leaves; in landward fringe also on *Nypa* fronds.

Range (Fig. 9.8). Southern Borneo; perhaps extending to Timor (a single record, doubtful since species not recorded at any intervening localities in Indonesia).

Records. MALAYSIA: SARAWAK: Santubong (DGR, BMNH, USNM, SM); Buntal (SM); INDONESIA: KALIMANTAN: Balikpapan Harbour (AMS); LESSER SUNDA IS.: Timor (RNHL, record doubtful).

REMARKS. Although common in Borneo, at least in Sarawak, *L. albicans* is rare in museum collections and does not seem to have been recognized as a distinct species in the literature since 1897. The white, lamellose shells of large adults are so distinctive that Tryon (1887) placed the species in a new subgenus, *Lamellilittorina*. This monotypic subgenus is retained here in recognition of the large protoconch (unique in the genus), the unusual shell sculpture (large number of primary grooves, strong axial microsculpture), small penis, distinctive radula and remarkable colouration of the animal.

In some other *Littoraria* species varices are formed during interruptions to growth corresponding with an annual reproductive season and possibly also during otherwise unfavourable periods (Section 13.4.7). It would seem difficult thus to account for the formation of as many as 20 varices in *L. albicans*, especially in an equatorial area without extremes of climate. However, it is possible that the longevity of this species is indeed much greater than others in the genus, for alone of species of *Littoraria* the shell fades to pure white, suggesting a most prolonged exposure to the sun.

SIMILAR SPECIES. This is one of the most distinctive of *Littoraria*

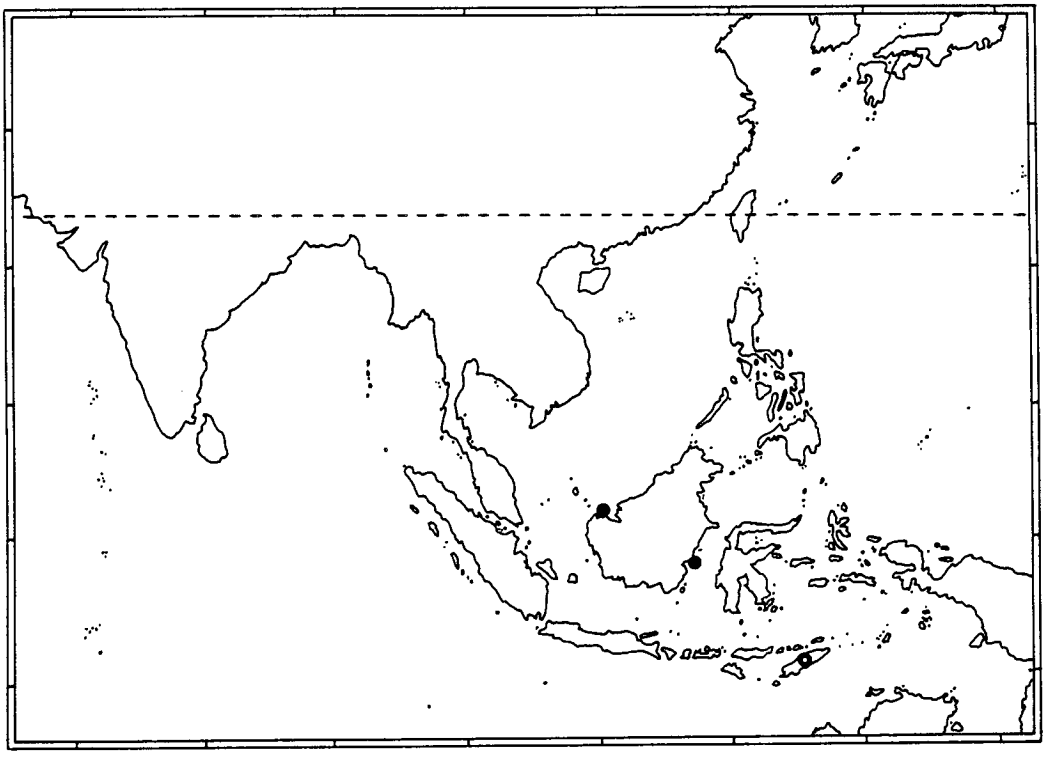


Fig. 9.8 Distribution of *Littoraria* (*Lamellilittorina*) *albicans*.

species and when large, with varices well developed, cannot be confused with any other. Small and immature shells are superficially close to *L. deltcatula* and *L. conica*, but are immediately distinguished by their very numerous primary grooves, large protoconch and characteristic microsculpture.

9.2.3 Subgenus *Littorinopsis*

Littorina (*Littorinopsis*) Mörch, 1876: 135 [type species by original designation *Littorina subangulata* Lamarck, error for *Littorina angulifera* (Lamarck, 1822)]

DIAGNOSIS. Shell often of thin texture; a few varices may be present; microsculpture, if present, is of spiral striae, usually only in grooves; shell colouration often polymorphic. Penial base bifurcate, glandular disc borne on a limb separate from that bearing filament; penial sperm groove open or closed. Sperm nurse cells not flagellate. Bursa copulatrix opens at anterior end of straight section of pallial oviduct; capsule glands absent. Development ovoviviparous. Radula with 'hooded' rachidian tooth.

9.2.3.1 *Littoraria* (*Littorinopsis*) *scabra* (Linnaeus, 1758)

Helix scabra Linnaeus, 1758: 770 [neotype here designated BMNH 198347; additional specimens from neotype lot AMS, USNM ; Magnetic I., N. Qld., Australia]; Linnaeus, 1767: 1243; Chemnitz, 1795: 283, pl. 210, fig. 2074 [in part]

Littorina scabra – Philippi, 1847, vol. 2: 221–223 [in part]; von Martens, 1871: 39; Weinkauff, 1878: 37–39, pl. 4, figs 7,12 [in part]; von Martens, 1880: 284 [in part]

Littorina scabra – Reeve, 1857: *Littorina* pl. 5, figs 21b,c [in part]; Nevill, 1885: 145 [in part]; von Martens, 1887: 169 [in part]; Fischer, 1891: 170 [in part]; Hidalgo, 1904–5: 207 [in part]; Nielsen, 1976: fig. 1c [in part; ecology]; Wilson & Gillett, 1979: 52, pl. 8, figs 5,5a; Kilburn & Rippey, 1982: 51, pl. 10, fig. 4

Littorina (*Melaraphe*) *scabra* – Tryon, 1887: 243–244, pl. 42, fig. 19 [in part]; Dautzenberg, 1929: 289 [in part]

Littorina (Malaraphe) scabra - Casto de Elera, 1896: 309 [in part]

Littorina (Littorinopsis) scabra - von Martens, 1897: 194; Schepman, 1909: 193-194 [in part]; Oostingh, 1927 [in part]; Adam & Leloup, 1938: 75, pl. 1, fig. 2a, text fig. 25A [radula]; Cernohorsky, 1972: 56, pl. 12, fig. 7

Littorinopsis scabra - Hirase & Taki (undated): pl. 79, fig. 13; Kuroda & Habe, 1952: 64; Oyama & Takemura, 1961: fig. 11; Brandt, 1974: 53-54 [in part]

Melaraphe (Littorinopsis) scabra - Abe, 1942: fig. 17, no. 11 [in part; ecology and behaviour]

Littoraria scabra - Azuma, 1960: 10; Habe, 1964: 29, pl. 9, fig. 32 right [in part]; Habe & Kosuge, 1966: pl. 6, fig. 16; Higo, 1973: 46

Littorina (Littorinopsis) scabra scabra - Rosewater, 1970: 456-461, pl. 325, figs 2,4; pl. 352, figs 1,11,32; pl. 353, figs B,C [in part]; Rosewater, 1980: figs 1,4,7,8

Buccinum lineatum Gmelin, 1791: 3493 [lectotype figure (Rosewater, 1970) Knorr, 1768: pl. 14, fig. 4; not da Costa, 1778]

Buccinum foliorum Gmelin, 1791: 3493 [lectotype figure here designated Rumphius, 1705: pl. 29, fig. Y; type locality restricted to Amboina, Moluccas]

Littorina novaehiberniae Lesson, 1831: 348 [Port Praslin, New Ireland; lectotype (Rosewater, 1970) MHNG]

Littorina angulifera - Quoy & Gaimard, 1832: 474-476, pl. 33, figs 1-3 [not Lamarck, 1822]

Phastanella angulifera - Deshayes & Milne Edwards, 1843: 244-245 [in part; not Lamarck, 1822]

Littorinopsis angulifera - Cossmann, 1916: pl. 3, figs 2,3 [not Lamarck, 1822]

Littorina (Littorinopsis) scabra angulifera - Rosewater, 1981: 20-23, pl. 2, fig. F [in part; not Lamarck, 1822]

Turbo striatus Schumacher, 1838: 198 [lectotype figure here designated Chemnitz, 1795: pl. 210, fig. 2074; not da Costa, 1778]

? *Litorina scabra* var. *flammulata* Philippi, 1847, vol. 2: 222

Littorina scabra subvar. *flammulata* - Nevill, 1885: 145

Littorina scabra var. *ventricosa* Philippi, 1847, vol. 2: 222, pl. 5, fig. 3 [not fig. 8 as cited in text; lectotype here designated BMNH 198341; type locality restricted to Cagayan, province of Misamis, Mindanao, Philippines; not *Littorina ventricosa* Brown, 1838]

Littorina scabra subvar. *tenuis* Nevill, 1885: 146 [Arakan [Burma]; lectotype here designated ZSI, 31.0 mm]

Littorina (*Melaraphe*) *scabra* var. *intermedia* - Tryon, 1887: 244 [in part, not Philippi, 1846]

Melarhaphe (*Littorinopsis*) *scabra intermedia* - Hirase, 1934: 47, pl. 79, fig. 13 [not Philippi, 1846]

NOMENCLATURE. Since the monograph of the genus *Littorina* by Philippi (1847-48) the name '*Littorina scabra*' has been generally accepted as applicable to the most frequently collected and well known of the Indo-Pacific mangrove littorinids. However, to equate the species with the name requires some justification. The original description by Linnaeus (1758) reads '*testa subcarinata imperforata ovata acuminata striata ... fascis fuscis dissectis, in inferiore anfractu linea elevata*', and is quite inadequate to define the species. No locality was given. Philippi (1847) argued that the colour pattern excluded the other carinate species recognized in his monograph, but his own concept of *Littorina* '*scabra*' embraced four species as here defined, and still others could equally well be described as subcarinate, with a pattern of dissected dark bands. Unfortunately, no Linnaean specimen is known to exist. Dance (1967) listed *Helix scabra* amongst the species described by Linnaeus which are not represented by specimens in the Linnaean shell collection, but noted that some of the missing specimens may be located amongst the residual unsorted material. An examination of this unauthenticated material revealed six unlabelled and unmarked specimens of this species, and four of *L. angulifera* (Lamarck), also with no data. From the comments of Dance on the containers used in the collection, these specimens are probably subsequent additions to the collection of Linnaeus and have no claim as type material. In edition ten of the *Systema Naturae* (Linnaeus, 1758), but not in

edition twelve (Linnaeus, 1767), the abbreviation 'M.L.U.' appeared following the description of *Helix scabra*, implying that a specimen of this species was contained in the Museum Ludovicae Ulricae. However, *Helix scabra* was not mentioned in the printed (Linnaeus, 1764) nor manuscript version (Hanley, 1860) of Linnaeus' catalogue of this collection, nor was the species listed by Odhner (1953) in the only modern account.

The identification of the present species with *Helix scabra* rests largely upon the observations of Hanley (1855) on a shell from the Linnaean collection which has since been lost. Hanley accepted an annotation in Linnaeus' personal copies of the *Systema Naturae* as evidence of the author's possession of *Helix scabra* (evidence which was disputed by Dance, 1967) and proceeded to identify as the holotype 'the shell, which alone of his collection agrees with the description' (Hanley, 1855, p. 365). Hanley added: 'It is the *Littorina scabra* of modern conchologists, and was described and illustrated by Chemnitz (Conch. Cab. vol. xi, pl. 210, f. 2074,2075) under the Linnaean name; that author having happily guessed at a species, which was neither defined by an adequate diagnosis nor illustrated by a reference to any engraving'. The monographs of the genus *Littorina* by Philippi (1847-48) and by Reeve (1857) can be taken as representative of the concept of the species '*Littorina scabra*' in Hanley's day. The varieties of *Litorina* '*scabra*' described by Philippi included four species as here recognized, chiefly *L. scabra s. s.* and *L. lutea*, but also *L. intermedia* and *L. pallescens*. Reeve illustrated *L. scabra s. s.*, *L. lutea* and *L. angulifera* (Reeve pl. 3, fig. 15a) as *Littorina* '*scabra*'. Of the two figures of Chemnitz referred to by Hanley, fig. 2074, although poorly drawn, is certainly the species here recognized as *L. scabra s. s.*, as indicated by the characteristic pattern, the concave spire outline and the description in the text of the wide, white columella. However, fig. 2075 is *L. angulifera*, as suggested by the colouration and outline, and confirmed by the locality Guinea.

Rosewater (1970) designated the figure 2074 of Chemnitz as

lectotype of *Helix scabra*, but such a designation is invalid since a lectotype must be either a specimen from a syntypic series or a figure quoted by the author of the species. In view of Hanley's comparison with the holotype, there would be some justification for the designation of the original shell of the Chemnitz figure as a neotype. There is in the Zoological Museum, Copenhagen, a specimen (inscribed 66/14; 38.3 mm) almost certainly from the collection of Spengler, which, according to T. Schiøtte (pers. comm.) and as suggested by Rosewater (1970) could be this figured specimen. This shell has been examined and neither pattern nor shape are closely similar to the published figure, although both are undoubtedly of the same species. Furthermore, in his text Chemnitz stated only that figure 2075 (of *L. angulifera*) was based on a shell belonging to Spengler; it is likely that the original of figure 2074 belonged to Chemnitz himself and is now lost.

In conclusion, none of the pieces of evidence presented above is of itself conclusive of the identity of the Linnaean species. However, restriction of the name '*scabra*' to the present species is consistent with all this evidence and does not conflict with accepted usage. To ensure future stability of nomenclature, a neotype is here designated, comprising both shell and preserved animal of a male specimen. No preserved specimens were available from Amboina, Moluccas, the type locality designated by Rosewater (1970) and the type locality of *Helix scabra* Linnaeus now becomes Magnetic Island, Queensland, Australia. This change in locality is unfortunate, but at Magnetic Island the ecology, reproduction, behaviour and anatomy have been studied in detail.

Of the synonyms of *L. scabra*, *Buccinum lineatum* and *B. foliorum* of Gmelin are based upon earlier figures by Knorr (1768) and Rumphius (1705) respectively. Schumacher (1838) proposed the new name *Turbo striatus* for the shells illustrated by Chemnitz as *Helix scabra*, objecting that the figures 2074 and 2075 depicted shells insufficiently depressed and carinate to be the Linnaean species. In fact, shells of *L. scabra* are often a little broader and the

periphery more strongly keeled than in these figures. As discussed above, figures 2074 and 2075 represent *L. scabra s. s.* and *L. angulifera* respectively, and to minimize confusion the former is designated lectotype of *Turbo striatus*. Of the varieties of *Litorina scabra* described by Philippi (1847), var. *flammulata* was not illustrated, but is probably this species, since none of the others included by Philippi under the name '*scabra*' can be described as flammulate. The lectotype of *Litorina scabra* var. *ventricosa* Philippi has been selected on the basis of an original label by Cuming, bearing one of the localities listed by Philippi, and with the name inscribed by Philippi himself (Section 3.1). Types of *Littorina novaehiberniae* Lesson and of *Littorina scabra* subvar. *tenuis* Nevill are typical specimens of *L. scabra*.

Rosewater (1981) designated a lectotype of *L. angulifera* from the collection of Lamarck in the MHNG. Unfortunately the supposed syntypic series is a mixed collection of *L. scabra* and *L. angulifera*, and the selected lectotype belongs to the former species. The original description by Lamarck (1822) could apply to both species, but the type locality was given as the Antilles, so that Rosewater's designation of an Indo-Pacific specimen is inappropriate. In order to maintain the accepted usage of the name '*angulifera*', the lectotype of *Phasianella angulifera* Lamarck is here re-designated as the specimen MHNG 1096/92-11. Although smaller than the dimension given by Lamarck, this shell shows an angulated periphery, conforming to his description.

DIAGNOSIS. Shell: large (25-35 mm); spire outline concave near apex; strong peripheral keel; columella wide, excavated, white; primary grooves 9-11; ribs low, numbering 36-41 on last whorl; microsculpture of spiral striae in grooves; colour pale with more or less dense pattern of black or dark brown dashes, aligned at suture and periphery to form oblique axial stripes numbering 9-14 on last whorl. Animal: penis bifurcate, ochraceous, limb with glandular disc large, filament small; ovoviviparous.

SHELL (Fig. 9.9). *Shape*. Height (15)25–35(44) mm. Teleoconch (6.5)7–8(8.5) whorls. Shell of moderate thickness, solid. Spire outline at first concave, becoming convex after whorls 5–6; whorls rounded; sutures impressed, narrowly channelled; peripheral keel prominent, becoming indistinct at end of last whorl. Adult lip a little thickened, not flared; varices absent. Columella wide, shallowly excavated; pillar straight or gently convex at base. Sexual dimorphism: males smaller, relatively lower spire and larger aperture.

Dimensions: Table 9.3.

Sculpture (Fig. 9.10a–d). Protoconch normal. First 2–3 whorls of teleoconch smooth. Primary grooves 9–11(12), almost equally spaced, posterior rib usually narrowest, sometimes 1–2 ribs below sutural rib are a little wider than the rest; 2 posterior grooves wider and deeper. On whorl 7 all, or only widest, primary ribs become divided each by a secondary groove at anterior $\frac{1}{3}$–$\frac{1}{2}$ width; single narrow riblets may be intercalated in primary grooves on last whorl. Tertiary sculpture absent. Ribs remain low and flattened, except for peripheral rib which is raised and rounded, and posterior rib which is pushed up to form a sutural channel; intercalated riblets always remain small and inconspicuous, less than $\frac{1}{2}$ width of ribs; total number of ribs on last whorl 36–41, rarely up to 59 when riblets are well developed. Primary grooves $\frac{1}{2}$–1 rib width, wider posteriorly; secondary grooves usually remain narrower. Sculpture becomes less distinct at end of whorl 8. Microsculpture of faint, irregular axial growth striae over surface; strong, regular spiral striae in grooves.

Colour. Rather constant; ground colour whitish, cream or pale brown, with dense pattern of long black or dark brown dashes, mostly on ribs; dashes aligned at suture and periphery to form oblique axial stripes, numbering 9–14 on last whorl; alignment sometimes complete from suture to base, especially on spire whorls; peripheral keel usually with conspicuous white gaps between dashes. Occasional

Fig. 9.9 *Littoraria* (*Littorinopsis*) *scabra*: (a) ♂, Moa I., Qld. (DGR); (b) Namalungo, Mozambique (NM); (c) Durban, S. Africa (WAM); (d) lectotype of *Littorina scabra* subvar. *tenuis* Nevill, Arakan, Burma (ZSI); (e) neotype of *Helix scabra* Linnaeus, ♂, Magnetic I., Qld. (BMNH 198347); (f) lectotype of *Litorina scabra* var. *ventricosa* Philippi, Cagayan, Mindanao, Philippines (BMNH 198341); (g) lectotype of *Littorina novaehiberniae* Lesson, Port Praslin, New Ireland (MHNG); (h) Green I., Qld. (NMV); (i) Pialba, Qld. (QM).

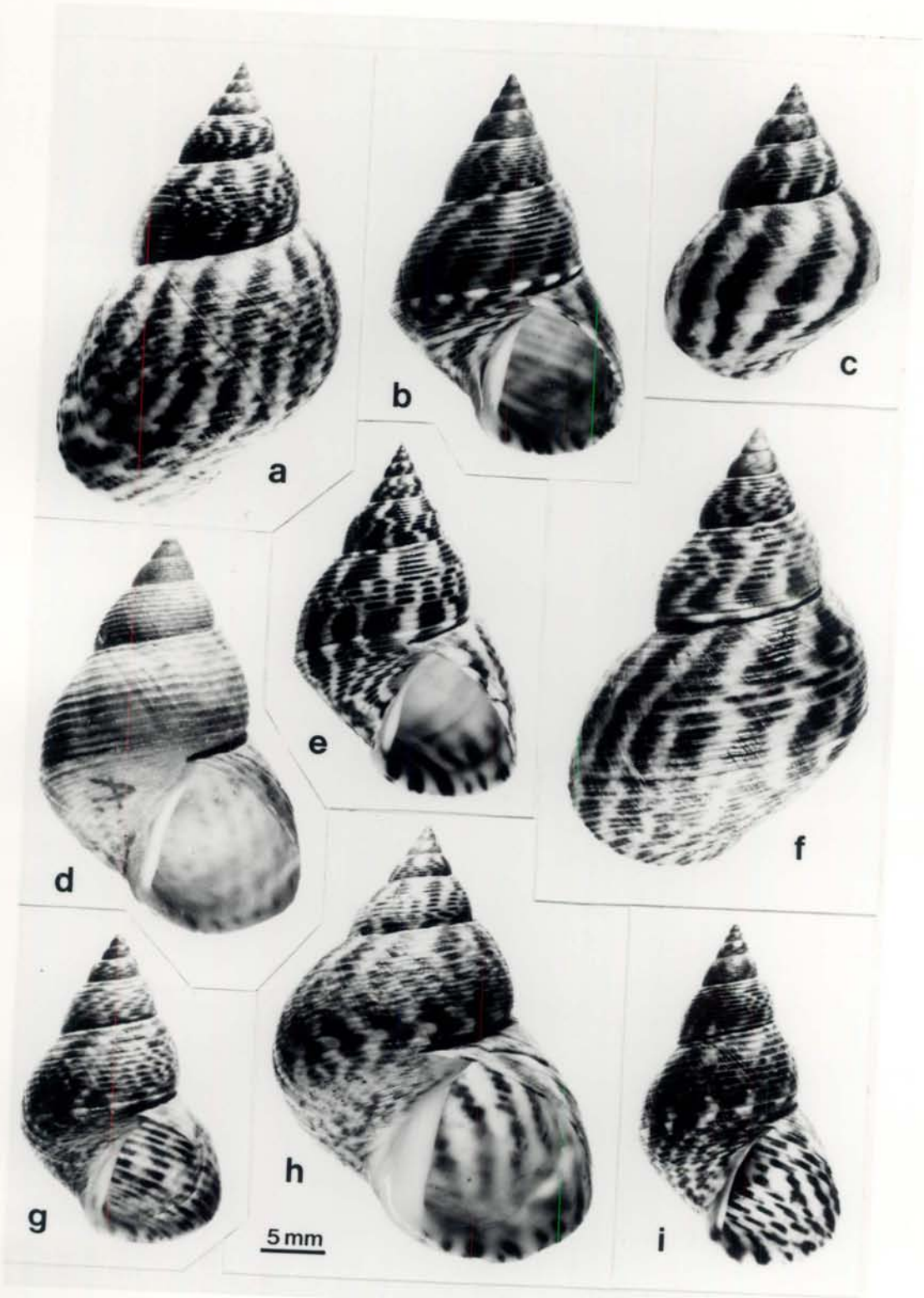
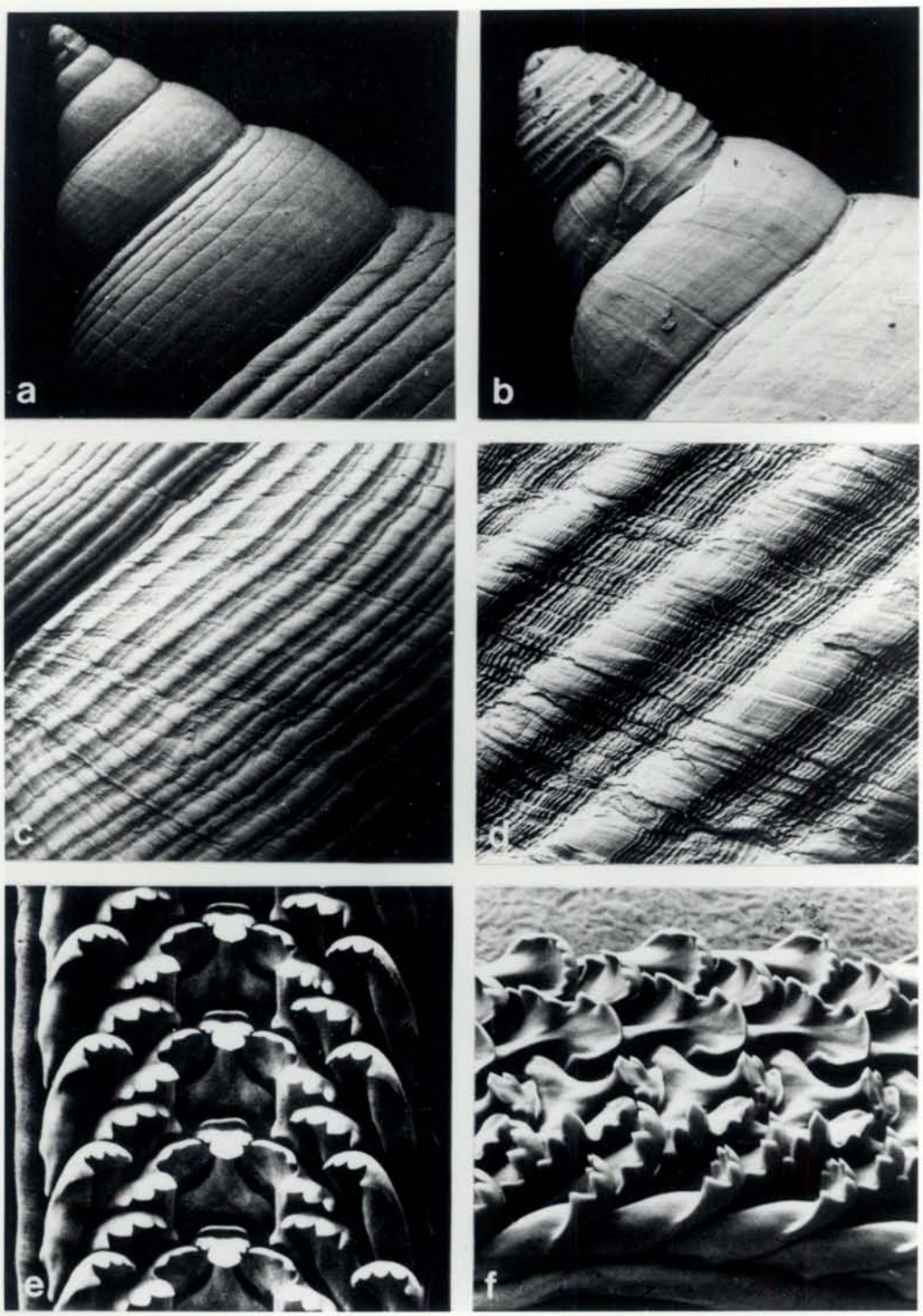

a
b
c
d
e
f
g
h
i
5 mm

Table 9.3 Dimensions of *Littoraria* (*Littorinopsis*) *scabra*.

Specimen	Locality	Sex	Primary grooves	H (mm)	B (mm)	LA (mm)	WA (mm)	C (mm)	PR	S	SH
Helix scabra neotype, BMNH 198347	Magnetic I., Qld.	♂	12	28.1	19.1	16.4	11.6	2.7	1.47	0.71	1.71
Littorina novaehiberniae lectotype, MHNG	Port Praslin, New Ireland		10	24.0	16.7	13.3	10.6	2.2	1.44	0.80	1.80
Littorina scabra var. *ventricosa* lectotype, BMNH 198341	Cagayan, Mindanao, Philippines		10	34.6	24.3	19.4	15.6	4.5	1.42	0.80	1.78
Littorina scabra subvar. *tenuis* lectotype, ZSI	Arakan, Burma		11	31.0	21.3	17.7	13.6	3.5	1.46	0.77	1.75
DGR	Magnetic I., Qld.	♀	11	40.6	25.8	21.8	15.7	3.9	1.57	0.72	1.86
DGR	Moa I., Qld.	♀	9	33.8	23.5	18.6	14.9	4.0	1.44	0.80	1.82
DGR	Moa I., Qld.	♂	10	32.2	20.9	17.8	12.8	3.2	1.54	0.72	1.81
AMS C.43106B	Mauritius		11	36.0	23.6	18.9	13.7	3.2	1.53	0.72	1.90
BMNH	Okinawa, Japan	♂	10	19.2	12.8	11.0	8.4	2.1	1.50	0.76	1.75
BMNH	Okinawa, Japan	♀	9	23.9	15.8	12.8	10.5	2.6	1.51	0.82	1.87
AMS C.131829	Ilha do Ibo, Mozambique	♂	9	21.7	14.0	11.7	8.9	2.4	1.55	0.76	1.85
AMS C.131829	Ilha do Ibo, Mozambique	♀	11	25.7	17.4	14.0	11.2	2.8	1.48	0.80	1.84
BMNH acc. 1838	Trincomalee, Sri Lanka		11	30.8	24.5	20.5	15.8	4.7	1.26	0.77	1.50
DGR, mean of 10	Moa I., Qld.	♂		32.37					1.450	0.754	1.759
standard error				0.51					0.019	0.009	0.014
DGR, mean of 10	Moa I., Qld.	♀		37.58					1.478	0.761	1.834
standard error				0.52					0.013	0.010	0.011
statistic t or U				7.158					63	57	93
probability				<.001					0.352	0.630	<.001

Fig. 9.10 *Littoraria* (*Littorinopsis*) *scabra*, Magnetic I., Qld.: (a) spire (×19); (b) protoconch (×85); (c) last whorl (×8); (d) detail (×30); (e,f) radula (×140).


a
b
c
d
e
f

pale shells lack alignment and show uniform speckling of grey or pale brown. Aperture pale yellow, external pattern visible as black or brown lines and dashes, obscured within by white or grey callus in larger shells. Columella almost invariably white, occasionally stained brown or purple at edge of inner apertural lip.

ANIMAL. *Colour* (Fig. 5.1). Pigmentation black; sides of foot mottled; head darkest, often with pale central streak; tentacles banded, unpigmented stripe each side of base.

Penis (Figs 5.1, 9.11a-d). Length to 11.0 mm. Base thick, bifurcate; limb bearing glandular disc the larger of the two; glandular disc bulbous. Filament small, tapering. Sperm groove open. Base ochraceous cream, darkest near glandular disc; disc opaque dark cream; filament off white.

Sperm (Fig. 5.3a,b). Eupyrene sperm 154–168 μm. Nurse cells (Fig. 9.11e,f) 21–37 μm, fusiform (sometimes oval); rods 2–3, central, projecting (rarely not so), usually one elongate and pointed, another small and oval; yolk granules small.

Pallial oviduct (Figs 5.7, 5.8). Length to 7.0 mm. Spiral section to 3.2 mm diam., $3\frac{1}{2}$ whorls; opaque albumen gland 1 whorl, cream to white; translucent albumen gland fawn to pale brown; capsule glands absent; spiral indistinct externally; egg groove only lightly pigmented. Straight section to 4.2 mm, fawn, terminating in a papilla. Bursa long, to 2.7 mm, anterior. Development ovoviviparous.

Radula (Fig. 9.10e,f). Length to 55 mm; relative length 0.91–1.54. Saw-toothed type; central rachidian cusp large, broad, edge slightly pointed, flanked by small cusp on each side; cusps of paired teeth almost equilaterally triangular; lateral with gap anterior to main cusp.

DISTRIBUTION. *Habitat*. Trunks and roots of *Rhizophora* trees near seaward edge of mangrove forests and on isolated trees, 0.5–2.0 m

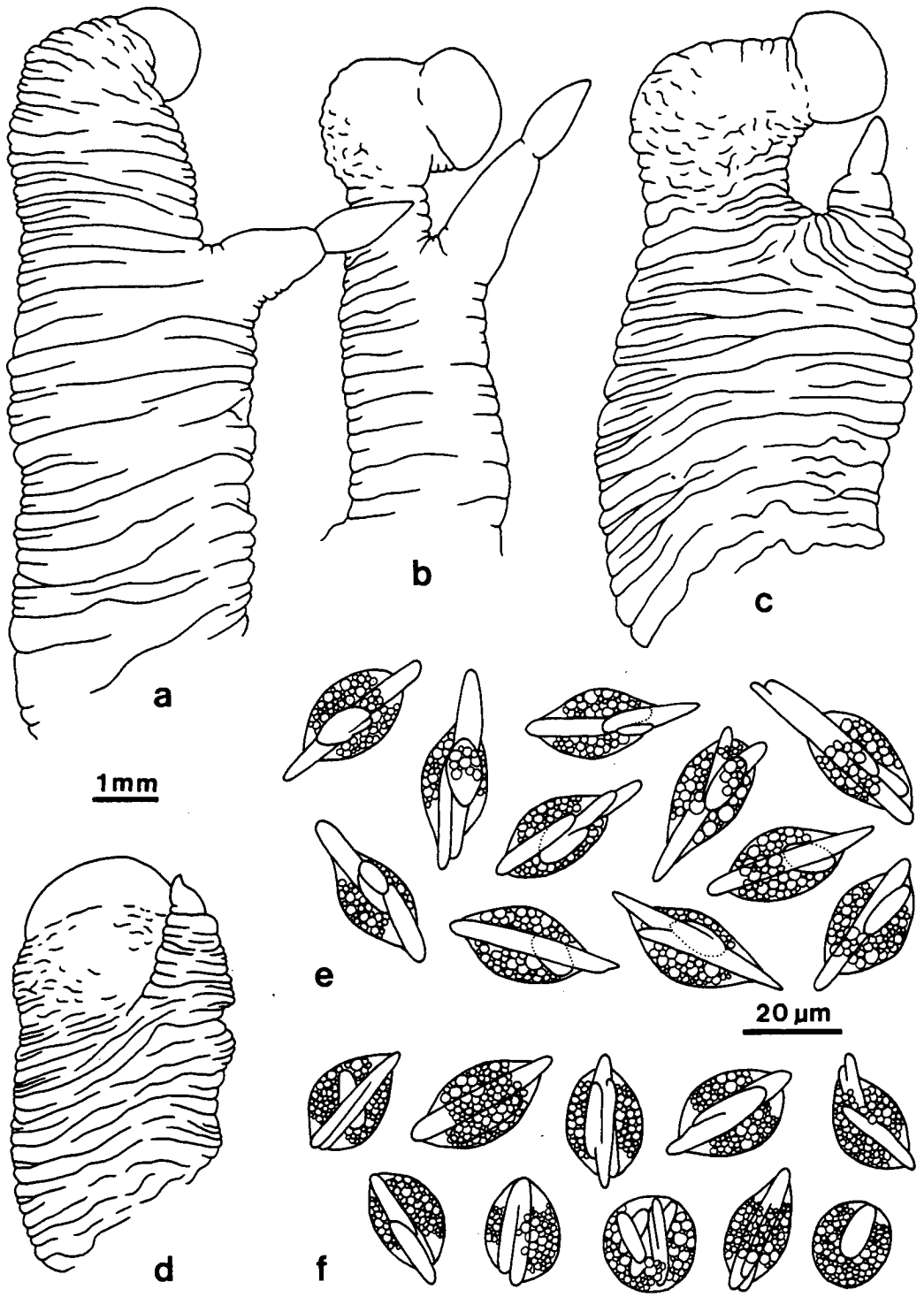


Fig. 9.11 *Littoraria (Littorinopsis) scabra*, Magnetic I., Qld.: (a–c) penes, relaxed; (d) penis, contracted; (e,f) sperm nurse cells.

above the ground; sometimes on trunks in *Avicennia* fringe; occasionally on trunks of *Hibiscus* or on driftwood on sandy shores where mangroves are absent; rarely on sheltered rocks. An oceanic species.

Range (Fig. 9.12). Throughout tropical and subtropical Indo-Pacific, excluding only northern Indian Ocean, northern Bay of Bengal and mainland South East Asia. Rare in Hawaiian Islands where mangroves were only established this century. Only 1 shell recorded from south-eastern Polynesia, where mangroves are absent.

Records. SOUTH AFRICA: Isipingo (BMNH); Durban Bay (NM, WAM); MOZAMBIQUE: Inhaca I. (NM); Porto Belmore, N.W. Nacala Bay (NM); Ilha do Ibo (AMS); TANZANIA: Bagamoyo (BMNH); Chukwani, Zanzibar (ANSP); KENYA: Shimoni (BMNH); MADAGASCAR: Tuléar (AMS, MCZ); Ile Ste. Marie (NMV); Nossi Bé (RNHL, ANSP); MAURITIUS: Le Chaland (AMS); Mouth of Camisard R. (ANSP); SEYCHELLES: Cosmoledo I. (BMNH, USNM); Mahé I. (BMNH, ANSP); ALDABRA ATOLL (BMNH); CHAGOS ARCH.: Diego Garcia (BMNH, USNM); MALDIVE IS.: Gan, Addu Atoll (ANSP); Fadiffolu Atoll (BMNH, ANSP); INDIA: Netravata R., Mangalore (USNM); Manali I., off Mandapam (MCZ); Madras (USNM); SRI LANKA: Trincomalee (BMNH); BURMA: Arakan (ZSI); ANDAMAN IS.: Port Blair (BMNH); NICOBAR IS. (BMNH); COCOS-KEELING IS. (BMNH, AMS, ANSP); THAILAND: Ao Nam Bor, Phuket I. (DGR); MALAYSIA: SABAH: Labuan I. (RNHL); Kudat Bay (ANSP); Po Bui I., Sandakan (USNM); SINGAPORE (BMNH); INDONESIA: SUMATRA: Weh I. (RNHL); Sinabang, Simeulue I. (RNHL); Bai I., Batu Is. (USNM); Sanding I., Mentawai Is. (USNM); JAVA: Djakarta Bay (RNHL); Menscheneter I. (ANSP); Tjilaoet Eureum (RNHL); LESSER SUNDA IS.: Koeta Beach, Bali (MCZ); Komodo (USNM); Maumere, Flores (USNM); Kambang I., Timor (RNHL); KALIMANTAN: Maratua I. (RNHL); Sandanan, S. Natuna Is. (NUS); SULAWESI: Manado (RNHL); Mamudju (RNHL); Makassar (RNHL); Gorontalo (RNHL); Tanah Djampea (RNHL); MOLUCCAS: Beo, Talaud I. (RNHL); Ternate, Halmahera (WAM); Taliabu I. (RNHL); Ambon I. (WAM); Mitak I., Tanimbar Is. (WAM); Tamberfane, Aru Is. (WAM); Kisar I. (RNHL); IRIAN JAYA: Manokwari (RNHL); Japen I., Schouten Is. (RNHL, AMS, ANSP); PHILIPPINES: Sanga Sanga I., Sulu

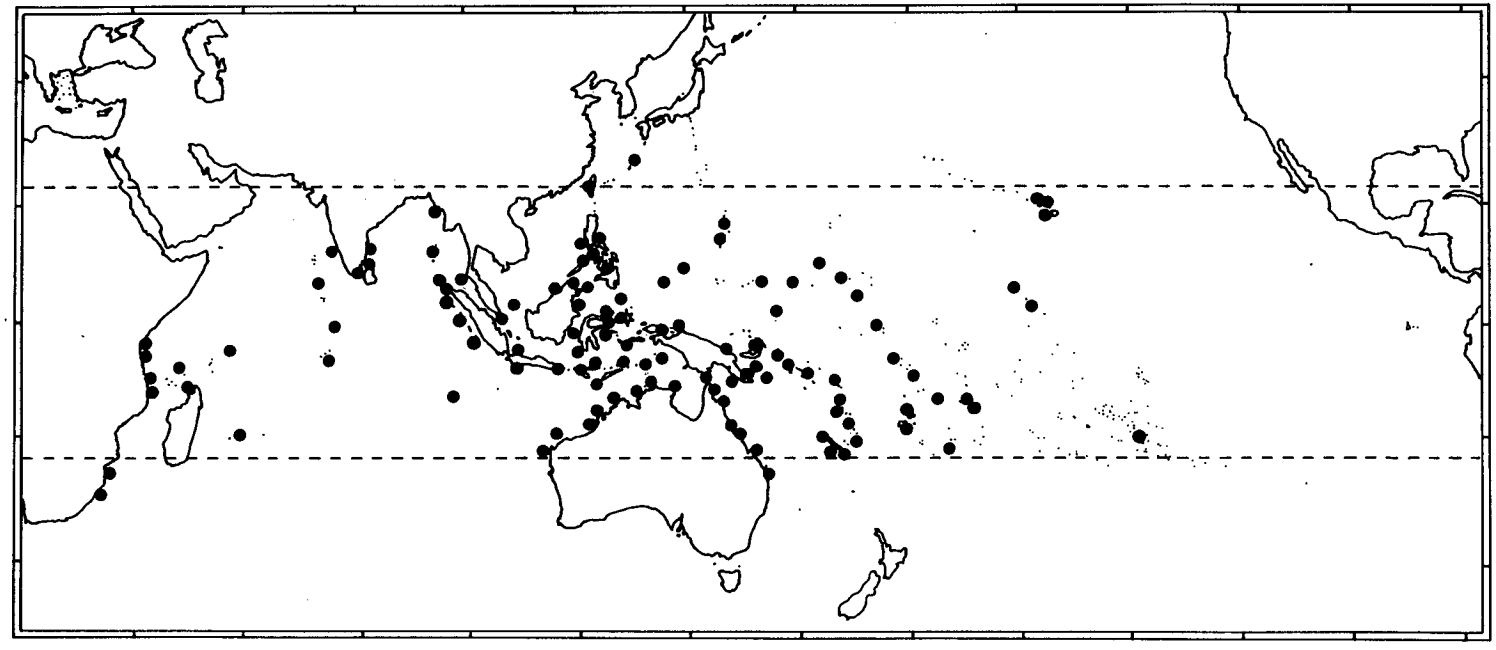


Fig. 9.12 Distribution of *Littoraria* (*Littorinopsis*) *scabra*.

Arch. (NMV, ANSP); Cagayan de Oro, Mindanao I. (BMNH); Banacon I., Bohol I. (AMS); Linapacan I. (USNM); Lubang I. (ANSP); Cuyo Is. (USNM); Catanauan, S. Quezon (WAM); Balibatikan, Batangas (ANSP); Panukulan, Polillo I., E. Quezon (WAM); TAIWAN (USNM); JAPAN: Toguchi, Kitanakagusuku, Okinawa, Ryukyu Is. (BMNH); PAPUA NEW GUINEA: Madang (AMS); Collingwood Bay (AMS); Kapa Kapa (AMS); Woodlark I. (AMS); Kuia I., Trobriand Is. (AMS); BISMARCK ARCH.: Duke of York Is., New Britain (AMS); AUSTRALIA: W.A.: Norwegian Bay, N. of Pt. Cloates (WAM); Barrow I. (WAM, USNM); Broome (NMV); Swan Pt. (NMV); Admiralty Gulf (WAM); N.T.: Darwin (DGR); Cape Don (AMS); Yirrkala, Arnhemland (USNM); QLD.: Thursday I., Torres Str. (DGR, QM); Quintell Beach (QM); Lizard I. (AMS); Green I. (NMV); Dunk I. (QM, NMV); Magnetic I. (DGR, AMS, USNM); Bowen (AMS); Proserpine (NMV); N. Keppel I. (NMV); Heron I. (AMS); Caloundra (QM); Stradbroke I. (QM, NMV, WAM); NEW CALEDONIA: Ile des Pins (AMS); Baie des Citrons, Nouméa (AMS); Poum (ANSP); NEW HEBRIDES: Aneityum and Tana (BMNH); Efate I. (AMS); Santo I. (AMS); Vanua Lava (BMNH); SOLOMON IS.: Santa Cruz I. (AMS); Malaita (BMNH, AMS); Choiseul I. (BMNH); Shortland I. (ANSP); CAROLINE IS.: Gorokotau I., Palau (ANSP); Yap I. (ANSP); Moen I., Truk Is. (BPBM); Ponape (BMNH); Werua, Kapingamarangi (USNM); MARIANA IS.: Saipan (ANSP); Guam (AMS, USNM); MARSHALL IS.: Eniwetok (USNM); Roi I., Kwajalein (BPBM); Enybor I., Jaluit (USNM); GILBERT IS.: Apaiang (MCZ); ELLICE IS.: Vaitupu (USNM); Nukulailai (USNM); WALLIS IS.: between Luanna and Fungalei Is. (USNM); FIJI: N.W. Vanua Levu (USNM); Nananu-i-ra I., N.N.E. Viti Levu (MCZ); Lomololo, S. Viti Levu (WAM); TONGA: Velitoa, nr. Tongatapu (BPBM); SAMOA IS.: Salua Pata, Upolu I. (ANSP); Tafuna Cove, Tutuila (USNM); LINE IS.: Fanning I. (USNM); Palmyra I. (ANSP); HAWAIIAN IS.: Coconut I., Kaneohe Bay, Oahu (DGR, BPBM); Molokai (BPBM); Puako, Hawaii (BPBM); TUAMOTU IS.: Tauere Atoll (USNM).

REMARKS. *L. scabra* has a very wide geographical distribution, but throughout the range the characters of both shell and animal are rather constant. In particular the penis shape is always diagnostic. In contrast to several other widely distributed *Littoraria* species,

no geographical forms can be recognized. Rather, variation in shell characters is mainly associated with habitat differences. Shells reach large size in mangrove forests, but are usually smaller if they occur on rocks or in other unfavourable habitats. On *Rhizophora* trees shells are heavily pigmented, while in those from *Avicennia* trees (e.g. Fig. 9.9d) the pattern is paler and more diffuse, or rarely almost absent. Fig. 9.9c,h,i illustrates several unusual shape and colour varieties.

SIMILAR SPECIES. Some shells of *L. intermedia* and of *L. pallescens* may approach *L. scabra* in shape and colouration, but lack the white columella, strong spiral microsculpture and smooth apical whorls of this species. The white columella and lack of an intercalated secondary rib in each primary groove separate *L. scabra* from *L. lutea*. *L. angulifera* from the tropical Atlantic is quite distinct (Figs 5.2o, 9.31e, 9.81d-f), with 67-91 ribs on the last whorl, indistinct or absent microsculpture, slight peripheral keel, lilac columella and large penial filament. The penial form of *L. scabra* is diagnostic.

9.2.3.2 *Littoraria* (*Littorinopsis*) *lutea* (Philippi, 1847)

Litorina scabra var. *lutea* Philippi, 1847, vol. 2: 222, *Litorina* pl. 5, fig. 11 [not fig. 6 as cited in text; fig. 11 here designated lectotype; type locality restricted to Masbate, Philippines]

Littorina scabra var. *lutea* - Nevill, 1885: 146 [in part]

Littorina (*Littorinopsis*) *scabra* var. *lutea* - Schepman, 1909: 194

Litorina scabra var. *punctata* Philippi, 1847, vol. 2: 222, *Litorina* pl. 5, fig. 5 [figure here designated lectotype; type locality restricted to Singapore; not *Littorina intermedia* var. *punctata* Philippi, 1846]

Littorina scabra var. *punctata* - Nevill, 1885: 145

? *Litorina scabra* var. *rubra* Philippi, 1847, vol. 2: 222 [Chemnitz

(1795) fig. 2075 is not the lectotype figure; type locality restricted to Mindoro, Philippines; not Anton, 1839]

Littorina scabra - Reeve, 1857: *Littorina* pl. 5, fig. 21a [in part; not Linnaeus, 1758]

Litorina scabra - Weinkauff, 1878: 37-39, pl. 4, figs 8-10 [in part; not Linnaeus, 1758]

Littorina (Melaraphe) scabra - Tryon, 1887: 243 [in part; not Linnaeus, 1758]

Littorina (Malaraphe) scabra - Casto de Elera, 1896: 309 [in part; not Linnaeus, 1758]

Littorina (Littorinopsis) scabra scabra - Rosewater, 1970: 456-461 [in part; not Linnaeus, 1758]

Littorina arboricola var. *philippiana* - Nevill, 1885: 148 [in part; not Reeve, 1857]

Littorina scabra var. *philippiana* - Hidalgo, 1904-5: 207 [in part; not Reeve, 1857]

Littorina pallescens ? var. *erronea* Nevill, 1885: 148 [Singapore; lectotype here designated ZSI, 28.9 mm]

NOMENCLATURE. This species has not hitherto been regarded as distinct, but on account of its similarity in shape to *L. scabra* has most often been considered a colour variety of that species. Some shell forms of *L. pallescens* resemble *L. lutea* closely, resulting in further confusion in the literature. In 1847 Philippi described seven varieties of *Littorina scabra*, based mainly upon differences in colour and pattern of the shell. In fact, the colouration of *L. scabra s. s.* is rather constant and four of Philippi's colour varieties are based wholly or in part upon the species here defined as *L. lutea*. Variety number 2, *Litorina scabra* var. *articulata*, is placed in the synonymy of *L. intermedia*, since the figured specimen is a large form of that species. However, the three paralectotypes are dark forms of *L. lutea* similar in appearance to the figure. No type specimen of variety number 3, var. *punctata*, is known to exist, but the figure is determined as *L. lutea* by reason of the spotted peripheral keel, colour pattern and shell shape. The name is preoccupied by *Littorina intermedia* var. *punctata* Philippi, 1846.

The figure of variety number 5, var. *lutea*, is here designated lectotype of the species, in the absence of a type specimen (see Section 9.2.3.5 for a discussion of the error in the original citation of the figure). The combination of yellow colour, purple columella and keeled outline leave no doubt as to the identity of the figure. Variety number 6, var. *rubra*, is not figured, but Philippi mentioned fig. 2075 of Chemnitz (1795), remarking that in the latter the keel was not sufficiently developed, and following the reference with a query. This figure of Chemnitz is clearly *L. angulifera*, from the shell shape and colour, as confirmed by the locality 'Guinea'. Philippi himself did not regard the Chemnitz figure as typical, so that it can hardly be designated as the lectotype of var. *rubra*, as proposed by Rosewater (1970). Furthermore, the localities Mindoro, Philippines, and Canton given by Philippi militate against the variety being a form of *L. angulifera*. Philippi's concept of *L. scabra* included, besides the Linnaean species, only *L. lutea* and a few forms closely resembling it, while *L. angulifera* was correctly recognized. Since pink shells of *L. lutea* are known, *Litorina scabra* var. *rubra* is tentatively included in the synonymy of this species.

The name *Litorina scabra* var. *concolor*, attributed to Weinkauff (1878), is listed in synonymies by Tryon (1887) and by Rosewater (1970). However, in Weinkauff's original text '*concolor*' is clearly the initial adjective in a Latin description and is not intended as a varietal name. The lectotype of *Littorina pallescens* ? var. *erronea* Nevill is a typical shell of *L. lutea*.

DIAGNOSIS. Shell: strong peripheral keel; columella wide, excavated, purple; primary grooves 8-11; secondary sculpture of single intercalated riblet in each primary groove; ribs low, numbering 33-50 on last whorl; microsculpture faint; colour polymorphic, usually yellow or pink, speckled with brown, keel spotted. Animal: penis bifurcate, filament large, glandular disc black; ovoviviparous.

SHELL (Fig. 9.13). *Shape*. Height 18–35 mm. Teleoconch 7–8 whorls. Shell of moderate thickness, solid. Spire outline gently convex, whorls rounded; suture impressed. Peripheral keel marked by a strong rib. Adult lip a little thickened, not flared; varices absent. Columella wide, excavated; pillar straight or slightly convex. Sexual dimorphism: males smaller, relatively lower spire and larger aperture.

Dimensions: Table 9.4.

Sculpture (Fig. 9.2e,f). Protoconch normal. First 1–2 whorls of teleoconch smooth. Primary grooves 8–11(12), equally spaced, posterior 2–3 grooves wider and deeper than others, posterior 3 ribs correspondingly narrower. Secondary sculpture develops on whorl 6, with intercalation of a single narrow riblet in each primary groove; primary ribs usually remain undivided, only rarely do 1 or 2 develop a secondary groove at about $\frac{1}{2}$ width. Narrow tertiary riblets may appear on whorl 8. On last whorl all primary ribs are flattened, but for the prominent rib at periphery; primary ribs of equal width, about twice as wide as secondary ribs intercalated between; total number of ribs 33–50. Grooves on last whorl less than $\frac{1}{3}$ maximum rib width; on whorls 6 and 7 posterior 2–3 grooves may equal width of intervening ribs. Microsculpture of irregular axial growth striae over surface; faint spiral striae sometimes visible in wider grooves.

Colour. Polymorphic; usually yellow, sometimes pink, with variable development of brown pattern. Ground colour pale yellow, whitish or orange pink. Pattern of dark brown or black dashes and flecks on ribs; darkest shells are densely patterned, with rough alignment at suture and periphery of spire whorls; pale shells may lack pigment entirely, but usually show a characteristic faint speckling, often developed only on last whorl; in most shells the keel is conspicuously spotted. Pattern visible within aperture only in darker shells, clouded by a cream callus. Columella and parietal callus dark purple or pink, pillar whitish.

Fig. 9.13 *Littoraria* (*Littorinopsis*) *lutea*: (a–c) Ubin I., Singapore (DGR); (a,b) ♂; (c) ♀; (d) Balikpapan, Kalimantan (AMS); (e,f) ♀, Ubin I., Singapore (DGR); (g) locality unknown (BMNH); (h) lectotype of *Littorina pallescens* ? var. *erronea* Nevill, Singapore (ZSI); (i) lectotype figure of *Litorina scabra* var. *lutea* Philippi, Masbate, Philippines (Philippi, 1847, *Litorina* pl. 5, fig. 11).

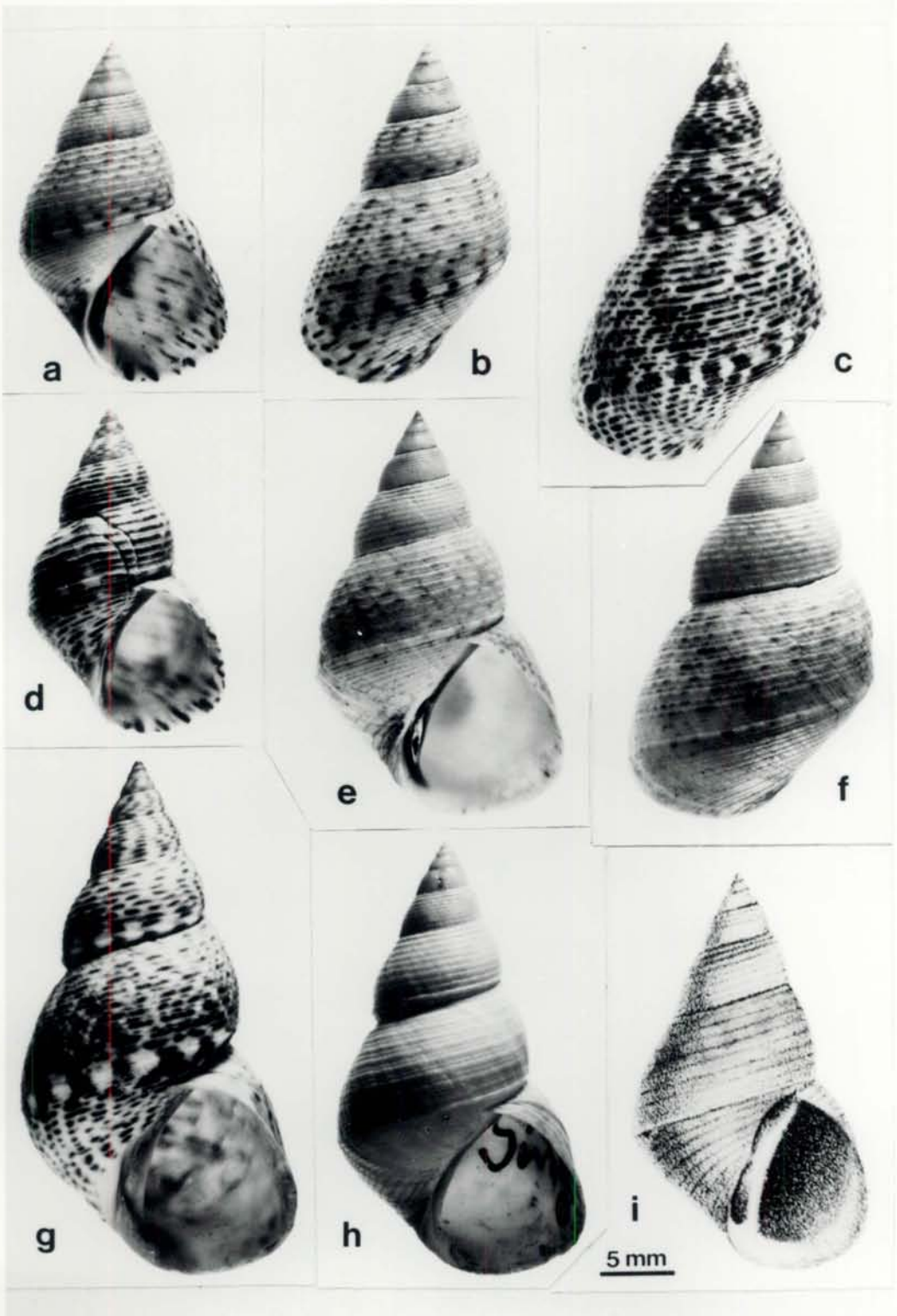

a
b
c
d
e
f
g
h
i
5 mm

Table 9.4 Dimensions of *Littoraria* (*Littorinopsis*) *lutea*.

Specimen	Locality	Sex	Primary grooves	H (mm)	B (mm)	LA (mm)	WA (mm)	C (mm)	PR	S	SH
Litorina scabra var. *lutea* lectotype figure (Philippi, 1847)	[Masbate, Philippines]			27.5	17.3	11.8	9.5		1.59	0.81	2.33
Littorina pallescens var. *erronea* lectotype, ZSI	Singapore		9	28.9	17.3	14.5	11.3	2.8	1.67	0.78	1.99
BMNH 1969381	Unknown		9	34.8	19.9	17.0	12.2	3.5	1.75	0.72	2.05
BMNH acc. 1829	Masbate, Philippines		8	23.2	14.7	12.5	9.9	2.6	1.58	0.79	1.86
AMS C.131831	Balikpapan, Kalimantan	♀	10	22.2	14.6	11.6	9.0	2.2	1.52	0.78	1.91
AMS C.131831	Balikpapan, Kalimantan	♂	8	22.5	14.5	12.7	10.0	2.7	1.55	0.79	1.77
DGR	Ubin I., Singapore	♂	10	23.4	15.2	13.5	10.0	2.6	1.54	0.74	1.73
DGR	Ubin I., Singapore	♀	8	26.3	17.7	14.6	11.1	2.7	1.49	0.76	1.80
DGR, mean of 10	Ubin I., Singapore	♂		22.81					1.584	0.745	1.764
standard error				0.36					0.019	0.007	0.021
DGR, mean of 10	Ubin I., Singapore	♀		26.01					1.565	0.768	1.859
standard error				0.70					0.021	0.009	0.012
statistic t or U				4.060					55	72	89
probability				0.001					0.740	0.106	0.002

ANIMAL. *Colour*. Pigmentation grey to black, correlated with shell colour; sides of foot sparsely mottled; head darkest; tentacles banded, unpigmented stripe each side of base.

Penis (Fig. 9.14a-e). Length to 7.7 mm. Base bifurcate. Filament fairly large, tapering at tip. Sperm groove open. Base pale ochre, filament white, penial glandular disc black to dark grey.

Sperm. Eupyrene sperm 152-164 μm. Nurse cells (Fig. 9.14f,g) 19-27 μm, oval to fusiform; rods 1-2(3), usually central, projecting, fusiform with rather pointed ends; yolk granules large.

Pallial oviduct (Fig. 9.14h,i). Length to 4.4 mm. Spiral section to 2.2 mm diam., $3\frac{1}{2}$ whorls; opaque albumen gland $\frac{1}{2}$ whorl, cream; translucent albumen gland pale brown; capsule glands absent; spiral indistinct externally; egg groove not darkly pigmented. Straight section to 2.5 mm, pale brown, terminating in a papilla. Bursa to 1.6 mm, anterior. Development ovoviviparous.

Radula (Fig. 9.2d). Length to 22 mm; relative length 0.88-0.90. Intermediate between saw- and chisel-toothed types; central rachidian cusp square, edge rounded; cusps of paired teeth obliquely triangular; lateral with gap anterior to main cusp.

DISTRIBUTION. *Habitat*. Trunks and occasionally leaves of trees in *Avicennia* fringe, to 1.7 m above ground; occasionally on roots and trunks of outermost trees of *Rhizophora* zone. A species of relatively clear water, and therefore 'oceanic' conditions, although range does not extend to the oceanic islands of the western Pacific.

Range (Fig. 9.15). Philippines, Indonesia and Singapore.

Records. SINGAPORE: Jelutong, Ubin I. (DGR); Tanjong Penuru (ANSP); MALASIA: SABAH: Labuan I. (BMNH); Tanjong Aru, Kota Kinabalu (ANSP); Po Bui I., Sandakan (USNM); INDONESIA: JAVA: Djakarta Bay (RNHL); Madura (RNHL); LESSER SUNDA IS.: Bali (AMS); Koeta Beach,

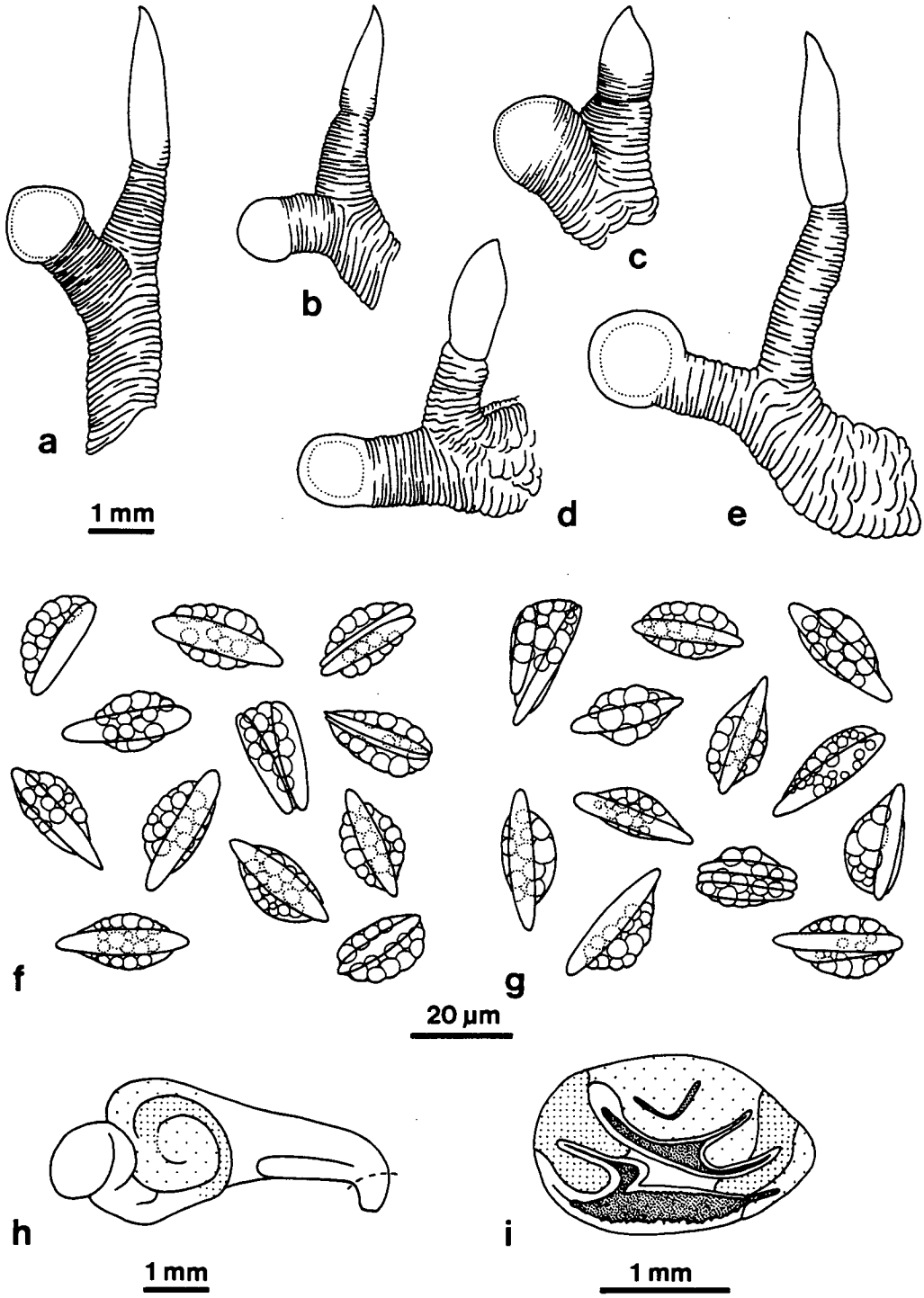


Fig. 9.14 *Littoraria* (*Littorinopsis*) *lutea*, Ubin I., Singapore: (a,b,d,e) penes, relaxed; (c) penis (a) contracted; (f,g) sperm nurse cells; (h,i) pallial oviduct, with transverse section.

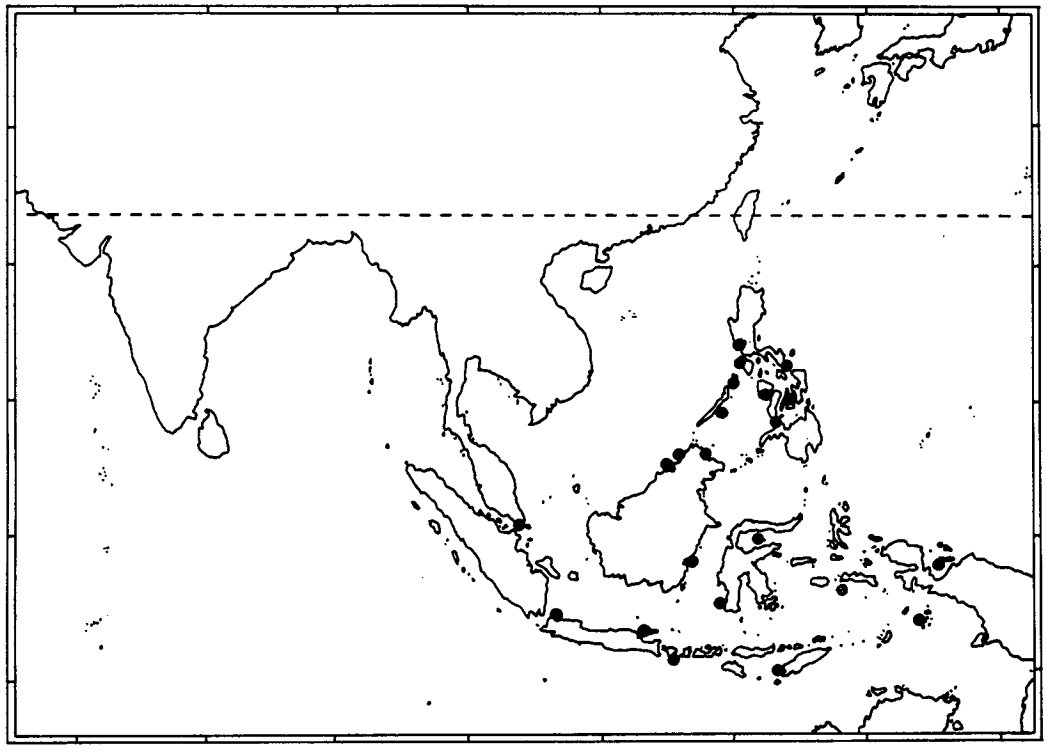


Fig. 9.15 Distribution of *Littoraria* (*Littorinopsis*) *lutea*.

Bali (MCZ); Bolang, S.W. Timor (RNHL); KALIMANTAN: Balikpapan (AMS); SULAWESI: Buka I., Gulf of Tomini (USNM); Makassar (RNHL); MOLUCCAS: Ambon I. (RNHL); Maikoor R., Aru Is. (USNM); IRIAN JAYA: Seroei, Japen I. (RNHL); PHILIPPINES: Puerto Princessa, Palawan I. (USNM); Dapitan, Mindanao I. (MCZ); Iloilo, Panay I. (BMNH); Hadayan I., Bohol I. (ANSP); Coron I. (USNM); Manoquid, Sorsogon, Luzon I. (AMS); Baruyan R., Calapan, Mindoro I. (MCZ); Manila, Luzon I. (ANSP, MCZ); Bacoor Bay, Luzon I. (USNM).

REMARKS. This species is rare in museum collections. Live material has been seen from Singapore and preserved specimens from Balikpapan, Borneo; from these collections the black penial disc appears to be characteristic of the species. Shell shape varies little and the regular intercalation of secondary ribs in the primary grooves is diagnostic. At Singapore, shells from *Rhizophora* trees were almost always dark brown and those from adjacent *Avicennia* trees yellow with pale patterning. No pink shells were seen at this locality, but do occur in the Philippines. *L. lutea* is apparently somewhat more tolerant of continental conditions than the typically oceanic species *L. scabra*.

SIMILAR SPECIES. Shells of *L. lutea* are similar in shape to those of *L. scabra*, but in the former the regular intercalation of secondary riblets in the primary grooves is diagnostic, spiral microsculpture in the grooves is faint or absent, and the columella is purple. Penial form, the shape of the sperm nurse cells and radular characters also distinguish these two species. The shape of the penis of *L. lutea* is somewhat similar to that of *L. philippiana*, although the glandular disc is black and the sperm groove open. The shell of *L. philippiana* is superficially similar, but secondary sculpture between the primary ribs is irregular and crowded, and the peripheral rib is not conspicuously spotted. Large forms of *L. intermedia* could be confused with *L. lutea*, but penial characters and the form of the secondary sculpture at once separate these two. Penial and sperm characters distinguish *L. pallescens*, and most shells lack secondary sculpture, but in the form of that species

described by Philippi as *L. sieboldii* (Fig. 9.16g) the shell is very close to that of *L. lutea*. In the '*sieboldii*' form of *L. pallescens* a transverse profile of the ribs and grooves is saw-toothed, secondary sculpture consists of incised lines in the V-shaped grooves, and secondary ribs do not become prominent, while the columella is white and the peripheral keel not marked with a conspicuous row of dashes or spots. In contrast, in *L. lutea* the primary ribs are rounded and the grooves wider, the intercalated secondary riblets are distinctive, and the columella always purple.

9.2.3.3 *Littoraria* (*Littorinopsis*) *pallescens* (Philippi, 1846)

Littorina pallescens Philippi, 1846: 142 [Cagayan, province of Misamis, Mindanao I., [Philippines]; lectotype (Rosewater, 1970) BMNH 1968277]; Reeve, 1857: *Littorina* pl. 9, fig. 43; Nevill, 1885: 148 [in part]; Hidalgo, 1904–5: 207

Litorina pallescens – Philippi, 1847, vol. 3: 10, *Litorina* pl. 6, fig. 4 [as *Litorina filosa* in text, corrected in index]; von Martens, 1871: 39; Weinkauff, 1882: 58–59, pl. 7, figs 14,15

Littorina (*Malaraphe*) *pallescens* – Casto de Elera, 1896: 310

Littorina filosa var. *pallescens* 'Reeve, *non* Philippi' – Hidalgo, 1904–5: 206

Littorina sieboldii Philippi, 1846: 142 [Japan; holotype BMNH 1968278]; Reeve, 1857: *Littorina* pl. 5, figs 23a,b

Litorina sieboldii – Philippi, 1847, vol. 3: 9–10, *Litorina* pl. 6, fig. 3; Weinkauff, 1882: 56, pl. 7, figs 6,7

Littorina (*Malaraphe*) *sieboldii* – Casto de Elera, 1896: 310

Littorinopsis sieboldii – Kuroda & Habe, 1952: 64

Littoraria sieboldii – Higo, 1973: 46

? *Litorina scabra* var. *suturalis* Philippi, 1847, vol. 2: 222, *Litorina* pl. 5, fig. 10 [not fig. 7 as cited in text; fig. 10 here designated lectotype]

Littorina arboricola Reeve, 1857: *Littorina*, pl.6, figs 27,27a

[Singapore; lectotype (Rosewater, 1970) BMNH 1968321]; Nevill, 1885: 147

Littorina (Melaraphe) scabra var. *filosa* - Tryon, 1887: 244, pl. 42, figs 25,26,30 [in part; not Sowerby, 1832]

Littorina (Littorinopsis) scabra var. *filosa* - Adam & Leloup, 1938: 75-77, pl. 1, figs 2b,c; text fig. 25B [radula]

Littorina (Malaraphe) scabra - Casto de Elera, 1896: 309 [in part; not Linnaeus, 1758]

Melaraphe (Littorinopsis) scabra - Abe, 1942: 391-435, fig. 17, nos 1-10 [in part; not Linnaeus, 1758; ecology and behaviour]

Littorina (Littorinopsis) scabra scabra - Rosewater, 1970: 456-461, pl. 325, fig. 1, pl. 352, figs 2,12,16,24,25 [in part; not Linnaeus, 1758]

Littorinopsis scabra - Brandt, 1974: 53-54 [in part; not Linnaeus, 1758]

Littorina scabra - Nielsen, 1976: fig. 1B [in part; not Linnaeus, 1758; ecology and behaviour]

Littorina scabra var. *philippiana* - Hidalgo, 1904-5: 207 [in part; not Reeve, 1857]

Littorinopsis intermedia - Oyama & Takemura, 1961: figs 12,13 [not Philippi, 1846]; Brandt, 1974: 54, pl. 4, fig. 62 [in part; not Philippi, 1846]

NOMENCLATURE. In the literature *L. pallescens* has been confused with other colourful, strongly ribbed and carinate forms under the name '*filosa*'. The species is common in collections, but the name '*pallescens*' has seldom been employed this century. There is no doubt that the syntypic series is the collection from which the species was described, since Cuming's original label, bearing Philippi's determination, accompanies the specimens. The lectotype may perhaps be the specimen figured by Philippi in 1847, although neither the type locality, nor material from the Cuming Collection was mentioned in the text. No specimen of *Littorina scabra* var. *suturalis* Philippi, 1847 has been traced; tentative placement of this variety in the synonymy of *L. pallescens* is based upon the colour pattern and wide, white columella, which seem to distinguish

the figure from the similar *L. lutea*.

DIAGNOSIS. Shell: columella wide, excavated, inner lip of aperture callused and rounded; primary grooves 9-10; secondary sculpture usually absent; ribs rounded or flattened, numbering 21-26 on last whorl; grooves wide or narrow; microsculpture faint; colour polymorphic; if present, dark pigment may form 6-10 axial stripes and a spiral band on base. Animal: penis bifurcate, filament small, glandular disc large, with thin, margined edge; ovoviviparous.

SHELL (Figs 9.16, 9.17). *Shape*. Height (9)15-25(31) mm. Teleoconch 6.5-8.5 whorls. Shell thick, solid. Spire outline gently convex; whorls rounded; sutures impressed. Peripheral keel evident on young shells, often indistinct on last whorl. Adult lip thickened, a little flared. Varices uncommon, usually strong growth lines only, sometimes up to 3 varices. Columella wide, excavated, pillar straight; inner lip of aperture callused and rounded in adult shells. Sexual dimorphism: males a little smaller (not quite significant in sample), relatively lower spire and larger aperture, aperture more elongate.

Dimensions: Table 9.5.

Sculpture (Figs 9.18, 9.35a). Protoconch normal. First 0-3 whorls of teleoconch smooth. Primary grooves (8)9-10(11), usually equally spaced and posterior 1-3 grooves deeper and wider, these sometimes also more closely spaced, so that posterior 1-2 ribs are narrowest. Secondary sculpture usually absent; rarely 1-2 ribs divide at anterior $\frac{1}{3}$-$\frac{1}{2}$ width on whorls 7-8; sometimes single minute riblets may appear by intercalation in the wider primary grooves of last whorl. Development of ribs and width of intervening grooves is variable: primary ribs may remain low and flattened on last whorl, of similar width, sometimes narrower posteriorly, often peripheral rib a little more prominent, primary grooves $\frac{1}{5}$-1 rib width or impressed lines only; frequently alternate, or even all, primary ribs become enlarged as prominent cords, primary grooves 1-3 times

Fig. 9.16 *Littoraria (Littorinopsis) pallescens*: lectotype of *Littorina pallescens* Philippi, Cagayan, Mindanao, Philippines (BMNH 1968277); (b) ♀, Gove, N.T. (DGR); (c) ♀, Ubin I., Singapore (DGR); (d) Polillo I., Philippines (WAM); (e) Sowek, Irian Jaya (AMS); (f) Hinchinbrook I., Qld. (DGR); (g) lectotype of *Littorina sieboldii* Philippi, Japan (BMNH 1968278); (h) Thursday I., Qld. (QM); (i) ♂, Phuket I., Thailand (DGR).

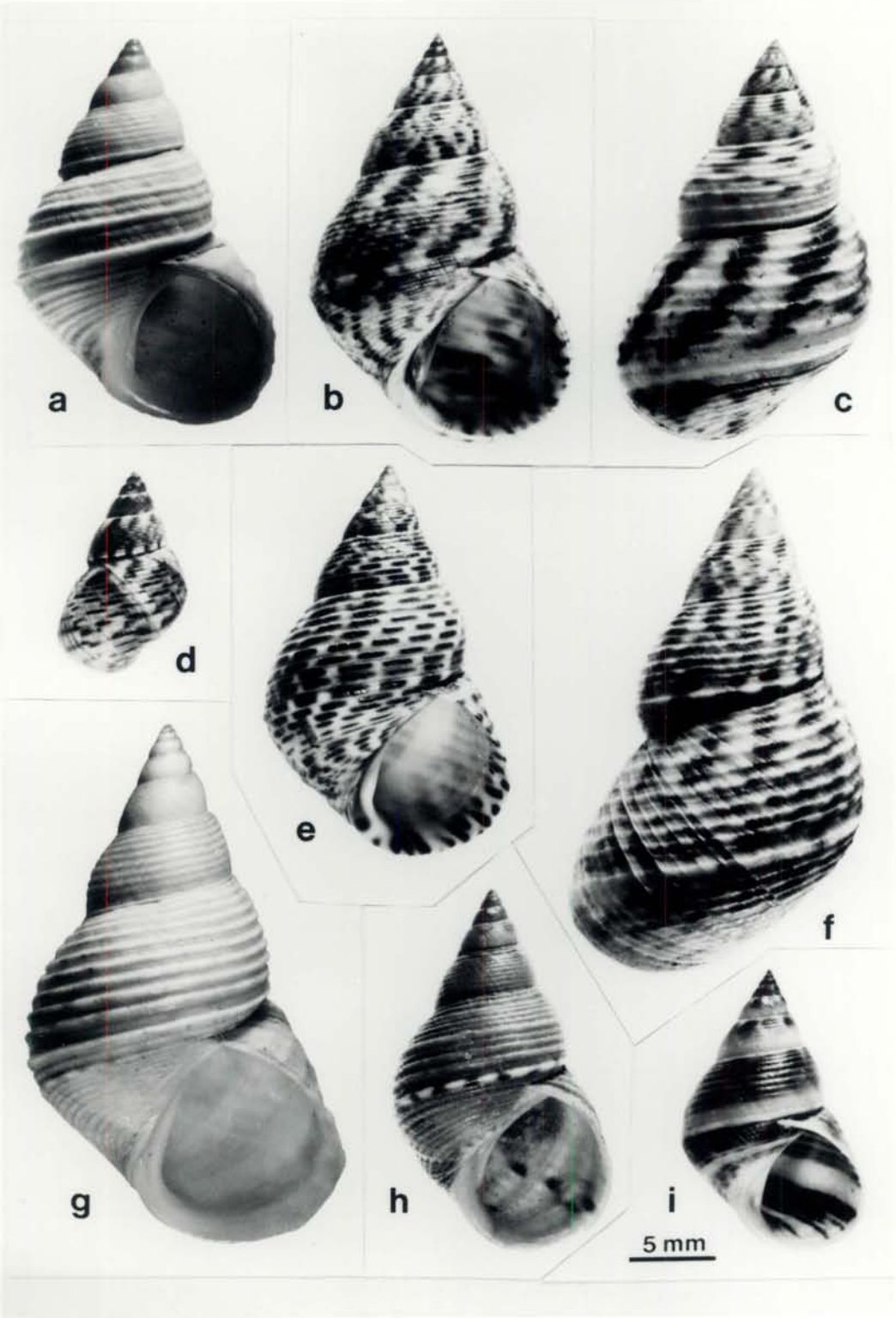

a
b
c
d
e
f
g
h
i
5 mm

Fig. 9.17 *Littoraria* (*Littorinopsis*) *pallescens*: (a) Kokenau, Irian Jaya (AMS); (b) Guadalcanal, Solomon Is. (AMS); (c) ♀, Balikpapan, Kalimantan (AMS); (d) ♂, Ubin I., Singapore (DGR); (e) ♀, Gove, N.T. (DGR); (f) Kokenau, Irian Jaya (AMS); (g) lectotype of *Littorina arboricola* Reeve, Singapore (BMNH 1968321); (h) Lunga Bay, Mozambique (NM); (i) Sebarok, Singapore (WAM).

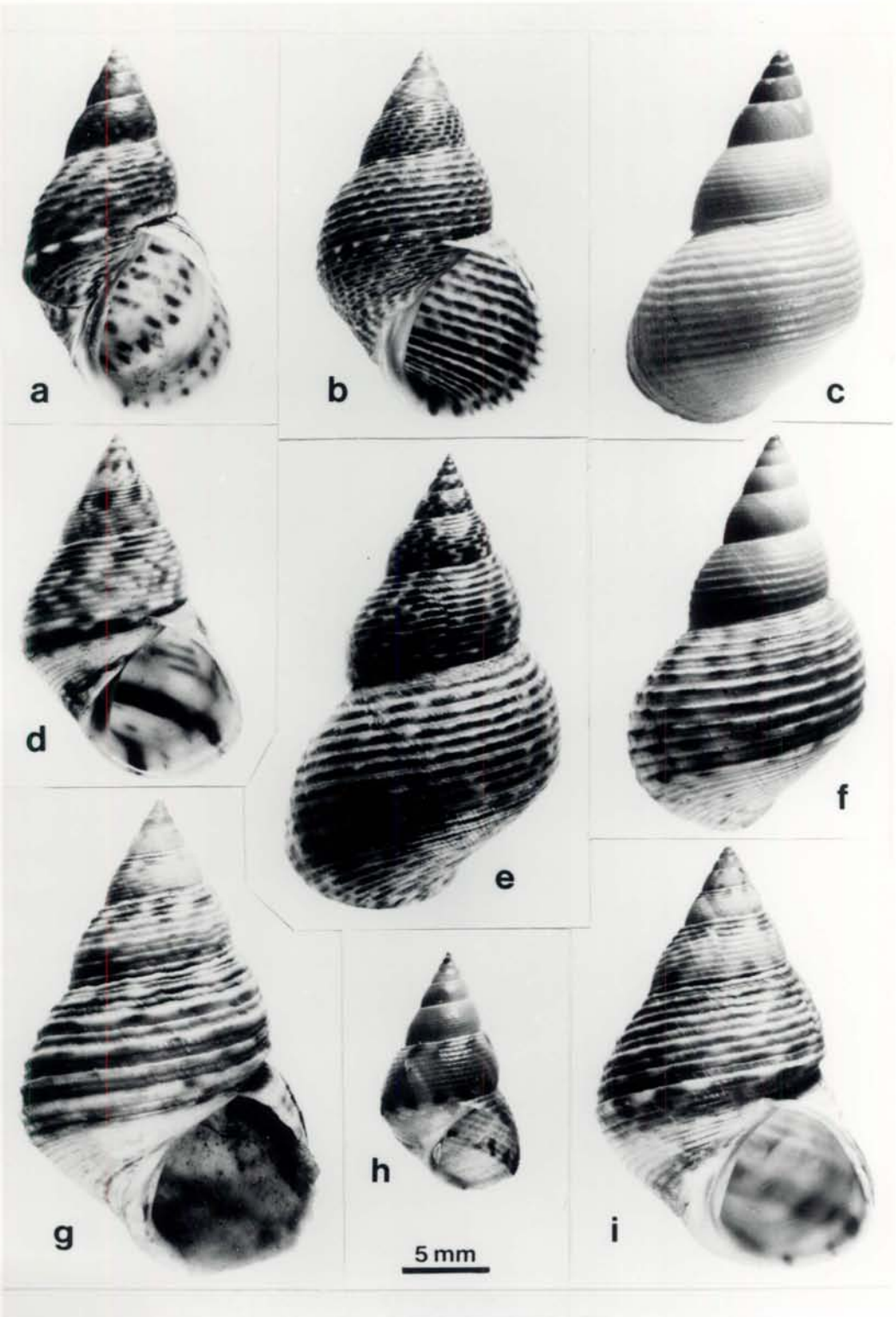
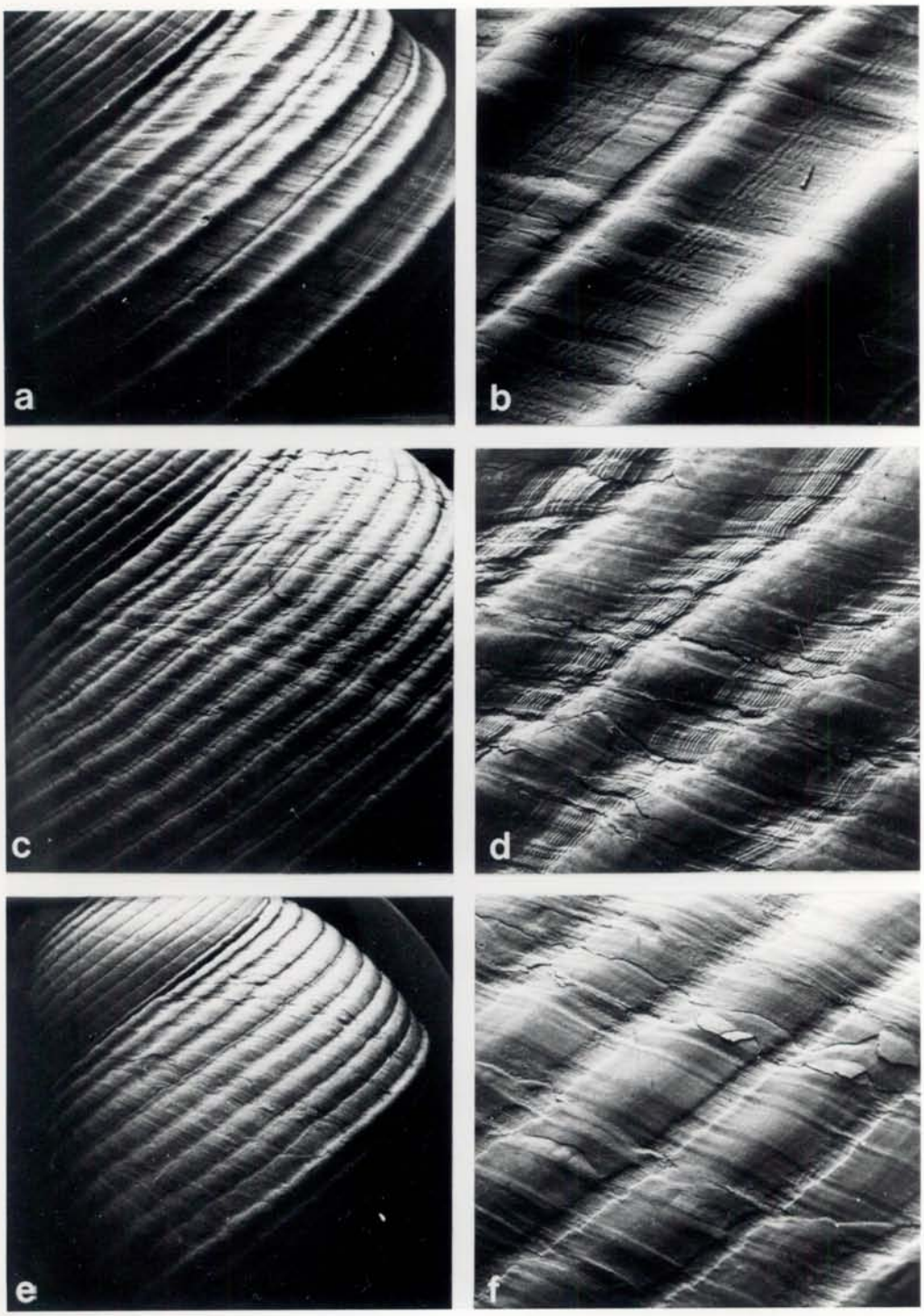

a
b
c
d
e
f
g
h
i
5 mm

Table 9.5 Dimensions of *Littoraria (Littorinopsis) pallescens*.

Specimen	Locality	Sex	Primary grooves	H (mm)	B (mm)	LA (mm)	WA (mm)	C (mm)	PR	S	SH
Littorina pallescens lectotype, BMNH 1968277	Cagayan, Mindanao, Philippines		9	22.1	15.3	12.4	9.9	3.1	1.44	0.80	1.78
Littorina sieboldii lectotype, BMNH 1968278	Japan		10	29.0	18.7	15.3	11.8	3.3	1.55	0.77	1.90
Littorina arboricola lectotype, BMNH 1968321	Singapore		8	26.8	17.4	13.2	10.6	2.5	1.54	0.80	2.03
DGR	Penang, Malaysia	♂	10	22.1	14.8	12.5	9.8	2.7	1.49	0.78	1.77
DGR	Penang, Malaysia	♀	9	29.0	18.9	14.2	11.7	2.7	1.53	0.82	2.04
DGR	Kanchanadit, Thailand	♀	9	31.3	18.8	15.6	11.9	3.0	1.71	0.76	2.01
DGR	Phuket I., Thailand		9	10.9	7.2	5.7	4.5	0.8	1.51	0.79	1.91
DGR	Ubin I., Singapore	♂	9	21.6	14.3	12.8	9.7	3.0	1.51	0.76	1.69
BMNH 1894.10.31	Solomon Is.		10	21.0	14.3	12.1	9.6	2.5	1.47	0.79	1.74
DGR	Gove, N.T.	♂	10	21.5	13.2	11.9	9.3	2.5	1.63	0.78	1.81
DGR	Gove, N.T.	♀	10	25.3	16.2	12.6	10.0	2.5	1.56	0.79	2.01
DGR, mean of 10	Ubin I., Singapore	♂		20.19					1.513	0.771	1.679
standard error				0.36					0.015	0.005	0.019
DGR, mean of 10	Ubin I., Singapore	♀		21.91					1.519	0.808	1.843
standard error				0.81					0.015	0.006	0.025
statistic t or U				1.947					55	95	97
probability				0.067					0.740	<.001	<.001

Fig. 9.18 *Littoraria* (*Littorinopsis*) *pallescens*: (a,b) Solomon Is.; (a) last whorl (×7); (b) detail (×32); (c,d) Gove, N.T.; (c) last whorl (×7); (d) detail (×32); (e,f) Phuket I., Thailand; (e) last whorl (×7); (f) detail (×28).


a
b
c
d
e
f

cord width; primary ribs between major cords may become obsolete on last whorl, leaving spaces between cords of 3–5 times their width. Total number of primary ribs on last whorl 21–26. Very rarely all primary ribs may divide and riblets are intercalated between, to produce as many as 43 ribs on last whorl, of which primary ribs remain most prominent. Microsculpture of axial growth striae covering surface, stronger in grooves; regular spiral striae may be visible in wide grooves.

Colour. Polymorphic; various shades of brown, yellow and sometimes pink, often striped or banded. Ground colour cream, pale brown, chrome yellow or dark orange pink. Most shells show black or dark brown dashes and flecks on ribs, sometimes densely covering surface, usually variously aligned to form 6–10 oblique axial stripes near suture or from suture to periphery; often with a continuous dark spiral band just below periphery, sometimes another around columella, with pale or unpigmented zones at periphery and on middle of base; the dark pigment fades to lilac grey. Predominantly yellow or cream shells may lack pigment, may show faint pattern of pale orange, or may possess dark pigment only in stripes at suture and in a subperipheral band; apical 4–5 whorls of such shells often tinged pink. Predominantly orange pink shells show a similar range of patterns, but sometimes develop conspicuous dashes on peripheral keel only. External pattern and colour visible within aperture, clouded by whitish callus. Columella purple in patterned shells, pillar and inner lip of aperture whitish; entire columella white in shells lacking dark pigment.

ANIMAL. *Colour*. Pigmentation pale grey to black, correlated with shell colour; sides of foot mottled; head darkest, sometimes with pale central streak; tentacles banded, unpigmented stripe each side of base.

Penis (Fig. 9.19a–f). Length to 8.6 mm. Base bifurcate. Glandular disc large, with thin, margined edge. Filament small, tapering. Sperm groove open. Base and filament ochre to cream, glandular disc

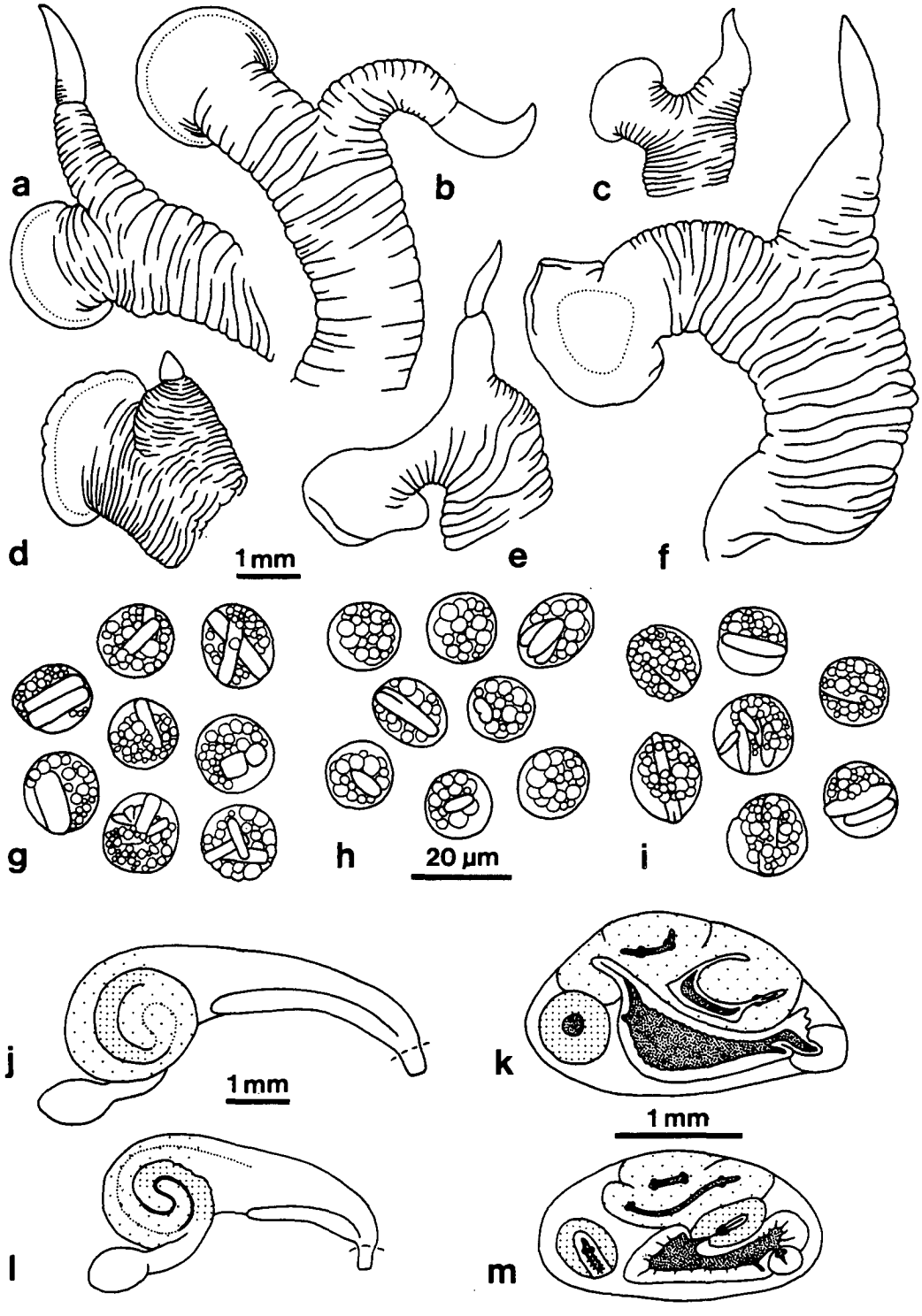


Fig. 9.19 *Littoraria (Littorinopsis) pallescens*: (a-c,e,f) penes, relaxed; (d) penis, contracted; (a,b,d) Ubin I., Singapore; (c) Aldabra; (e) Santa Isabel, Solomon Is.; (f) Gove, N.T.; (g-i) sperm nurse cells; (g) Ubin I., Singapore; (h) Phuket I., Thailand; (i) Gove, N.T.; (j-m) pallial oviducts, with transverse sections; (j,k) Gove, N.T.; (l,m) Phuket I., Thailand.

opaque cream or ochre, sometimes brown.

Sperm. Eupyrene sperm 180–185 μm. Nurse cells (Fig. 9.19g–i) 14–22 μm, round (sometimes somewhat oval); rods 1–2(3), small, variable in shape, elongate or oval, not projecting, sometimes absent; yolk granules fairly large.

Pallial oviduct (Fig. 9.19j–m). Length to 6.5 mm. Spiral section to 2.0 mm diam., $3\frac{1}{2}$ whorls; opaque albumen gland $\frac{3}{4}$–1 whorl, white to cream; translucent albumen gland off white, sometimes reddish; capsule glands absent; spiral indistinct externally unless egg groove is pigmented. Straight section to 5.0 mm, off white, terminating in a papilla. Bursa long, anterior, to 3.8 mm. Development ovoviviparous.

Radula (Fig. 9.35b). Length to 23 mm; relative length 0.85–1.10. Intermediate between saw- and chisel-toothed types; central rachidian cusp square, edge rounded; cusps of paired teeth obliquely triangular; lateral with gap anterior to main cusp.

DISTRIBUTION. *Habitat*. Typically on leaves in *Rhizophora* forest, less frequently on trunks and roots, 1.0–4.5 m above ground, most common at seaward edge, but extending into *Bruguiera* zone; also on leaves and sometimes trunks in *Avicennia* fringe, 0.7–2.0 m above ground; occasionally on leaves of *Sonneratia* and *Aegialitis*. An oceanic species.

Range (Fig. 9.20). Throughout the tropical Indo-Pacific, from central East Africa to Sri Lanka, Ryukyu Is., Marshall Is. and Samoa. Three old and doubtful records from Hawaiian Is. This species is largely restricted to oceanic situations, occurring only rarely on the continental shores of the Gulf of Siam, north-western Borneo, Hong Kong, eastern and north-western Australia (although common in Arnhemland).

Records. MOZAMBIQUE: Lunga Bay to Memba Bay (NM); TANZANIA:

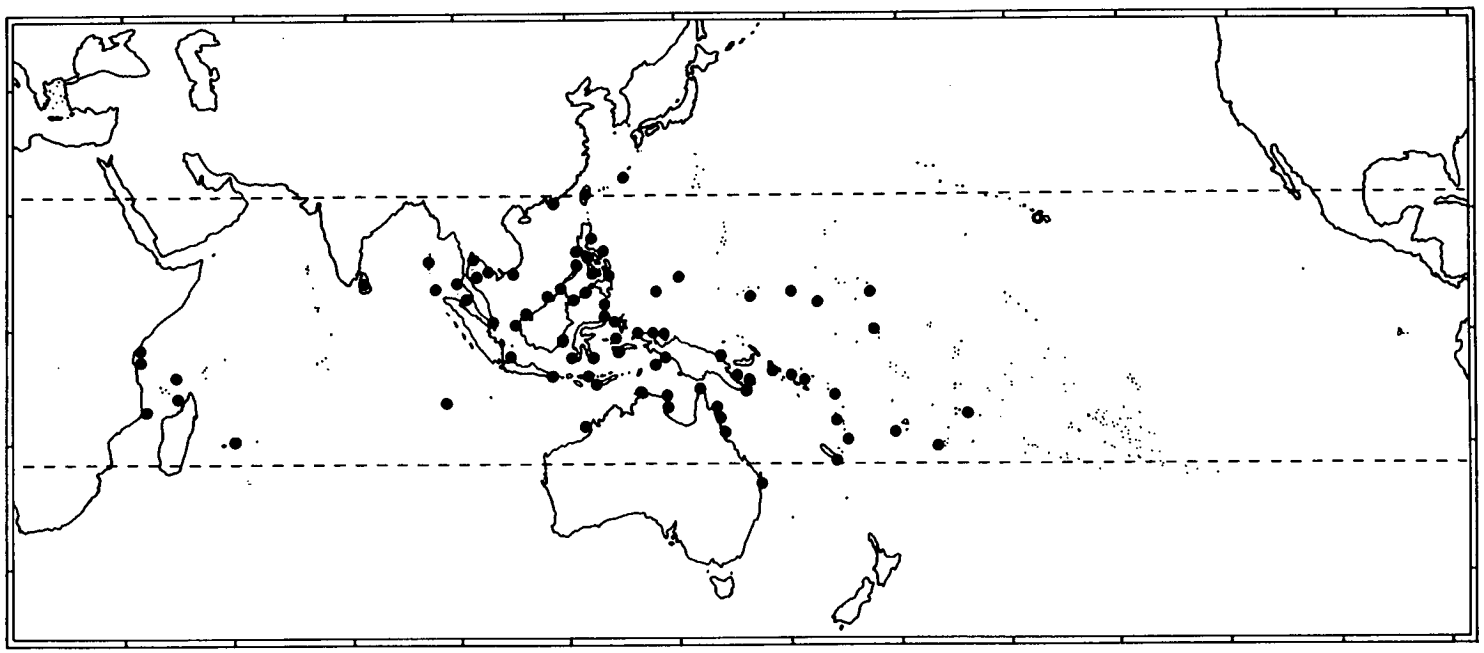


Fig. 9.20 Distribution of *Littoraria* (*Littorinopsis*) *pallescens*.

Chukwani, Zanzibar (ANSP); Tanga (MCZ); KENYA: Port Reitz, Mombasa (BMNH); MADAGASCAR: Nossi Bé (ANSP); ALDABRA ATOLL (BMNH); MAURITIUS: Mouth of Camisard R. (ANSP); SRI LANKA (MCZ); ANDAMAN IS. (BMNH, NMW); NICOBAR IS. (BMNH); COCOS-KEELING IS. (BMNH, ANSP); THAILAND: Ao Nam Bor, Phuket I. (DGR); Tanga I., Butang Group (USNM); Surat Thani (DGR); Bang Pakong R. (ANSP); Chantaburi (BMNH); Koh Kut (USNM); VIETNAM: Chilins, Vung Tau district (ANSP); MALAYSIA: PENINSULA: Penang (DGR); Pisang I. (NUS); SABAH: Tanjong Aru, Kota Kinabalu (ANSP); Kudat Bay (ANSP); Sandakan (ANSP, USNM); SARAWAK: Santubong (SM); BRUNEI: Bandar Seri Begawan (RNHL); SINGAPORE: Jelutong, Ubin I. (DGR); Sebarok (WAM); INDONESIA: JAVA: Djakarta Bay (RNHL); Menscheneter I. (ANSP); LESSER SUNDA IS.: Koeta Beach, Bali (MCZ); Larantuka, Flores (RNHL); Maumere, Flores (USNM); Bolang, Timor (RNHL); KALIMANTAN: Lemukutan I. (RNHL); Balikpapan (AMS); SULAWESI: Manado (MCZ); Makassar (RNHL); Wowoni I. (MCZ); MOLUCCAS: Dago Bay, Sangihe I. (MCZ); Kahatola I., S. Loloda Is. (MCZ); Obi I. (BMNH); Ambon I. (BMNH; RNHL); Maikoor R., Aru Is. (USNM); IRIAN JAYA: Sorong (AMS); Doreh Bay (RNHL); Japen I., Schouten Is. (ANSP, RNHL); Kokenau (AMS); PHILIPPINES: Sanga Sanga I., Sulu Arch. (RNHL, ANSP); Tapiantana I. (USNM); Taganaan, Surigao, Mindanao (MCZ); Iloilo, Panay (USNM); Linapacan I. (USNM); Lopez Bay, S. Quezon (WAM); Matabunkay Cove, Batangas (ANSP); Prieto Diaz, Sorsogon (ANSP); Panukulan, N.W. Pollilo I. (WAM); HONG KONG: Shin Han (BMNH); Rocky Harbour and Port Shelter (ANSP); TAIWAN (USNM, MCZ, ANSP); JAPAN: Fukuchi R., Okinawa I., Ryukyu Is. (BMNH); PAPUA NEW GUINEA: Madang (AMS); Popondetta (AMS); Losuia, Kiriwina Is., Trobriand Is. (AMS); East Cape (AMS); AUSTRALIA: W.A.: Broome (NMV); N.T.: Grose I. (AMS); Port Essington (AMS); Gove Peninsula, Arnhemland (DGR); Groote Eylandt (AMS); QLD.: Thursday I., Torres Str. (QM); Lizard I. (AMS); Machans Beach, Cairns (AMS); Dunk I. (NMV); Magnetic I. (DGR); Moreton Bay (MCZ); NEW CALEDONIA: San Gabriel, nr. Yaté (USNM); NEW HEBRIDES: Eromanga (AMS); Port Stanley, Malekula (BMNH); SOLOMON IS.: Santa Cruz I., Vanikoro Is. (USNM); Auki, Malaita (BMNH); Santa Isabel (BMNH); Shortland I. (ANSP); CAROLINE IS.: Babelthuap I., Palau Is. (USNM); Yap I. (T. Smalley); Ponape (BMNH); Tol Is., Truk Atoll (BPBM); Kusaie I.

(USNM, BPBM); MARSHALL IS.: Bikarej I., Arno Atoll (USNM); GILBERT IS.: Apaiang (MCZ); FIJI: Lautoka, N.W. Viti Levu (MCZ); Nadi Bay, Viti Levu (AMS); TONGA: Velitoa (BPBM); SAMOA IS.: Tafuna Cove, Tutuila (USNM); HAWAIIAN IS. (RNHL, USNM, BPBM, all doubtful records).

REMARKS. Shells of *L. pallescens* are sometimes closely similar to those of *L. philippiana* and *L. lutea*; these three species show parallel colour polymorphism and somewhat similar shell shape, sculpture and columellar characters. Nevertheless, there can be no doubt that these are distinct species, for although the geographical range of *L. pallescens* overlaps that of each of the others, the diagnostic penial differences remain constant. Furthermore, details of shell sculpture and pattern can alone be used to identify all but a very few specimens. However, even when *L. philippiana* and *L. lutea* are separated from *L. pallescens*, there remains a wide variety of shell types, so that as here defined *L. pallescens* is the most variable of all the Indo-Pacific *Littoraria* species. Despite the range of sculpture, size and colour, there seems no reason to subdivide the species. Anatomical characters are constant and in particular the form of the penis at once separates *L. pallescens* from all other species in the genus. The existence of geographical forms accounts for much of the variation in shell characters, but even within local populations shells are variable in shape and sculpture, besides being colour polymorphic. Some of the variation in size and colour may be attributed to environmental effects (Section 15.5.1).

The principal geographical forms are illustrated in Figs 9.16, 9.17 and 9.18. The typical form of the species occurs in the western Pacific islands, southern Japan, Indonesia, eastern Australia and the Indian Ocean; shells are rather small, secondary sculpture absent or limited to a few secondary grooves, yellow and orange pink shells are common, while in pigmented shells the pattern is of discrete dashes aligned near the sutures and prominent at the periphery. Sometimes, especially in pure yellow shells, the primary

ribs become alternately prominent and obsolete (Figs 9.16a, 9.18a,b), as in the lectotype. In south-western Thailand, the Andaman and Nicobar Islands, pigmented shells frequently show a pattern of continuous spiral bands, especially on the base; primary grooves are narrow and ribs flattened (Figs 9.16i, 9.18e,f). The form typical of Malaysia and Singapore was named *L. arboricola* by Reeve; shells are large and generally yellow, with axial stripes near the sutures and a spiral band on the base (Figs 9.16c, 9.17d,g,i). In a form from northern Australia, the Moluccas and parts of New Guinea, the shells are large and solid, the ribs equal and separated by wide grooves, the periphery of the last whorl rounded and the colour pattern similar to that of *L. intermedia* (Figs 9.16b,e, 9.17e, 9.18c,d).

In only two rare forms is secondary sculpture regularly present. The first is the form described by Philippi as *L. sieboldii*, in which the shell is large, the spire rather elongate and the ribs sharp; the primary grooves are at first narrow, but on the last whorl each contains a secondary groove or an indistinct rib (Figs 9.16g, 9.17c). This form is known only from Balikpapan, Borneo (AMS) and Japen Island, Irian Jaya (RNHL), besides the rather doubtful type locality of 'Japan'. The second is a very curious form seen in a few collections from Irian Jaya (AMS, RNHL, ANSP), Sulawesi (RNHL) and Negros Island, Philippines (USNM) in which shells are thin and sculpture is indistinguishable from that of *L. philippiana*, with 2-3 secondary ribs between each primary rib. While female shells of this form are of normal shape (Fig. 9.17f), the males develop an extremely elongate, patulous aperture, usually after the first varix (Fig. 9.17a). Males of other forms develop a relatively larger aperture than females, but dimorphism is not so extreme. None of these varieties is sufficiently distinct to justify taxonomic recognition and numerous intermediates exist between them.

As in some other species variation of shells within local populations suggests that the environment may influence shell size and colour. Specimens from small mangrove bushes in full sunlight

and at high tidal levels are small, reaching a maximum size of only 9–11 mm in one collection from Phuket Island, Thailand. On *Avicennia*, *Sonneratia* and *Aegialitis* trees, shell pigmentation is in general paler and yellow shells more frequent than on *Rhizophora* trees where brown colour morphs predominate (Section 15.4.3).

SIMILAR SPECIES. The small penial filament and marginate glandular disc distinguish *L. pallescens* from all other species, and the round sperm nurse cells are found elsewhere only in *L. subvittata* and *L. philippiana*. Shells of *L. pallescens* are almost always separable from those of *L. philippiana* by their lack of secondary sculpture, by the rounded inner apertural lip and often by the pattern of more discrete dashes confined to the ribs. From *L. lutea* this species can be distinguished by the narrower primary grooves on the early whorls and by the absence of the single intercalated secondary rib in each primary groove on the last whorl. The form found in northern Australia, the Moluccas and parts of New Guinea may resemble *L. intermedia* in shell characters, but grooves tend to be wider and the shell broader; penial form clearly separates these two species. The only other *Littoraria* with such a diversity of colour forms is *L. filosa*, which is easily recognized by its narrow columella and thin shell.

9.2.3.4 *Littoraria* (*Littorinopsis*) *philippiana* (Reeve, 1857)

Littorina philippiana Reeve, 1857: *Littorina* pl. 5, figs 22a,b ['Philippine Islands', in error, type locality here corrected to E. Queensland, Australia; holotype BMNH 1968307]

Litorina philippiana – Weinkauff, 1882: 54–55, pl. 7, figs 2,3

Littorina arboricola var. *philippiana* – Nevill, 1885: 148 [in part]

Litorina philippina von Martens, 1900: 584 [unjustified emendation of *Littorina philippiana* Reeve, 1857]

Littorina (*Melaraphe*) *scabra* var. *filosa* – Tryon, 1887: 244, pl. 42,

fig. 27 [in part; not Sowerby, 1832]

Littorina (Littorinopsis) scabra scabra - Rosewater, 1970: 456-461, pl. 352, fig. 13 [in part; not Linnaeus, 1758]

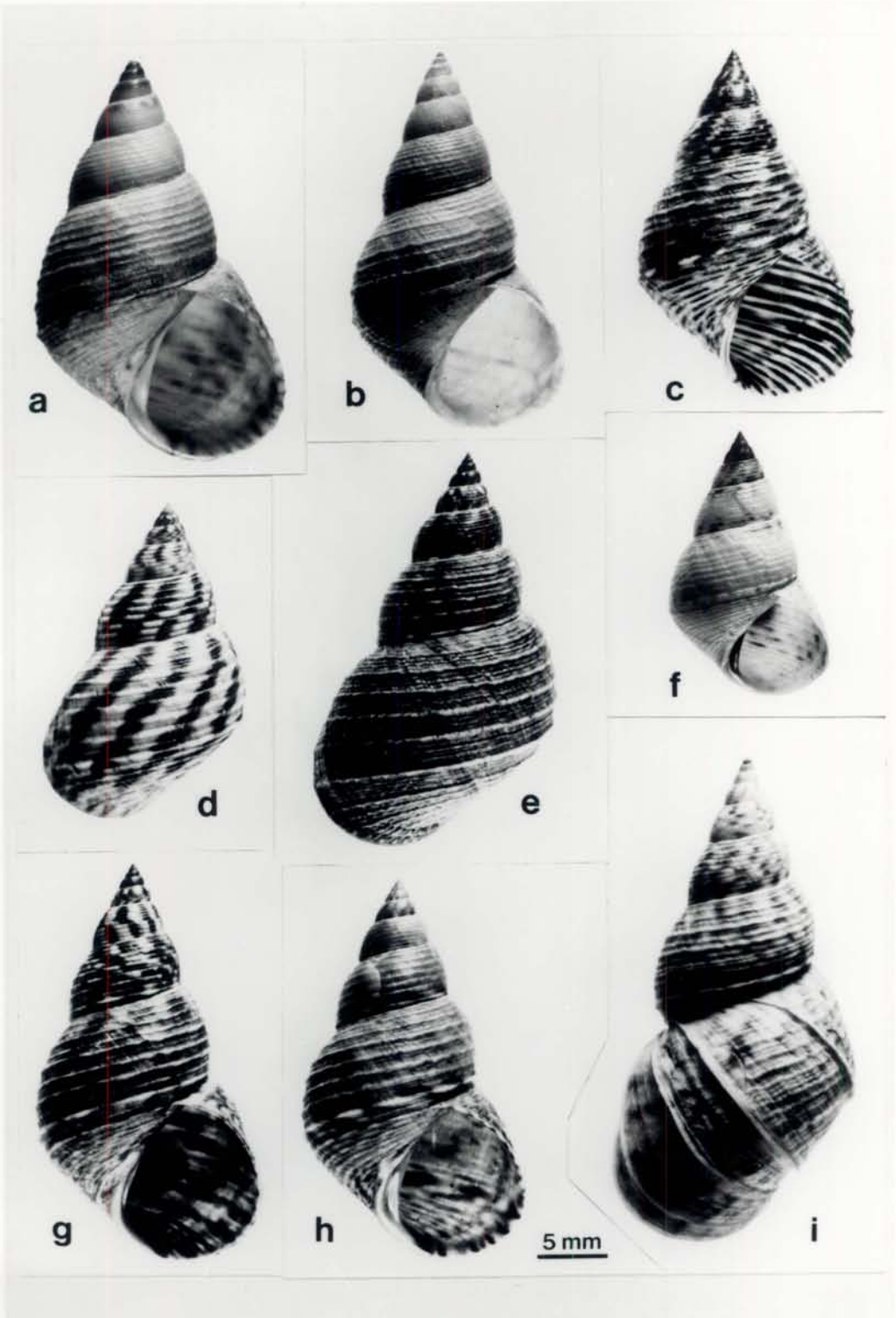
Littorina scabra - Wilson & Gillett, 1979: 52, pl. 8, fig. 5b [in part; not Linnaeus, 1758]

NOMENCLATURE. It is fitting that a littorinid should bear the name of Philippi, in recognition of his pioneering and accurate contribution to the study of the group. Although there is no doubt that the lectotype designated by Rosewater (1970) is the specimen figured by Reeve, there has clearly been a confusion of localities and labels. Reeve gave the type locality as the Philippine Islands, but the shell certainly belongs to a species endemic to Australia and south-eastern New Guinea. Accompanying the figured specimens are two shells of the form of *L. filosa* found in north-western Australia and the Lesser Sunda Islands, together with labels inscribed 'Kangaroo Is., S.A.' (presumably South Australia, where no *Littoraria* species occur). Since these two shells do not correspond with the description given by Reeve and this locality is not mentioned, they cannot be part of a syntypic series. The figured specimen therefore becomes the holotype.

DIAGNOSIS. Shell: columella wide, excavated, purple; primary grooves 8-9; secondary and tertiary sculpture well developed; primary ribs are raised as 13-18 narrow cords on last whorl, with 1-3 riblets and irregular striations in each interspace; microsculpture of irregular spiral striae in grooves; colour polymorphic, brown predominating, pattern diffuse. Animal: penis bifurcate, limb bearing glandular disc is long, disc small, filament long, sperm groove closed as a duct; ovoviviparous.

SHELL (Fig. 9.21). *Shape*. Height (18)23-33(38) mm. Teleoconch 7.5-8.5(9) whorls. Shell of moderate thickness, solid. Spire gently concave; whorls rounded; sutures impressed. Peripheral keel prominent in young shells, often becoming obsolete on last whorl. Adult lip somewhat thickened, a little flared. Varices 0-3(7).

Fig. 9.21 *Littoraria* (*Littorinopsis*) *philippiana*: (a) holotype of *Littorina philippiana* Reeve (BMNH 1968307); (b) Elliott R., Qld. (QM); (c) ♀, Orpheus I., Qld. (DGR); (d,e) Magnetic I., Qld. (DGR); (d) ♀; (e) ♀; (f) ♀, Moa I., Qld. (DGR); (g,h) Magnetic I., Qld. (DGR); (g) ♂; (h) ♀; (i) ♀, Bohle R., Townsville, Qld. (DGR).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Columella wide, excavated, pillar straight, narrowed at base. Sexual dimorphism: males with relatively lower spire and larger aperture.

Dimensions: Table 9.6.

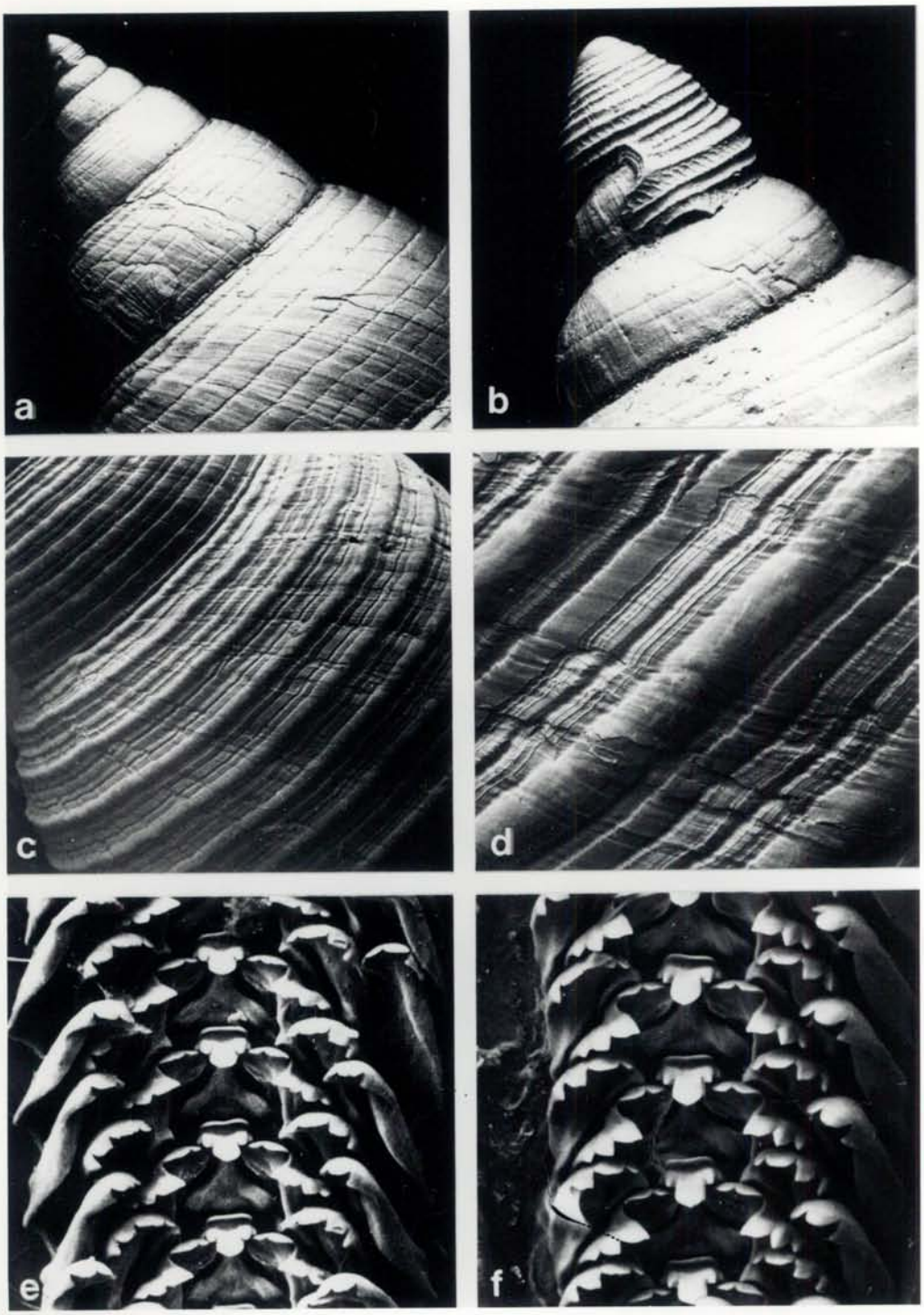
Sculpture (Fig. 9.22a–d). Protoconch normal. First 0.5–1 whorl of teleoconch smooth. Primary grooves (7)8–9(11), equally spaced anteriorly, posterior 2–3 more closely spaced, deeper and broader. Secondary grooves appear on whorls 6–7, dividing each primary rib at anterior $\frac{1}{4}$–$\frac{1}{2}$ width; secondary riblets may also form by intercalation, especially in the wider posterior grooves. Higher orders of sculpture appear on whorls 7 and 8, as fine grooves and riblets in the broad spaces between major ribs. All primary ribs become raised and rounded on penultimate whorl, and on last whorl develop into prominent, rather narrow cords, numbering 13–18; peripheral rib is most prominent, those near suture least so; secondary riblets remain narrow, but may become rounded. Grooves remain small; on last whorl the spaces between primary ribs are 4–6 times cord width, each containing 1–3 riblets and numerous small, irregularly spaced grooves and striations. Microsculpture of axial growth striae, strongest between cords, and of fine, irregularly spaced spiral striae, only between cords; in some specimens the intersection of axial and spiral sculpture produces a beaded appearance between the ribs.

Colour. Polymorphic; dark brown shells predominate, sometimes pink, rarely yellowish. Ground colour pale brown, cream, orange pink or yellow, with pattern of diffuse dashes and flecks of dark brown or black, fading to grey. On early whorls dark dashes are aligned at sutures to form short axial stripes; on last two whorls pattern is more diffuse, although indistinct, oblique, axial stripes numbering 10–11 per whorl are often visible. Most shells are densely patterned; palest pink or yellow shells show a faint orange or brown mottling or a marbled pattern, often with darkest pigment dashes at sutures and periphery. External pattern visible within aperture as lines and dashes of purple brown, clouded by grey or lilac callus.

Table 9.6 Dimensions of *Littorarta* (*Littorinopsis*) *philippiana*.

Specimen	Locality	Sex	Primary grooves	H (mm)	B (mm)	LA (mm)	WA (mm)	C (mm)	PR	S	SH
Littorina philippiana holotype, BMNH 1968307	[eastern Qld.]		7	29.8	18.4	15.5	12.1	2.8	1.62	0.78	1.92
DGR	Thursday I., Qld.	♀	8	35.8	21.9	18.0	14.4	2.9	1.63	0.80	1.99
DGR	Thursday I., Qld.	♀	9	36.1	19.2	17.5	12.7	3.1	1.88	0.73	2.06
DGR	Moa I., Qld.	♂	8	17.9	11.4	9.5	7.2	1.5	1.57	0.76	1.88
DGR	Moa I., Qld.	♀	8	19.6	12.4	9.7	8.0	1.6	1.58	0.82	2.02
DGR	Bohle R., Qld.	♂	8	26.8	15.5	13.5	10.5	2.1	1.73	0.78	1.99
DGR	Bohle R., Qld.	♂	8	23.2	14.4	12.7	10.6	2.6	1.61	0.83	1.83
DGR	Bohle R., Qld.	♀	9	33.4	19.0	15.9	12.5	2.3	1.76	0.79	2.10
DGR	Bohle R., Qld.	♀	10	30.2	18.0	14.9	12.3	2.3	1.68	0.83	2.03
DGR, mean of 10	Magnetic I., Qld.	♂		27.44					1.684	0.794	1.936
standard error				1.28					0.041	0.009	0.021
DGR, mean of 10	Magnetic I., Qld.	♀		28.75					1.664	0.803	2.014
standard error				0.47					0.020	0.005	0.021
statistic t or U				0.963					50	56.5	82
probability				0.348					1	0.657	0.014

Fig. 9.22 *Littorarta* (*Littortnopsis*) *philippiana*: (a,b) Magnetic I., Qld.; (a) spire (×17); (b) protoconch (×80); (c,d) Orpheus I., Qld.; (c) last whorl (×7); (d) detail (×28); (e) radula, Lizard I., Qld. (×225); (f) radula, Magnetic I., Qld. (×235).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Columella purple or lilac.

ANIMAL. *Colour*. Pigmentation dark grey to black; sides of foot darkly mottled; head darkest, sometimes pale patch in centre; tentacles banded, unpigmented stripe each side of base.

Penis (Fig. 9.23a–d). Length to 10.0 (15.0) mm. Base bifurcate, limb bearing glandular disc long, disc small. Filament long, tapering towards tip. Sperm groove closed as a duct. Base and filament white to fawn; glandular disc opaque white to pale brown.

Sperm (Fig. 5.3d). Eupyrene sperm 160–187 μm. Nurse cells (Fig. 9.23e–g) 14–24 μm, rounded (sometimes somewhat oval); rods often absent, but if present 1–2, central, not projecting, parallel sided, blunt; yolk granules large.

Pallial oviduct (Fig. 9.23h,i). Length to 5.8 mm. Spiral section to 2.3 mm diam., $3\frac{1}{2}$ whorls; opaque albumen gland $\frac{3}{4}$ whorl, white to cream; translucent albumen gland white to fawn; capsule glands absent; spiral indistinct externally; egg groove not pigmented. Straight section to 3.9 mm, white to fawn, terminating in a papilla. Bursa to 2.0 mm, anterior. Reproduction ovoviviparous.

Radula (Fig. 9.22e,f). Length to 21 mm; relative length 0.63–0.79. Saw-toothed type; central rachidian cusp square, edge slightly pointed; cusps of paired teeth almost equilaterally triangular; lateral with gap anterior to main cusp.

DISTRIBUTION. *Habitat*. Characteristic of *Rhizophora* forests, usually on trunks, sometimes on leaves, 0.5–5.2 m above the ground; found also on trunks and leaves in the *Avicennia* fringe. A continental species.

Range (Fig. 9.24). Eastern Australia from Botany Bay, N.S.W. to Torres Strait and south-eastern Papua New Guinea; rare in N.S.W. Three records from N.T. and W.A. are doubtful, either old

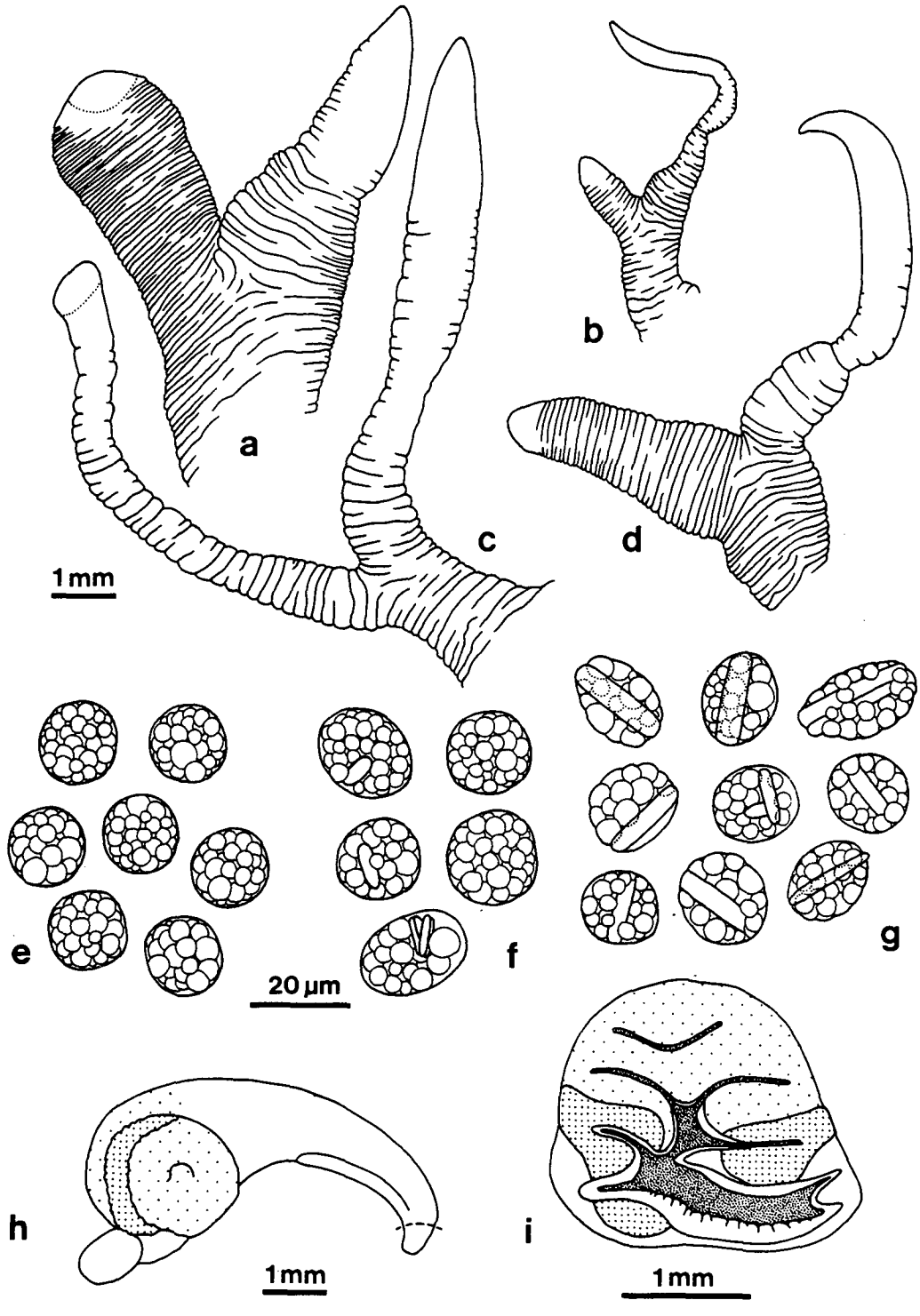

Fig. 9.23 *Littoraria* (*Littorinopsis*) *philippiana*, Magnetic I., Qld.: (a) penis, partially relaxed; (b-d) penes, relaxed; (e-g) sperm nurse cells; (h,i) pallial oviduct, with transverse section.

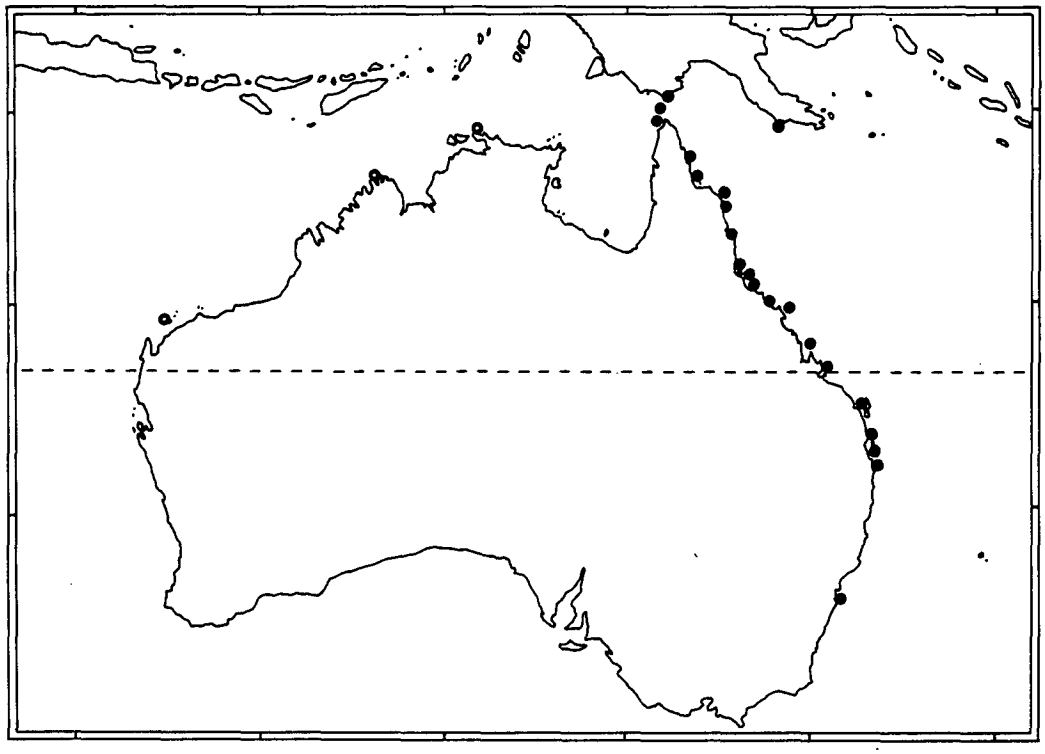

Fig. 9.24 Distribution of *Littoraria (Littorinopsis) philippiana*.

collections or shells which could belong to the similar *L. pallescens*. Nineteenth century material from Solomon Is., New Hebrides, New Caledonia and Philippine Is. is almost certainly incorrectly localized.

Records. AUSTRALIA: N.S.W.: Bayview, Pittwater (AMS); Kurnell Penin. (DGR); Tweed Heads (NMV); QLD.: Dunwich, Stradbroke I. (WAM, QM); Caloundra (QM); Pialba (QM, AMS); Wathumba Creek, Fraser I. (AMS); Yeppoon (AMS, NMV); Percy I. (BMNH); Cannonvale Beach, Proserpine (AMS); Hayman I. (AMS); Bowen (AMS, WAM); Magnetic I. (DGR); Orpheus I., Palm Is. (DGR); Missionary Bay, Hinchinbrook I. (DGR); Dunk I. (QM, NMV); Machans Beach, Cairns (NMV); Port Douglas (AMS); Low Isles (AMS); Lizard I. (AMS); Claremont I. (QM); Quintell Beach (QM); Thursday I., Torres Str. (DGR, QM, WAM); Moa I., Torres Str. (DGR); Saibai I., Torres Str. (AMS); N.T.: Port Essington (BMNH, doubtful record); W.A.: Vansittart Bay (AMS, doubtful record); Barrow I. (WAM, doubtful record); PAPUA NEW GUINEA: Kapa Kapa (AMS); Marshall Lagoon (AMS).

REMARKS. The shell of *L. philippiana* is rather constant in sculpture, although colouration is variable. Specimens from *Rhizophora* forests are invariably darkly pigmented, whilst in those from *Avicennia* trees the pattern is usually paler and the pink or yellow ground colour visible (Section 15.4.3). Of the anatomical characters the closed penial sperm duct is noteworthy, a feature shared only with *L. subvittata* and *L. intermedia* in the same subgenus. Sperm nurse cells are also similar in these species and the three are probably closely related. Shells of *L. pallescens* are sometimes extremely similar to those of *L. philippiana*, and sperm nurse cells are the same, although penial form differs in the two species. Where their ranges overlap in eastern Australia they seldom occur together, since *L. pallescens* is an oceanic species, while *L. philippiana* occurs in continental situations. Only on high islands close to the north Queensland coast are both found together (Magnetic I., Hinchinbrook I., Dunk I., Lizard I., Thursday I.). However, despite their similarities there is no doubt that the two

species are distinct, since at localities where both occur the diagnostic penial characters remain constant and shells can usually be distinguished.

SIMILAR SPECIES. As mentioned above, although penial form differs in the two species *L. philippiana* and *L. pallescens*, their shells can in some cases be closely similar. *L. philippiana* can usually be distinguished by its larger size, the sharp inner lip of the aperture adjacent to the columella, and most importantly by the presence of numerous secondary and tertiary grooves in the spaces between the primary ribs. In addition there are differences in colour pattern; although both species are polymorphic, the pattern of *L. philippiana* is rather diffuse, while in *L. pallescens* the spiral dashes tend to be discrete and confined to the ribs. Neither pure yellow shells nor continuous spiral bands of pigment are found in *L. philippiana* and the columella is never white. Only a very few shells cannot be separated using shell characters alone. Of other similar species, *L. filosa* can bear a close resemblance in shell sculpture, but the columella is narrow and not excavated, and on the apical whorls the spacing of the primary grooves is unequal. *L. luteola* and *L. ardouiniana* can be superficially similar, but both lack the wide and excavated columella of *L. philippiana*. Sculptural details and penial form readily distinguish this species from *L. subvittata*, *L. intermedia* and *L. lutea*.

9.2.3.5 *Littoraria* (*Littorinopsis*) *intermedia* (Philippi, 1846)

Littorina intermedia Philippi, 1846: 141 [in part; lectotype here designated BMNH 198343 ; type locality here restricted to Tahiti]; Reeve, 1858: *Littorina* pl. 18, fig. 101; Issel, 1869: 192; Nevill, 1885: 146 [in part]; Sowerby, 1892: 37; Dautzenberg, 1923: 49; Turton, 1932: 131; Fischer, 1970: 99

Litorina intermedia – Philippi, 1847, vol. 2: 223; Krauss, 1848:

103; von Martens, 1871: 39; von Martens, 1880: 284 [all in part]

Littorina (Melaraphe) scabra var. *intermedia* - Tryon, 1887: 244, pl. 42, figs 21,22,24 [in part]

Littorina (Malaraphe) intermedia - Casto de Elera, 1896: 309-310 [in part]

Littorina (Melaraphe) intermedia - Dautzenberg & Fischer, 1905: 146; Dautzenberg, 1929: 288-289 [both in part]

Littorinopsis intermedia - Kuroda & Habe, 1952: 64

Littoraria intermedia - Higo, 1973: 46

Littorina intermedia var. *punctata* Philippi, 1846: 141 [objective synonym of *Littorina intermedia* Philippi, 1846; not a secondary homonym of *Turbo punctatus* Gmelin, 1791 = *Nodilittorina punctata*]

Littorina intermedia var. *punctata* - Philippi, 1847, vol. 2: 223, *Littorina* pl. 5, fig. 6 [not fig. 11 as cited in text]

Littorina scabra var. *articulata* Philippi, 1847, vol. 2: 222, *Littorina* pl. 5, fig. 4 [lectotype (Rosewater, 1970) BMNH 1968354; type locality here corrected Jimaimilan [Himamaylan], Negros I., Philippines; not *Littorina intermedia* var. *articulata* Philippi, 1846]

Littorina ambigua Philippi, 1848, vol. 3: 62-63, *Littorina* pl. 7, fig. 6 [Sandwich Is. [= Hawaiian Is.]; lectotype (Rosewater, 1970) BMNH 1968314]

Littorina ambigua - Reeve, 1857: *Littorina* pl. 12, fig. 64; Hidalgo, 1904-5: 206

Littorina newcombi Reeve, 1857: *Littorina* pl. 6, figs 28a,b [Sandwich Is. [= Hawaiian Is.]; lectotype (Rosewater, 1970) BMNH 1968308]; Pease, 1868: 128; Nevill, 1885: 144; Sowerby, 1892: 37

Littorina newcombi - von Martens, 1871: 39

Littorina scabra var. *newcombi* - Dautzenberg, 1923: 49

Littorina (Melaraphe) scabra var. *newcombi* - Dautzenberg, 1929: 289

Littorina fraseri Reeve, 1857: *Littorina* pl. 10, fig. 47 [Lagos, West Africa, in error; corrected to Indo-Pacific; lectotype (Rosewater, 1981) BMNH 1968312]

Littorina (Melaraphe) punctata var. *fraseri* - Tryon, 1887: 248, pl. 44, figs 62,63

Littorina pintado - Pease, 1868: 127; Kay, 1979: 72 [both in part;

not Wood, 1828]

Litorina pintado - von Martens, 1871: 39 [in part; not Wood, 1828]

Littorina (Melaraphe) pintado - Tryon, 1887: 250 [in part; not Wood, 1828]

Littorina (Littcraria) pintado pintado - Rosewater, 1970: 447-449, pl. 346, figs 3,4 [in part; not Wood, 1828]

Litorina scabra - Weinkauff, 1878: 37-39, pl. 4, figs 16-18 [not Linnaeus, 1758]

Littorina (Melaraphe) scabra - Tryon, 1887: 243, pl. 42, fig. 20 [in part; not Linnaeus, 1758]

Littorina (Malaraphe) scabra - Casto de Elera, 1896: 309 [in part; not Linnaeus, 1758]

Littorina scabra - Risbec, 1942 [anatomy]; Whipple, 1965: figs 3c,4, pl. 25, figs 3a-c; Struhsaker, 1966 [reproduction and development]; Salvat & Rives, 1975: 263, no. 38; Nielsen, 1975: fig. 1a; Kay, 1979: 73, fig. 24g [all not Linnaeus, 1758]

Littoraria scabra - Habe, 1964: 29, pl. 9, fig. 32 left [in part; not Linnaeus, 1758]

Littorina (Littorinopsis) scabra scabra - Rosewater, 1970: 456-461, pl. 352, figs 6,10,14,15,19 [in part; not Linnaeus, 1758]

Littorina (Littorinopsis) scabra - Tadjalli-Pour, 1974: 58, pl. 20, fig. 3 [not Linnaeus, 1758]

Littorinopsis scabra - Brandt, 1974: 53-54, pl. 4, fig. 60 [in part; not Linnaeus, 1758]

Littorina (Melaraphe) planaxis - Tryon, 1887: 248, pl. 43, fig. 56 [in part; not Philippi, 1847]

Littorina scabra var. *philippiana* - Hidalgo, 1904-5: 206 [in part; not Reeve, 1857]

Littorina (Melaraphe) scabra var. *rhodea* Biggs, 1958: 272 [Bundar Abbas, S. Persia; holotype BMNH 1958.6.13.23]

Littorina (Littoraria) cingulifera - Rosewater, 1981: 18-20 [in part; not Dunker, 1845]

NOMENCLATURE. The identity of this species has been the subject of much confusion in the literature, as indicated by the lengthy synonymy. This has arisen firstly because the name '*intermedia*' has

been applied to a group comprising at least three species, *L. articulata*, *L. strigata* and *L. intermedia s. s.*, and probably also including *L. subvittata*. Secondly, the species is so variable that several forms have been named and subsequently often incorrectly placed in the synonymies of other species.

Difficulties begin with the original diagnosis (Philippi, 1846) of *Littorina intermedia*, which was not sufficiently precise to define the species, and was followed by diagnoses of the principal colour varieties *punctata*, *articulata* and *strigata*. The varieties *punctata* and *strigata* were figured by Philippi in 1847, although the figures of his plate 5 were incorrectly cited in the text. From the accompanying descriptions it is evident that Philippi's plate 5, fig. 6 illustrates var. *punctata* and plate 5, figs 7,8,9 var. *strigata*. From these figures and the type localities given, each variety is recognizable as the type of a species here considered distinct, and it must be decided to which the name '*intermedia*' should be applied. Following the diagnosis of *Littorina intermedia*, Philippi (1846) gave the following dimensions: '*Altit.* 10, *diam.* $7\frac{1}{2}$, *altit. aperturae* $5\frac{1}{2}$ *lin.*' (22.0, 16.5, 12.1 mm respectively). Since neither *L. articulata* nor *L. strigata* ever attain such large size, the epithet '*intermedia*' is thereby restricted to the variety *punctata*. All the taxa described by Philippi (1846), and their locality records, were based on specimens in the Cuming Collection, now in the BMNH. In 1846, Philippi gave no localities for the variety *punctata*. However, of the localities listed for *Littorina intermedia*, the original material upon which the records were based has now been identified for the localities Natal, Elizabeth Island and Tahiti. All are the species illustrated by Philippi (1847) as *Littorina intermedia* var. *punctata*, as, from the known distribution of the species, was the record from the Red Sea. The majority of the specimens that Philippi had before him were therefore of the variety *punctata*, and in 1847 he listed all these localities for this variety. Only two other localities were given beneath the diagnosis of *Littorina intermedia*, which are the type localities of *L. articulata* and *L. strigata*. It seems that Philippi

himself considered the variety *punctata* to be the typical colour form of his species, and on each occasion listed it as the first of the three varieties.

When Rosewater (1970) examined the collections of the BMNH, he distinguished only the type material of *Littorina intermedia* var. *strigata*, from which he designated the lectotype of *Littorina intermedia*. From the evidence presented above, this designation is inappropriate. The original specimen of Philippi's figure of *Littorina intermedia* var. *punctata* has now been identified, on the basis of correspondence of pattern and dimensions. The original label bears the locality 'Tahiete' inscribed by Cuming and '*intermedia* Ph.' in the hand of Philippi himself (Section 3.1). Tahiti is one of the localities given by Philippi for *Littorina intermedia* (1846) and for *Litorina intermedia* var. *punctata* (1847), although the origin and owner of the figured specimen were not explicitly stated. This specimen is here designated lectotype of *Littorina intermedia* Philippi, 1846, with type locality Tahiti. *Littorina intermedia* var. *punctata* becomes an objective synonym of this species. This redesignation of a lectotype for *L. intermedia* stabilizes the concept of the species as it has most frequently been used in the literature.

Of the several junior synonyms of *L. intermedia*, *Litorina scabra* var. *articulata* Philippi, 1847 was based upon an unusually large specimen of *L. intermedia*. The lectotype selected by Rosewater (I970) is probably the specimen figured by Philippi, but the original label does not bear the type locality given by Rosewater, which is corrected accordingly. The three paralectotypes are *L. lutea* (Philippi, 1847), to which the lectotype does indeed bear a close resemblance. *Litorina ambigua* Philippi, 1848 has been placed in the synonymy of *L. pintado* by several authors. Although the lectotype is an eroded shell, there is no doubt that it is a specimen of the Hawaiian form of *L. intermedia*. *Littorina newcombi* Reeve, 1857 is also the large Hawaiian form. Reeve (1857) gave the locality of *Littorina fraseri* as 'Lagos, West Africa', which misled

Tryon (1887) to list it as a variety of *Littorina punctata* (Gmelin) and Rosewater (1981) to place the species in the synonymy of *L. cingulifera*. The type specimens are typical *L. intermedia*, however, and the type locality is therefore presumably incorrect. *Littorina (Melaraphe) scabra* var. *rhodea* Biggs, 1958 ia a reddish shell lacking the usual colour pattern, and similar small, pallid shells are common in the N.W. Indian Ocean. The name '*Litorina scabra* var. *minor*', attributed to Weinkauff (1878) in synonymies given by Tryon (1887) and Rosewater (1970), has arisen from a misreading of the original text, in which '*minor*' is used merely as the initial adjective in a Latin description and not as a varietal name.

DIAGNOSIS. Shell: periphery rounded; columella wide, excavated, purple; primary grooves 8–10; secondary sculpture on last whorl only, not usually well developed; ribs low, except posterior rib which is often prominent, total number of ribs on last whorl 17–32; grooves narrow; microsculpture indistinct; colour variable, but shells often show dense pattern of discrete black or brown dashes, aligned to form 13–20 axial series on last whorl. Animal: penis bifurcate, base ochraceous, filament white and large, tip mucronate, sperm groove closed as a duct; ovoviviparous.

SHELL (Figs 9.25, 9.26). *Shape*. Height (10)14–26(32) mm. Teleoconch 6.5–7.5(8) whorls. Shell usually thick, solid. Spire outline gently convex; whorls rounded; sutures impressed. Peripheral keel evident in young shells, becoming obsolete on last whorl. Adult lip slightly thickened, sometimes a little flared. Varices absent, but strong growth ridges may remain behind lip. Columella wide, excavated; pillar slightly convex, sharply pinched at base. Sexual dimorphism: males smaller, relatively lower spire and larger aperture.

Dimensions: Table 9.7.

Sculpture (Fig. 9.27a–e). Protoconch normal. All whorls of teleoconch sculptured by spiral grooves. Primary grooves (7)8–10(11), almost equally spaced, but all or one of the 3

Fig. 9.25 *Littoraria* (*Littorinopsis*) *intermedia*: (a) lectotype of *Littorina fraseri* Reeve, locality unknown (BMNH 1968312); (b) ♂, Sungei Merbok estuary, Malaysia (DGR); (c) Pearl Harbour, Hawaiian Is. (AMS); (d) lectotype of *Litorina ambigua* Philippi, Hawaiian Is. (BMNH 1968314); (e) lectotype of *Littorina newcombi* Reeve, Hawaiian Is. (BMNH 1968308); (f) holotype of *Littorina* (*Melaraphe*) *scabra* var. *rhodea* Biggs, Bundar Abbas, Iran (BMNH 1958.6.13.23); (g) lectotype of *Litorina scabra* var. *articulata* Philippi, Himamaylan, Negros I., Philippines (BMNH 1968354); (h) Aqaba, Jordan (DGR); (i) lectotype of *Littorina intermedia* Philippi, Tahiti (BMNH 198343).

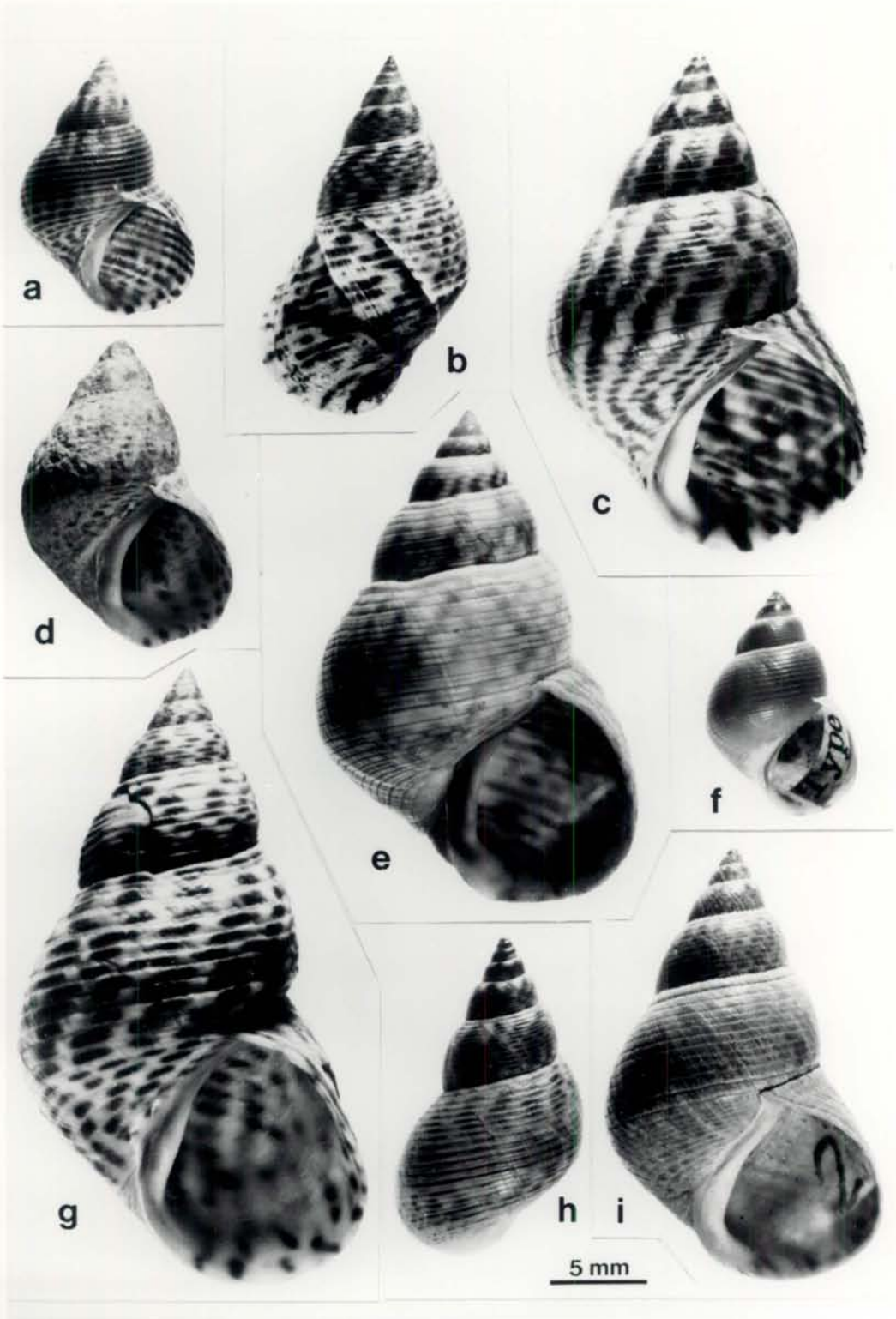
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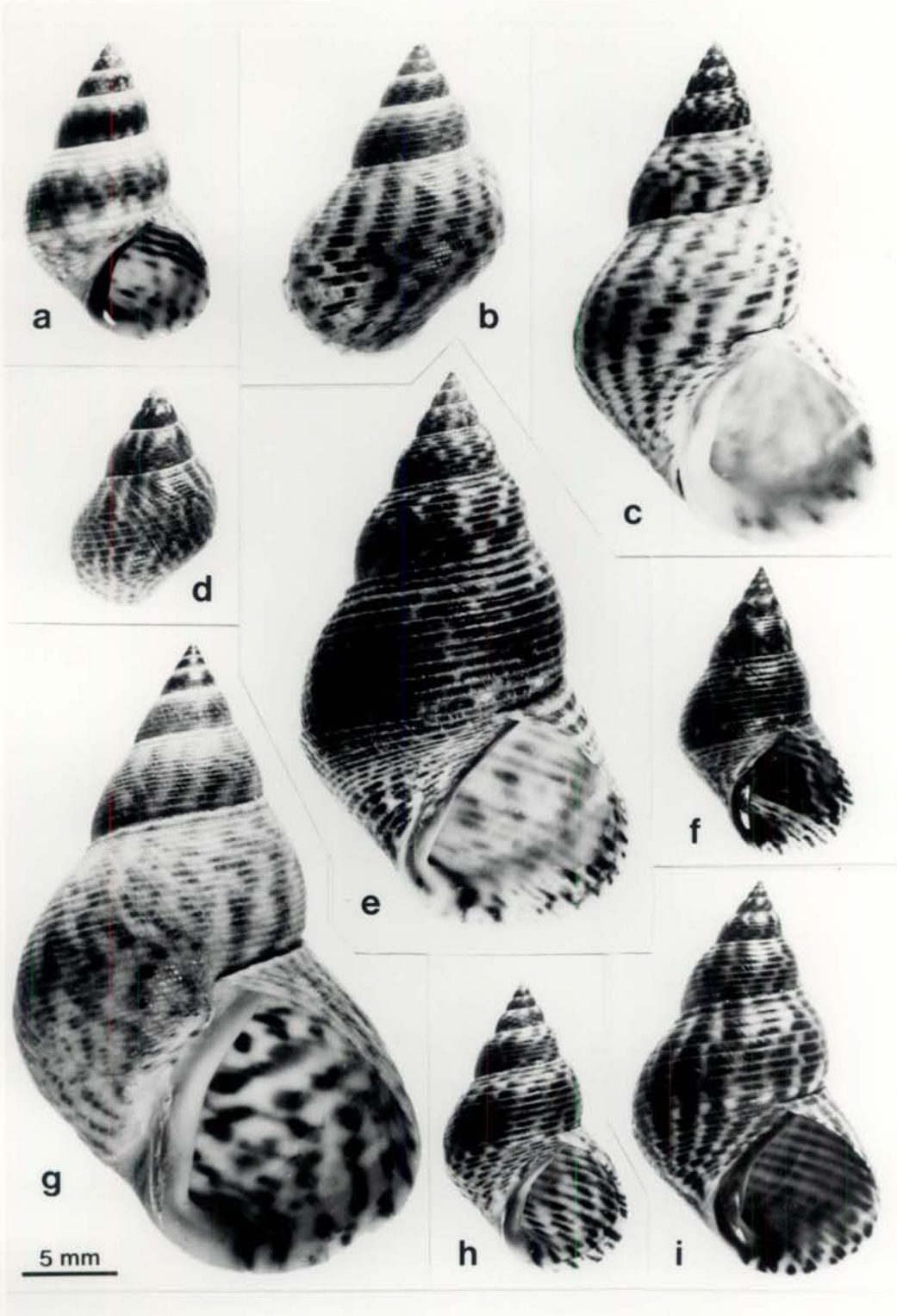
Fig. 9.26 *Littoraria* (*Littorinopsis*) *intermedia*: (a) Okinawa, Japan (BMNH); (b) Ile Ste. Marie, Madagascar (NMV); (c) ♀, Gove, N.T. (DGR); (d) Mangareva I., Gambier Is. (WAM); (e) ♀, Penang, Malaysia (DGR); (f) ♂, Phuket I., Thailand (DGR); (g) Trincomalee, Sri Lanka (BMNH); (h) Polillo I., Philippines (WAM); (i) ♀, Magnetic I., Qld. (DGR).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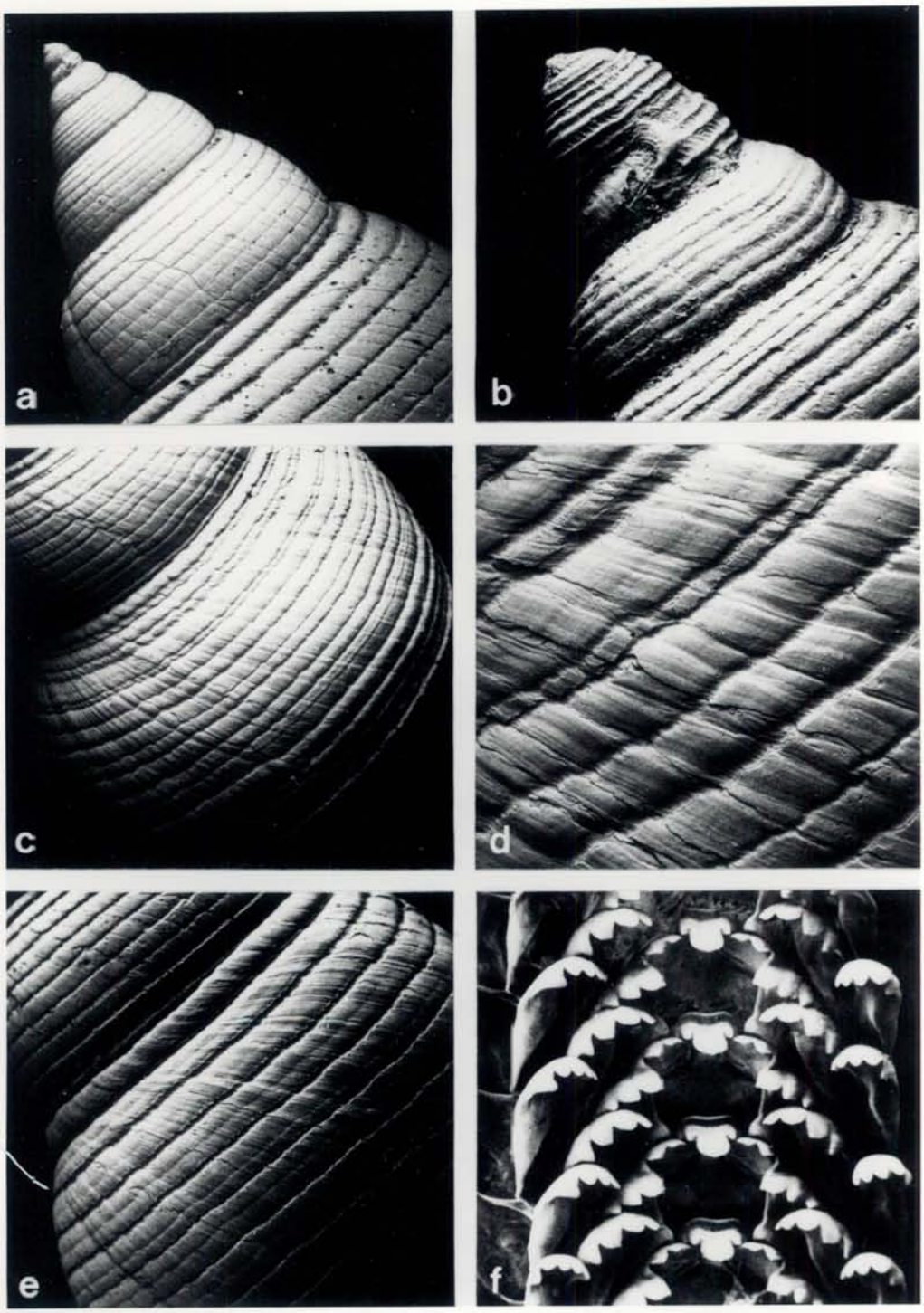
5 mm

Table 9.7 Dimensions of *Littoraria* (*Littorinopsis*) *intermedia*.

Specimen	Locality	Sex	Primary grooves	H (mm)	B (mm)	LA (mm)	WA (mm)	C (mm)	PR	S	SH
Littorina intermedia lectotype, BMNH 198343	Tahiti		10	22.7	15.3	12.8	10.2	2.6	1.48	0.80	1.77
Litorina scabra var. *articulata* lectotype, BMNH 1968354	Himamaylan, Negros I., Philippines		8	31.9	19.0	16.1	12.2	3.0	1.68	0.76	1.98
Litorina ambigua lectotype, BMNH 1968314	Hawaiian Is.		8	15.8	11.7	9.1	7.6	1.8	1.35	0.84	1.74
Littorina newcombi lectotype, BMNH 1968308	Hawaiian Is.		8	25.4	17.2	13.4	10.4	2.7	1.48	0.78	1.90
Littorina fraseri lectotype, BMNH 1968312	[Indo-Pacific]		10	13.5	9.8	7.8	6.0	1.6	1.38	0.77	1.73
Littorina scabra var. *rhodea* holotype, BMNH 1958.6.13.23	Bundar Abbas, Iran		10	11.6	8.4	6.6	4.7	0.6	1.38	0.71	1.76
DGR	Magnetic I., Qld.	♂	9	18.8	12.5	10.2	8.2	2.2	1.50	0.80	1.84
DGR	Magnetic I., Qld.	♀	9	21.4	14.0	10.7	9.2	2.2	1.53	0.86	2.00
DGR	Penang, Malaysia	♂	10	22.2	14.5	13.0	10.0	2.8	1.53	0.77	1.71
DGR	Penang, Malaysia	♀	10	26.6	16.5	13.7	10.4	1.9	1.61	0.76	1.94
BMNH 1969357	Trincomalee, Sri Lanka		8	31.0	21.2	17.4	13.8	3.0	1.46	0.79	1.78
BMNH 1969357	Trincomalee, Sri Lanka		8	23.0	16.5	13.9	10.9	3.3	1.39	0.78	1.65
DGR, mean of 10	Magnetic I., Qld.	♂		17.37					1.501	0.786	1.778
standard error				0.33					0.015	0.006	0.021
DGR, mean of 10	Magnetic I., Qld.	♀		19.67					1.516	0.803	1.881
standard error				0.45					0.011	0.009	0.022
statistic t or U				4.116					57	65.5	87
probability				<.001					0.630	0.264	0.004

Fig. 9.27 *Littoraria* (*Littorinopsis*) *intermedia*: (a,b) Magnetic I., Qld.; (a) spire (×19); (b) protoconch (×90); (c,d) Phuket I., Thailand; (c) last whorl (×7); (d) detail (×29); (e,f) Magnetic I., Qld.; (e) last whorl (×9); (f) radula (×210).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posterior ribs usually wider than others; posterior rib almost always most prominent since posterior groove is deepest. Some or rarely all primary ribs may be divided by secondary grooves at $\frac{1}{2}$ width on whorls (6)7-8, although secondary sculpture often absent. Tertiary grooves on largest shells only. Ribs remain low and flattened, except posterior rib which is rounded, prominent, undivided and, on last whorl, often appears pushed up over suture; peripheral rib sometimes a little wider and more prominent than others; total number of primary ribs on last whorl 17-21, up to 32 ribs if secondary sculpture well developed. Intercalation of single, narrow secondary riblets occurs infrequently in the wider primary grooves of last whorl. Primary grooves remain narrow, usually less than $\frac{1}{5}$ rib width on last whorl, but posterior groove and that at periphery may reach $\frac{1}{2}$ rib width; secondary grooves are incised lines only. Microsculpture of faint axial growth striae over surface; spiral microsculpture usually absent, but faint spiral striae occasionally visible on ribs of spire whorls and in wider grooves of last whorl.

Colour. Variable over entire geographical range, but usually rather constant at each locality. Ground colour usually grey, sometimes pale brown, cream, whitish or rarely orange pink. Pattern of discrete black or dark brown dashes, closely spaced on ribs, often roughly aligned at suture or over entire whorl to form axial series, numbering 13-20 on last whorl; alignment usually especially prominent at suture of spire whorls, where ground colour is palest. Degree of pigmentation variable, although grooves remain pale; some shells almost entirely black with pale patches at suture and periphery; palest shells only faintly mottled with light brown; sometimes with spiral paler zones at suture, periphery and around columella. Aperture with black lines and streaks, corresponding to external ribs, clouded with greyish callus. Columella and parietal callus dark purple or pink; columellar pillar usually paler pink or whitish.

ANIMAL. *Colour*. Pigmentation black; sides of foot densely mottled;

head darkest, sometimes with pale central patch; tentacles banded, unpigmented stripe each side of base.

Penis (Fig. 9.28a–h). Length to 8.2 mm. Base bifurcate; glandular disc relatively small. Filament large, broad, tip mucronate. Sperm groove closed as a duct. Base ochraceous, darkest at base of filament and near disc, filament white, glandular disc dark ochre to cream.

Sperm. Eupyrene sperm 133–146 μm. Nurse cells (Fig. 9.28i–k) 18–24(27) μm, slightly irregularly oval to reniform; rods often indistinct, 1–4, narrow, pointed, central, usually not projecting or only minutely so (occasionally strongly); yolk granules large, indistinct.

Pallial oviduct (Fig. 9.28l–o). Length to 4.1(5.7) mm. Spiral section to 1.9(2.7) mm diam., $3\frac{1}{2}$ whorls; opaque albumen gland $\frac{1}{2}$–$\frac{3}{4}$ whorl, white; translucent albumen gland white to fawn; capsule glands absent; spiral indistinct externally, egg groove not usually darkly pigmented. Straight section to 2.5(3.4) mm, pale brown, terminating in a papilla. Bursa long, to 2.1(2.8) mm, anterior. Development ovoviviparous.

Radula (Fig. 9.27f). Length to 26 mm; relative length 0.76–1.07. Saw-toothed type; central rachidian cusp square, edge slightly pointed; cusps of paired teeth almost equilaterally triangular; lateral with gap anterior to main cusp.

DISTRIBUTION. *Habitat*. On roots and trunks throughout *Rhizophora* forests, 0.3–2.0 m (rarely to 3.5 m) above the ground. Occasional on trunks in *Bruguiera* forests and in *Avicennia* fringe. Not infrequent on sheltered rocks. An oceanic species.

Range (Fig. 9.29). Throughout tropical and subtropical Indo-Pacific, including South Africa, Red Sea and Persian Gulf, but excluding Bay of Bengal, north-western Australia and much of

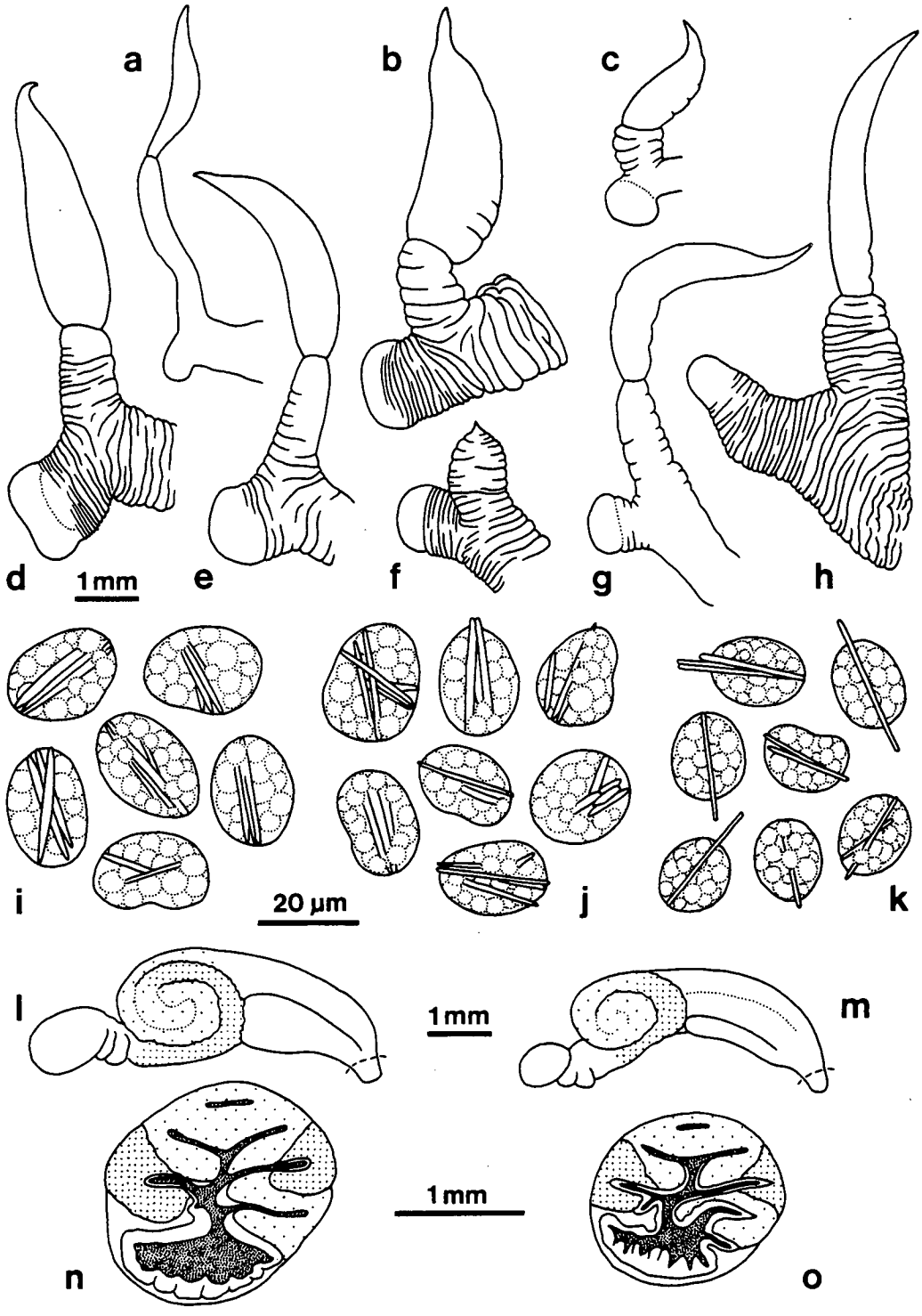


Fig. 9.28 *Littoraria* (*Littorinopsis*) *intermedia*: (a–e,g,h) penes, relaxed; (f) penis, contracted; (a) Nxaxo R., S. Africa; (b) Penang, Malaysia; (c) Magnetic I., Qld.; (d) Coconut I., Oahu, Hawaiian Is.; (e) Vaiore Bay, Tahiti; (f,g) Magnetic I., Qld.; (h) Gove, N.T.; (i–k) sperm nurse cells; (i) Ubin I., Singapore; (j) Magnetic I., Qld.; (k) Penang, Malaysia; (l–o) pallial oviducts, with transverse sections, Magnetic I., Qld.

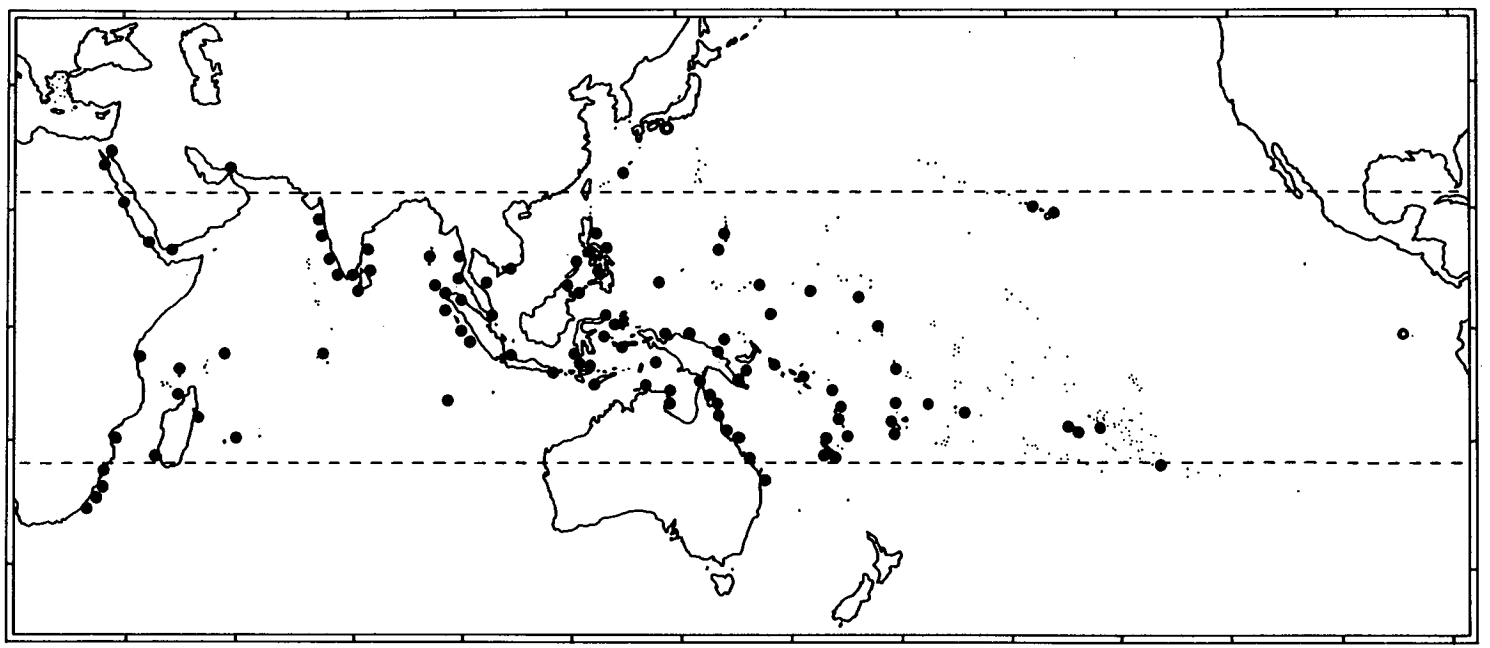


Fig. 9.29 Distribution of *Littoraria (Littorinopsis) intermedia*.

mainland South East Asia and Borneo. Extends as far eastwards as Hawaiian Is. and Polynesia; a single shell is doubtfully recorded from the Galapagos Is.

Records. SOUTH AFRICA: Umtata R. mouth (NM); Nxaxo R. mouth (ANSP); Isipingo (BMNH); Durban (BMNH, NM); St. Lucia, Zululand (NMW, NM); MOZAMBIQUE: Inhaca I. (NM); Beira (BMNH, NMW); TANZANIA: North Reef, Dar-es-Salaam (AMS); Chukwani, Zanzibar (ANSP); MADAGASCAR: Tuléar (AMS, MCZ); Nossi Bé (ANSP); Ile Ste. Marie (NMV); MAURITIUS: (BMNH, NMW); Poste de Flacq (ANSP); SEYCHELLES: Mahé I. (BMNH); ALDABRA ATOLL (BMNH); CHAGOS ARCH: Diego Garcia (BMNH); ETHIOPIA: Melita Bay, Gulf of Zula (ANSP); Dahlak Kebir I. (USNM); EGYPT: Halieb (USNM); Hurghada (RNHL); ISRAEL: Eilat (USNM); JORDAN: Aqaba (DGR); YEMEN: Aden (BMNH); IRAN: Bundar Abbas (BMNH); INDIA: Bombay (USNM, MCZ); Vengurla, N. of Goa (USNM); Netravata R., Mangalore (USNM); Beypore Estuary (BMNH); between Wallarpat I. and Bolghatti, Cochin Harbour (ANSP); Manali I., off Mandapam (MCZ); Tuticorin (USNM); Madras (BMNH, USNM); SRI LANKA: Galle (BMNH); Trincomalee (BMNH); ANDAMAN IS.: Port Blair (BMNH); NICOBAR IS. (BMNH); COCOS-KEELING IS. (AMS, WAM); BURMA: King I., Mergui Arch. (BMNH); THAILAND: Ao Nam Bor, Phuket I. (DGR); Tanga I., Butang Group (USNM); MALAYSIA: PENINSULA: Penang (DGR); Sungei Merbok estuary, Kedah (DGR); Perhentian I., 50 km S. of Kota Bharu (ANSP); SABAH: Po Bui I., Sandakan (USNM); SINGAPORE: Loyang Besar (WAM); Jelutong, Ubin I. (DGR); VIETNAM: Chilins, Vung Tau district (ANSP); INDONESIA: SUMATRA: Belawan R. (RNHL); Weh I. (RNHL); Sinabang, Simeulue I. (RNHL); Bai I., Batu Is. (USNM); Sanding I., Mentawai Is. (USNM); JAVA: Njamoek Besar, Djakarta Bay (RNHL); LESSER SUNDA IS.: Sanur Beach, Bali (AMS); Maumere, Flores (USNM); Tanahdjampea I. (RNHL); Kambang I., 20 km S.W. of Kupang, Timor (RNHL); SULAWESI: Manado (MCZ); Makassar (RNHL); MOLUCCAS: Ternate, Halmahera (WAM); Kasirota I. (MCZ); Taliabu I., Sula Is. (RNHL); Ambon (RNHL); Tamberfane, Aru Is. (WAM); IRIAN JAYA: Sorendidori, Schouten Is. (ANSP); Japen I. (RNHL, ANSP); Djajapura (RNHL); PHILIPPINES: Sanga Sanga I., Sulu Arch. (RNHL, ANSP); Jolo I., Sulu Arch. (ANSP); Makibojoc Bay, Bohol I. (WAM); Viejo Victorias, Negros I. (USNM);

Batangas Bay, Luzon I. (WAM); Legaspi, Albay Prov., Luzon I. (ANSP); Panukalan, N.W. Polillo I. (WAM); Linapacan I. (USNM); JAPAN: Toguchi, Kitanakagusuku, Okinawa I., Ryukyu Is. (BMNH); Kii Peninsula, Honshu (Habe, 1964); PAPUA NEW GUINEA: Madang (AMS); Collingwood Bay (AMS); Losuia, Kiriwina Is., Trobriand Is. (AMS); BISMARCK ARCH.: New Britain (AMS); Koruniat I., Admiralty Is. (ANSP); Bouin, Bougainville I. (ANSP); AUSTRALIA: N.T.: Cape Don (AMS); Port Essington (AMS): Gove, Arnhemland (DGR); Groot Eylandt (WAM); QLD.: Thursday I., Torres Str. (DGR, QM); Moa I., Torres Str. (DGR); Quintell Beach, Iron Range (QM); Lizard I. (AMS, ANSP); Annan R. (AMS); Double I., Cairns (NMV); Dunk I. (QM); Magnetic I. (DGR); Hayman I. (AMS); N. Keppel I. (NMV); Heron I. (AMS); Caloundra (QM); Dunwich, Stradbroke I. (QM, NMV); Currumbin Creek, N. of Coolangatta (AMS); NEW CALEDONIA: Ile des Pins (AMS); Noumèa (AMS); Hienghène (ANSP); NEW HEBRIDES: Aneiteum and Tana (BMNH); Port Stanley, Malekula (BMNH); Pakea, Banks Group (AMS); SOLOMON IS.: Santa Cruz I., Vanikoro Is. (USNM); Auki, Malaita (BMNH); CAROLINE IS.: Babelthuap I., Palau (USNM, ANSP); Ulali I., Truk (BPBM); Kapingamarangi (USNM); Kusaie (BPBM); MARIANA IS.: Tanapag Harbour, Saipan (ANSP); Guam (USNM); MARSHALL IS.: Enybor I., Jaluit Atoll (USNM); GILBERT IS.: Apaiang (MCZ); ELLICE IS.: Vaitupu (USNM); WALLIS IS.: Rotuma I. (BMNH); between Luanna and Fungalei Is. (USNM); FIJI: Deuba, Viti Levu (AMS); Suva (RNHL, USNM); Lautoka, Viti Levu (MCZ); SAMOA IS.: Upolu I. (ANSP, BPBM); Tutuila I. (ANSP, USNM); SOCIETY IS.: Tahaa (USNM); Raiatea (USNM, ANSP); Moorea (USNM); Vaiore Bay, Tahiti (USNM); TUAMOTU IS.: Anaa (USNM); GAMBIER IS.: Mangareva I. (AMS, WAM); HAWAIIAN IS.: Hilo, Hawaii (BPBM); Coconut I., Kaneohe Bay, Oahu (DGR, AMS, USNM); Pearl Harbour, Oahu (NMV, ANSP); GALAPAGOS IS.: Wreck Bay, Chatham I. (ANSP, doubtful record).

REMARKS. *L. intermedia* is the most widely distributed of the species in the genus which are associated with mangroves. Throughout its range penial shape remains relatively constant and is always distinctive. The penial sperm groove is closed as a duct, a feature found elsewhere in the subgenus only in *L. subvittata* and *L.*

philippiana. Sperm nurse cells were found to be similar, and diagnostic of the species, in specimens from North Queensland; Gove, N.T.; Phuket Island, south-western Thailand; Singapore; Penang, Malaysia and Oahu, Hawaiian Islands, although some variation was shown in the degree to which the rods project from the cell.

Several rather characteristic geographical forms of the shell can be recognized, but do not deserve taxonomic recognition. Specimens from the Hawaiian Islands and Polynesia (as far west as Samoa) are often of larger size, the grooves narrow and shallow, and the colouration pallid or with continuous axial stripes (Fig. 9.25c,e,i); the lectotype is of this form. The most characteristic shell type is found in Australia, the western Pacific islands, South East Asia and the Indian Ocean, usually on roots of *Rhizophora* trees. In this type the colouration is dark, the pattern is of regular axial series of black dashes and the primary grooves are conspicuous (Fig. 9.26c,h,i). Occasional giant forms of this type occur, such as the lectotype of *Litorina scabra* var. *articulata* (Fig. 9.25g). Specimens from south-western Thailand, Penang and India have rather thin shells, the colour pattern is dark but irregular and the shells are sometimes of large size (Figs 9.25b, 9.26e,f). Such shells occur together with the common form found on *Rhizophora* at Phuket Island, south-western Thailand; intermediates can be found and there are no differences in the anatomy of the two forms. In the Persian Gulf, Red Sea and parts of the western Indian Ocean the shells are often small and the secondary sculpture well developed, the shell colour is whitish or pink, and the pigmented pattern pale and indistinct, or even absent (Fig. 9.25f,h). Similar forms are found in other regions on rocks, and this may be an ecotype rather than a geographical form.

In several parts of the range shells are sometimes found with an orange pink ground colour, usually with a normal pattern of darker pigment. This colour form is especially frequent in Arnhemland, N.T., Australia, where it occurs on *Rhizophora* trees and is probably a local genetic form. In other areas the species is not polymorphic

in the descriptive sense employed here, for variation is continuous and the range of colour forms not great. Reference has already been made to variation between habitats. Shells from rocks are often small, pigmentation is pale and pinkish shells are not unusual. Specimens from *Rhizophora* forests are almost invariably darkly pigmented, but on *Avicennia* trunks the shells may be paler in colour.

Kuroda & Habe (1952) recorded the species from a latitude of 37°N on the west coast of Korea, although in the absence of a figure correct identification cannot be certain. Amongst other *Littoraria* species in the *scabra* group, only *L. luteola* (in Australia) reaches such a high latitude. The distribution of the species demonstrates its preference for oceanic situations, since it is absent from such sheltered and turbid areas as Bengal, the Gulf of Siam and north-western Borneo. The distribution of *L. intermedia* in Australia deserves comment. The species is frequent on peninsulas and islands on the east coast, but the westernmost record is from the Coburg Peninsula, N.T. This is curious, since the species is abundant elsewhere in the Indian Ocean, and both *L. scabra* and *L. pallescens*, the two other almost equally widely distributed species, are recorded further west in Australia.

SIMILAR SPECIES. *L. intermedia* has been persistently confused with *L. articulata* in the literature, but can be immediately distinguished from the latter, as from *L. strigata*, by characters of the penis, sperm nurse cells and oviduct. Using shell characters, *L. intermedia* may be separated from these two species by the larger size, darker ground colour and interior, and by the greater number of axial series of dashes on the last whorl. *L. vespacea* is closer in shell pattern, but in *L. intermedia* the whorls are less inflated, the spire taller, and the columella less deeply excavated. Again anatomical characters are distinctive of each species. Small specimens of *L. scabra* are sometimes similar, but *L. intermedia* is distinguished by the purple columella, characteristically enlarged posterior rib adjacent to the suture, sculptured apical whorls of

the postlarval shell, absence of spiral microsculpture in the grooves, and by the shape of the penis. In *L. subvittata* the penial form is similar, although the filament is smaller and lacks the prominent basal constriction of *L. intermedia*. However, shells of the species differ, that of *L. subvittata* being thinner, more elongate and of a distinctive pattern. Shells of *L. intermedia* are approached most closely by some uncommon forms of *L. pallescens*; whilst the pattern of *L. intermedia* is usually more regular, axial alignment of dashes more complete and grooves narrower, a very few specimens are separable only by means of penial characters. Dark forms of *L. lutea* should not be confused with *L. intermedia*, since in the former the arrangement of narrow, intercalated, secondary riblets is diagnostic.

9.2.3.6 *Littoraria* (*Littorinopsis*) *subvittata* n. sp.

TYPES. Holotype: BMNH 198346, Aldabra Atoll, Indian Ocean. Paratypes: BMNH, AMS, USNM, NM.

ETYMOLOGY. Latin: *sub-*, almost, *vittatus*, longitudinally striped.

? *Litorina intermedia* var. *strigata* Philippi, 1847, vol. 2: 223, *Litorina* pl. 5, fig. 9 [in part; not conspecific with lectotype here designated, p. 290]

Littorina ahenea - Sowerby, 1892: 36; Bartsch, 1915: 120; Turton, 1932: 131 [all not Reeve, 1857]

Littorina borbonica Barnard, 1951: 100, pl. 13, fig. 13 [*nomen nudum*]

Littorina (*Littorinopsis*) *scabra scabra* - Rosewater, 1970: 456-461, pl. 352, figs 20,21 [in part; not Linnaeus, 1758]; Kilburn, 1972: 403 [not Linnaeus, 1758]

NOMENCLATURE. One of the three shells illustrated by Philippi (1847)

as *Litorina intermedia* var. *strigata* resembles this species, although no locality was given. (The designation of a lectotype establishes *L. strigata* (Philippi) as a different species, p. 290). It seems likely that records of '*Littorina ahenea*' from South Africa refer to *L. subvittata*, for Reeve's species was based upon the rather similar colour form of *L. angulifera* with prominent axial stripes on the shell. *L. angulifera* does not occur in South Africa and of the *Littoraria* species found there, only *L. subvittata* bears a resemblance to it. In a popular text book, Barnard (1951) figured *Littorina borbonica* and although only a drawing, there is little doubt that the shell is the species here described. Despite careful search, no other reference to *Littorina borbonica* has been traced. The accompanying text is so brief that the name must be considered a *nomen nudum* until an earlier description is discovered.

DIAGNOSIS. Shell: spire rather tall; peripheral keel usually weak or absent; columella of moderate width, excavated, pinkish brown; primary grooves 10–12; ribs remain low, numbering 40–60 on last whorl; grooves narrow; microsculpture indistinct; colour variable, usually cream with red brown dashes conspicuously aligned to produce axial stripes from suture to base, which number 8–12 on last whorl. Animal: penis bifurcate, filament large and uniformly tapering, sperm groove closed as a duct; ovoviviparous.

SHELL (Fig. 9.30). *Shape*. Height 13–34 mm. Teleoconch 7–9 whorls. Shell of moderate thickness, solid. Spire tall, outline only slightly convex; whorls lightly rounded, sutures distinct. Peripheral keel usually absent, but periphery accentuated by colour pattern; occasional large shells are keeled, but keel becomes obsolete on last whorl. Adult lip hardly thickened, only slightly or not at all flared. Varices 0–2, occasional. Columella of moderate width, excavated; pillar gently convex, pinched at base. Sexual dimorphism: males smaller, relatively lower spire and larger aperture, broader shell.

Dimensions: Table 9.8.

Fig. 9.30 *Littoraria* (*Littorinopsis*) *subvittata*: (a,b) holotype, ♂, Aldabra (BMNH 198346); (c,d) paratypes, Aldabra (BMNH); (e) Port Shepstone, S. Africa (NM); (f) Lake St. Lucia, S. Africa (NM); (g) Mauritius (AMS); (h) Tuléar, Madagascar (AMS); (i) paratype, Aldabra (BMNH).

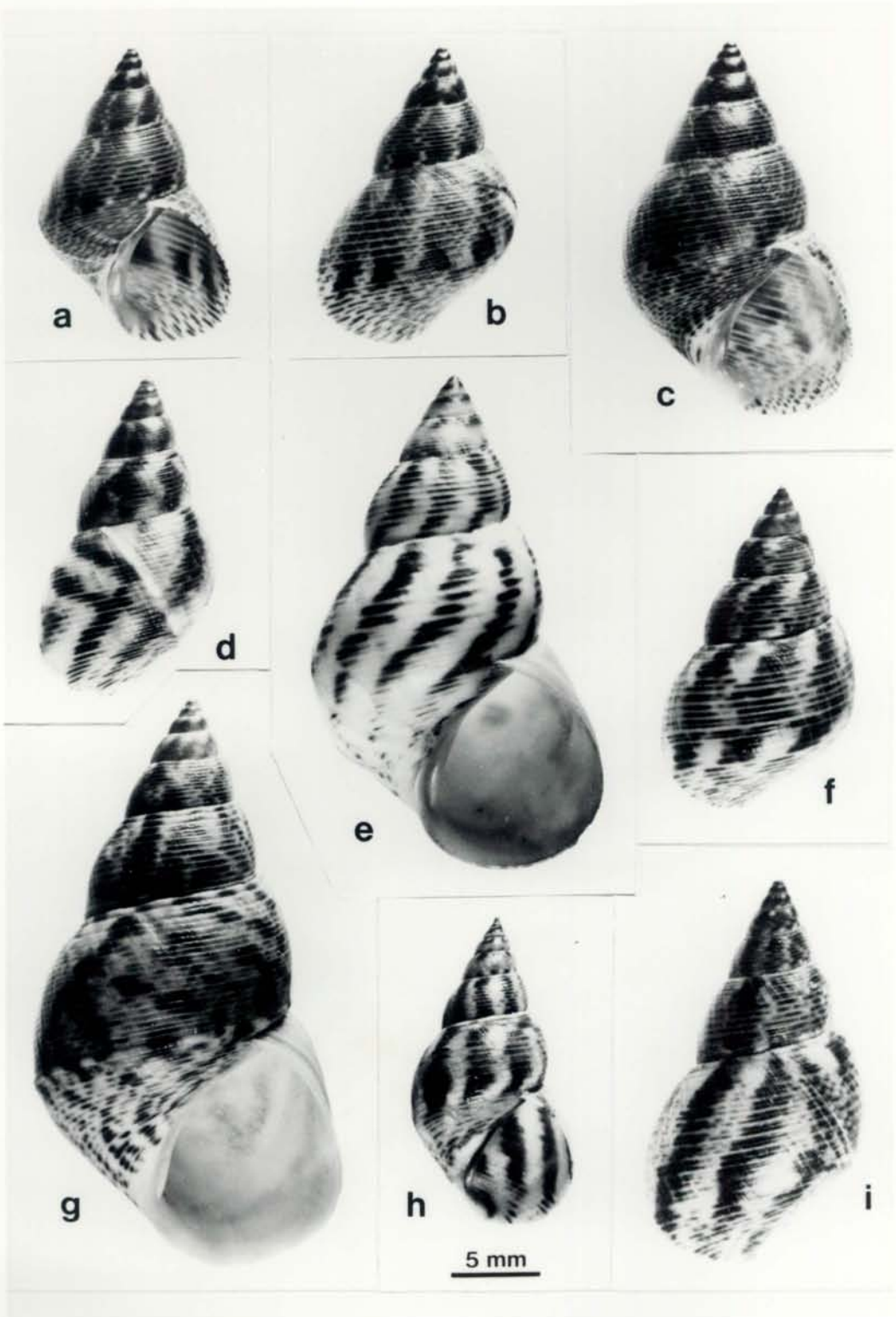

a
b
c
d
e
f
g
h
i
5 mm

Table 9.8 Dimensions of *Littoraria* (*Littorinopsis*) *subvittata*.

Specimen	Locality	Sex	Primary grooves	H (mm)	B (mm)	LA (mm)	WA (mm)	C (mm)	PR	S	SH
L. subvittata holotype, BMNH 198346	Aldabra	♂	11	16.5	11.1	9.4	7.2	1.9	1.49	0.77	1.76
BMNH	Aldabra	♂	10	16.7	10.6	8.5	6.5	1.0	1.58	0.76	1.96
BMNH	Aldabra	♂	11	16.1	9.5	8.3	6.4	1.0	1.69	0.77	1.94
BMNH	Aldabra	♀	11	22.3	12.0	10.1	7.6	1.0	1.86	0.75	2.21
BMNH	Aldabra	♀	10	19.2	10.8	9.0	6.5	1.0	1.78	0.72	2.13
AMS C.43106A	Mauritius		12	32.1	18.1	15.4	11.3	2.4	1.77	0.73	2.08
AMS C.43106A	Mauritius		10	24.3	14.2	12.0	8.9	1.6	1.71	0.74	2.03
AMS C.100070	Tuléar, Madagascar		11	16.9	10.0	8.4	6.4	1.2	1.69	0.76	2.01
AMS C.100070	Tuléar, Madagascar		11	16.6	10.7	9.0	6.6	1.2	1.55	0.73	1.84
AMS C.100070	Tuléar, Madagascar		11	13.8	8.0	6.5	4.7	0.6	1.73	0.72	2.12
BMNH, mean of 10	Aldabra	♂		15.14					1.624	0.728	1.914
standard error				0.41					0.021	0.011	0.018
BMNH, mean of 10	Aldabra	♀		18.49					1.762	0.737	2.119
standard error				0.76					0.028	0.007	0.017
statistic t or U				3.877					90	56	100
probability				0.001					0.002	0.684	<.001

Sculpture (Fig. 9.31a-d). Protoconch normal. First teleoconch whorl smooth. Primary grooves 10-12, equally spaced; posterior 1-2 sometimes deeper. Secondary grooves form on whorl 6, at mid point of each primary rib; ribs at suture and periphery divide later, and consequently may appear more prominent than others on last two whorls. Ribs flat, of equal width, totalling 40-60 on last whorl; all grooves remain as narrow impressed lines. Sculpture becomes almost obsolete after first major varix. Microsculpture of faint axial growth striae over whole surface.

Colour. Variable; ground colour shades of chrome yellow, cream, orange or pale brown, overlain by dark red brown or blackish brown pattern of dashes on ribs. Pattern usually conspicuously aligned to form oblique axial stripes from suture to base, numbering 8-12 on last whorl, although alignment may be less perfect on shoulder and base. Degree of pigmentation variable: dashes may join to form continuous spiral lines; axial stripes may be narrow, and faint or absent below periphery, but shells never lack pigment entirely. Pattern frequently reduced or absent after first varix. External pattern visible within aperture. Columella usually pinkish brown, seldom white.

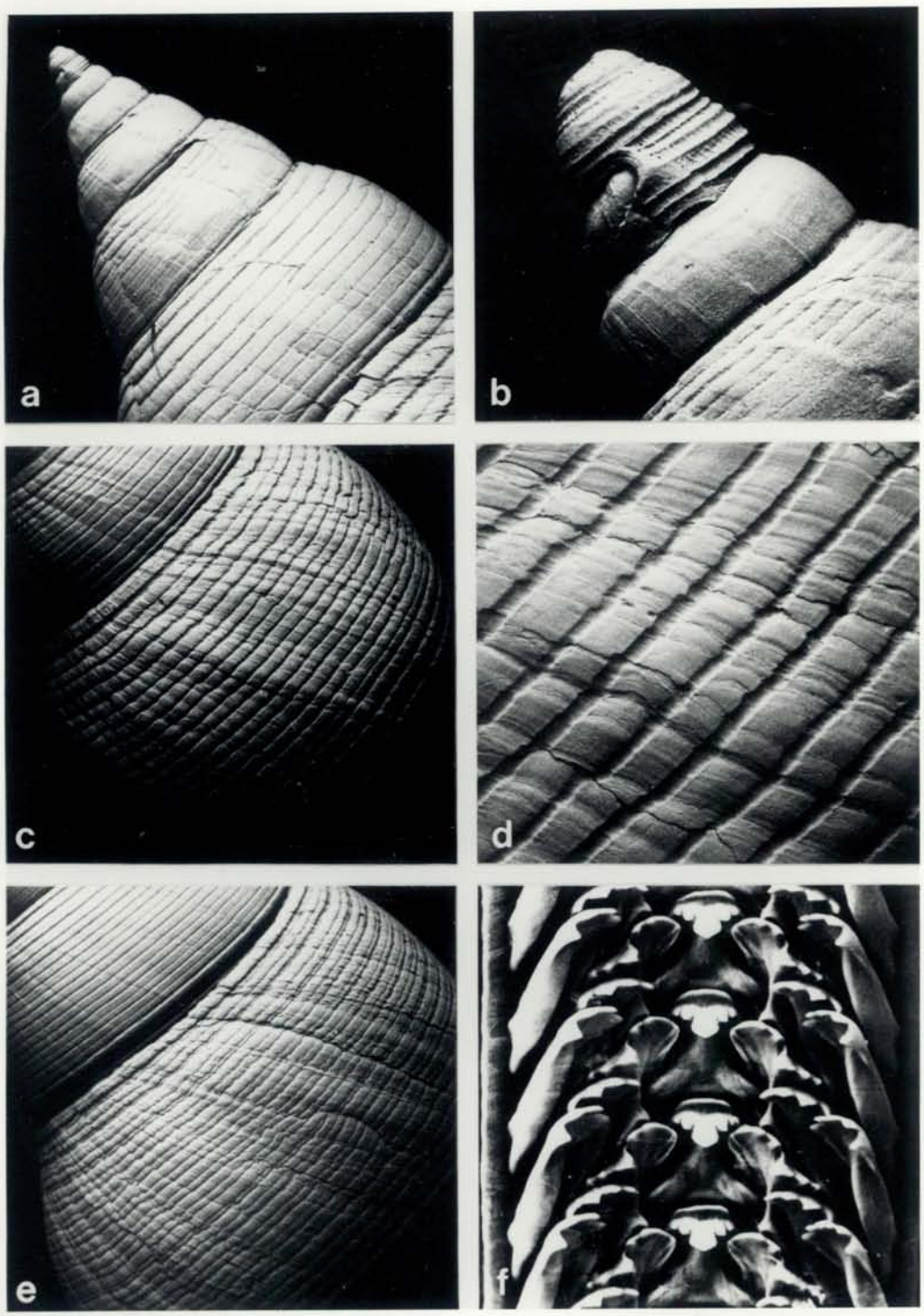
ANIMAL. *Colour*. Pigmentation grey to black; sides of foot pale mottled to dark grey; head darkest, sometimes with pale central streak; tentacles banded, unpigmented stripe each side of base.

Penis (Fig. 9.32a-g). Length to 7.5 mm. Base bifurcate; limb bearing glandular disc short; disc rather irregular. Filament long, uniformly tapering. Sperm groove closed as a duct. Base and filament off white or cream, glandular disc cream to pale brown.

Sperm. Nurse cells (Fig. 9.32l,m) 8-10(15) μm; rounded to oval; no rods visible; yolk granules large.

Pallial oviduct (Fig. 9.32h-k). Length to 3.0 mm. Spiral section to 1.9 mm diam., $2\frac{1}{2}$ whorls; opaque albumen gland $\frac{1}{3}$ whorl, not

Fig. 9.31 (a–d) *Littoraria (Littorinopsis) subvittata*, Aldabra: (a) spire (×18); (b) protoconch (×80); (c) last whorl (×8); (d) detail (×34). (e) *Littoraria (Littorinopsis) angulifera*, Sanibel I., Florida, last whorl (×7). (f) *Littoraria (Littorinopsis) subvittata*, Aldabra, radula (×250).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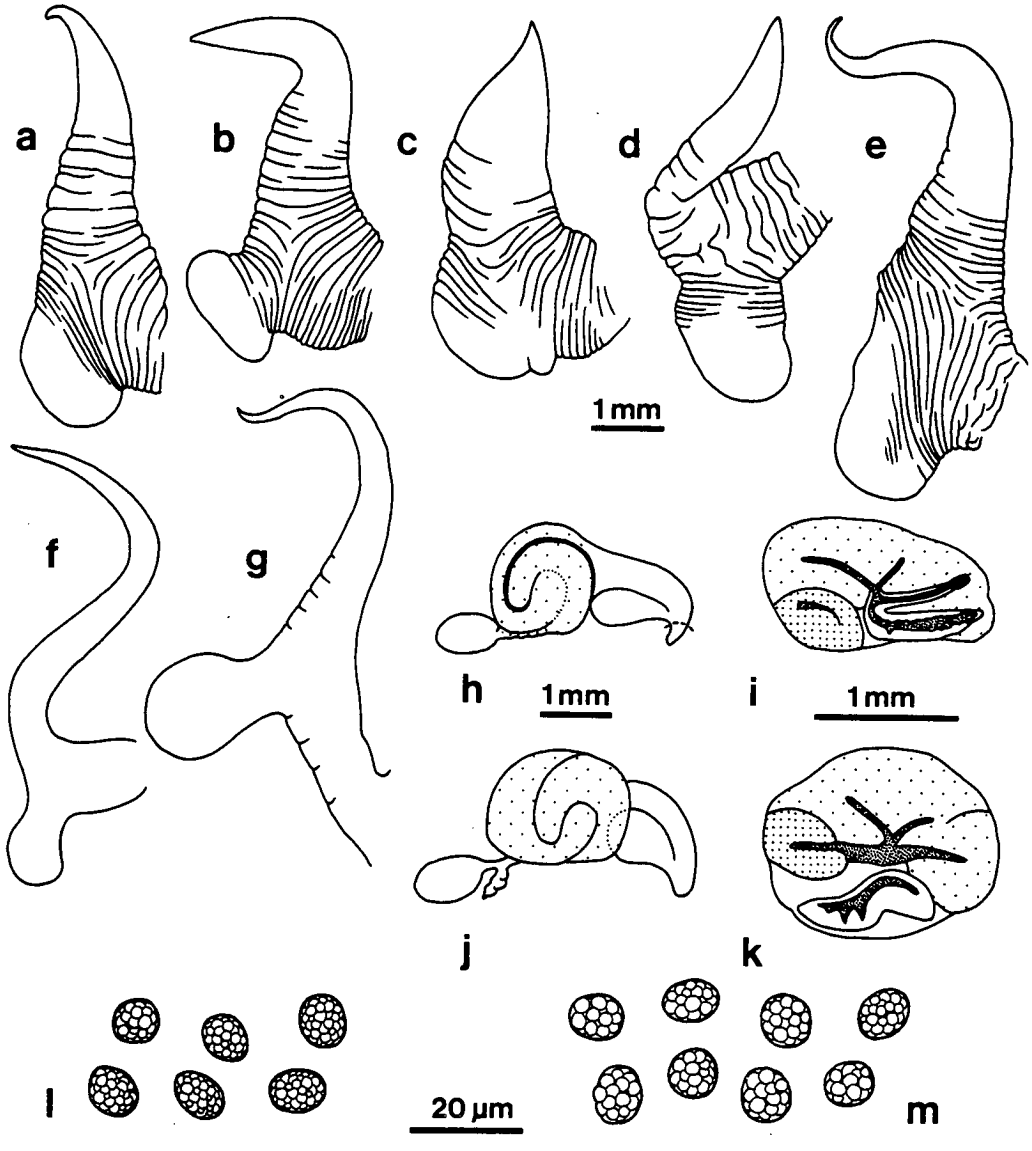

Fig. 9.32 *Littoraria* (*Littorinopsis*) *subvittata*: (a–g) penes; (a–d) Aldabra; (e) Buffalo Harbour, S. Africa; (f,g) Nxaxo R., S. Africa; (h–k) pallial oviducts, with transverse sections, Aldabra; (l,m) sperm nurse cells, Aldabra.

visible externally, white; translucent albumen gland off white; capsule glands absent; spiral distinct externally, especially if egg groove is pigmented. Straight section to 1.3 mm, pale; terminating in a papilla. Bursa to 1.1 mm, anterior. Development ovoviviparous.

Radula (Fig. 9.31f). Length to 19 mm; relative length 0.82–0.89. Saw-toothed type; central rachidian cusp rather elongate and pointed; cusps of paired teeth almost equilaterally triangular; lateral with gap anterior to main cusp.

DISTRIBUTION. *Habitat*. Mangroves, marsh grass, wooden pilings and sheltered rocks. Probably an oceanic species.

Range (Fig. 9.33). Indian Ocean, from Aden to eastern Cape Province, South Africa, and east to Mauritius, Maldive Is. and Cocos-Keeling Is.

Records. SOUTH AFRICA: Zwartkops R. mouth, Algoa Bay (NM); Port Alfred (BMNH, AMS, MCZ); Gonubie R. mouth, East London (ANSP); Umtata R. mouth (NM); Port St. Johns (DGR); Nxaxo R. mouth (ANSP); Port Shepstone (NM); Durban Bay (BMNH, WAM, NM, RNHL); St. Lucia, Zululand (NMW, NM); MOZAMBIQUE: Lourenço Marques (DGR); Inhaca I., Delagoa Bay (NM); Lunga Bay to Memba Bay (NM); Ilha do Ibo (AMS); TANZANIA: Bagamoyo (MCZ); Chukwani, Zanzibar (ANSP); Tanga (BMNH, MCZ); KENYA: Gazi (NMW); Mombasa (BMNH); Mkunumbi (BMNH); SOMALIA: Mogadisho (MCZ); YEMEN: Aden (BMNH); MADAGASCAR: Tuléar (AMS, MCZ); Ile Ste. Marie (MCZ); Nossi Bé (ANSP); ALDABRA ATOLL (BMNH); SEYCHELLES: Menai I., Cosmoledo Atoll (USNM); St. Joseph I., Amirante Is. (BMNH); MAURITIUS (BMNH, AMS, MCZ); Camisard R. mouth (ANSP); MALDIVE IS.: Male Harbour (ANSP); COCOS-KEELING IS.: S.E. side of North Lagoon, West I. (ANSP).

REMARKS. It is surprising that such a common, widely distributed and fairly distinctive species should have remained unrecognized. It is sympatric with *L. scabra*, *L. intermedia* and *L. pallescens* over most of its range, and has perhaps been confused with *L. scabra* in the

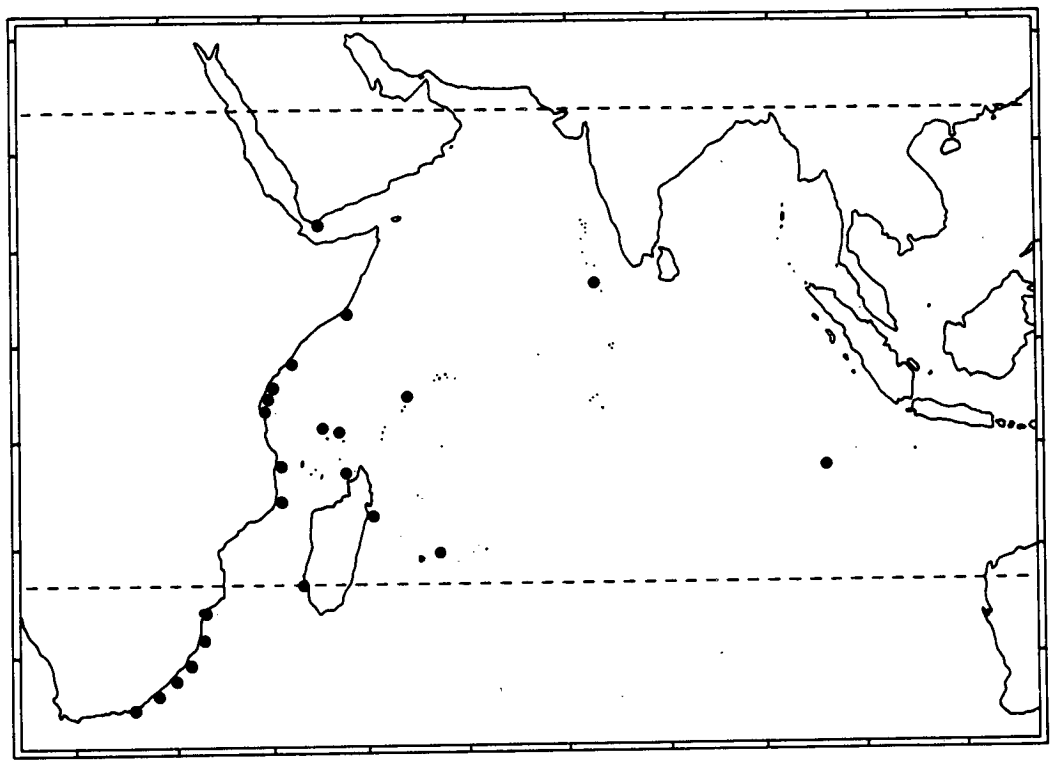

Fig. 9.33 Distribution of *Littoraria (Littorinopsis) subvittata*.

early faunistic lists for this region (e.g. von Martens, 1880; Smith, 1906; Dautzenberg, 1923, 1929; Viader, 1937). *L. subvittata* is in most respects rather constant over its range, although size varies considerably. The sperm nurse cells illustrated (Fig. 9.32l,m) are unusually small for the genus; these were drawn from material preserved in formalin and it is not known if they are typical.

SIMILAR SPECIES. Large specimens of *L. subvittata* can be confused with *L. scabra*, but are distinguished by their higher spire, more numerous ribs on the last whorl, narrower grooves which lack microsculpture, brown columella and by penial characters. Most specimens of *L. intermedia* have fewer ribs on the last whorl, but rarely east African shells may approach small specimens of *L. subvittata* and penial characters must then be used for separation. The excavated columella and closed penial groove distinguish *L. subvittata* from *L. ardouiniana*. *L. angulifera* from the tropical Atlantic (Figs 5.2o, 9.31e, 9.81d–f) shows more numerous ribs on the last whorl, a wide and usually lilac columella, lower spire and a penis with an open sperm groove and larger filament.

9.2.3.7 *Littoraria* (*Littorinopsis*) *filosa* (Sowerby, 1832)

Littorina filosa Sowerby, 1832: *Littorina* fig. 5 ['S. America' in error, here corrected to E. coast of Queensland, Australia; lectotype figure here designated]; Mitchell, 1838: pl. 2, fig. 5; Reeve, 1857: *Littorina* pl. 5, figs 24 a–c; Nevill, 1885: 148 [in part]

Littorina filosa – Philippi, 1848, vol. 3: 61, *Littorina* pl. 7, figs 1,2 [not pl. 6, fig. 4, corrected to *Littorina pallescens* in index]; Weinkauff, 1882: 57–58, pl. 7, figs 10,11

Littorina (*Melaraphe*) *scabra* var. *filosa* – Tryon, 1887: 244, pl. 43, figs 31, 31a [in part]

Littorina (Littorinopsis) carinifera - von Martens, 1897: 198 [in part; not Menke, 1830]

Littorina (Littoraria) luteola - Shikama & Horikoshi, 1963: pl. 16, fig. 7 [not Quoy & Gaimard, 1832]

Littorina (Littorinopsis) scabra scabra - Rosewater, 1970: 456-461, pl. 325, fig. 3, pl. 352, figs 22,23,33,34 [in part; not Linnaeus, 1758]

Littorina scabra - Wilson & Gillett, 1979: 52, pl. 8, fig. 5c [in part; not Linnaeus, 1758]

NOMENCLATURE. The name '*filosa*' is not uncommon in the older literature, but does not seem to have been correctly applied since 1882. Since then it has sometimes been used for other brightly coloured or carinate species, especially *L. pallescens*. Sowerby's figure leaves no doubt as to the identity of the species, for the elongate outline and strong carinae are unique in the family. The locality was erroneously given as 'S. America'. However, Mitchell (1838: 15) reported that a collection of 'fossil shells from the basin of the Hunter, &c' made in 1831 was sent to Sowerby for description, and listed '*Turbo filosa* Sowerby (new species)', while figuring an apparently recent shell as '*Littorina filosa*'. The specimens were stated to have been deposited in the Australian Museum, Sydney. It seems likely that this was the origin of Sowerby's shell, but no type specimen could be located in the AMS or BMNH. The locality given by Mitchell seems to apply to the small collection of fossils; it is unlikely that the shell could have originated near the Hunter River (Newcastle, N.S.W.) since only one specimen has been recorded from the state. The type locality has therefore been corrected to eastern Queensland.

DIAGNOSIS. Shell: thin; columella narrow, rounded; primary grooves 5-7(9), spacing markedly unequal, increasing anteriorly; last whorl with 9-11 strong, narrow carinae, the spaces between with numerous irregularly spaced spiral grooves; colour highly polymorphic, brown, yellow or orange pink, with or without pattern of brown dashes aligned at suture to form short stripes, numbering 10-12 on last

whorl. Animal: penis bifurcate, filament large, narrowing only at tip; ovoviviparous.

SHELL (Fig. 9.34). *Shape*. Height 16–35 mm. Teleoconch 7–8 whorls. Shell thin, translucent. Spire outline only slightly convex; whorls rounded; sutures distinct. Peripheral keel conspicuous until whorl 7, last whorl more uniformly rounded, but strongly carinate. Adult lip thin, slightly flared. Varices 0–2(4), not common. Columella narrow, rounded, not excavated; pillar straight to slightly convex. Sexual dimorphism: not significant; males tend to be a little smaller, adult lip is more strongly flared and varices correspondingly more frequent.

Dimensions: Table 9.9.

Sculpture (Fig. 9.35c,e,f). Protoconch normal. First two whorls of teleoconch smooth. Primary grooves 5–7; spacing unequal, showing 3- or 4-fold increase from suture to periphery; primary grooves remain as narrow, incised lines. Secondary sculpture develops on whorls 5–6, grooves appearing at anterior $\frac{1}{4}$–$\frac{1}{2}$ rib width. Tertiary and higher orders of grooves develop in same manner on primary and secondary ribs of whorls 6 and later. On whorls 7–8 each primary rib becomes a strong, narrow carina, numbering 9–11 in total; peripheral carina most prominent; spacing between carinae up to 5 times carina width, widest near periphery. Secondary ribs do not usually become carinate. Microsculpture: carinae smooth; spaces between with 2–4 flat secondary and tertiary ribs, between which run irregular fine spiral striae. Entire surface between carinae crossed by fine axial growth striae, which may give a microscopically decussate or pitted pattern where they cross the spiral microsculpture. Specimens from northern W.A., and some from the Lesser Sunda Is., differ from the foregoing description as follows: primary grooves 7–9, spacing subequal, only a 2-fold increase towards the periphery; total number of primary ribs on last whorl 12–15, of which usually only that at periphery is sufficiently developed to be termed carinate.

Fig. 9.34 *Littoraria* (*Littorinopsis*) *filosa*: (a) ♀, Broome, W.A. (DGR); (b) ♂, Thursday I., Qld. (DGR); (c) Weipa, Qld. (BMNH); (d) ♂, Broome, W.A. (DGR); (e) ♀, Gove, N.T. (DGR); (f) ♀, Magnetic I., Qld. (DGR); (g) lectotype figure of *Littorina filosa* Sowerby, locality unknown (Sowerby, 1832, *Littorina* fig. 5); (h) ♀, Moa I., Qld. (DGR); (i) ♀, Gove, N.T. (DGR).

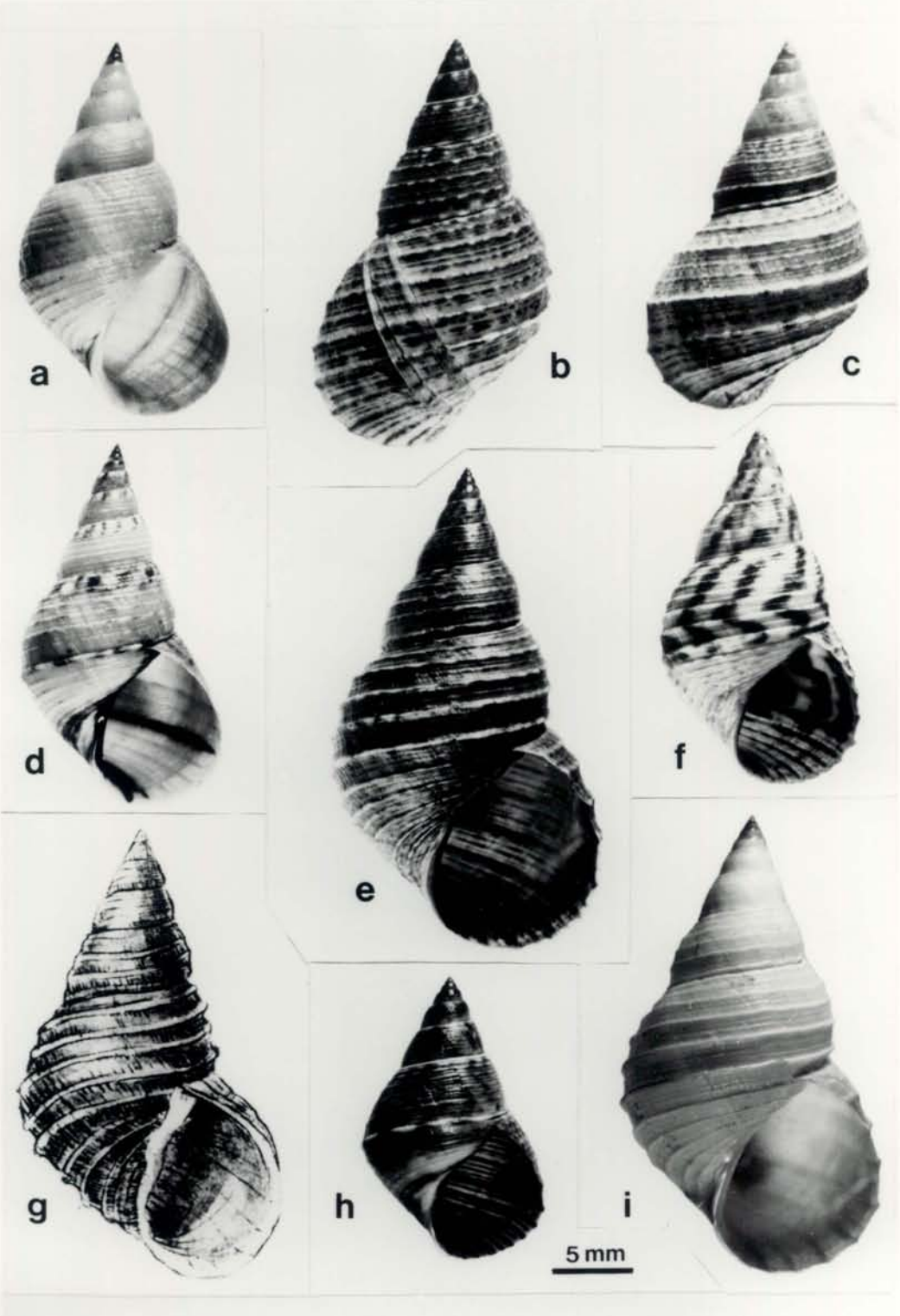
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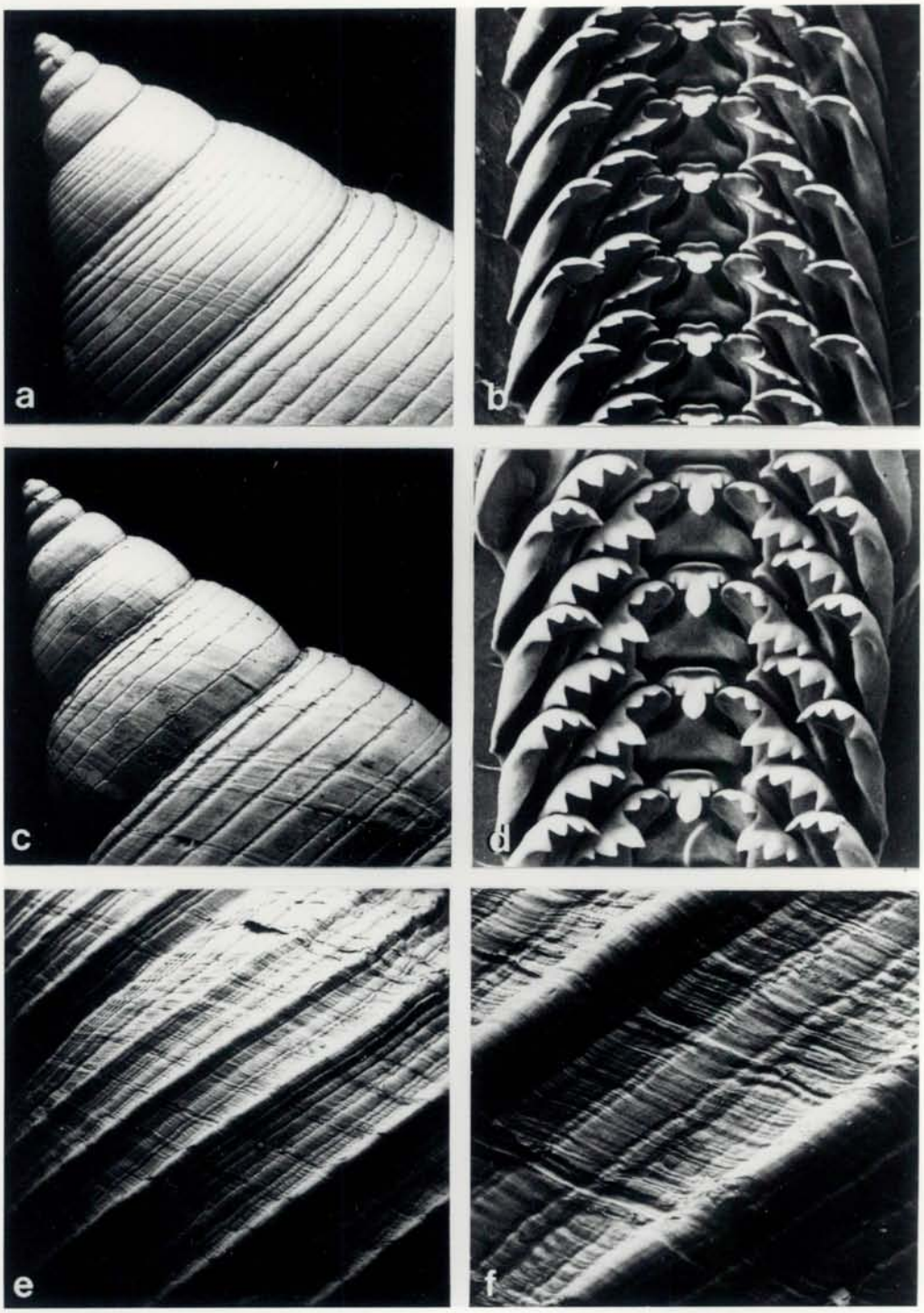
Table 9.9 Dimensions of *Littoraria* (*Littorinopsis*) *filosa*.

Specimen	Locality	Sex	Primary grooves	H (mm)	B (mm)	LA (mm)	WA (mm)	C (mm)	PR	S	SH
Littorina filosa lectotype figure (Sowerby, 1832)	[eastern Qld.]			27.8	16.5	12.0	9.0		1.68	0.75	2.32
DGR	Thursday I., Qld.	♂	7	29.0	18.0	15.9	11.7	1.6	1.61	0.74	1.82
DGR	Thursday I., Qld.	♀	5	34.6	21.9	17.5	13.0	1.9	1.58	0.74	1.98
DGR	Magnetic I., Qld.	♂	6	23.6	13.8	11.9	8.8	1.0	1.71	0.74	1.98
DGR	Magnetic I., Qld.	♀	6	26.5	16.0	13.1	10.3	1.3	1.66	0.79	2.02
DGR	Darwin, N.T.	♂	5	24.2	14.9	12.8	9.9	1.2	1.62	0.77	1.89
DGR	Darwin, N.T.	♀	5	24.1	16.0	12.8	9.2	1.2	1.51	0.72	1.88
DGR	Broome, W.A.	♂	8	23.3	13.8	12.6	9.3	1.4	1.69	0.74	1.85
DGR	Broome, W.A.	♀	8	27.5	15.7	13.3	9.5	1.4	1.75	0.71	2.07
DGR, mean of 10	Darwin, N.T.	♂		24.60					1.614	0.762	1.939
standard error				0.37					0.016	0.007	0.013
DGR, mean of 10	Darwin, N.T.	♀		25.20					1.580	0.759	1.978
standard error				0.36					0.015	0.007	0.023
statistic t or U				1.167					69	54	64.5
probability				0.259					0.166	0.796	0.297

Fig. 9.35 (a,b) *Littoraria* (*Littorinopsis*) *pallescens*: (a) spire (×17), Phuket I., Thailand; (b) radula (×200), Gove, N.T. (c-f) *Littoraria* (*Littorinopsis*) *filosa*, Magnetic I., Qld.: (c) spire (×20); (d) radula (×230); (e) last whorl (×8); (f) detail (×32).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Colour. Polymorphic; yellow and shades of brown most frequent, pink shells not uncommon. Ground colour chrome yellow, brown or orange pink. Apical 3 whorls with dark brown suture. Pattern dark brown, fading to lilac grey in large, old shells. Shells with sparse pattern: brown dashes confined to primary and secondary ribs, axially aligned near suture to form short stripes, numbering 10–12 on last whorl; base pale but for dark band around columella. Dark shells: entire surface may be suffused or marbled with brown, occasionally alignment of dashes is complete, producing oblique stripes from suture to base. Pink and yellow shells commonly lack brown patterning and may fade almost to white. In all shells carinae are composed of more opaque material, appearing paler than rest of surface. Brown pattern visible within aperture. Columella white in shells lacking pattern, otherwise purple or pinkish brown. Shells from northern W.A. frequently show dark pigment only near sutures, on peripheral keel, and in a band around the columella (a pattern rare elsewhere), columella and parietal callus almost always very dark purple brown, spiral white stripe at base of pillar, outlined by narrow purple band within aperture; only in those few yellow or pink shells lacking dark pigment are the columella and callus white.

ANIMAL. *Colour*. Pigmentation correlated with shell colour, from unpigmented to dark grey or black; sides of foot may be pale grey mottled; head darkest; tentacles may be banded, white stripe on each side of base. Unpigmented animals cream, red buccal mass.

Penis (Fig. 9.36a–f). Length to 12 mm. Base bifurcate; limb bearing glandular disc not long. Filament large, narrowing only near slightly mucronate tip. Sperm groove open. Base and filament off white; glandular disc opaque white or cream.

Sperm. Eupyrene sperm 100–120 μm. Nurse cells (Fig. 9.36j–l) 12–20 μm; oval; rods 1(2), central, not or scarcely projecting, parallel sided, ends rounded; yolk granules moderately large. (Rarely, abnormal individuals may have rounded nurse cells lacking rods, or with small, rounded rod pieces).

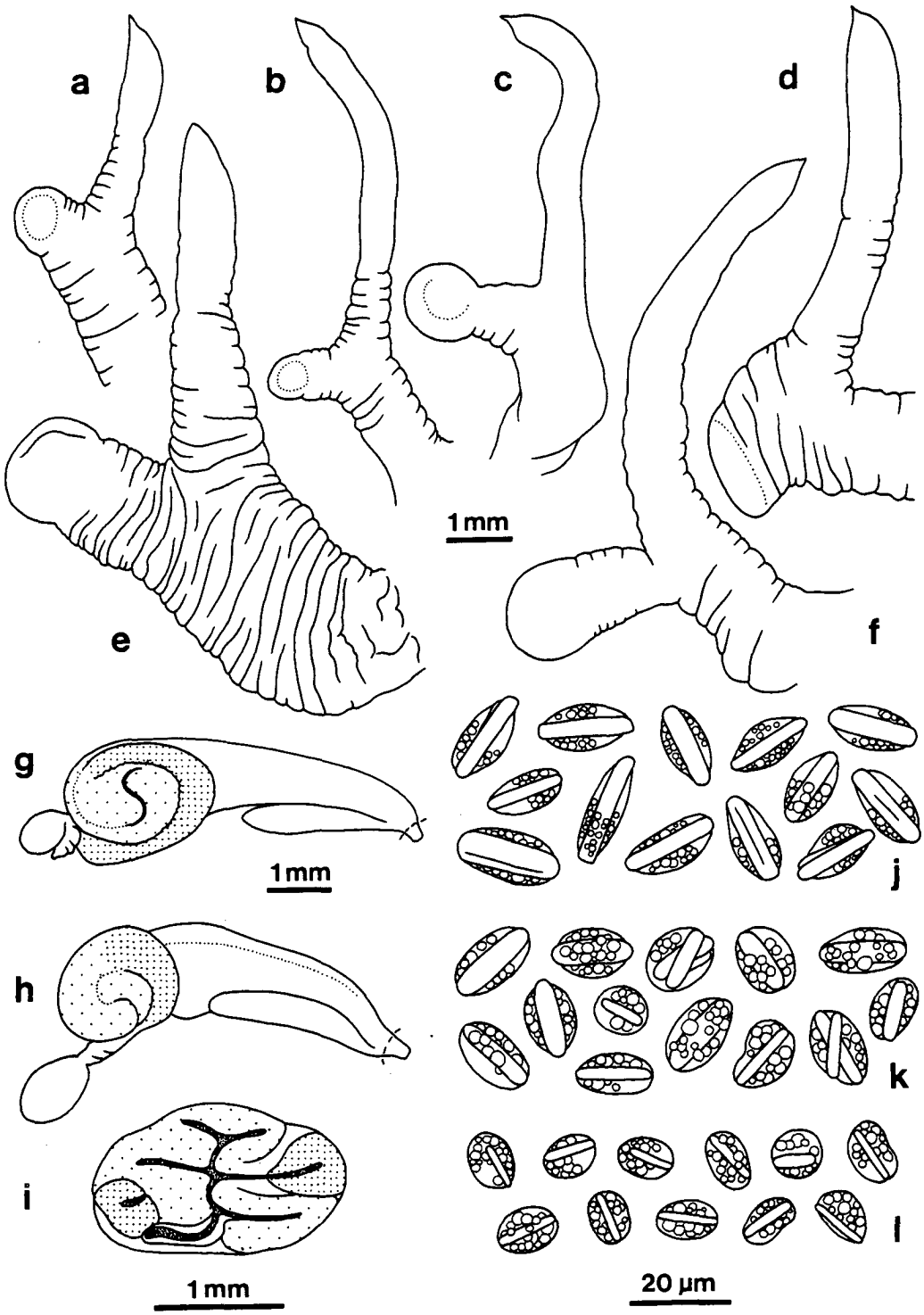


Fig. 9.36 *Littoraria* (*Littorinopsis*) *filosa*: (a-f) penes; (a) Broome, W.A.; (b-d) Magnetic I., Qld.; (e) Broome, W.A.; (f) Magnetic I., Qld.; (g-i) pallial oviducts, with transverse section; (g) Darwin, N.T.; (h,i) Gove, N.T.; (j-l) sperm nurse cells; (j) Broome, W.A.; (k,l) Magnetic I., Qld.

Pallial oviduct (Fig. 9.36g–i). Length to 5.3 mm. Spiral section to 2.4 mm diam., $3\frac{1}{2}$ whorls; opaque albumen gland $\frac{1}{2}\frac{2}{3}$ whorl, white or cream; translucent albumen gland off white to pale brown; capsule glands absent; spiral indistinct externally; egg groove not usually darkly pigmented. Straight section relatively long, to 3.6 mm; off white to fawn; terminating in a papilla. Bursa long, to 2.6 mm, anterior. Development ovoviviparous.

Radula (Fig. 9.35d). Length to 17 mm; relative length 0.58–0.98. Saw-toothed type; central rachidian cusp elongate and pointed; cusps of paired teeth equilaterally triangular; lateral with slight gap anterior to main cusp.

DISTRIBUTION. *Habitat*. *Avicennia* fringe, especially on leaves, but also on trunks, 0.2–3.0 m above ground; usually scarce on leaves and trunks in *Rhizophora* forest; occasional in *Ceriops* zone; also on *Aegialitis*. A continental species.

Range (Fig. 9.37). From Botany Bay, N.S.W., around east and north coasts of Australia, to Exmouth Gulf, W.A.; south coast Papua New Guinea; Lesser Sunda Is. (Nineteenth Century material from Philippines and Solomon Is. almost certainly incorrectly localized).

Records. INDONESIA: LESSER SUNDA IS.: Bali (AMS); Bolang, S.W. Timor (RNHL); IRIAN JAYA: Merauke (AMS, RNHL); PAPUA NEW GUINEA: Oriomo R. (MCZ); Port Moresby (AMS); AUSTRALIA: W.A.: Bay of Rest, Exmouth Gulf (WAM); Barrow I. (WAM); Monte Bello Is. (WAM); 10 km W. of Cape Preston (WAM); Broome (DGR, AMS, WAM, NMV); Cape Leveque (WAM, NMV); Port Warrender, Admiralty Gulf (WAM); Troughton I. (BMNH); Vansittart Bay (AMS); Napier Broome Bay (WAM); N.T.: Grose I. (AMS); Ludmilla Creek, Darwin (DGR); Cape Gambier, Melville I. (AMS); Boucaut Bay (AMS); Glyde R., Arnhemland (AMS); Nhulunbuy, Gove Pen. (DGR); Groote Eylandt (AMS); QLD: Karumba (AMS); Thursday I. (DGR, QM); Moa I. (DGR); Murray Is. (AMS); Claremont Is. (QM); Cooktown (AMS); Port Douglas (AMS); Dunk I. (AMS, QM); Magnetic I. (DGR); Bowen (AMS, NMV); Hayman I. (AMS); Sarina (AMS); Yeppoon

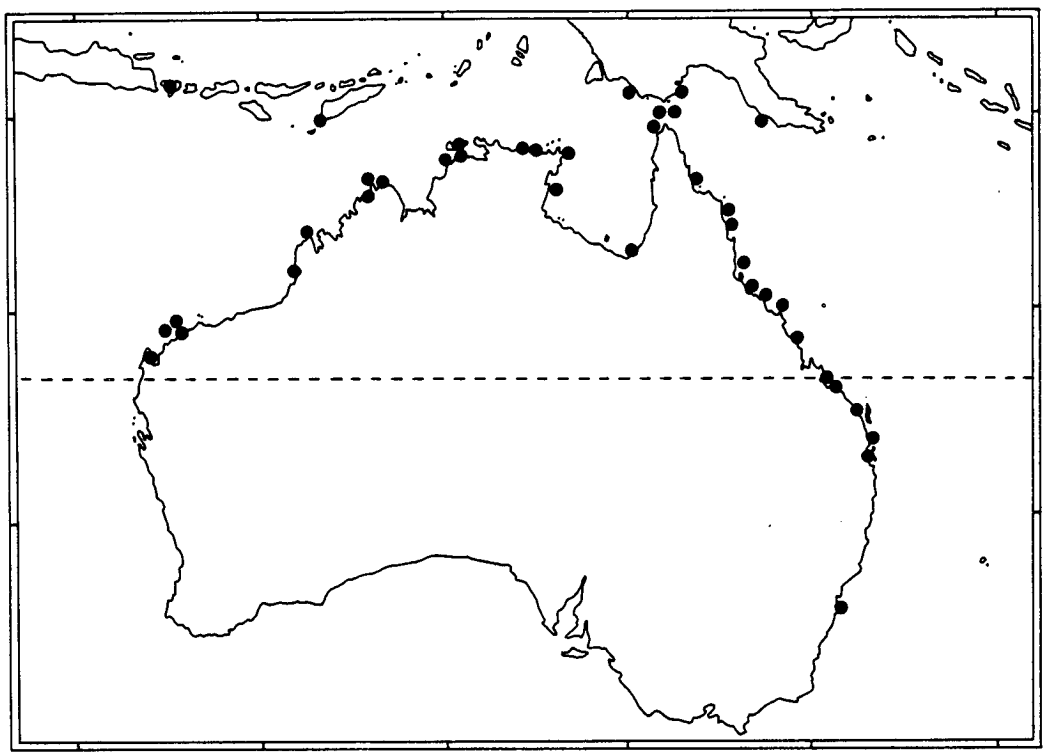


Fig. 9.37 Distribution of *Littoraria* (*Littorinopsis*) *filosa*.

(AMS, NMV); Port Curtis (AMS); Pialba (QM); Maroochydore (AMS); Wellington Point, Moreton Bay (QM); N.S.W.: Kurnell Pen. (DGR).

REMARKS. Of all *Littoraria* species, *L. filosa* exhibits the most striking colour polymorphism. The proportions of colour morphs show some variation both with habitat and geographical area, but all populations are highly polymorphic. There is little variation in shell shape on the east coast of Australia, but in the Torres Strait, Northern Territory and Papua New Guinea the shells are of large size, rather broad and solid. In this region many of the yellow and pink shells are speckled with brown pigment, whereas entirely unpigmented yellow and pink shells are common elsewhere. The most characteristic geographical form (Fig. 9.34a,d) occurs from Cape Leveque to Exmouth Gulf, W.A., and also in Timor, and is described above. Collections from the Admiralty Gulf, W.A., and further north and east, are normal. The differences in sculpture and colouration are not considered sufficient to warrant taxonomic recognition, since anatomical features remain constant, and occasional carinate shells occur in this region of north-western Australia, while rather smooth shells are occasionally found elsewhere.

From Moreton Bay southwards *L. filosa* appears to be replaced as the dominant species on *Avicennia* leaves by *L. luteola*, while to the north of Australia *L. pallescens* takes over the habitat.

SIMILAR SPECIES. The typical carinate form may be confused with *L. philippiana* and *L. pallescens*, but is distinguished by its narrow, rounded columella and by the smaller number and unequal spacing of the primary ribs. *L. filosa* and *L. cingulata* are separated by the form of the primary, secondary and microsculpture, by colour and by penial characters. *L. luteola* is superficially similar, but again sculptural details are diagnostic.

9.2.3.8 *Littoraria* (*Littorinopsis*) *cingulata cingulata* (Philippi, 1846)

Littorina cingulata Philippi, 1846: 142 [north coast of Australia; lectotype (Rosewater, 1970) BMNH 1968352]; Reeve, 1857: *Littorina* pl. 6, fig. 25

Littorina cingulata – Philippi, 1847, vol. 3: 11–12, *Litorina* pl. 6, fig. 5; Weinkauff, 1882: 58, pl. 7, fig. 13

Littorina filosa – Nevill, 1885: 148 [in part; not Sowerby, 1832]

Littorina (*Melaraphe*) *scabra* var. *filosa* – Tryon, 1887: 244, pl. 42, fig. 29 [in part; not Sowerby, 1832]

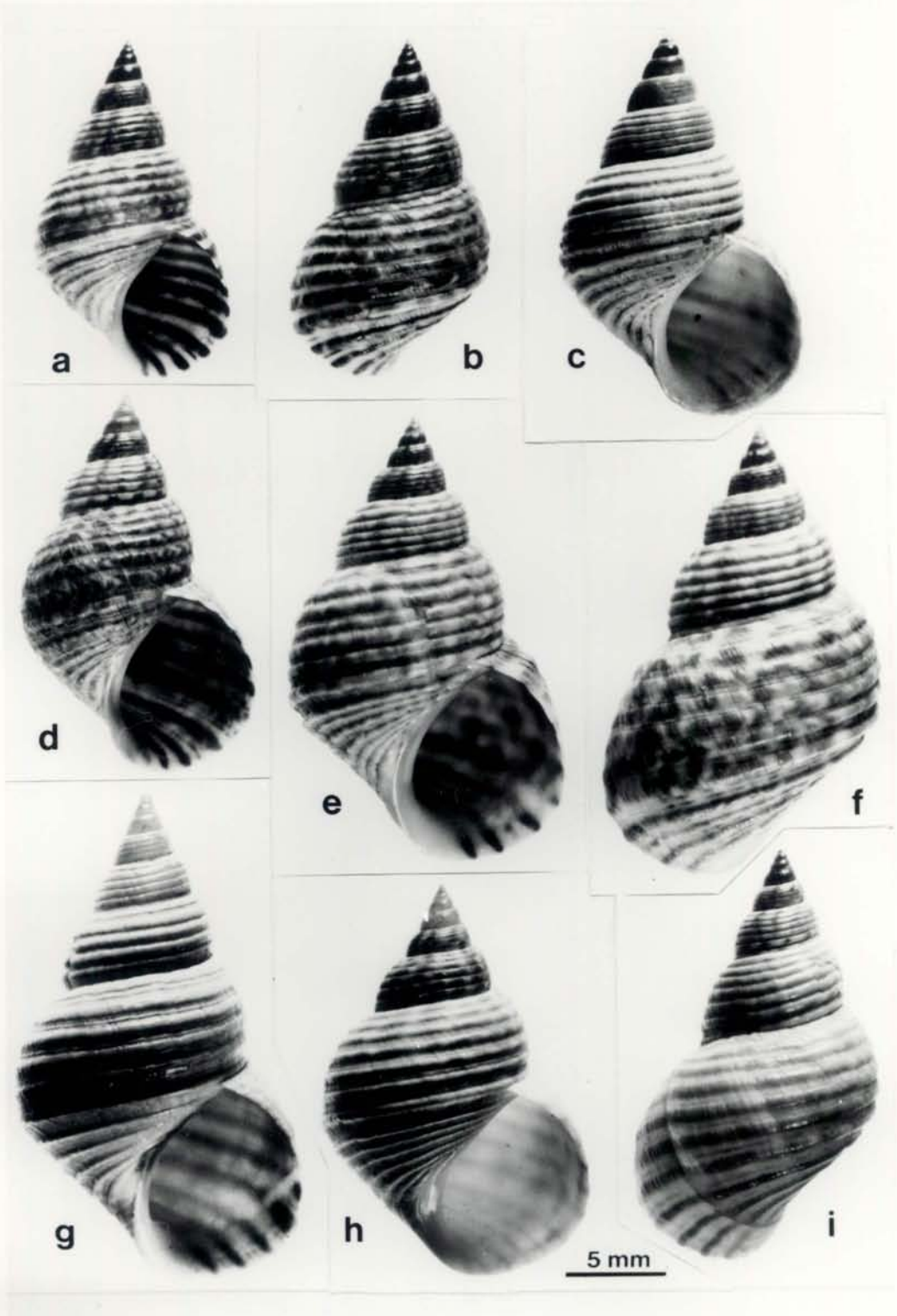
Littorina (*Littorinopsis*) *scabra scabra* – Rosewater, 1970: 456–461, pl. 352, figs 7,26,27,30 [in part; not Linnaeus, 1758]

NOMENCLATURE. The species was described and later figured by Philippi from specimens in the Cuming Collection; the lectotype designated by Rosewater (1970) is the figured specimen.

DIAGNOSIS. Shell: columella rounded, usually purplish; primary grooves 5–6, primary ribs rounded and prominent, 11–13 on last whorl, separated by grooves $\frac{1}{2}$–1 times rib width; secondary sculpture of minor riblets on last whorl only; microsculpture of regular spiral striae in grooves; colour cream with marbled pattern of orange brown on ribs, apical whorls often blue grey. Animal: penis bifurcate, base thick, filament fairly short and tapering; ovoviviparous.

SHELL (Fig. 9.38). *Shape*. Height 13–25 mm. Teleoconch 7.5–8.5 whorls. Shell thick, solid. Spire outline straight; whorls rounded; sutures impressed. Peripheral keel marked by largest rib in young shells, becoming less conspicuous on last whorl. Adult lip slightly thickened and flared. Varices unusual, 0–2. Columella of moderate width, rounded; sometimes very slightly excavated in largest shells; pillar gently concave. Sexual dimorphism: males smaller, with relatively lower spire and larger aperture, adult lip a little more

Fig. 9.38 *Littoraria (Littorinopsis) cingulata cingulata*: (a,b) ♂, Broome, W.A. (DGR); (c) lectotype of *Littorina cingulata* Philippi, N. Australia (BMNH 1968352); (d–f) Broome, W.A. (DGR); (d) ♂; (e,f) ♀; (g) Cape Leveque, W.A. (NMV); (h) Broome, W.A. (NMV); (i) Sunday I., W.A. (WAM).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flared.

Dimensions: Table 9.10.

Sculpture (Fig. 9.39a,c,d). Protoconch normal. First two whorls of teleoconch smooth. Primary grooves 5-6(7); spacing almost equal, posterior 1 or 2 ribs may be a little narrower. Secondary sculpture confined to whorl 8, where 1-3 riblets develop in each primary groove, and primary ribs may become divided by single narrow grooves. Primary ribs rounded and prominent, largest at periphery, 11-13 in total on last whorl, spacing between is $\frac{1}{2}$-1 times rib width. Secondary ribs and grooves remain narrow and inconspicuous. Microsculpture: primary ribs smooth but for faint axial growth striae; regular spiral striae confined to grooves.

Colour. Rather constant. Ground colour whitish, cream or blue grey. First 6 whorls often conspicuously blue grey, with ribs whitish, especially at sutures. Irregular marbled pattern of orange brown or dark brown confined to ribs; pattern sometimes faint and ribs unicolorous orange brown; sometimes aligned to form axial stripes, especially on spire. Aperture with purple brown lines or dashes corresponding to ribs of body whorl, darkest at margin, glazed with whitish, pale pink or cream callus within. Columella dark purple, pale lilac pink, or sometimes white. Parietal callus often conspicuously purple, especially at posterior limit of aperture.

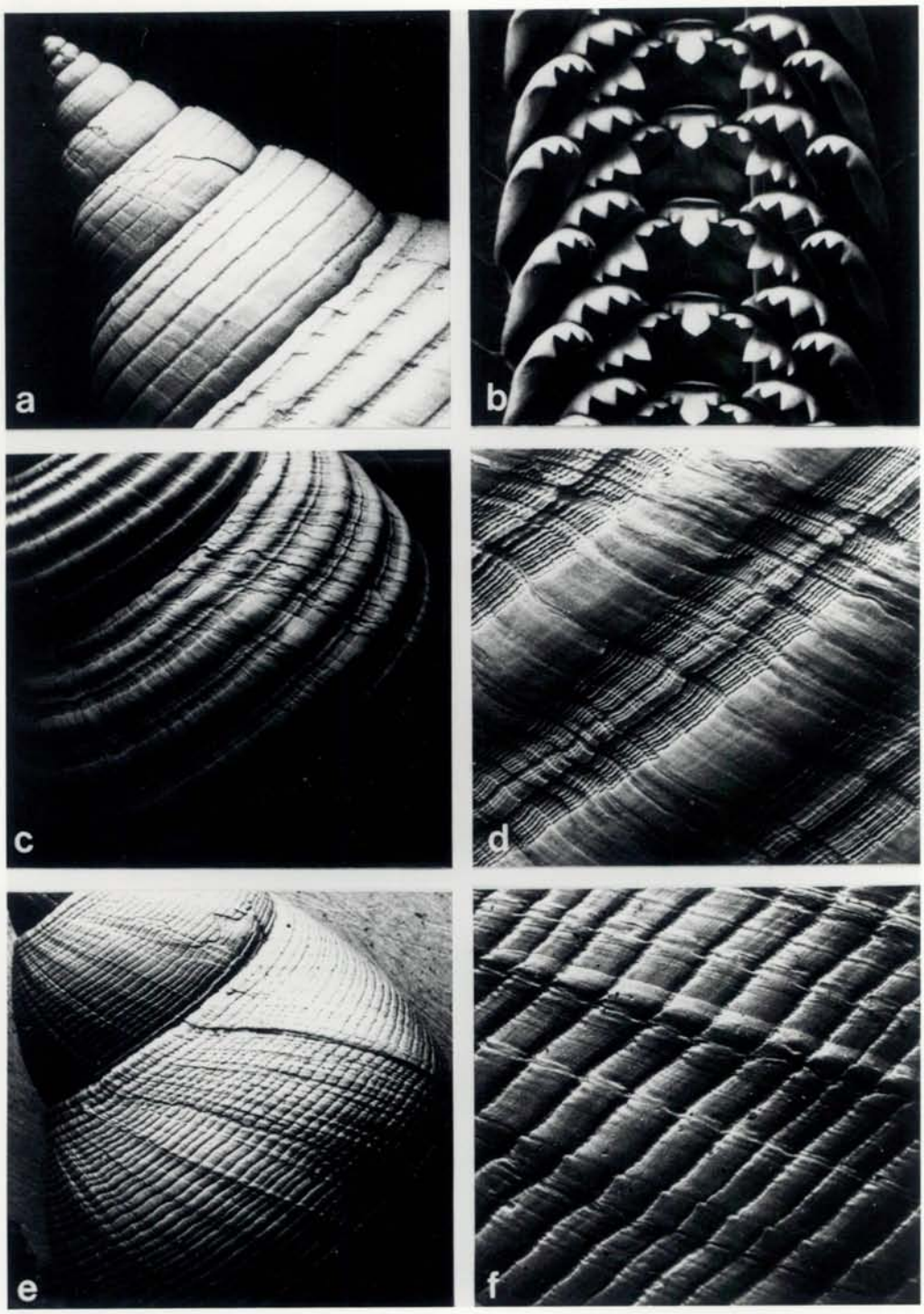
ANIMAL. *Colour*. Pigmentation pale grey to black; sides of foot pale mottled; head darkest, sometimes with pale central streak; tentacles banded, unpigmented stripe each side of base.

Penis (Fig. 9.40a-e). Length to 6.0 mm. Base thick, bifurcate; limb bearing glandular disc usually short. Filament fairly short, tapering. Sperm groove open. Base fawn, filament cream, glandular disc pale brown.

Table 9.10 Dimensions of *Littoraria (Littorinopsis) cingulata cingulata.*

Specimen	Locality	Sex	Primary grooves	H (mm)	B (mm)	LA (mm)	WA (mm)	C (mm)	PR	S	SH
Littorina cingulata lectotype, BMNH 1968354	N. coast of Australia		6	19.2	12.2	10.0	7.5	1.5	1.57	0.75	1.92
DGR	Broome, W.A.	♂	6	18.8	11.6	9.4	7.0	1.1	1.62	0.74	2.00
DGR	Broome, W.A.	♂	6	17.6	11.5	9.4	6.5	1.1	1.53	0.69	1.87
DGR	Broome, W.A.	♀	5	22.4	14.1	11.1	8.0	1.4	1.59	0.72	2.02
DGR	Broome, W.A.	♀	6	19.7	12.2	9.6	7.1	1.3	1.61	0.74	2.05
DGR, mean of 10	Broome, W.A.	♂		17.14					1.569	0.742	1.923
standard error				0.27					0.027	0.007	0.029
DGR, mean of 10	Broome, W.A.	♀		17.92					1.618	0.742	2.035
standard error				0.18					0.017	0.007	0.019
statistic t or U				2.366					74	53	83
probability				0.029					0.076	0.854	0.012

Fig. 9.39 (a–d) *Littorarta* (*Littorinopsis*) *cingulata cingulata*, Broome, W.A.: (a) spire (×17); (b) radula (×220); (c) last whorl (×8); (d) detail (×32). (e–f) *Littorarta* (*Littorinopsis*) *delicatula*, Port Canning, Bengal, India: (e) last whorl (×9); (f) detail (×32).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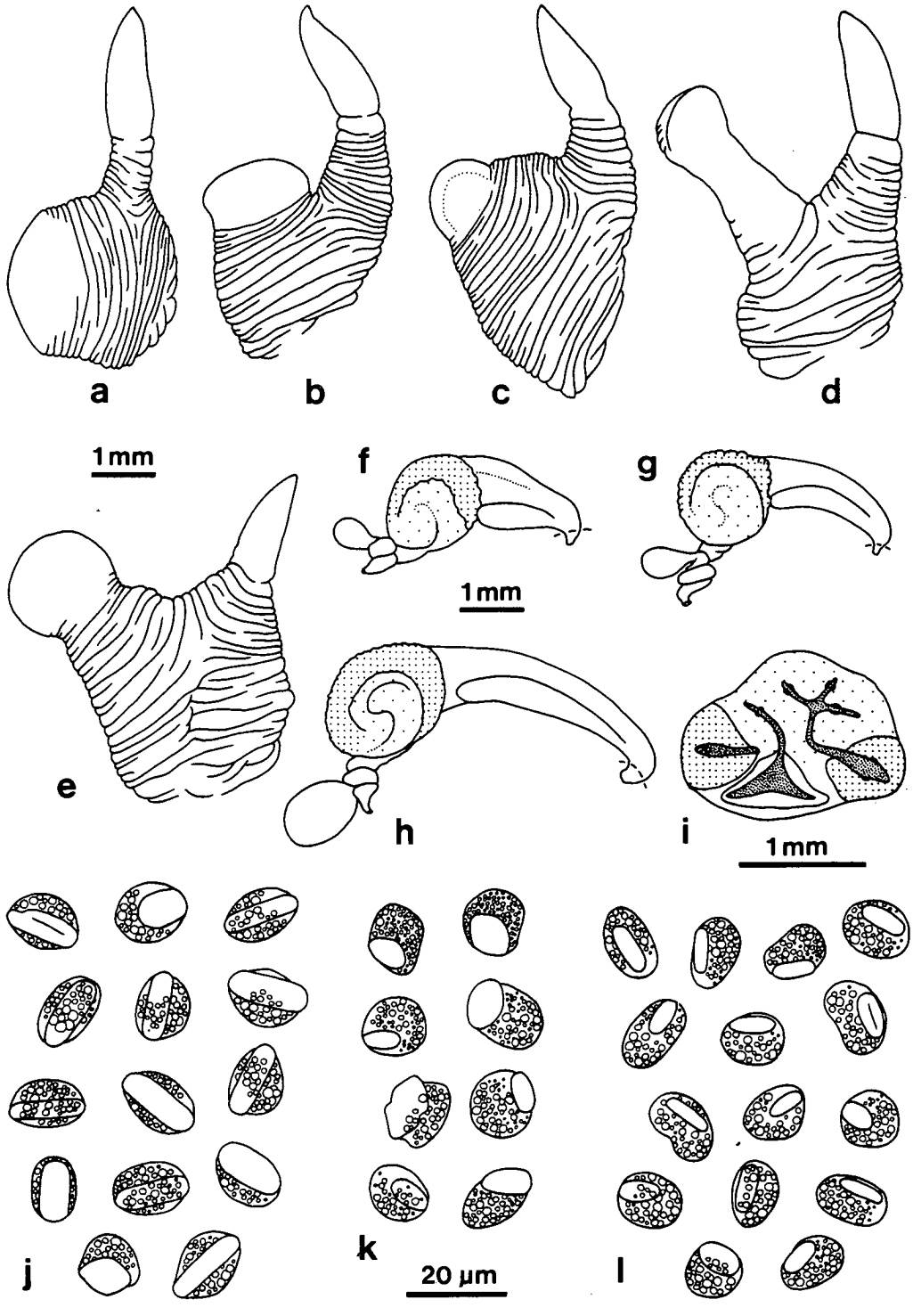


Fig. 9.40 *Littoraria (Littorinopsis) cingulata cingulata*, Broome, W.A.: (a-e) penes; (f-i) pallial oviducts, with transverse section; (j-l) sperm nurse cells.

Sperm. Eupyrene sperm 147–164 μm. Nurse cells (Fig. 9.40j–l) 12–15 μm; rounded to oval; rods single, central or asymmetrically placed, not projecting, parallel sided with rounded ends, or oval; yolk granules small.

Pallial oviduct (Fig. 9.40f–i). Length to 5.0 mm. Spiral section to 2.0 mm diam., $3\frac{1}{2}$ whorls; opaque albumen gland $\frac{2}{3}$–1 whorl, white; translucent albumen gland off white; capsule glands absent; spiral indistinct externally, egg groove not darkly pigmented. Straight section to 3.4 mm, white, terminating in a papilla. Bursa long, to 3.2 mm, anterior. Development assumed ovoviviparous.

Radula (Fig. 9.39b). Length to 15.5 mm; relative length 0.70–0.94. Saw-toothed type; central rachidian cusp rather elongate, pointed; cusps of paired teeth equilaterally triangular; lateral with no gap anterior to main cusp.

DISTRIBUTION. *Habitat*. At Broome, W.A., occurs near back of forest entirely of *Avicennia*, 0–2.0 m above ground, on trunks and sometimes leaves; occasionally on *Rhizophora* roots; rarely on sheltered rocks.

Range (Fig. 9.41). North-western Australia, from mouth of King Sound to Exmouth Gulf.

Records. AUSTRALIA: W.A.: Bay of Rest, Exmouth Gulf (WAM); Barrow I. (WAM, AMS, USNM); Cossack (BMNH); Port Hedland (AMS); Broome (DGR, WAM, NMV); West I., Lacepede Group (AMS); Cape Leveque (NMV); Sunday I. (WAM); Buccaneer Arch. (AMS).

REMARKS. As a result of the remote and restricted distribution of this species, specimens are rare in museum collections outside Australia. For this reason and perhaps also because of confusion with the sympatric *L. filosa* and *L. sulculosa*, it has not been listed as a distinct species for a century. *L. cingulata cingulata* shows constant shell characters throughout its range. The relationship of the typical form with the geographical subspecies *L.*

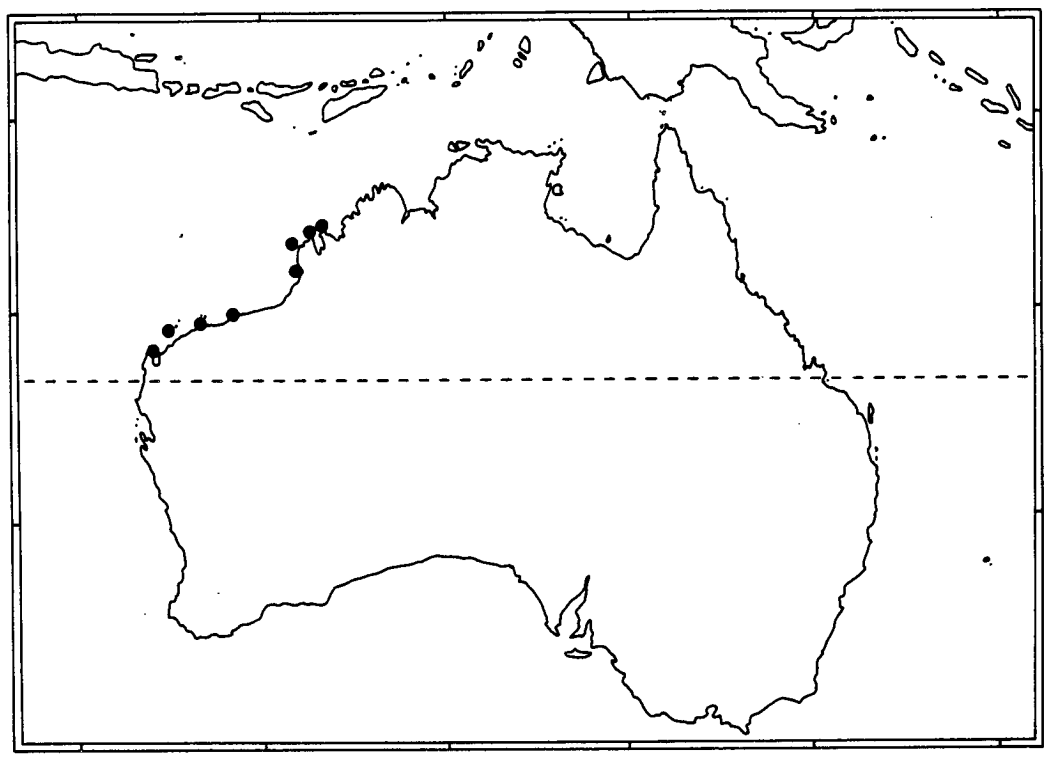


Fig. 9.41 Distribution of *Littoraria* (*Littorinopsis*) *cingulata cingulata*.

cingulata pristissini is discussed in the remarks on the latter.

SIMILAR SPECIES. Although characters of penis, sperm nurse cells and pallial oviduct place *L. cingulata cingulata* and *L. sulculosa* in different subgenera, their shells are closely similar. They can, however, always be immediately separated by the microsculpture between the conspicuous ribs, of axial striae in *L. sulculosa* and spiral striae in *L. c. cingulata*. In the field, *L. c. cingulata* is distinguished by its diffusely marbled pattern, columella often flushed with purple, 11-13 primary ribs on last whorl and thinner shell; in comparison, *L. sulculosa* has a pattern of long dashes or continuous spiral lines, usually a white columella, 9-11 primary ribs on last whorl and a thicker shell. *L. filosa* is only superficially similar, the shell is much thinner, the ribs narrow and often carinate, the microsculpture irregular and the species is colour polymorphic. Separation of the two subspecies of *L. cinguata* is usually straightforward, based on the more numerous ribs and inflated whorls of *L. c. pristissini*.

9.2.3.9 *Littoraria* (*Littorinopsis*) *cingulata pristissini* n. subsp.

TYPES. Holotype: AMS C.138323, Little Lagoon, Denham, Shark Bay, Western Australia. Paratypes: AMS, WAM, BMNH, USNM.

ETYMOLOGY. Latin: *pristis*, shark, and *sinus*, bay, after type locality.

DIAGNOSIS. Shell: outline slightly convex, whorls inflated, periphery rounded; columella rounded, lilac or white; primary grooves 7-9; development of secondary and tertiary sculpture variable, usually 40-60 low ribs on last whorl; grooves narrow; microsculpture usually of strong spiral striae in grooves; colour polymorphic, brown predominating, often 10-17 axial stripes on last

whorl. Animal: penis bifurcate, base thick, filament fairly short and tapering; ovoviviparous.

SHELL (Fig. 9.42). *Shape*. Height 17–30 mm. Teleoconch 8–8.5 whorls. Shell of moderate thickness, solid. Spire outline slightly convex; whorls inflated; sutures impressed. Peripheral keel weak until whorl 7, usually absent on last whorl, but sometimes marked by an enlarged rib. Adult lip slightly thickened, not flared. Varices absent, or present only as strong growth lines. Columella of moderate width, rounded, slightly flattened or hollowed in largest shells; pillar concave. Sexual dimorphism: males smaller, relatively lower spire and larger aperture.

Dimensions: Table 9.11.

Sculpture (Fig. 9.43a,c–f). Protoconch normal. First 2 whorls of teleoconch smooth. Primary grooves (6)7–9(10), equally spaced. Secondary grooves form at $\frac{1}{2}$ width of primary ribs on whorls 5 and 6; posterior rib may remain undivided until whorl 7, therefore appearing the most prominent on whorls 4–6. Tertiary grooves form in the same way on whorl 7; ribs may also be intercalated in primary grooves. Depending upon development of tertiary sculpture, ribs on last whorl total 40–60; usually all remain low and flat, peripheral rib sometimes a little enlarged; grooves narrow, less than $\frac{1}{2}$ rib width. Rarely secondary sculpture is delayed or absent, last whorl then sculptured by as few as 14–16 raised, rounded ridges, separated by primary grooves of up to twice rib width, sometimes with intercalated secondary riblets. At opposite extreme, shells may be almost smooth, with only posterior primary groove and basal grooves developed. Microsculpture of fine, irregular axial growth striae over whole surface; spiral striae sometimes absent, but usually strong and regular in grooves of shells in which groove width is greatest, rarely developed over whole shell surface.

Colour. Polymorphic; shades of brown predominate, pink occasional, yellow rare. Ground colour whitish, orange pink or cream

Fig. 9.42 *Littoraria (Littorinopsis) cingulata pristissini*: (a–c) Denham, W.A.; (a) paratype, ♀ (BMNH); (b) holotype, ♂ (AMS C.138323); (c) paratype, ♀ (BMNH); (d) Herald Bight, W.A. (WAM); (e) paratype, ♂, Denham, W.A. (BMNH); (f) Herald Bight, W.A. (WAM); (g) Dirk Hartog I., W.A.; (h) paratype, ♂, Denham, W.A. (BMNH); (i) Dirk Hartog I., W.A. (WAM).

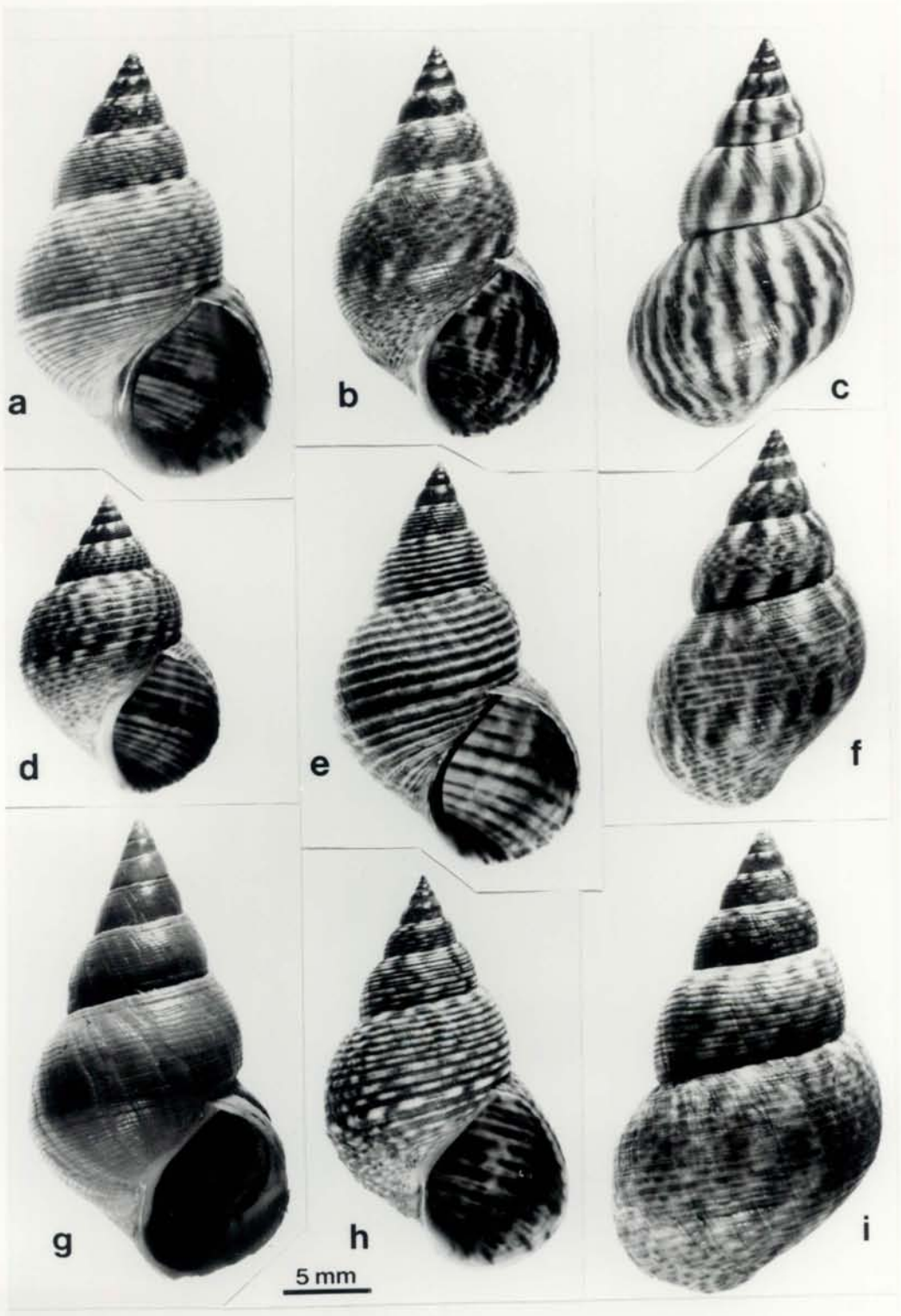
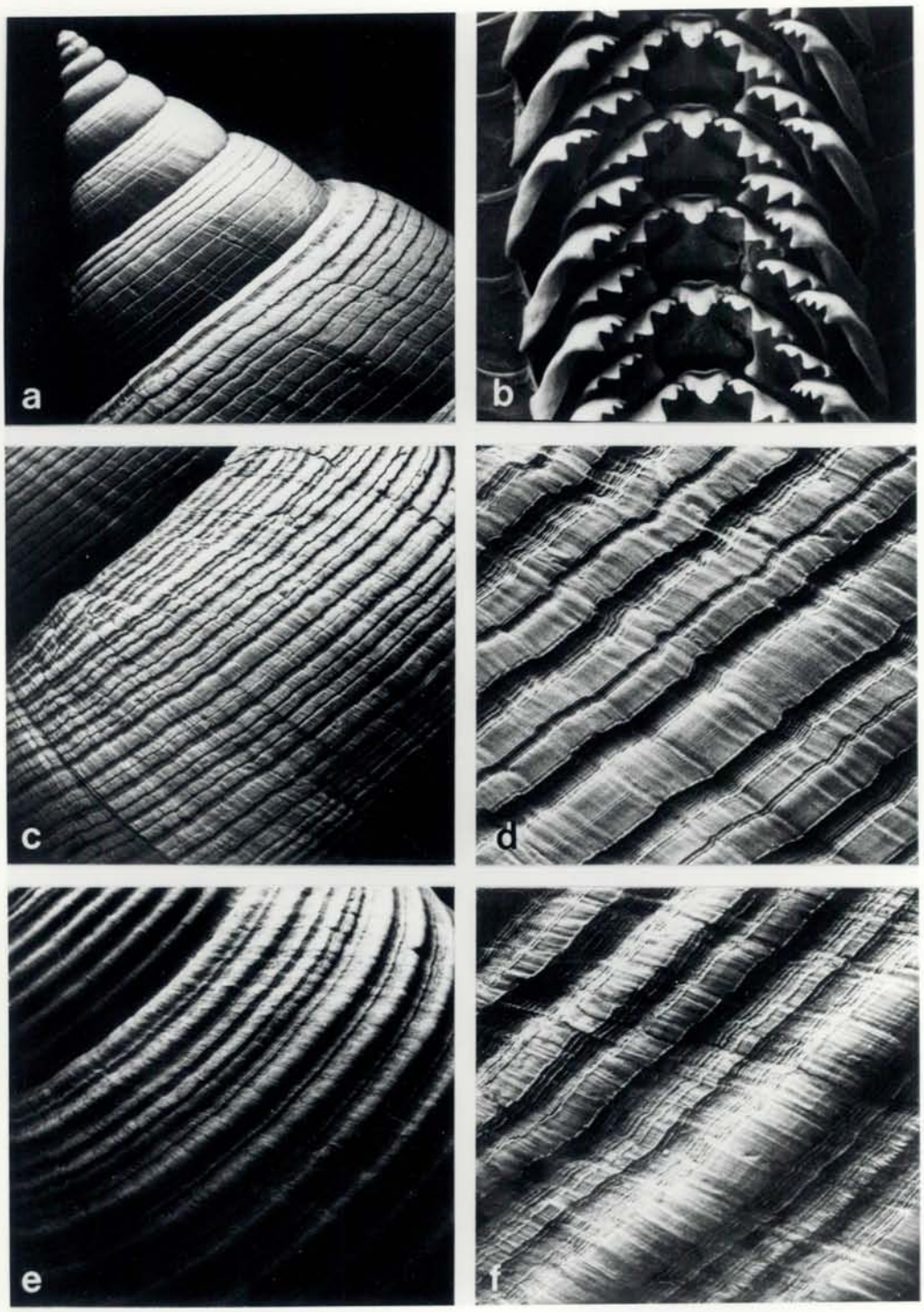

a
b
c
d
e
f
g
h
i
5 mm

Table 9.11 Dimensions of *Littorarta (Littorinopsis) cingulata pristissini*.

Specimen	Locality	Sex	Primary grooves	H (mm)	B (mm)	LA (mm)	WA (mm)	C (mm)	PR	S	SH
L. c. pristissini holotype, AMS C.138323	Denham, W.A.	♂	8	22.8	14.2	11.6	8.6	1.2	1.61	0.74	1.97
DGR	Denham, W.A.	♂	7	22.1	13.4	11.0	8.5	1.4	1.65	0.77	2.01
DGR	Denham, W.A.	♂	8	19.3	11.4	9.4	6.8	1.3	1.69	0.72	2.05
DGR	Denham, W.A.	♂	7	21.4	14.8	11.5	8.6	1.8	1.45	0.75	1.86
DGR	Denham, W.A.	♀	7	21.0	14.4	11.3	8.8	1.5	1.46	0.78	1.86
DGR	Denham, W.A.	♀	7	25.2	16.0	12.1	9.3	1.7	1.58	0.77	2.08
DGR	Denham, W.A.	♀	7	24.9	14.2	11.6	8.2	1.5	1.75	0.71	2.15
DGR, mean of 10	Denham, W.A.	♂		21.15					1.533	0.759	1.933
standard error				0.59					0.043	0.006	0.021
DGR, mean of 10	Denham, W.A.	♀		23.02					1.622	0.758	2.069
standard error				0.51					0.023	0.006	0.021
statistic t or U				2.405					72	53.5	93.5
probability				0.027					0.106	0.825	<.001

Fig. 9.43 *Littoraria* (*Littorinopsis*) *cingulata pristissini*, Denham, W.A.: (a) spire (×17); (b) radula (×220); (c) last whorl (×7); (d) detail (×30); (e) last whorl (×7); (f) detail (×30).


a
b
c
d
e
f

yellow. In dark shells pattern is of red brown or dark brown flecks densely scattered over surface, sometimes aligned only at sutures, especially on spire; first 6 whorls blue grey with conspicuous alternation of brown and white spots at suture; not infrequently entire shell marked by 10–17 vertical or oblique continuous axial stripes; occasionally shell uniform reddish black throughout. Pink, white or yellow shells may lack pattern entirely, or show a uniform speckling of pale orange brown. Aperture marked by purple brown oblique stripes or irregular spots, corresponding to external pattern; rarely spiral lines; glazed by a lilac or cream callus within. Columella lilac, or white in palest shells.

ANIMAL. *Colour*. Pigmentation pale grey to black, correlated with shell colour; sides of foot pale, mottled; head darkest, sometimes pale in centre; tentacles banded, unpigmented stripe each side of base.

Penis (Fig. 9.44a–d). Length to 10.5 mm. Base thick, bifurcate, limb bearing glandular disc rather short, except when extremely relaxed. Filament tapering. Sperm groove open. Base cream to fawn; filament cream; glandular disc pale brown.

Sperm (Fig. 5.3c). Eupyrene sperm 154–171 μm. Nurse cells (Fig. 9.44h–j) 14–24 μm; oval to fusiform; rods 1–2, central, often projecting, parallel sided, ends bluntly rounded; yolk granules small.

Pallial oviduct (Fig. 9.44e–g). Length to 3.7 mm. Spiral section to 1.9 mm diam., $3\frac{1}{2}$ whorls; opaque albumen gland $\frac{1}{2}$–1 whorl, white; translucent albumen gland off white; capsule glands absent; spiral distinct externally; egg groove not pigmented. Straight section to 2.3 mm, off white, terminating in a papilla. Bursa long, to 2.2 mm, anterior. Reproduction assumed ovoviviparous.

Radula (Fig. 9.43b). Length to 21 mm; relative length 0.68–0.88. Saw-toothed type; central rachidian cusp square, edge rounded or

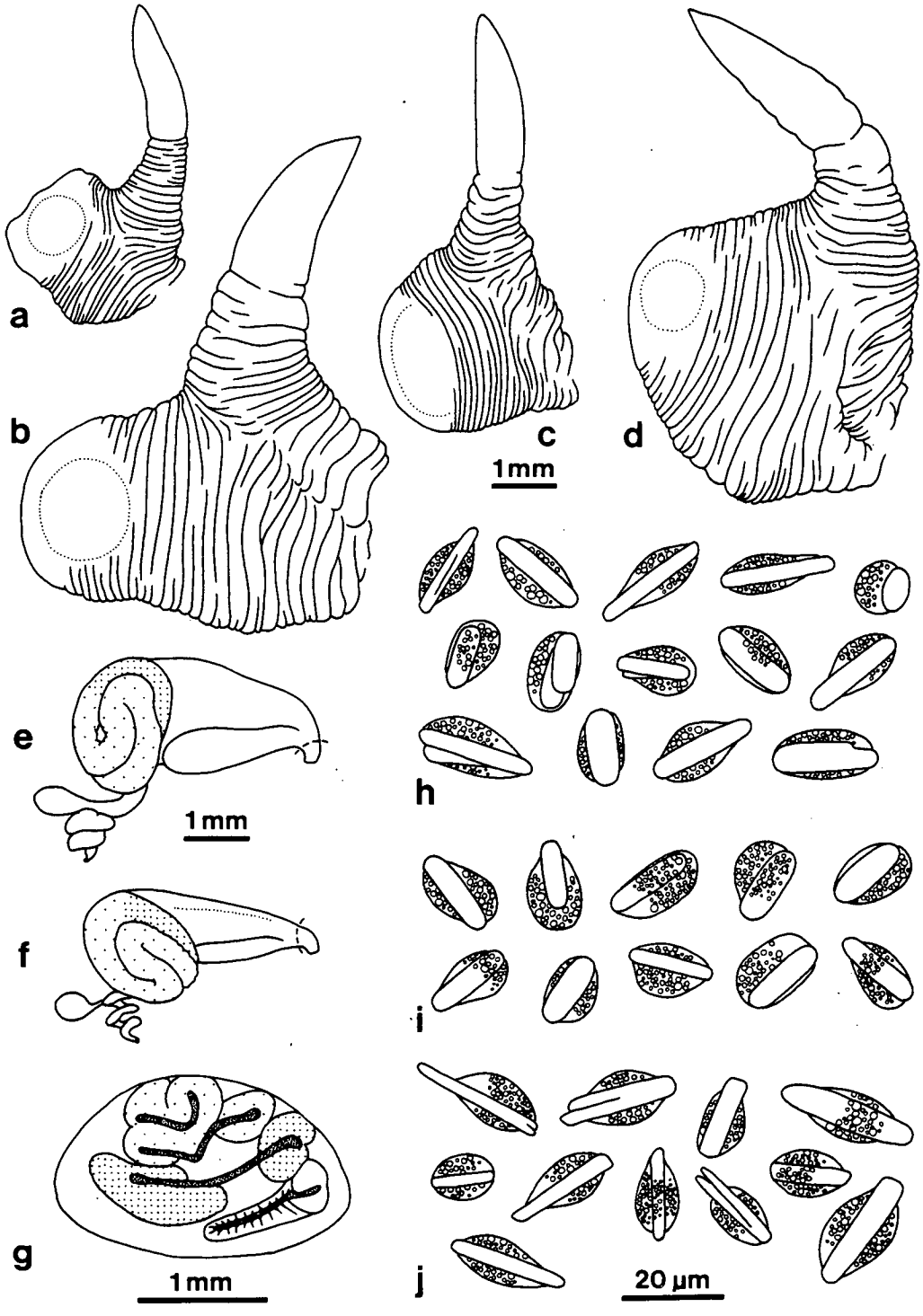


Fig. 9.44 *Littoraria* (*Littorinopsis*) *cingulata pristissini*, Denham, W.A.: (a–d) penes; (e–g) pallial oviducts, with transverse section; (h–j) sperm nurse cells.

slightly pointed; cusps of paired teeth equilaterally triangular; lateral with no gap anterior to main cusp.

DISTRIBUTION. *Habitat*. At type locality, on pneumatophores of *Avicennia* fringing creek between lagoon and sea, 0–0.2 m above ground; in broader *Avicennia* fringe found up to 0.6 m on trunks of outermost trees, occasionally on leaves, while found under logs at ground level further back; abundant amongst samphires at edges of sandy lagoons; occasional under stones at high tide level on sheltered rocky shores.

Range (Fig. 9.45). Restricted to Shark Bay, Western Australia.

Records. AUSTRALIA: W.A.: Useless Inlet (AMS); Denham (DGR, AMS, WAM); Tetradon Loop, off Dirk Hartog I. (WAM); Herald Bight, Peron Peninsula (WAM); Monkey Mia (DGR, WAM); Faure I. (WAM); Carnarvon (DGR, AMS, WAM); Quobba Point (WAM); 32 km N. of Cardabia (subfossil, WAM).

REMARKS. Typical specimens of *L. cingulata pristissini* and *L. cingulata cingulata* are so distinctive that a close relationship between them could be doubted. The shells are usually easily separated. In *L. c. pristissini* the whorls are rounded, the aperture relatively small, the sculpture usually of 40–60 narrow spiral ribs on the last whorl, and the colour highly polymorphic, often with a pattern of axial stripes. In *L. c. cingulata* the shell is usually keeled, the last whorl sculptured by 11–13 rounded ribs and the colour is a uniform marbled orange brown. However, the sculpture of *L. c. pristissini* is extremely variable, even within local populations, ranging from shells almost smooth to others with only 14–16 rounded ribs (Fig. 9.42e). The strongly ribbed shells comprise only a small fraction of the population (3.8%, n = 367, sampled from 4 localities) and are usually males (13 of 177 males, 1 of 190 females, $\chi^2 = 9.8$, $0.001<P<0.005$). The ribbed shells approach *L. c. cingulata* closely, not only in sculpture, but also in colour, which is never pink, yellow or axially striped as in typical *L. c.*

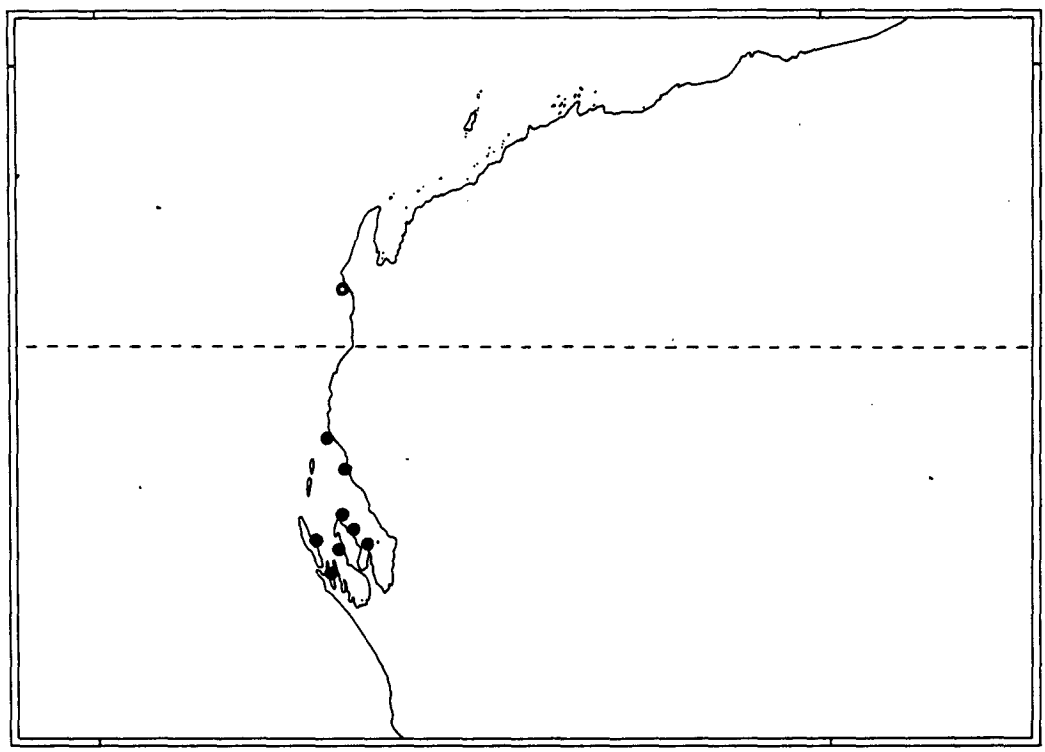


Fig. 9.45 Distribution of *Littoraria (Littorinopsis) cingulata pristissini*. Open circle, subfossil occurrence.

pristissini. However, in shape and in number of primary grooves (usually 7 or more) the shells resemble the Shark Bay subspecies, with which they are linked by an entire range of intermediates. Despite the conchological differences, anatomically the two subspecies are closely similar. Small differences shown by *L. c. pristissini* include the more obvious spiral form of the oviduct, the less elongate central cusp of the rachidian tooth and the more oval sperm cells with longer rods. There is no difference in the form of the penis.

L. c. pristissini is the only species of *Littoraria* to be found in Shark Bay and on the basis of available museum specimens seems to be geographically isolated from *L. c. cingulata*, which does not occur further south than Exmouth Gulf. This discontinuity is probably real, for according to G.W. Kendrick (WAM, pers. comm.) the only area of mangroves between Exmouth Gulf and the Gascoyne River is located 30 km south from North West Cape on the western coast, and he has been unable to find any living molluscs there. Little is known of coastal currents in the area, but they are said to be variable and weak (Phillips *et al.*, 1979) or southwards across the mouth of Shark Bay in autumn and winter (Legeckis & Cresswell, 1981). It is thus conceivable that the 300 km stretch of inhospitable coast between Shark Bay and Exmouth Gulf effectively isolates the two subspecies at the present time, although both probably have a lengthy planktonic larval phase (Section 7.2).

Since these two closely related forms are allopatric, their taxonomic status can only be judged on the basis of degree of morphological difference as compared with other examples of inter- and intraspecific variation in the genus (Mayr, 1969, pp. 196-197). Several species of *Littoraria*, including *L. pallescens*, *L. carinifera* and *L. filosa*, show regional variation in shell sculpture, but not to such a degree as *L. cingulata*. Shell colour is known to be influenced by substrate in some *Littoraria* species (Section 15.5.1), but in *L. cingulata* the habitats of the two forms, chiefly on *Avicennia* bushes, are similar. It would seem that the

polymorphism of the Shark Bay population may be determined genetically. Amongst other species, only *L. intermedia* is polymorphic over a part of its range and then the polymorphism is less striking than that of *L. c. pristissini*. The anatomical differences enumerated above are no greater than the normal range of intraspecific variation in other *Littoraria* species. Clearly the combination of shell sculpture, colour polymorphism and anatomical details distinguishing *L. c. pristissini* are more significant than other cases of intraspecific variation and are worthy of taxonomic recognition. Throughout the present work penis shape has been used as a diagnostic character, constant within species, which suggests that it might be used in species recognition by the animals themselves during copulation (Section 5.2). If this is so, the identity of the penes in the two forms of *L. cingulata* is circumstantial evidence that, were their ranges to meet, there would be no barrier to interbreeding. Since the taxa are closely related, taxonomically distinct, but allopatric, the category of subspecies is appropriate.

The known distributions of these two subspecies suggests that differentiation may have taken place following the isolation of the Shark Bay population from a once continuously distributed ancestral species. In the middle Holocene there were areas of mangroves in lagoons and embayments along the coast from Shark Bay to Exmouth Gulf, which have since almost completely disappeared (G.W. Kendrick, pers. comm.). Two subfossil shells of *L. c. pristissini* have been seen from a locality 32 km north of Cardabia (WAM), showing that this subspecies did in the past extend further north than Shark Bay. This time period might seem too short for such a level of differentiation to be achieved between isolated populations. However, the ancestral population might well have shown geographical variation before isolation was complete, as in the case of *L. filosa* in north-western Australia. Alternatively, more ancient episodes of habitat resriction may have caused the initial isolation. It is noteworthy that local populations of *L. c. pristissini* are highly variable in shell sculpture and shape. This might suggest that

differentiation from the nominate subspecies is relatively recent, or even that isolation is incomplete, with some gene flow from the northern population. Further fossil material may provide evidence of the history of these subspecies.

SIMILAR SPECIES. The relationship between *L. c. pristissini* and the nominate subspecies is discussed above. *L. angulifera* and *L. subvittata* are similar in shell characters, but in each the columella is excavated. Specimens might be confused with *L. ardouiniana*, but in *L. c. pristissini* the primary grooves are fewer, varices are absent and the microsculpture is often more prominent.

9.2.3.10 *Littoraria (Littorinopsis) luteola* (Quoy & Gaimard, 1832)

Littorina luteola Quoy & Gaimard, 1832: 477–478, pl. 33, figs 4–7 [Port Jackson, near Sydney [N.S.W., Australia]; lectotype (Rosewater, 1970) MNHNP]; Deshayes & Milne Edwards, 1843: 210–211

Melarhaphe luteola – Hedley, 1918a: M51

Melarapha luteola – Iredale & McMichael, 1962: 38

Littorina scabra – Angas, 1871: 95; Whitelegge, 1889: 264 [both not Linnaeus, 1758]; Muggeridge, 1979 [not Linnaeus, 1758; reproductive biology]

Littorina (Littorinopsis) scabra scabra – Rosewater, 1970: 456–461, pl. 352, fig. 9 [in part; not Linnaeus, 1758]

Littorina filosa var. *subcingulata* Nevill, 1885: 149 [Port Jackson [N.S.W., Australia]; lectotype here designated ZSI, 17.7 mm]

Littorina (Melaraphe) scabra var. *filosa* – Tryon, 1887: 244 [in part; not Sowerby, 1832]

Littorina (Melaraphe) flammea – Tryon, 1887: 245, pl. 43, fig. 36 [in part; not Philippi, 1847]

NOMENCLATURE. Rosewater (1970) designated a lectotype from the syntypic series in MNHNP. This specimen was unavailable for loan,

but Rosewater's figure leaves no doubt as to its identity. Fig. 9.46a herein is a specimen collected by Quoy & Gaimard which may perhaps be a paralectotype (P. Bouchet, pers. comm.), although labelled 'Port Western'.

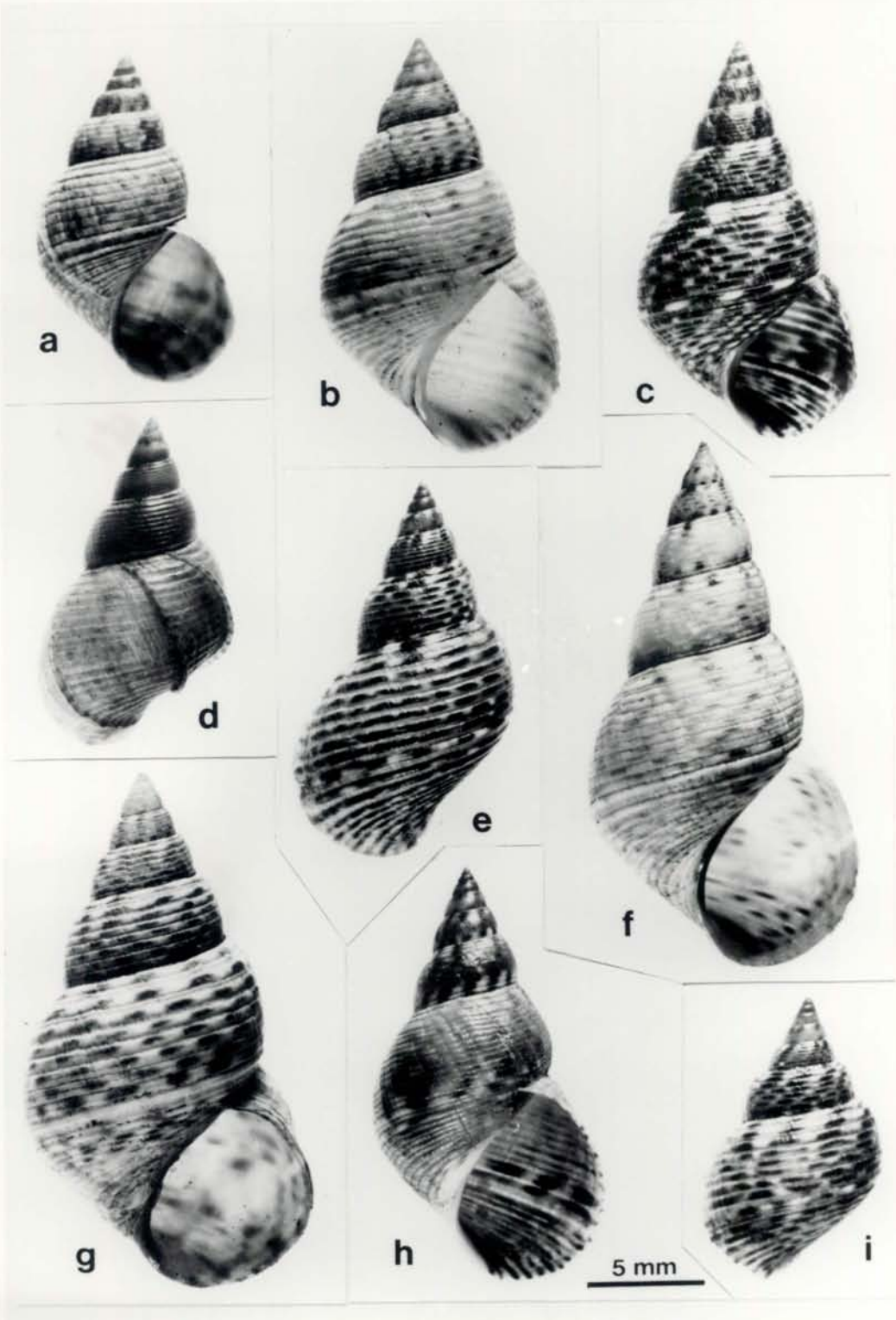
DIAGNOSIS. Shell: thin; spire elongate, outline convex; lip flared, varices 0–2; columella narrow, rounded, purple; primary grooves 8–10; 18–23 rounded ribs on body whorl, of which 2 at periphery are most prominent; secondary sculpture may be absent; colour polymorphic, dashes of dark pigment may be aligned to form short stripes at suture and periphery numbering 9–11 on last whorl. Animal: penis bifurcate, glandular disc large, filament small and tapering; ovoviviparous.

SHELL (Fig. 9.46). *Shape*. Height 8–23(28) mm. Teleoconch 7–9 whorls. Shell thin and delicate. Spire elongate, outline distinctly convex; whorls rounded or slightly turreted; sutures impressed. Whorls weakly keeled, although periphery is made prominent by 2 strong ribs, and often also by colour pattern. Adult lip thin and flared. Varices 0–2(4). Columella narrow, rounded, not excavated; pillar concave. Sexual dimorphism: males smaller, relatively lower spire and larger aperture, broader shell, adult lip more strongly flared and varices more frequent.

Dimensions: Table 9.12.

Sculpture (Fig. 9.47a,c–f). Protoconch normal. First whorl of teleoconch smooth. Primary grooves 8–10(11); spacing almost equidistant, but for posterior 3 grooves which are somewhat further apart; posterior 1 or 2 grooves deeper and wider than the rest, consequently posterior 2 or 3 ribs of spire whorls are the most prominent, this prominence often accentuated by colour pattern; posterior rib slightly narrower than the 2 ribs below. Secondary sculpture may develop on whorl 7, where larger ribs near suture and periphery divide at $\frac{1}{2}$ width; small shells often lack secondary sculpture; all ribs may divide in large shells. Occasionally single,

Fig. 9.46 *Littorarta* (*Littorinopsis*) *luteola*: (a) specimen collected by Quoy & Gaimard, Port Western (MNHNP); (b) lectotype of *Littorina filosa* var. *subcingulata* Nevill, Port Jackson, N.S.W. (ZSI); (c) ♀, Kurnell, N.S.W. (DGR); (d) Thursday I., Qld. (QM); (e,f) Kurnell, N.S.W. (DGR); (e) ♂; (f) ♀; (g) Uralla Bay, N.S.W. (NMV); (h) ♂, Kurnell, N.S.W. (DGR); (i) Tallebudgera, S.E. Qld. (QM).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g
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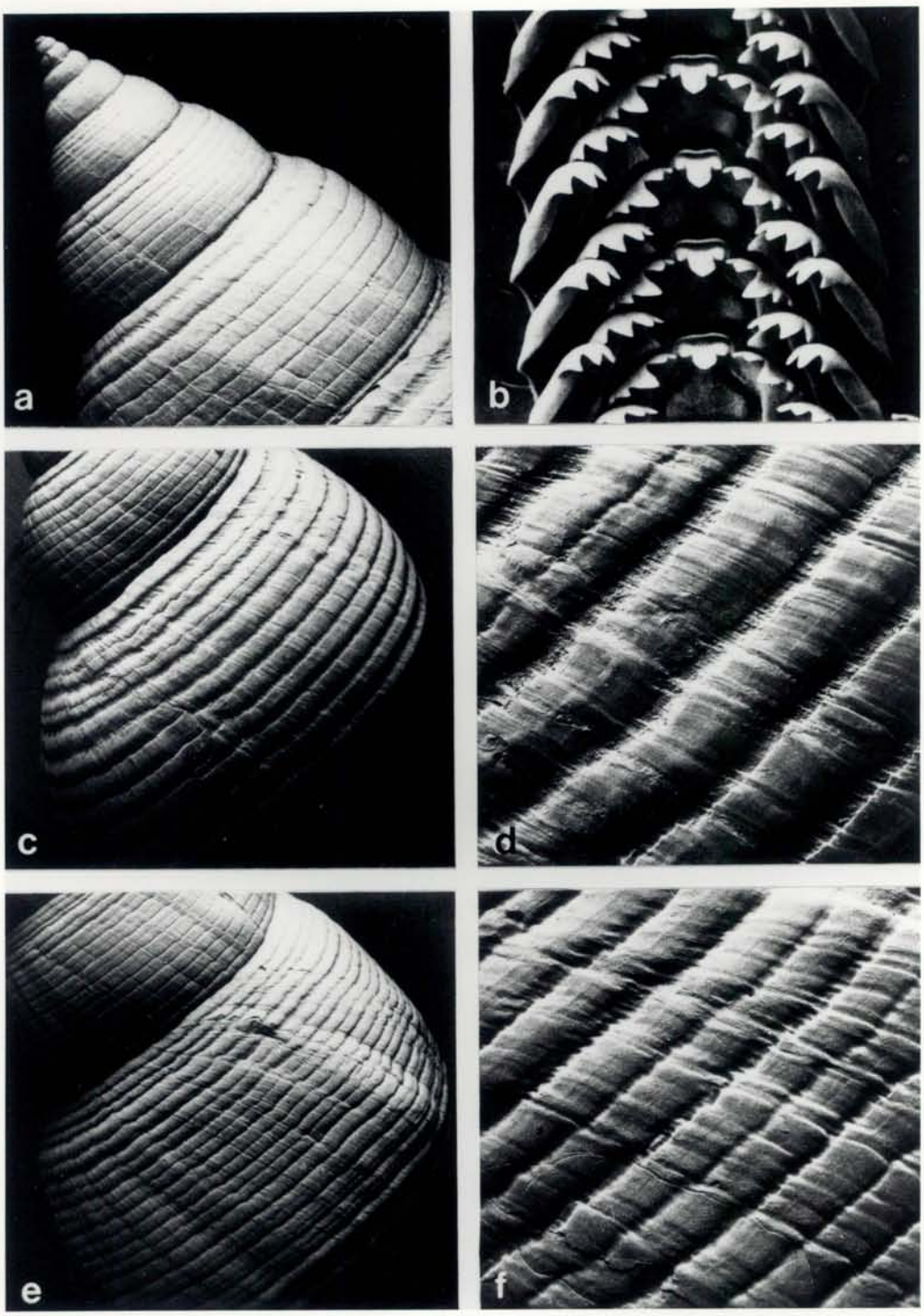
i
5 mm

Table 9.12 Dimensions of *Littorarta* (*Littorinopsis*) *luteola*.

Specimen	Locality	Sex	Primary grooves	H (mm)	B (mm)	LA (mm)	WA (mm)	C (mm)	PR	S	SH
Littorina luteola lectotype[1], MNHNP	Port Jackson, N.S.W.			16.3							
MNHNP[2]	Port Western		8	14.3	9.1	7.3	5.8		1.57	0.79	1.96
Littorina filosa var. *subcingulata* lectotype, ZSI	Port Jackson, N.S.W.		9	17.7	10.8	8.8	6.2	0.9	1.64	0.70	2.01
DGR	Kurnell, N.S.W.	♀	8	22.0	11.9	9.9	7.1	0.9	1.85	0.72	2.22
DGR	Kurnell, N.S.W.	♀	9	17.4	9.5	8.0	5.9	0.8	1.83	0.74	2.18
DGR	Kurnell, N.S.W.	♂	9	14.8	8.7	8.2	6.0	0.7	1.70	0.73	1.80
DGR	Kurnell, N.S.W.	♂	9	16.9	10.3	9.3	6.9	0.8	1.64	0.74	1.82
DGR	Magnetic I., Qld.	♀	9	19.4	10.2	8.8	6.1	1.0	1.90	0.69	2.20
DGR	Magnetic I., Qld.	♂	11	9.5	5.6	4.9	3.7	0.5	1.70	0.76	1.94
DGR, mean of 10	Kurnell, N.S.W.	♂		12.98					1.644	0.744	1.827
standard error				0.65					0.026	0.011	0.023
DGR, mean of 10	Kurnell, N.S.W.	♀		16.06					1.751	0.726	2.102
standard error				1.14					0.031	0.008	0.038
statistic t or U				2.335					81	67	98
probability				0.031					0.018	0.218	<.001

1 – shell height from Rosewater (1970, p. 459); 2 – specimen collected by Quoy & Gaimard.

Fig. 9.47 *Littoraria* (*Littorinopsis*) *luteola*, Kurnell, N.S.W.: (a) spire (×18); (b) radula (×230); (c) last whorl (×8); (d) detail (×33); (e) last whorl (×9); (f) detail (×39).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narrow secondary riblets are intercalated in widest primary grooves at periphery and near suture. Tertiary sculpture usually absent. Body whorl sculptured by rounded primary and secondary ribs numbering 18–23(28); most prominent are 2 ribs at periphery (peripheral rib and first basal rib), which remain undivided and are separated by widest of primary grooves, equal to rib width. Posterior groove up to $\frac{1}{2}$ average rib width; other grooves narrow, less than $\frac{1}{3}$ average rib width. Microsculpture of axial growth striae covering surface, strongest in widest grooves; faint spiral striae often visible, on ribs only; occasional large shells show single rows of beads in widest grooves.

Colour. Polymorphic; brown most frequent, yellow or red not uncommon. Ground colour pale brown, cream yellow or dark orange pink. Pattern of dark brown dashes on ribs; dashes axially aligned on 3 large subsutural ribs and 2 large peripheral ribs, making these parts of the whorls conspicuous by alternation of pale and dark colour stripes, which number 9–11 around suture of last whorl; elsewhere dashes may be so dense as to almost cover surface, may be sparsely scattered in a marbled pattern, or all pigmentation may be faint or even absent. External pattern clearly visible within aperture. Columella purple or red brown; spiral white stripe at base of pillar within inner apertural lip, outlined by narrow purple band within aperture.

ANIMAL. *Colour*. Pigmentation pale to dark grey or black, correlated with shell colour; sides of foot mottled; head darkest, sometimes with pale central streak; tentacles banded, unpigmented stripe each side of base.

Penis (Fig. 9.48a–e). Length to 3.9 mm. Base bifurcate; glandular disc large, somewhat irregular. Filament small, tapering, tip slightly mucronate. Sperm groove open. Base and filament off white, opaque white zone between filament and base; glandular disc white to pale brown.

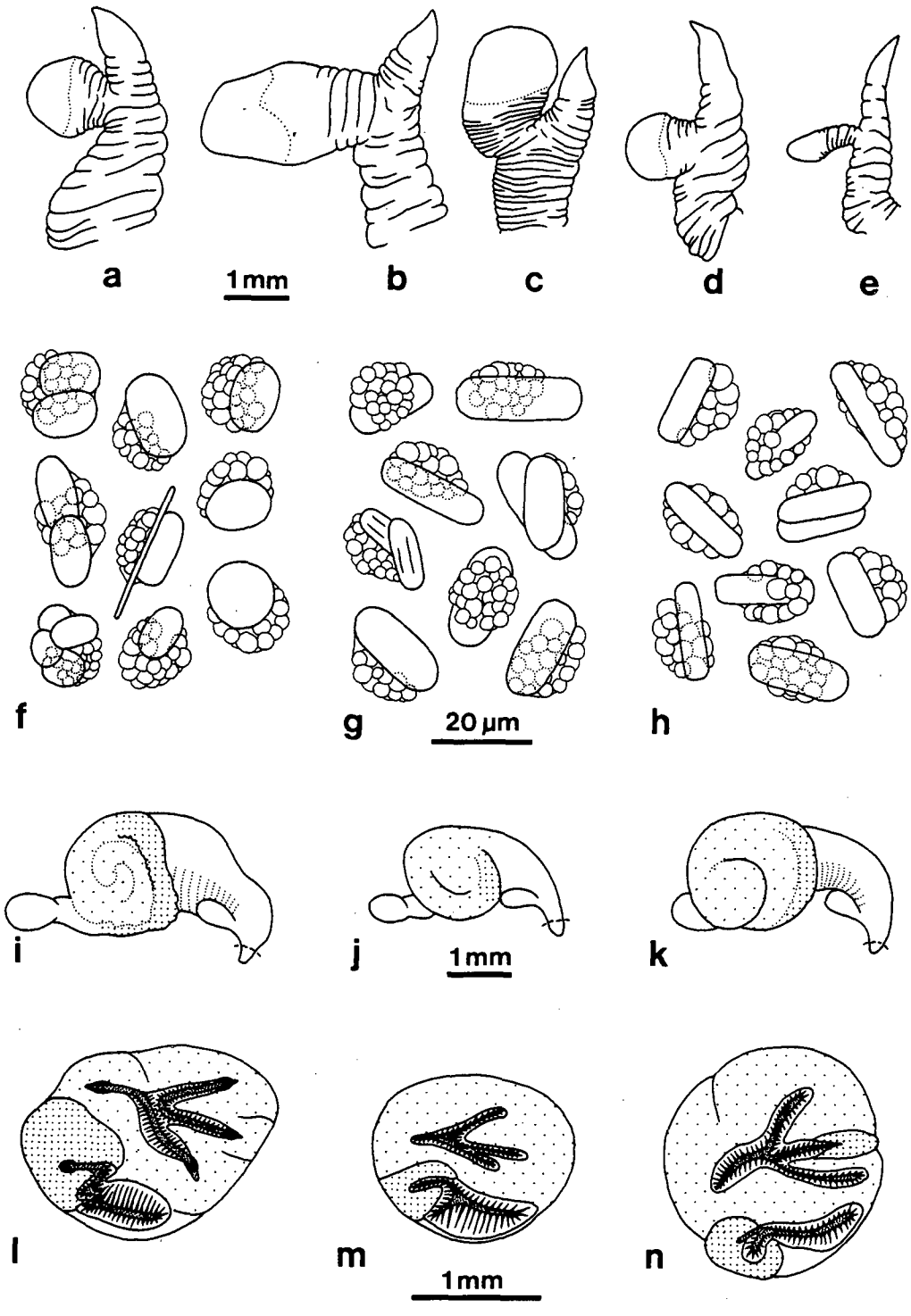


Fig. 9.48 *Littoraria* (*Littorinopsis*) *luteola*: (a–e) penes; (a,b) Kurnell, N.S.W.; (c) Pittwater, N.S.W.; (d) Kurnell, N.S.W.; (e) Magnetic I., Qld.; (f–h) sperm nurse cells; (f,g) Pittwater, N.S.W.; (h) Kurnell, N.S.W.; (i–n) pallial oviducts, with transverse sections, Kurnell, N.S.W.

Sperm. Eupyrene sperm 114–137 μm. Nurse cells (Fig. 9.48f–h) 17–26 μm; oval to rounded; rods 1–2(4), often asymmetrically placed, somewhat projecting, broad, rectangular and usually with rounded ends, or even oval; yolk granules large.

Pallial oviduct (Fig. 9.48i–n). Length to 3.2 mm. Spiral section to 1.9 mm diam., $2\frac{1}{2}$ whorls; opaque albumen gland $\frac{1}{2}$ whorl, white; translucent albumen gland cream to fawn; capsule glands absent; spiral indistinct externally; internal structure rather characteristic, with thick, red epithelial lining and last revolution of egg groove meeting lowermost chamber rather far forward; egg groove not usually darkly pigmented. Straight section relatively short, to 2.0 mm, fawn, reddish epithelial lining visible posteriorly; terminating in a papilla. Bursa small, to 0.6 mm, anterior. Development ovoviviparous.

Radula (Fig. 9.47b). Length to 11 mm; relative length 0.52–0.69. Saw-toothed type; central rachidian cusp square, edge slightly pointed; cusps of paired teeth equilaterally triangular; lateral with only slight gap anterior to main cusp.

DISTRIBUTION. *Habitat*. Leaves and trunks of *Avicennia*; in forests consisting entirely of *Avicennia* (southern N.S.W.), occurs from seaward edge to back of forest, 0.4–2.2 m above ground; in more complex forests (Qld.) occurs in *Avicennia* fringe and *Ceriops* zone; also found at back of swamps in saltmarsh vegetation and on and under driftwood at ground level. A continental species.

Range (Fig. 9.49). Endemic to eastern Australia, from southern N.S.W. to Torres Strait Is. (Old material from Solomon Is., New Britain and other Pacific islands almost certainly incorrectly localized).

Records. AUSTRALIA: Qld.: Thursday I. (QM); Murray Is. (QM); Cooktown (AMS); Yule Point (WAM); Dunk I. (QM); Missionary Bay, Hinchinbrook I. (DGR); Magnetic I. (DGR); Bowen (AMS); Sarina (AMS);

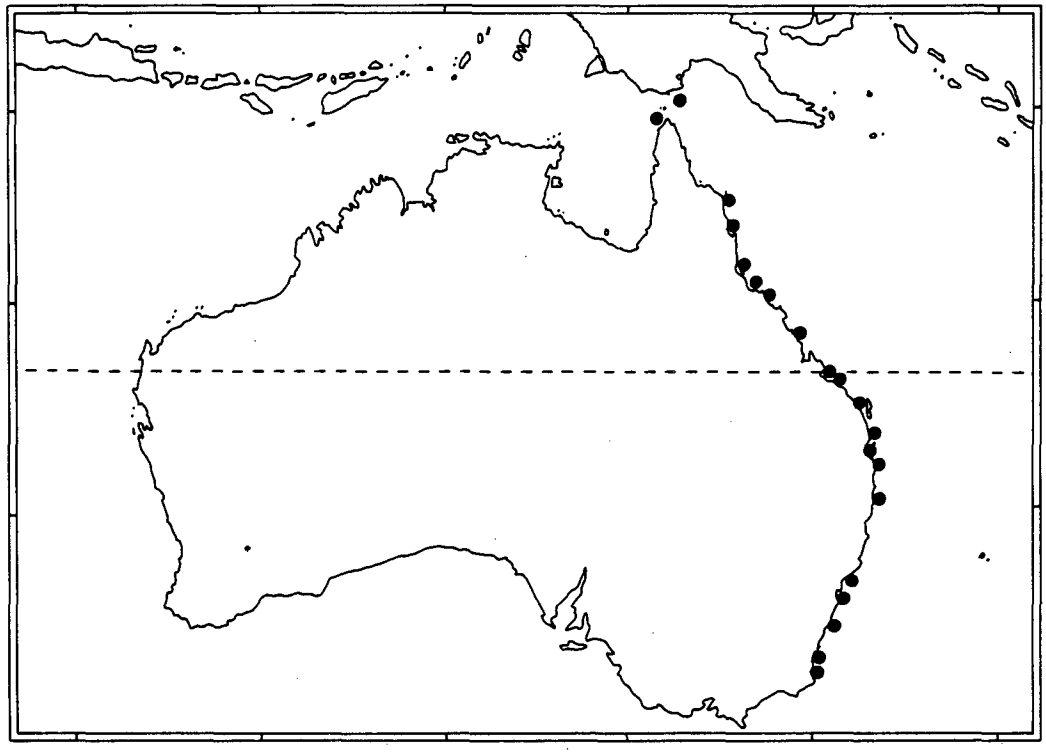


Fig. 9.49 Distribution of *Littoraria* (*Littorinopsis*) *luteola*.

Yeppoon (AMS); Eurimbula Creek, S. of Bustard Head (AMS); Pialba (QM); Caloundra (QM); Dunwich, Stradbroke I. (WAM, NMV); Tallebudgera, near Coolangatta (QM); N.S.W.: Brunswick Heads (AMS); Yamba (AMS); Port Stephens (AMS); Palm Beach, Pittwater (AMS); Kurnell Pen. (DGR); Huskisson, Jervis Bay (AMS); Narooma (AMS, NMV); Merimbula (AMS).

REMARKS. This species is little known and has not been recognized as distinct by authors outside Australia for about a century. *L. luteola* shows little geographical variation over its range, but sexual dimorphism is very marked. Shells from the leaves of *Avicennia* trees tend to be highly colour polymorphic, while those from bare trunks within thick forests and from driftwood in salt marshes are usually dark brown in colour. *L. luteola* extends as far into the temperate zone as any of the mangrove-associated species of *Littoraria*, reaching 37°S (*L. intermedia* is recorded from 37°N by Kuroda & Habe, 1952); mangroves are, however, found at still higher latitudes. This is by far the most abundant and often the only species of *Littoraria* in the mangroves of N.S.W., but becomes scarce north of about Rockhampton in Queensland, where it is gradually replaced as the dominant species on *Avicennia* leaves by *L. filosa*. The reproductive biology of the species has been studied in detail by Muggeridge (1979).

SIMILAR SPECIES. The narrow and rounded columella immediately distinguishes *L. luteola* from the larger *L. philippiana* and from the thicker shelled *L. intermedia*. In the same geographical range only *L. filosa* has a similar columella, but is larger, broader, and is usually strongly carinate. Confusion is most likely with small specimens of *L. ardouiniana*, although the distributions do not overlap; *L. ardouiniana* is distinguished by its finer and more numerous spiral ribs, and by the lack of the 2 large peripheral ribs which are characteristic of *L. luteola*. The form of the oviduct is unique to *L. luteola*.

9.2.3.11 *Littoraria* (*Littorinopsis*) *ardouiniana* (Heude, 1885)

Leptopoma (?) *ardouinianum* Heude, 1885: 95–96, pl. 25, figs 8,8a [A-long, Tonkin [Vietnam]; type in Academia Sinica, Peking? (P. Bouchet, pers. comm.)]

Littorina (*Lamellilittorina*) *ardouiniana* – Tryon, 1887: 253, pl. 46, fig. 28

Littorina ardouiniana – Fischer, 1891: 170

Melarhaphe scabra – Yen, 1942: 195 [not Linnaeus, 1758]

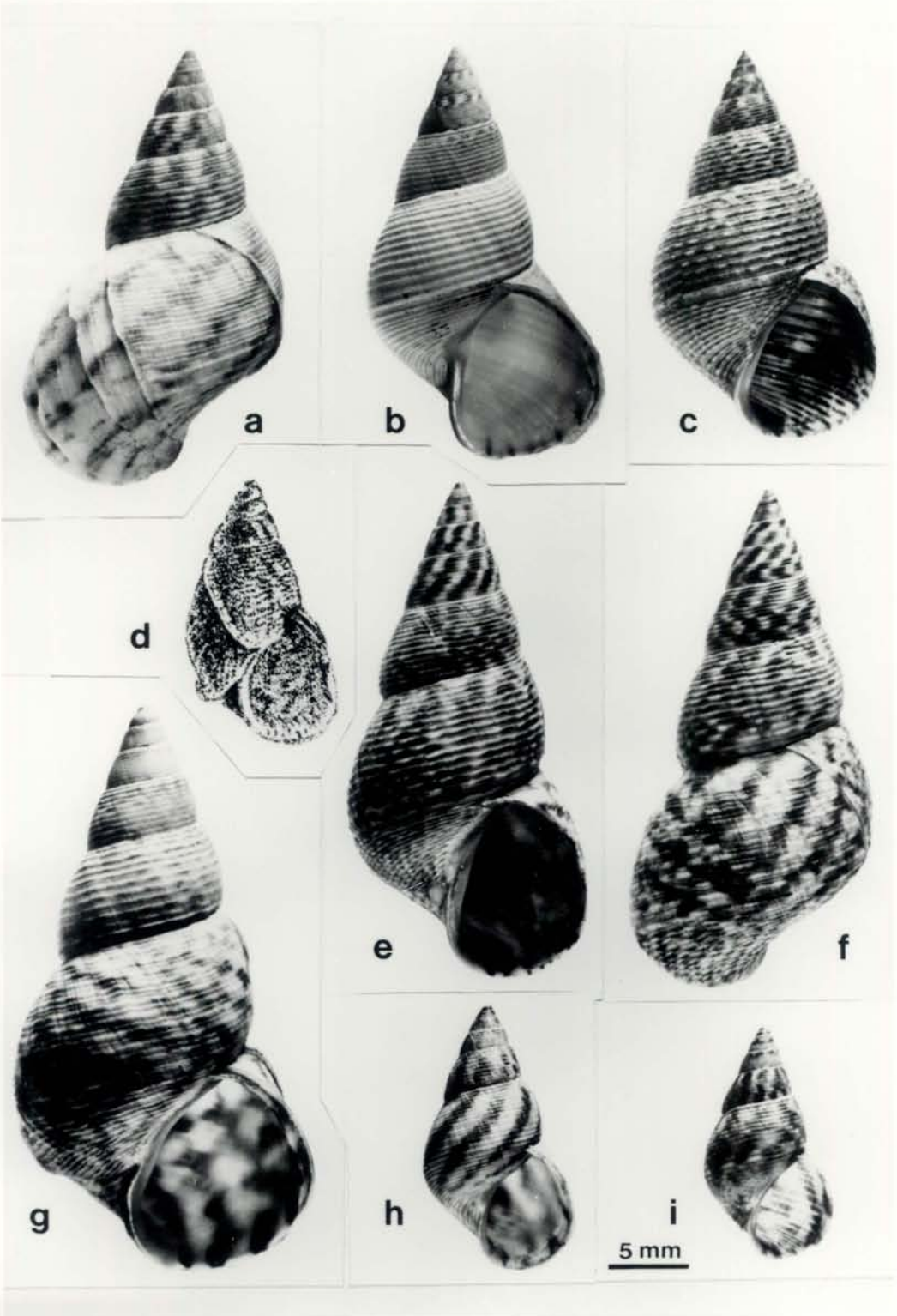
Littorina (*Littorinopsis*) *scabra scabra* – Rosewater, 1970: 456–461 [in part; not Linnaeus, 1758]

NOMENCLATURE. The type of this species could not be obtained, but Heude's figure (Fig. 9.50d herein) leaves little doubt as to its identity. The fine spiral sculpture (Heude's fig. 8a), prominent varices, indistinct axial stripes and narrow columella are all clearly shown and are characteristic of the species.

DIAGNOSIS. Shell: moderately thin; spire tall, whorls rounded; lip flared; varices 0–3; columella fairly narrow, rounded; primary grooves 10–13; body whorl with 37–78 rounded primary and secondary ribs; colour polymorphic, brown dashes may be aligned to form oblique axial stripes numbering 8–11 on last whorl. Animal: penis bifurcate, filament large and broad with sharply tapering tip, base ochraceous; ovoviviparous.

SHELL (Fig. 9.50). *Shape*. Height 11–30(36) mm. Teleoconch 7–9 whorls. Shell moderately thin, becoming solid at large size. Spire tall, outline convex; whorls lightly rounded, sutures impressed. Peripheral keel absent on last whorl; in smaller shells a slight angulation may be accentuated by a rib more prominent than the others. Adult lip thin, flared. Varices 0–3(7). Columella fairly narrow, usually rounded, sometimes slightly flattened, not excavated; pillar straight to gently convex. Sexual dimorphism: males smaller, relatively lower spire and larger aperture, shell

Fig. 9.50 *Littoraria* (*Littorinopsis*) *ardouiniana*: (a,b) Three Fathoms Cove, Hong Kong (BMNH); (a) ♂; (b) ♂; (c) ♀, Ubin I., Singapore (DGR); (d) figure of *Leptopoma* (?) *ardouinianum* Heude, Along, Tonkin (Heude, 1885, pl. 25, fig. 8); (e-g) Three Fathoms Cove, Hong Kong (BMNH); (e,f) ♀; (g) ♀; (h) Tai Po, S. China (BMNH); (i) China (BMNH).


a
b
c
d
e
f
g
h
i
5 mm

relatively wider.

Dimensions: Table 9.13.

Sculpture (Fig. 9.78e,f). Protoconch of normal shape, sculpture not seen. Probably all whorls of teleoconch sculptured by spiral grooves (apices of available specimens not well preserved). Primary grooves (9)10–13, equally spaced. Secondary sculpture may appear as early as whorls 5–6, more usually on whorl 7, where 1–4 ribs, generally on shoulder, become divided each by a secondary groove at $\frac{1}{3}$–$\frac{1}{2}$ width; rarely all ribs are thus divided. On whorls 7–8 1–3 small secondary riblets form by intercalation in each primary groove, usually appearing just before and continuing strongly after the first varix. Primary ribs of equal width; until last whorl all remain low, but for slightly more prominent peripheral rib; secondary riblets remain small, usually less than $\frac{1}{2}$ width of primary ribs; all ribs become more prominently raised and rounded on last whorl; total number of primary and secondary ribs beyond first varix 37–78. Primary grooves $\frac{1}{2}$–1 rib width on penultimate whorl, widest at and just below periphery; up to 4 times rib width on last whorl, but crowded with secondary riblets. Microsculpture of faint, irregular axial growth striae covering surface, stronger in grooves; a few irregular spiral striae confined to grooves.

Colour. Polymorphic; brown patterned shells predominate. Ground colour pale yellow, pale brown or orange pink. Pattern of indistinct brown dashes and flecks on ribs, often aligned at suture and periphery, or over whole surface, to form irregular, oblique axial stripes, numbering 8–11 on last whorl, or sometimes producing a coarsely marbled pattern. Pink or yellow shells may lack dark pigment entirely, or may have short axial stripes only at suture and periphery; some shells show paler spiral zones at periphery and middle of base. Aperture cream, external pattern visible within, obscured by whitish or pink callus in larger shells. Columella usually pink or purple, may be entirely white in pale shells.

Table 9.13 Dimensions of *Littorarta (Littorinopsis) ardouiniana*.

Specimen	Locality	Sex	Primary grooves	H (mm)	B (mm)	LA (mm)	WA (mm)	C (mm)	PR	S	SH
Leptopoma ardouinianum original figure (Heude, 1885)	Along, Tonkin			17.6	11.4	8.7	6.8		1.54	0.78	2.02
BMNH	China		13	17.7	10.3	8.9	6.5	0.8	1.72	0.73	1.99
BMNH	China		13	14.9	8.5	7.4	5.6	0.7	1.75	0.76	2.01
BMNH 1969391	unknown		12	23.4	12.7	10.5	7.4	1.1	1.84	0.70	2.23
BMNH	Okinawa, Japan	♀	11	15.5	8.7	7.5	4.8	0.5	1.78	0.64	2.07
BMNH 1947.8.15.112	Tai Po, China		10	16.5	9.6	8.5	6.1	0.6	1.72	0.72	1.94
AMS C.131826	Tai Tam, Hong Kong	♂	11	14.2	7.8	6.7	4.8	0.6	1.82	0.72	2.12
BMNH	Three Fathoms Cove, Hong Kong	♂	10	26.9	16.1	14.1	10.9	1.4	1.67	0.77	1.91
BMNH	Three Fathoms Cove, Hong Kong	♂	10	27.1	15.7	14.1	10.6	1.7	1.73	0.75	1.92
BMNH	Three Fathoms Cove, Hong Kong	♀	10	35.8	18.5	15.9	12.3	1.7	1.94	0.77	2.25
BMNH	Three Fathoms Cove, Hong Kong	♀	13	30.2	15.9	12.8	9.0	1.5	1.90	0.70	2.36
BMNH, mean of 10	Three Fathoms Cove, Hong Kong	♂		24.85					1.730	0.757	1.924
standard error				0.44					0.017	0.006	0.009
BMNH, mean of 10	Three Fathoms Cove, Hong Kong	♀		28.29					1.845	0.740	2.236
standard error				1.29					0.025	0.011	0.036
statistic t or U				2.518					87	67	100
probability				0.021					0.004	0.218	<.001

ANIMAL. *Colour*. Pigmentation grey to black; sides of foot darkly mottled; head darkest; tentacles banded, unpigmented stripe each side of base.

Penis (Fig. 9.51a–d). Length to 6.0 mm. Base bifurcate, limb bearing glandular disc not long. Filament large, broad, tip sharply tapering. Sperm groove open. Base pale ochraceous brown, filament cream, glandular disc opaque cream.

Sperm. Nurse cells (Fig. 9.51e–g) 16–29 μm, oval; rods 1–3, central, usually projecting, parallel sided, blunt; yolk granules small.

Pallial oviduct (Fig. 9.51h–k). Length to 5.1 mm. Spiral section to 2.3 mm diam., $2\frac{1}{2}$ whorls; opaque albumen gland $\frac{3}{4}$ whorl, cream; translucent albumen gland pale brown; capsule glands absent; epithelial lining reddish; spiral distinct externally; egg groove with a little black pigment. Straight section to 3.0 mm, pale brown, terminating in a papilla. Bursa long, to 2.2 mm, anterior. Development assumed ovoviviparous.

Radula (Fig. 9.78d). Length to 21 mm; relative length 0.59–0.90. Saw-toothed type; central rachidian cusp square, edge sometimes slightly pointed; cusps of paired teeth equilaterally triangular; lateral with no gap anterior to main cusp.

DISTRIBUTION. *Habitat*. Leaves and trunks in *Avicennia* fringe, to 1.5 m above ground and probably higher. Also reported on *Aegiceras* and *Kandelia* (B.S. Morton and M. Nishihira, pers. comm.), on rocks (Heude, 1885; Fischer, 1891) and in marsh grass (collection in AMS, coll. W.F. Ponder & B.S. Morton). A continental species.

Range (Fig. 9.52). Okinawa I. to Singapore.

Records. SINGAPORE: Jelutong, Ubin I. (DGR); VIETNAM: Chilins, Vung Tau district (ANSP); Bay of Along (Heude, 1885); HONG KONG:

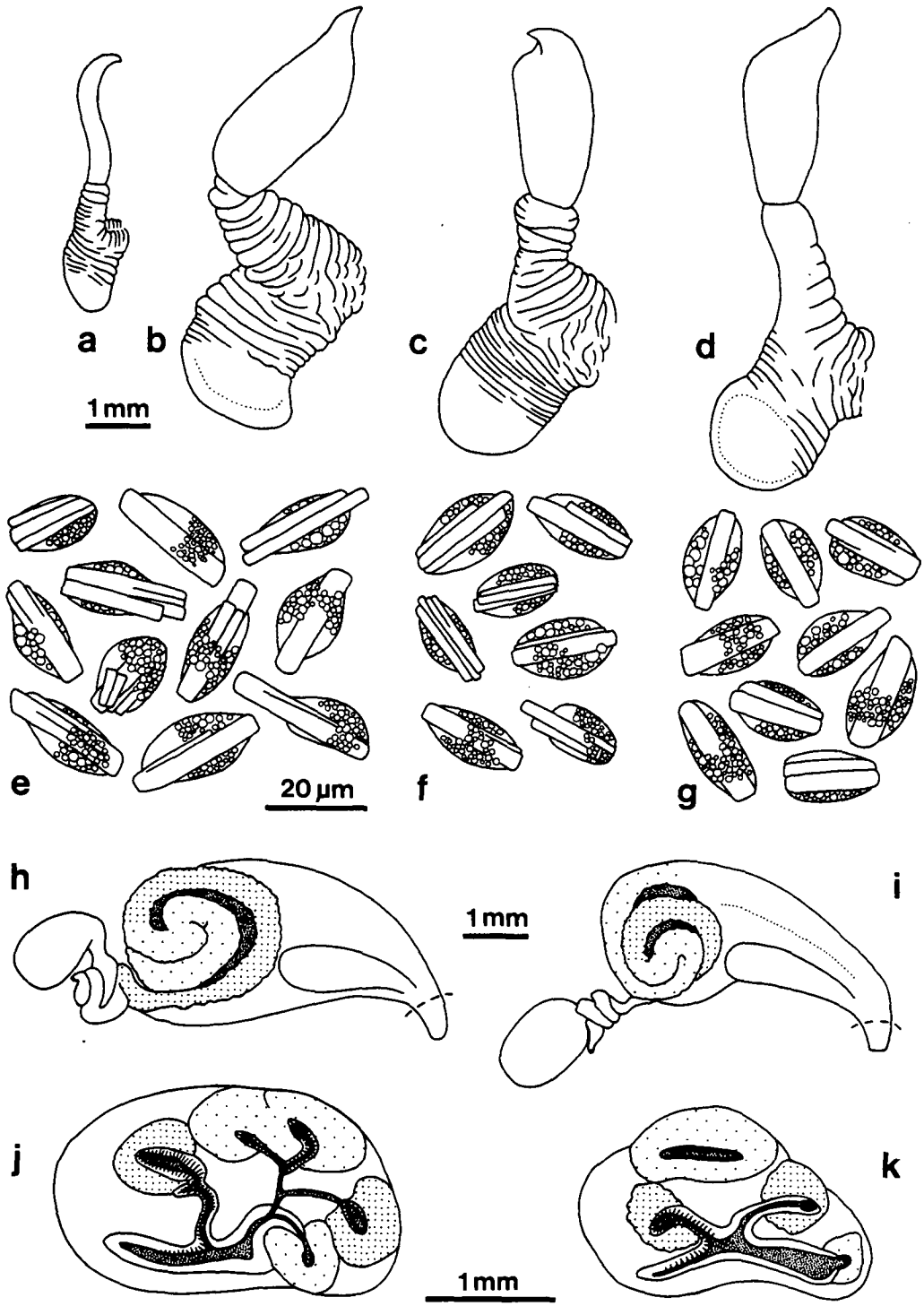


Fig. 9.51 *Littoraria* (*Littorinopsis*) *ardouiniana*: (a–d) penes; (a) Tai Tam Harbour, Hong Kong; (b–k) Three Fathoms Cove, Hong Kong; (e–g) sperm nurse cells; (h–k) pallial oviducts, with transverse sections.

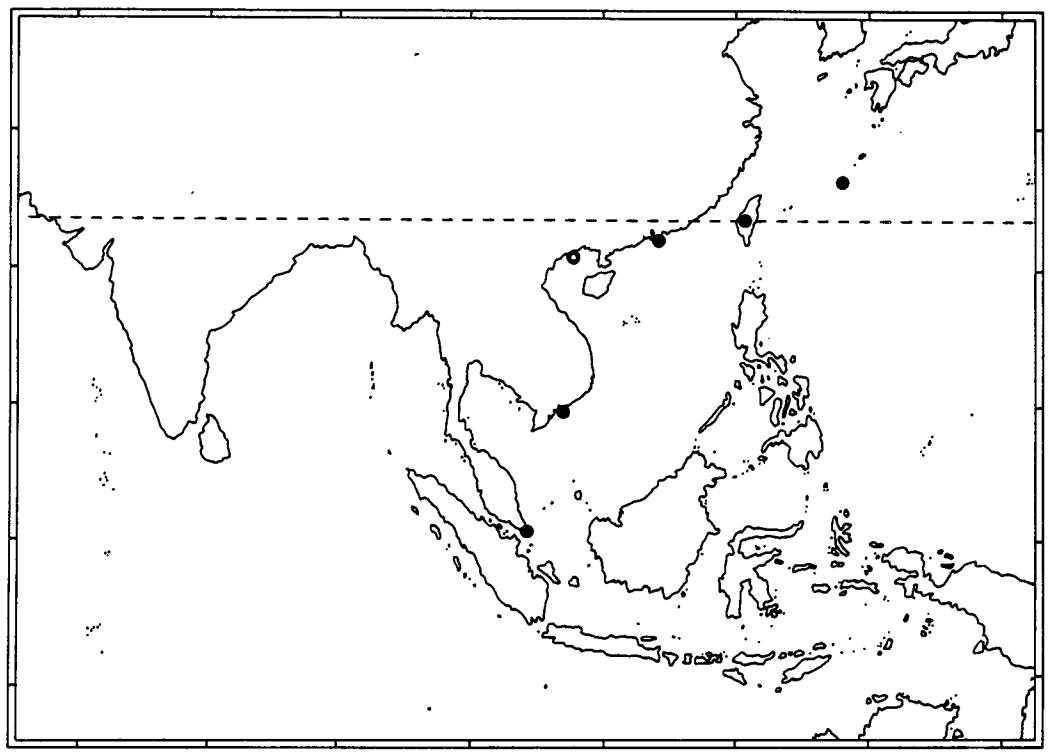


Fig. 9.52 Distribution of *Littoraria* (*Littorinopsis*) *ardouiniana*.

Three Fathoms Cove, New Territories (BMNH); West Point (BMNH); Tai Tam Harbour (AMS); TAIWAN (MCZ); JAPAN: Okkubi R., Okinawa I. (BMNH).

REMARKS. Specimens of *L. ardouiniana* are rare in museum collections and the species has apparently not been mentioned as distinct in the literature since 1891. The shell is highly colour polymorphic and this, together with the thin texture and prominent varices, suggests that the typical habitat may be at rather high levels on leaves of mangroves. There is considerable variation in adult shell size and in the number of ribs on the body whorl. The rather numerous varices led Tryon (1887) to place this species in the subgenus *Lamellilitorina*; however, details of shell sculpture, protoconch and oviduct preclude any close relationship with the only known member of that subgenus, *L. albicans*.

SIMILAR SPECIES. *L. ardouiniana* may be confused with a number of other species on account of its variation in size, sculpture and colour. Shells may superficially resemble those of *L. subvittata*, *L. lutea*, *L. philippiana* and *L. angulifera* in the rather fine spiral ribs and diffusely striped colour pattern, but specimens of *L. ardouiniana* are separated by the narrow and rounded columella pillar. Amongst species which share this character, *L. cingulata pristissini* is one of the closest in appearance, but the primary spiral grooves on the early whorls are more numerous in *L. ardouiniana*, varices are more prominent and microsculpture scarcely present. Small shells could be confused with *L. luteola* or *L. delicatula*. From the former, *L. ardouiniana* is distinguished by the more numerous and finer ribs on the last whorl and absence of the two enlarged ribs at the periphery. Some small specimens do approach rather closely to *L. delicatula*, but in *L. ardouiniana* the sculpture is of more prominent and unequal ribs, separated by wider grooves, the periphery is more rounded, the shell thicker and the columella not excavated. Penial characters and the form of the sperm nurse cells separate *L. ardouiniana* from all the similar species mentioned above, with the exception of *L. delicatula* in which the anatomy is

not known.

9.2.3.12 *Littoraria* (*Littorinopsis*) *delicatula* (Nevill, 1885)

Littorina conica var. *delicatula* Nevill, 1885: 149–150 [Port Canning and False Point, Bengal [India]; holotype ZSI]

Littorina delicatula – Annandale & Prashad, 1919: 246, fig. 2c [radula], pl. 20, fig. 4

Littorina conica var. *subintermedia* Nevill, 1885: 150 [Port Canning and False Point [Bengal, India]; lectotype ZSI, 16.5 mm, here designated]

Littorina subintermedia – Annandale & Prashad, 1919: 245–246, fig. 2b [radula], pl. 20, fig. 3

Littorina (*Melaraphe*) *undulata* – Tryon, 1887: 244 [in part; not Gray, 1839]

Littorina (*Littoraria*) *undulata* – Rosewater, 1970: 436–439 [in part; not Gray, 1839]

Littorina (*Littorinopsis*) *scabra scabra* – Rosewater, 1970: 456–461 [in part; not Linnaeus, 1758]

NOMENCLATURE. Nevill (1885) described both *delicatula* and *subintermedia* as varieties of *L. conica*, which indeed they do in some respects resemble and which, according to Nevill, occurs at the same locality. The name *delicatula* was proposed for the very thin shelled, brightly coloured form. The lectotype of *subintermedia* is a little more solid, the sculpture more coarse (38 grooves on last whorl) and the colour pattern darker, but the two seem, from shell characters alone, to be conspecific. Nevertheless, Annandale & Prashad (1919) separated the two as distinct species on the basis of shell shape, thickness, colour and radular characters. The radular cusps of *L. subintermedia* were said to be transversely striate, but to judge by an accompanying drawing of the radula of *L. melanostoma*, the accuracy of observation could be doubted. Until anatomical

evidence is available, *L. subintermedia* is tentatively regarded as a synonym of *L. delicatula*.

DIAGNOSIS. Shell: thin, often extremely delicate; sutures only slightly impressed; peripheral keel becoming obsolete on last whorl; lip flared; primary grooves 11-14; 35-50 flat ribs on last whorl, separated by impressed lines; colour polymorphic, yellow, brown or pink, often with brown pattern in short axial stripes only at suture and periphery, numbering 9-11 on last whorl. Animal: unknown.

SHELL (Fig. 9.53). *Shape*. Height 13-19 mm. Teleoconch 6.5-7.5 whorls. Shell thin, translucent, often extremely delicate. Spire only slightly convex; whorls but lightly rounded; sutures only slightly impressed. Peripheral keel prominent in young shells, becoming obsolete on last whorl. Adult lip thin, flared; varices 0-1(3). Columella narrow, excavated; pillar straight to slightly concave. Sexual dimorphism: males smaller, relatively lower spire and larger aperture, adult lip more strongly flared, varices more frequent (after Nevill, 1885; and pers. obs. of dimorphic empty shells).

Dimensions: Table 9.14.

Sculpture (Fig. 9.39e-f). Protoconch normal. First whorl of teleoconch smooth. Primary grooves (10)11-14; spacing almost equal, posterior 3 or 4 a little closer together. Secondary grooves form on whorls 5-6, at $\frac{1}{2}$ width of primary ribs. Rib width remains almost equal throughout, only peripheral rib and sometimes sutural rib are a little wider and more prominent; ribs number 35-50 on last whorl, all are low and flattened. Primary and secondary grooves alike are narrow, impressed lines. Microsculpture of faint axial growth striae over whole surface.

Colour. Polymorphic; yellow, brown and pink shells occur. Ground colour pale yellow, cream or orange pink, overlain by brown dashes on ribs. Pattern variable; dark pigment often absent; pale shells

Fig. 9.53 *Littoraria* (*Littorinopsis*) *delicatula*: (a) locality unknown (BMNH); (b,c) holotype of *Littorina conica* var. *delicatula* Nevill, Port Canning and False Point, Bengal, India (ZSI); (d–f) Port Canning, Bengal, India (BMNH); (g,h) locality unknown (BMNH); (i) lectotype of *Littorina conica* var. *subintermedia* Nevill, Port Canning and False Point, Bengal, India (ZSI).

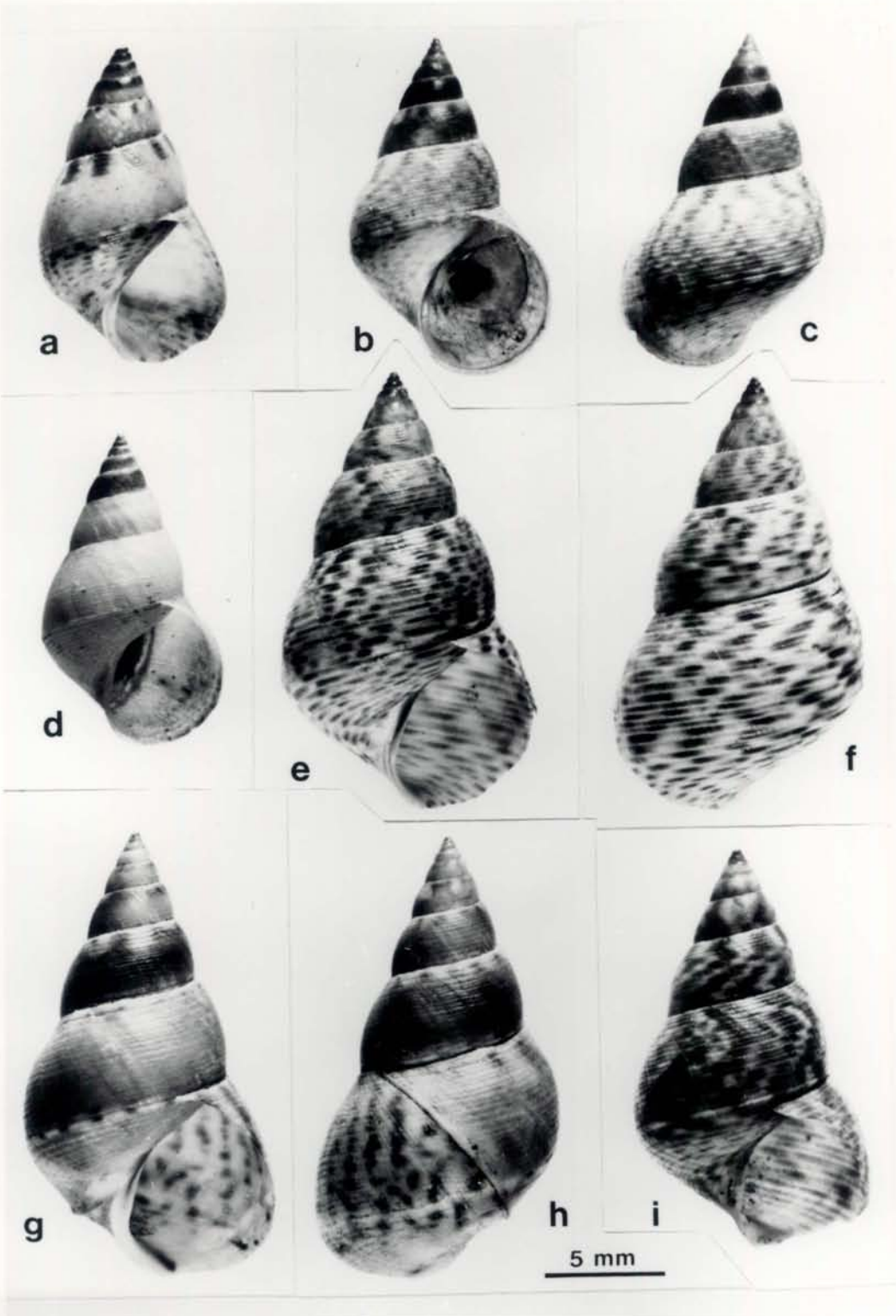

a
b
c
d
e
f
g
h
i
5 mm

Table 9.14 Dimensions of *Littoraria* (*Littorinopsis*) *delicatula*.

Specimen	Locality	Sex	Primary grooves	H (mm)	B (mm)	LA (mm)	WA (mm)	C (mm)	PR	S	SH
Littorina conica var. *delicatula* holotype, ZSI	Port Canning and False Point, Bengal, India	?♂	12	14.2	8.5	7.9	5.9	0.8	1.67	0.75	1.80
Littorina conica var. *subintermedia* lectotype, ZSI	Port Canning and False Point, Bengal, India	?♀	11	16.5	10.2	7.9	6.0	0.9	1.62	0.76	2.09
BMNH acc. 1944	Port Canning, Bengal	?♂	14	14.2	8.9	7.8	5.7	0.8	1.60	0.73	1.82
BMNH acc. 1944	Port Canning, Bengal	?♂	14	13.1	8.1	7.5	5.4	0.7	1.62	0.72	1.75
BMNH acc. 1944	Port Canning, Bengal	?♀	13	14.7	8.9	7.0	5.7	0.8	1.65	0.81	2.10
BMNH acc. 1944	Port Canning, Bengal	?♀	13	17.8	9.7	8.2	6.3	0.8	1.84	0.77	2.17
BMNH acc. 1944	unknown	?♀	12	18.5	10.7	9.1	7.0	1.2	1.73	0.77	2.03
BMNH	Port Canning, Bengal	?♀	12	17.9	11.0	8.3	6.1	0.5	1.63	0.73	2.16
BMNH 1969407	Andaman Is.	?♀	10	18.5	11.3	9.4	7.0	1.4	1.64	0.74	1.97

Sex of shells based on description of dimorphism by Nevill (1885).

may show brown dashes at suture and periphery only; darker shells heavily speckled, dashes aligned at suture and near periphery, forming short axial stripes, numbering 9–11 at suture of last whorl, a dark band just below periphery and around columella. Pattern clearly visible within aperture. Columella white or tinged with purple.

ANIMAL. Unknown.

DISTRIBUTION. *Habitat*. 'Trees and bushes far above high-tide mark' (Annandale & Prashad, 1919, p. 246). A habitat on leaves of mangroves would be predicted from the extreme fragility and bright colouration of the shell.

Range (Fig. 9.54). Bengal and Andaman Is.

Records. INDIA: Port Canning, Bengal (BMNH, USNM); ANDAMAN IS. (BMNH).

REMARKS. This species is very rare in museum collections. Shell thickness is variable; specimens from Port Canning, Bengal, are mostly extremely fragile, while a shell from the Andaman Islands is solid. Thin shells and colour polymorphism are typical of species living at high levels on leaves (e.g. *L. filosa*, *L. luteola*, *L. albicans*) so it is likely that *L. delicatula* occurs in a similar habitat. Characters of the animal are unknown, but the thin, colour polymorphic and sometimes varicose shell supports classification in the subgenus *Littorinopsis*.

SIMILAR SPECIES. *L. delicatula* is most likely to be confused with small, thin shells of *L. conica*. However, *L. delicatula* has a taller spire, varices are sometimes present, fresh shells are brilliantly coloured (Nevill, 1885) and the protoconch is not papillose. If the subgeneric placement of *L. delicatula* is correct, anatomical characters should immediately separate it from *L. conica*. Small specimens of *L. ardouiniana* may be similar, but *L. delicatula* can be

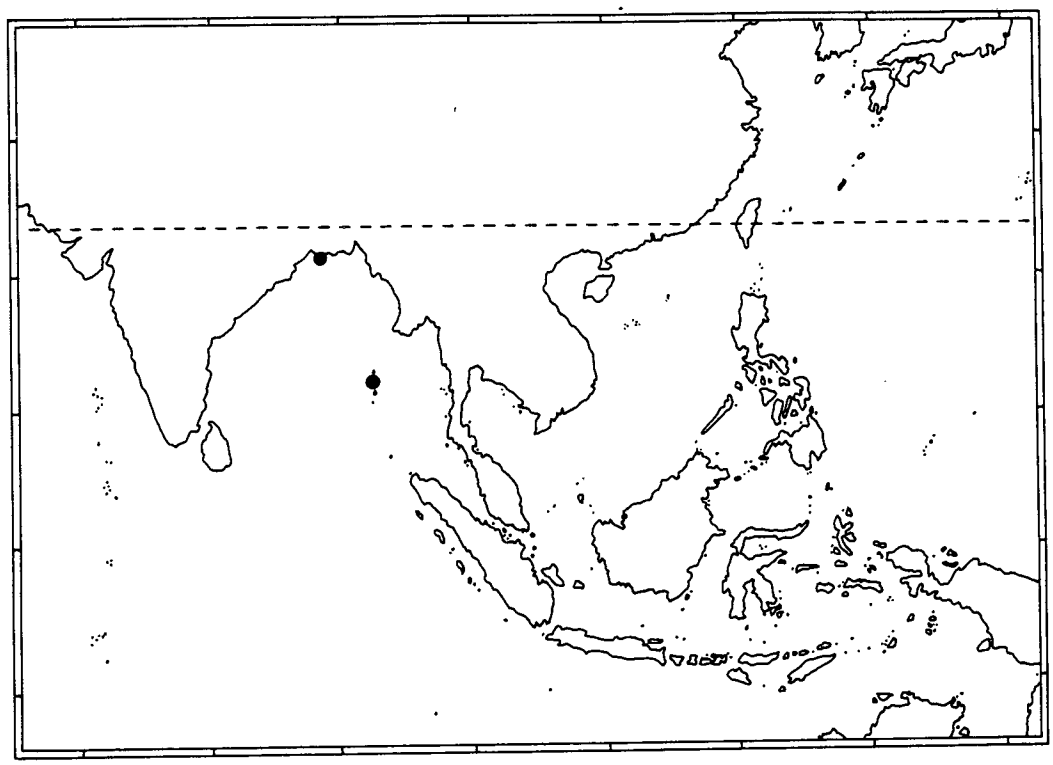


Fig. 9.54 Distribution of *Littoraria* (*Littorinopsis*) *delicatula*.

distinguished by its finer sculpture of almost equal ribs, separated by narrow grooves, by the more angular periphery, the thinner shell and the narrowly excavated columella. This last mentioned character is not always useful, since in specimens of *L. delicatula* with the thinnest shells the columella may be so narrow that the excavation is scarcely apparent, while in *L. ardouiniana* the columella is sometimes a little flattened. The ranges of *L. ardouiniana* and *L. delicatula* are not known to overlap. It is conceivable that additional specimens and anatomical evidence might indicate a closer relationship between these two species, but from present evidence they seem always to be distinct. *L. filosa, L. luteola* and *L. albicans* are only superficially similar to *L. delicatula*. Confusion with *L. undulata* should never arise.

9.2.4 Subgenus *Palustorina* n. subgen.

TYPE SPECIES: *Littoraria melanostoma* (Gray, 1839)

ETYMOLOGY. Condensation of Latin: *palustris*, swamp, and *Littorina*.

DIAGNOSIS. Shell usually solid; microsculpture, if present, of spiral striae on ribs and axial striae in grooves; shell colouration variable but not polymorphic; outer lip of aperture rarely flared; varices usually absent. Penial base simple, not bifurcate, glandular disc incorporated into base; penial sperm groove open. Sperm nurse cells flagellate. Bursa copulatrix opens near posterior end of straight section of pallial oviduct; capsule glands present. Development oviparous. Radula with 'hooded' rachidian tooth.

9.2.4.1 *Littoraria* (*Palustorina*) *melanostoma* (Gray, 1839)

Littorina melanostoma Gray, 1839: 140 [Penang, Malaysia; lectotype (Rosewater, 1970) BMNH 1968364]; Reeve, 1857: *Littorina* pl. 9, figs 45a,b; Nevill, 1885: 151; von Martens, 1887: 170; Annandale & Prashad, 1919: 245, fig. 2a [radula]; Yen, 1933: 94; Berry & Chew, 1973 [reproductive biology, ecology]

Litorina melanostoma – Philippi, 1847, vol. 2: 224–225, *Litorina* pl. 5, fig. 16; Weinkauff, 1878: 41, pl. 4, fig. 19

Litorina (*Melaraphe*) *melanostoma* – Tryon, 1887: 245, pl. 43, figs 42,43; Dautzenberg & Fischer, 1905: 148

Littorina (*Malaraphe*) *melanostoma* – Casto de Elera, 1896: 311

Littorina (*Littorinopsis*) *melanostoma* – von Martens, 1897: 199; Oostingh, 1923: 49–50, fig. 2; Rosewater, 1970: 462–464, pl. 325, figs 28,29, pl. 355, figs 1–4

Littoraria melanostoma – Habe & Kosuge, 1966: pl. 6, fig. 8

Littorinopsis melanostoma – Brandt, 1974: 55, pl. 4, fig. 63

Littorina melanostoma var. *articulata* Nevill, 1885: 151 [Hong Kong; lectotype here designated ZSI, 12.1 mm; not Philippi, 1846]

NOMENCLATURE. *Littorina melanostoma* var. *articulata* Nevill is simply a small form of the species; the lectotype is evidently adult, showing a somewhat thickened apertural lip, and resembles the dwarf forms found in salt marshes in Hong Kong.

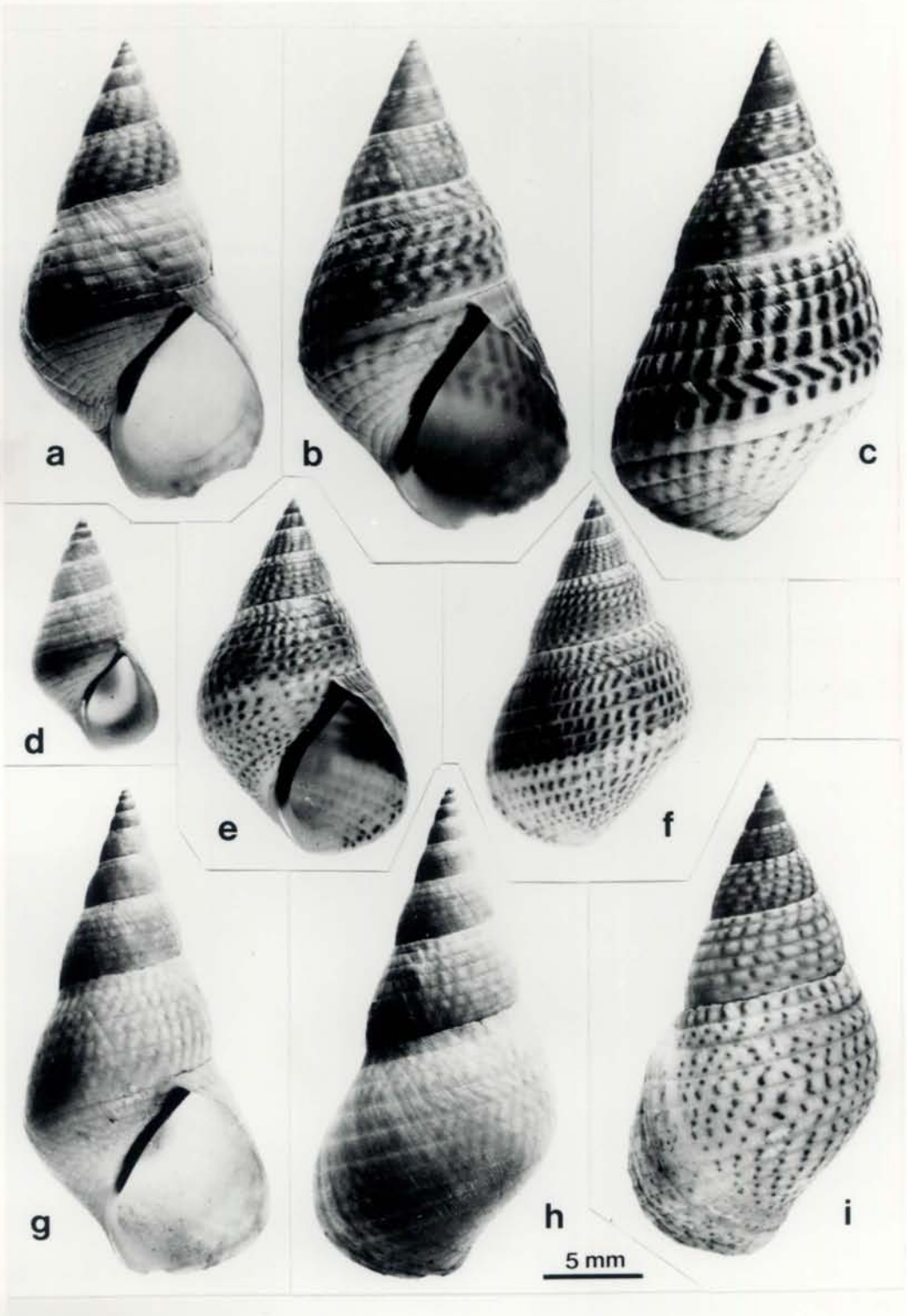
DIAGNOSIS. Shell: solid; spire tall, sides almost flat, sutures not impressed; periphery rounded; aperture elongate, somewhat quadrangular; columella narrow, rounded; primary grooves 6–8; secondary sculpture absent; ribs flat, numbering 15–17 on last whorl; grooves narrow; microsculpture of spiral striae on ribs, axial lines or pits in grooves; colour cream or yellow, usually with small brown spots aligned into axial series or stripes, numbering 27–40 on last whorl, aperture yellow, parietal callus and upper part of columella dark purple brown. Animal: penis not bifurcate, coarse annular wrinkles at posterior edge, filament fairly long; oviparous.

SHELL (Fig. 9.55). *Shape*. Height (12)20–31 mm. Teleoconch whorls 6.5–7.5. Shell of moderate thickness, solid. Spire tall, outline straight or slightly convex; whorls almost flat; sutures not impressed. Periphery roundly angled in young shells, last whorl more evenly rounded. Aperture rather elongate, somewhat quadrangular; adult lip scarcely thickened, not flared. Varices absent. Columella narrow, rounded, not excavated; pillar concave. Sexual dimorphism: not significant.

Dimensions: Table 9.15.

Sculpture (Fig. 9.56a,c,d). Protoconch normal. All whorls of teleoconch sculptured with spiral grooves. Primary grooves 6–8, equally spaced or 2 posterior ribs narrower. Secondary sculpture absent. Ribs remain flat, of approximately equal width, often a little narrower at suture and periphery, numbering (13)15–17(19) on last whorl. Grooves narrow, less than $\frac{1}{6}$ width of ribs on last

Fig. 9.55 *Littoraria* (*Palustorina*) *melanostoma*: (a) lectotype of *Littorina melanostoma* Gray, Penang, Malaysia (BMNH 1968364); (b,c) Port Canning, Bengal, India (BMNH); (d) lectotype of *Littorina melanostoma* var. *articulata* Nevill, Hong Kong (ZSI); (e,f) ♀, Ubin I., Singapore (DGR); (g,h) Mergui Arch., Burma (BMNH); (i) ♂, Kanchanadit, Thailand (DGR).


a
b
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g
h
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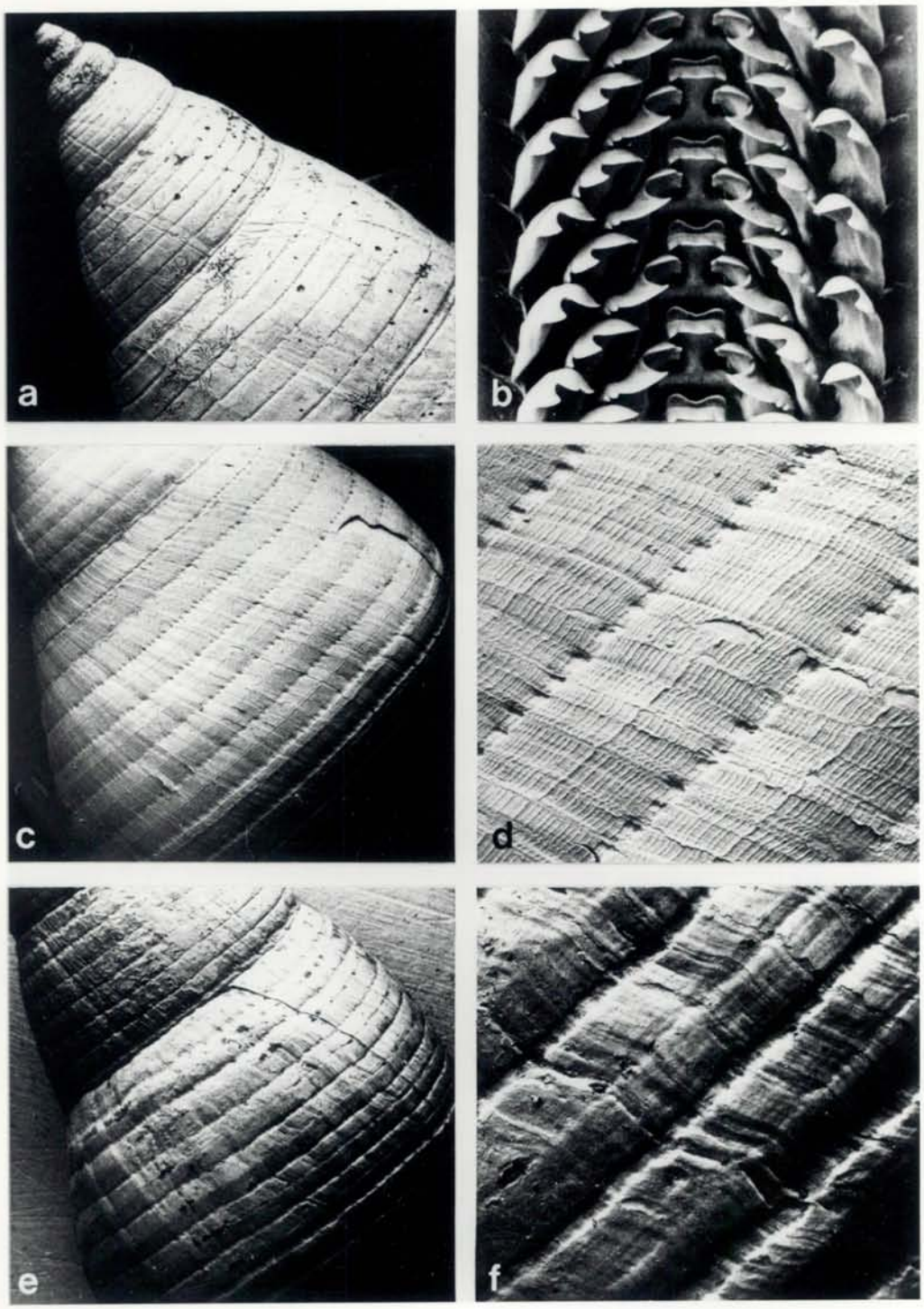
5 mm

Table 9.15 Dimensions of *Littoraria* (*Palustorina*) *melanostoma*.

Specimen	Locality	Sex	Primary grooves	H (mm)	B (mm)	LA (mm)	WA (mm)	C (mm)	PR	S	SH
Littorina melanostoma lectotype, BMNH 1968364	Penang, Malaysia		7	23.7	13.7	12.3	8.1		1.73	0.66	1.93
Littorina melanostoma var. *articulata* lectotype, ZSI	Hong Kong		6	12.1	7.1	6.5	4.5	0.7	1.70	0.69	1.86
BMNH acc. 2176	Port Canning, Bengal, India		7	29.9	16.5	14.6	10.0	1.8	1.79	0.68	2.05
BMNH	Port Canning, Bengal, India		7	28.7	16.9	15.5	10.1	1.5	1.70	0.65	1.85
DGR	Kanchanadit, Thailand	♂	6	29.0	16.2	14.2	9.0	1.5	1.79	0.63	2.04
DGR	Kanchanadit, Thailand	♂	6	19.7	10.7	9.9	6.1	0.9	1.84	0.62	1.99
DGR	Kanchanadit, Thailand	♀	6	24.0	13.4	12.0	8.0	1.3	1.79	0.67	2.00
DGR	Kanchanadit, Thailand	♀	6	20.6	11.1	10.4	6.4	1.1	1.86	0.62	1.98
DGR, mean of 10	Kanchanadit, Thailand	♂		24.80					1.801	0.639	1.980
standard error				0.58					0.019	0.007	0.019
DGR, mean of 10	Kanchanadit, Thailand	♀		23.83					1.753	0.647	1.952
standard error				0.58					0.018	0.005	0.026
statistic t or U				1.183					72	65	62
probability				0.252					0.106	0.280	0.394

Fig. 9.56 (a–d) *Littoraria* (*Palustorina*) *melanostoma*: (a) spire, Ubin I., Singapore (×20); (b) radula, Kanchanadit, Thailand (×170); (c,d) Ubin I., Singapore; (c) last whorl (×8); (d) detail (×31). (e,f) *Littoraria* (*Palustorina*) *flammea*, China: (e) last whorl (×8); (f) detail (×31).


a
b
c
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e
f

whorl. Microsculpture of strong, regular, spiral striae covering surface; stria at mid point of each rib may be a little more prominent, but never develops into a secondary groove. Faint axial growth lines are stronger in grooves, which may appear pitted on last whorl.

Colour. Rather constant. Ground colour pale yellow or cream, fading to white; very rarely pale pink. Pattern of numerous red brown vertical bars on ribs, aligned to form narrow axial stripes, 27-40 on last whorl; pattern sometimes reduced to lines of dots or to a scarcely visible mottling; in darkest shells stripes almost cover surface, but pattern becomes abruptly paler below periphery. Apical 5 whorls may be tinged lilac grey or pink. Aperture pale yellow, exterior pattern only visible in darkest shells. Parietal callus and upper part of columellar pillar dark purple brown, lower part of pillar white.

ANIMAL. *Colour*. Pigmenation pale grey to black; sides of foot pale, mottled, and with conspicuous opaque white flecks; snout grey to black, rest of head pale; tentacles banded, broad unpigmented patch at base, dark stripe behind eye.

Penis (Fig. 9.57a-g). Length to 5.8 mm. Base simple, incorporating glandular disc; prominent annular wrinkles at posterior edge. Filament fairly long, tapering near tip. Sperm groove open. Base and filament white to cream, glandular disc opaque white.

Sperm. Eupyrene sperm 256-287 μm. Nurse cells (Fig. 9.57j-l) 33-50 μm, elongate oval, tapering at base; basal flagellum to 160 μm; rods 1-4, usually basal, narrowly elongate; yolk granules small, becoming larger towards base.

Pallial oviduct (Figs 5.5, 5.6). Length to 8.2 mm. Spiral section to 7.3 mm diam., $6\frac{1}{2}$ whorls; opaque albumen gland $\frac{1}{3}$ whorl, white; translucent albumen gland white to pale grey; opaque capsule gland

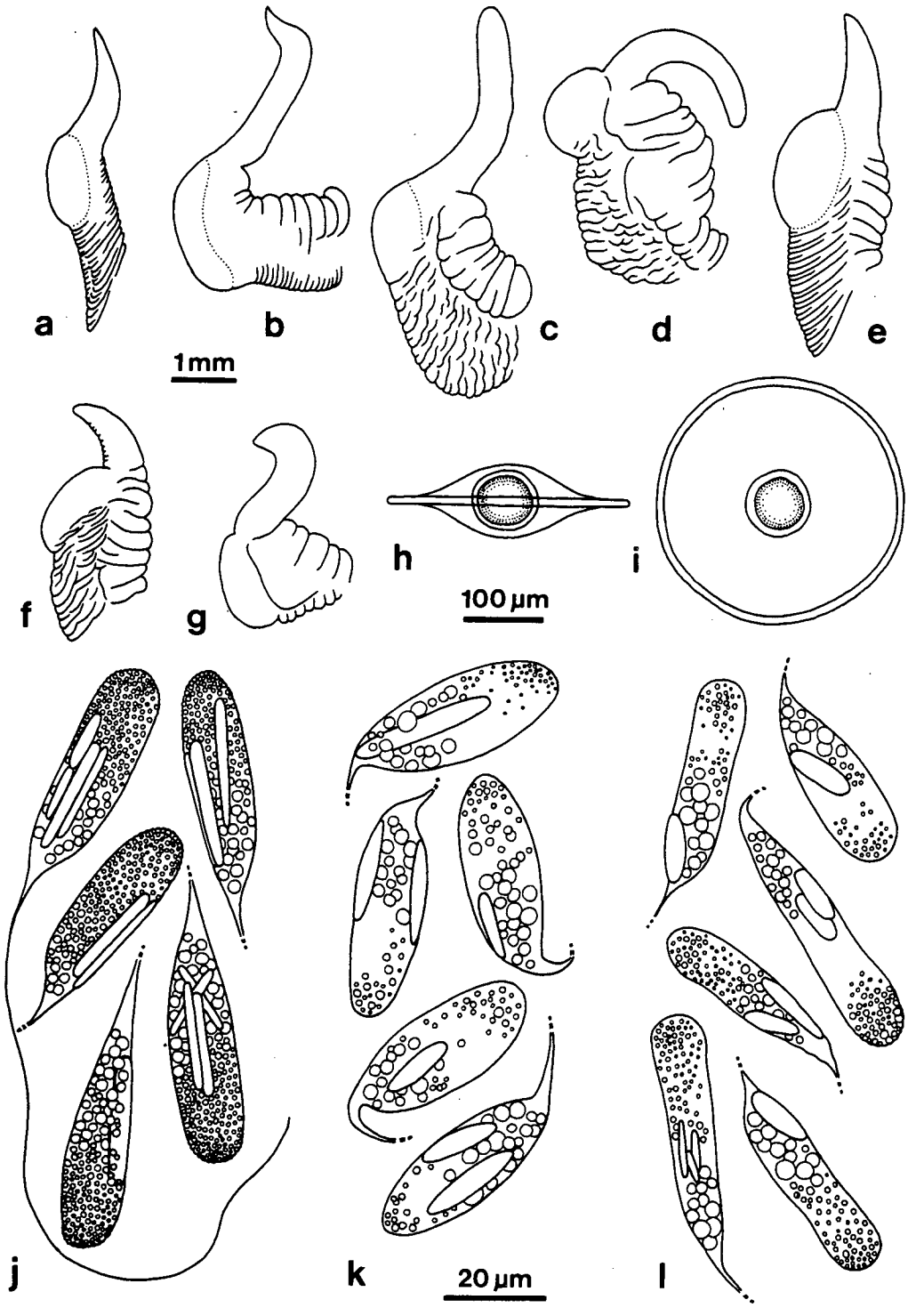

Fig. 9.57 *Littoraria (Palustorina) melanostoma*: (a-g) penes; (a,b) Santubong, Sarawak; (c) Kanchanadit, Thailand; (d) Three Fathoms Cove, Hong Kong; (e,f) Ubin I., Singapore; (g) Three Fathoms Cove, Hong Kong; (h,i) egg capsule, W. Malaysia (after Berry & Chew, 1973); (j-l) sperm nurse cells, flagellum shown on one only; (j) Kanchanadit, Thailand; (k,l) Ubin I., Singapore.

1½ whorls, pale pink; translucent capsule gland red brown; spiral distinct externally; egg groove darkly pigmented. Straight section to 3.5 mm, pale grey to brown; no terminal papilla. Bursa posterior, extending into spiral section. Development oviparous (Berry & Chew, 1973).

Egg capsules (Fig. 9.57h,i, after Berry & Chew, 1973). Capsule 290–310 μm diam., symmetrically biconvex disc, with narrow circumferential flange; containing single ovum 120–140 μm diam.

Radula (Fig. 9.56b). Length to 26 mm; relative length 0.61–0.94. Chisel-toothed type; central rachidian cusp wide, same length as two small flanking cusps, giving almost continuous cutting edge; cusps of paired teeth extremely obliquely triangular, minor cusps reduced; lateral with gap anterior to main cusp.

DISTRIBUTION. *Habitat*. On trunks and sometimes leaves in *Avicennia* fringe, 0.3–1.8 m above ground, only on the outermost trees in very sheltered situations; most common at back of *Avicennia* zone and in outer parts of *Rhizophora* forest; roots and occasionally leaves in *Rhizophora* forest, 0.2–0.6 m above ground; scarce in *Bruguiera* zone. Juveniles occur mainly on leaves. Berry & Chew (1973) report juveniles amongst marsh grass. A continental species.

Range (Fig. 9.58). South East Asia, from southern India and Bay of Bengal to north coast of Java and southern China.

Records. INDIA: Manali I., off Mandapam (MCZ); Port Canning, Bengal (BMNH, RNHL); Calcutta (BMNH, AMS); ANDAMAN IS.: Port Blair (BMNH); SRI LANKA (BMNH); BURMA: Pegu Estuary (BMNH); Mergui (BMNH); THAILAND: Chonburi (ANSP, RNHL); Kanchanadit, near Surat Thani (DGR); Pakpun, Nakhon Si Thammarat (USNM); MALAYSIA: PENINSULA: Batu Maung, Penang (DGR); Kuala Selangor (ANSP); 10 km N. of Port Kelang (DGR); SARAWAK: Santubong (DGR); SINGAPORE: Jelutong, Ubin I. (DGR); Kranji (BMNH); INDONESIA: SUMATRA: Weh I. (RNHL); JAVA: Tandjong Priok, Djakarta (RNHL); Tjirebon (RNHL); Pandjang I., near Djepara

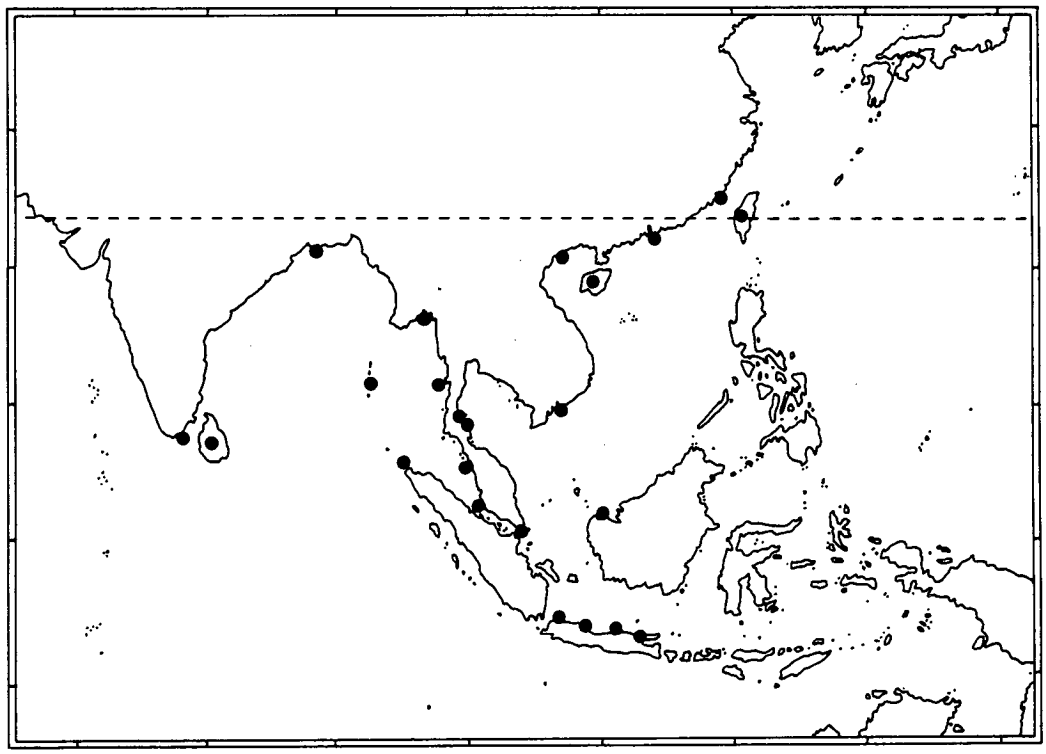

Fig. 9.58 Distribution of *Littoraria* (*Palustorina*) *melanostoma*.

(RNHL); Surabaja (RNHL); VIETNAM: Chilins, Vung Tau district (ANSP); Do Son, Tonkin (RNHL); CHINA: Hainandao I. (ANSP); Amoy (ANSP, RNHL); HONG KONG: Three Fathoms Cove, New Territories (BMNH); Tai Tam Harbour (AMS); TAIWAN (USNM).

REMARKS. This is a well known and distinctive species. As the type of the new subgenus *Palustorina*, the anatomy, especially that of the female reproductive tract, is discussed in some detail in the introductory sections. The radula is remarkable for the reduction in numbers of effective cusps, a feature shared with *L. conica*, but not found to such an extent in other members of the genus. Shell shape is constant, but degree of pigmentation shows some variation. The occurrence of a very few shells with pale pink ground colour is noteworthy, since this colour form is extremely rare in the subgenus, recorded elsewhere only in *L. articulata*. A possibly homologous pink morph is more frequent in the polymorphic species of the subgenus *Littorinopsis*. The relationship of *L. melanostoma* with *L. flammea* is discussed in the remarks upon the latter species.

SIMILAR SPECIES. *L. melanostoma* is so distinctive that confusion with any other species should not arise. *L. flammea* is the most similar, but the shell of *L. melanostoma* is more solid, the sides of the spire are straight, and the axial stripes or rows of aligned dots are more numerous.

9.2.4.2 *Littoraria (Palustorina) flammea* (Philippi, 1847)

Litorina flammea – Philippi, 1847, vol. 3: 16, *Litorina* pl. 6, fig. 21 [China; lectotype here designated MNHNP, 19.5 mm]; Weinkauff, 1882: 56–57, pl. 7, figs 9,12

Littorina flammea – Reeve, 1857: *Littorina* pl. 9, figs 46a,b

Littorina (Melaraphe) flammea – Tryon, 1887: 245, pl. 43, figs 34,35 [in part]

Littorina (Malaraphe) flammea - Casto de Elera, 1896: 311 [in part]
Melarhaphe flammea - Yen, 1942: 196
Littorina fortunei Reeve, 1857: *Littorina* pl. 9, figs 42a,b [China; lectotype (Rosewater, 1970) BMNH 1968309]
Littorina (Littorinopsis) scabra scabra - Rosewater, 1970: 456-461, pl. 352, figs 3,4 [in part; not Linnaeus, 1758]

NOMENCLATURE. Rosewater (1970) designated the lectotype of *Litorina flammea* from amongst a lot of four specimens in the Cuming Collection (BMNH), supposing that the shell was that figured by Philippi (1847). The resemblance of the shell to the figure is indeed close. However, there is no documentary evidence to support the designation since, regarding the origin of the shell, Philippi merely notes the locality as China and that it was received from Largilliert. An old label accompanying the specimens and another by Tomlin record the locality of the shells as the Philippines. Nevertheless, Philippi did not in every case mention the origin of figured specimens when these were from Cuming (e.g. *L. intermedia*) and some mixing of labels could have occurred. The lectotype *Littorina fortunei* Reeve was selected by Rosewater from the same lot, but does not bear close resemblance to Reeve's figure, although shell and figure are undoubtedly of the same species. Evidently Reeve himself did not recognize these shells as syntypes of Philippi's species, for he figured a broader shell from another lot as *Littorina flammea* Philippi. In the MNHNP are three shells of *L. flammea* from the Largilliert Collection housed in the Natural History Museum in Rouen (P. Bouchet, pers. comm.). It seems appropriate to redesignate as lectotype one of these which closely resembles Philippi's figure.

DIAGNOSIS. Shell: rather thin; spire tall, outline convex, whorls lightly rounded; aperture elongate; varices may be present; columella narrow, rounded; primary grooves 7-9; secondary sculpture absent; total of 16-20 low, rounded ribs on last whorl, with narrow grooves between; microsculpture of spiral striae on ribs, axial striae or pits in grooves; colour white to cream, pattern of narrow,

brown, oblique axial stripes from suture to periphery, numbering 9–10 on last whorl; columella and parietal callus purple brown.

SHELL (Fig. 9.59). *Shape*. Height 16–20 mm. Teleoconch of about 7 whorls. Shell rather thin. Spire tall, outline gently convex; whorls only slightly rounded; sutures a little impressed. Peripheral keel absent. Aperture elongate; adult lip a little flared, not thickened. Varices 0–1(4). Columella narrow, rounded, not excavated; pillar concave. Sexual dimorphism: unknown.

Dimensions: Table 9.16.

Sculpture (Fig. 9.56e,f). Protoconch not seen. Primary grooves 7–9, equally spaced, or posterior 2 ribs a little narrower. Secondary sculpture absent. Ribs remain low and rounded, of similar width, but slightly narrower at suture and periphery; total of 16–20 on last whorl. Grooves narrow, $\frac{1}{6}$–$\frac{1}{3}$ rib width on last whorl; widest groove is that just below peripheral rib, which is $\frac{1}{2}$–1 width of this rib. Microsculpture of spiral striae on ribs, sometimes indistinct; on last whorl central stria of each rib is pronounced, but does not develop into secondary sculpture, seeming to be only a projection of the periostracum; irregular axial growth striae cover surface, stronger in grooves, which may appear pitted on last whorl.

Colour. Ground colour whitish or cream; pattern of red brown, oblique axial stripes from suture to periphery; stripes are narrow and distant, usually interrupted by primary grooves, and number 9–10 on last whorl; pattern becomes faint on base. External pattern visible within aperture. Columella and parietal callus purple brown or pink.

ANIMAL. Unknown.

DISTRIBUTION. *Habitat*. Unknown.

Fig. 9.59 *Littoraria (Palustorina) flammea*, China: (a,b) lectotype of *Litorina flammea* Philippi (MNHNP); (c) specimen designated lectotype of *Litorina flammea* Philippi by Rosewater (1970) (BMNH 1968310); (d) (BMNH); (e) lectotype of *Littorina fortunei* Reeve (BMNH 1968309); (f) (BMNH); (g) paralectotype (MNHNP); (h,i) paralectotype (MNHNP).

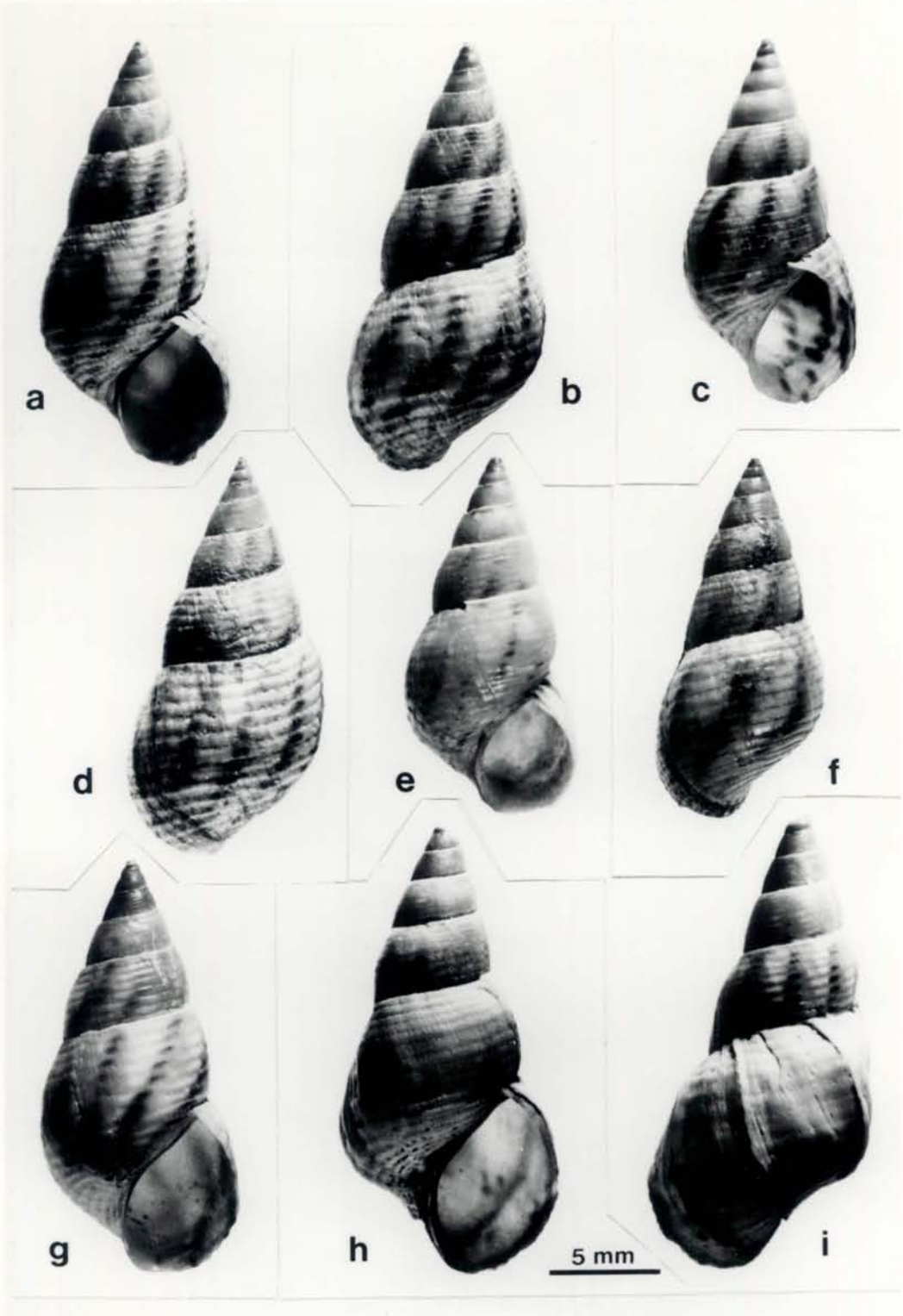
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Table 9.16 Dimensions of *Littorarta* (*Palustorina*) *flammea*.

Specimen	Locality	Sex	Primary grooves	H (mm)	B (mm)	LA (mm)	WA (mm)	C (mm)	PR	S	SH
Litorina flammea lectotype, MNHNP	China		8	19.5	9.2	8.0	5.1	0.6	2.12	0.64	2.44
paralectotype, MNHNP	China		9	20.5	9.9	9.4	6.3	0.8	2.07	0.67	2.18
Littorina fortunei lectotype, BMNH 1968309	[China]		8	16.1	8.5	6.5	4.6		1.89	0.71	2.48
BMNH 1968310	[China]		8	16.7	7.4	7.9	4.8	0.6	2.26	0.61	2.11
BMNH acc. 1829	China		8	16.1	8.9	7.8	4.8	0.5	1.81	0.62	2.06
BMNH acc. 1829	China		7	15.9	8.0	7.3	4.6	0.4	1.99	0.63	2.18
BMNH acc. 1829	China		8	17.8	9.1	8.5	4.9	0.5	1.96	0.58	2.09
BMNH acc. 1829	China		8	15.4	8.0	7.0	4.4	0.4	1.93	0.63	2.20

Range. Recorded from 'China' in literature and on museum labels. A doubtful record from Mindoro, Philippines (Casto de Elera, 1896).

Records. CHINA (BMNH, MNHNP, MCZ).

REMARKS. This species is very rare in museum collections; all material seen dates from the early nineteenth century and none is localized more precisely than 'China'. Since the species is not known from Indochina, Hong Kong or Japan, it is possible that it occurs on the shores of the East China Sea or the Yellow Sea. Despite the record by Casto de Elera (1896) and the label accompanying one collection in the BMNH, occurrence in the Philippines appears most unlikely, for large collections of other littorinids are available from the area.

The animal of *L. flammea* is unknown, but the species is placed in the subgenus *Palustorina* on the basis of the resemblance of the shell to that of *L. melanostoma*. The most significant similarity is the type of microsculpture, but other points of resemblance include the dark colouration of the parietal callus, narrow columella, elongate spire and pronounced axial alignment of the colour pattern. Despite these similarities, it does not at present seem possible that *L. flammea* could be a form of *L. melanostoma*. The latter is a species of constant characters throughout its rather wide range; even specimens from Hong Kong and Amoy on the Chinese coast are entirely typical and do not approach *L. flammea*. Furthermore, the few shells of *L. flammea* available are closely similar to each other.

SIMILAR SPECIES. *L. flammea* could be confused only with *L. melanostoma*, but is distinguished from that species by its thinner shell, more convex spire outline and by the pattern of fewer axial stripes. Authors have compared this species with *L. luteola*, but in the latter the shell sculpture and colouration are quite different, as, if the subgeneric placement of *L. flammea* is correct, the animal may be also.

9.2.4.3 *Littoraria* (*Palustorina*) *conica* (Philippi, 1846)

Littorina conica Philippi, 1846: 141 [Java; lectotype (Rosewater, 1970) BMNH 1968225]; Reeve, 1857: *Littorina* pl. 8, figs 36a,b; Nevill, 1885: 149 [in part]

Litorina conica – Philippi, 1847, vol. 3: 9, *Litorina* pl. 6, figs 1,2; Weinkauff, 1882: 54, pl. 7, figs 1,4

Littorina (*Melaraphis*) *conica* – Tapparone-Canefri, 1874: 48

Littorina (*Littorinopsis*) *conica* – von Martens, 1897: 198; Prashad, 1921: 485; Oostingh, 1927

Littorinopsis conica – Kuroda & Habe, 1952: 64; Brandt, 1974: 55, pl. 4, fig. 64

Littoraria conica – Higo, 1973: 46

Littorina (*Melaraphe*) *undulata* – Tryon, 1887: 244, pl. 43, fig. 41 [in part; not Gray, 1839]

Littorina (*Littorinopsis*) *carinifera* – Rosewater, 1970: 464–465, pl. 355, figs 10,11 [in part; not Menke, 1830]

NOMENCLATURE. Philippi described *Littorina conica* from specimens in the Cuming Collection, giving the type locality as Java. Rosewater (1970) designated as lectotype a shell in a lot from this collection which bears some resemblance to the figure of Philippi (1847). However, no original label exists and labels in Tomlin's hand give the locality as 'Japan', possibly misled by Reeve (1857) who also gives this locality for his figure. This might perhaps be an error for 'Java'; no specimens with reliable data have been seen from Japan, although the species appears in several Japanese faunal lists, possibly on the basis of Reeve's record. Philippi (1847) did not mention the owner of the figured shell in this case, but did not invariably do so (e.g. *L. intermedia* and its 'varieties'). From the available evidence the lectotype designation seems acceptable. Sowerby (1825) described *Turbo conicus*, a species of Upper Albian age from the Blackdown Greensand and subsequently (1840) referred it to the genus *Littorina*. This is a problematical species, but does not belong to either of the genera *Littorina* or *Littoraria* (N.J.

Morris & R. Cleevely, pers. comm.).

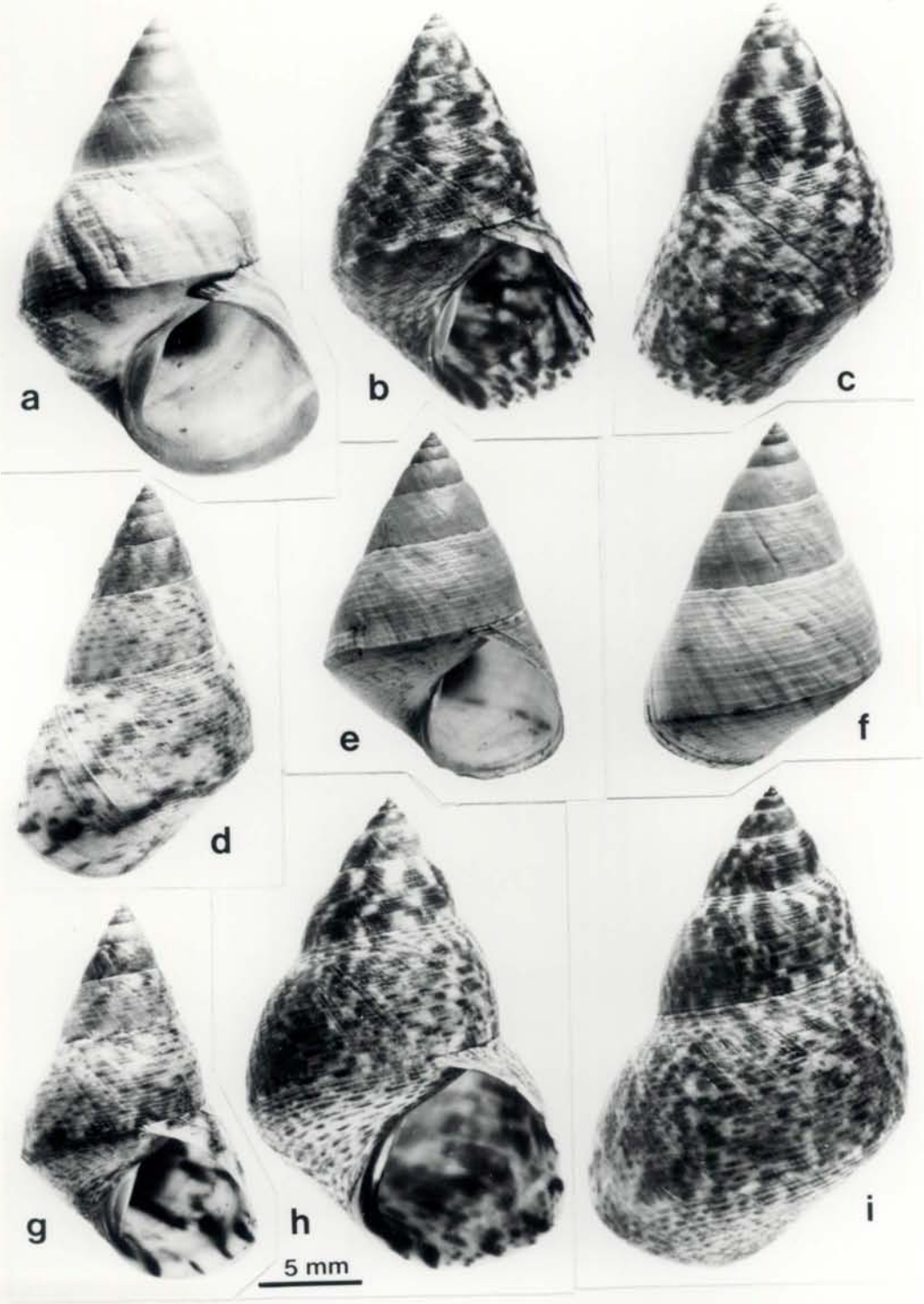
DIAGNOSIS. Shell: apex blunt with papillose protoconch; spire outline convex, whorls flattened, sutures scarcely impressed; peripheral keel prominent; columella excavated, pillar convex; primary grooves 10–12; total of 50–70 flat ribs on last whorl, with narrow grooves between; microsculpture indistinct; colour variable, cream, usually with dense pattern of brown flecks, aligned into axial stripes only on spire whorls. Animal: penis not bifurcate, filament long, tapering; oviparous.

SHELL (Fig. 9.60). *Shape*. Height 16–25 mm. Teleoconch 5.5–6.5 whorls. Shell of moderate thickness, solid. Spire outline convex; first whorls of teleoconch are broad, so that apex appears blunt with a papillose protoconch; first 3 whorls rounded, subsequent whorls become flattened; sutures scarcely impressed. Peripheral keel prominent, becoming obsolete at end of last whorl. Adult lip only slightly thickened, not usually flared. Varices rare, usually merely strong growth lines behind lip. Columella of moderate width, excavated; pillar noticeably convex, narrowed at base. Sexual dimorphism: males smaller, relatively lower spire and larger aperture, aperture more elongate.

Dimensions: Table 9.17.

Sculpture (Fig. 9.61a,c,d). Protoconch of normal shape (sculpture not seen). First whorl of teleoconch probably smooth. Primary grooves (9)10–12(13) by whorl 4; posterior 4 ribs about half width of the equally spaced ribs over rest of whorl, having been formed by division of 2 larger ribs on earlier whorls. On whorls 4–5 primary ribs become divided by secondary grooves at anterior $\frac{1}{3}$–$\frac{1}{2}$ width; posterior 4 ribs divide later. Tertiary grooves appear on whorl 6. Grooves remain narrow, less than $\frac{1}{5}$ width of widest ribs on last whorl; all grooves are of similar size, spaced rather unevenly across surface of last whorl to produce 50–70 ribs. All ribs remain low and flat, that at periphery often a little more prominent owing

Fig. 9.60 *Littoraria* (*Palustorina*) *conica*: (a) lectotype of *Littorina conica* Philippi, Java (BMNH 1968225); (b,c) ♂, Santubong, Sarawak (DGR); (d–g) Sungei Merbok estuary, Malaysia (DGR); (d,g) ♂; (e,f) ♀; (h,i) ♀, Santubong, Sarawak (DGR).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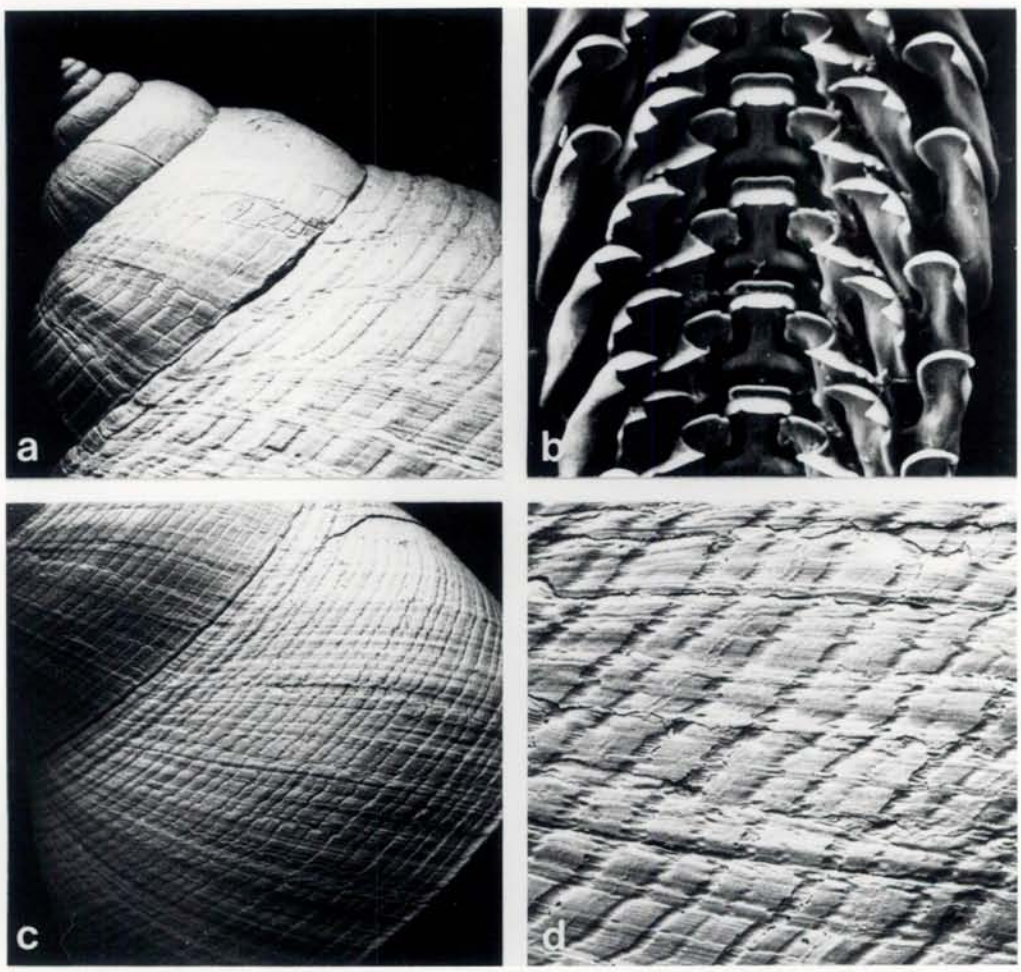
5 mm

Table 9.17 Dimensions of *Littoraria (Palustorina) conica*.

Specimen	Locality	Sex	Primary grooves	H (mm)	B (mm)	LA (mm)	WA (mm)	C (mm)	PR	S	SH
Littorina conica lectotype, BMNH 1968225	Java		11	22.3	15.5	12.8	9.5	2.1	1.44	0.74	1.74
DGR	Sungei Merbok, Malaysia	♂	11	18.2	11.9	10.3	7.5	1.5	1.53	0.73	1.77
DGR	Sungei Merbok, Malaysia	♀	10	21.5	14.3	11.7	9.2	2.0	1.50	0.79	1.84
DGR	Santubong, Sarawak	♂	11	19.7	14.2	12.0	8.6	1.4	1.39	0.72	1.64
DGR	Santubong, Sarawak	♂	10	18.9	13.1	11.1	8.2	1.7	1.44	0.74	1.70
DGR	Santubong, Sarawak	♀	10	22.6	15.9	13.0	10.2	2.5	1.42	0.78	1.74
DGR	Santubong, Sarawak	♀	10	21.3	14.6	12.4	9.5	2.3	1.46	0.77	1.72
DGR, mean of 10	Santubong, Sarawak	♂		18.12					1.428	0.734	1.687
standard error				0.48					0.011	0.004	0.013
DGR, mean of 10	Santubong, Sarawak	♀		20.59					1.431	0.761	1.730
standard error				0.67					0.011	0.004	0.010
statistic t or U				2.999					55.5	94	79
probability				0.008					0.712	<.001	0.028

Fig. 9.61 *Littoraria* (*Palustorina*) *conica*: (a) spire, Santubong, Sarawak (×18); (b) radula, Penang, Malaysia (×220); (c,d) Santubong, Sarawak; (c) last whorl (×7); (d) detail (×27).


a
b
c
d

to slightly greater width and to sharp angulation of shell. Microsculpture of irregular axial growth striae covering surface, stronger in grooves, which may appear pitted on last whorl; faint spiral striae sometimes visible.

Colour. Variable. Ground colour cream or pale brown, usually with pattern of dark brown flecks and dashes densely scattered over surface. Pattern often roughly aligned on spire to form axial stripes numbering 11–13 per whorl, but last whorl is uniformly speckled and flecked with dark pigment. Degree of pigmentation varies; uniform cream shells entirely lacking pigment are not infrequent. Purple brown flecks and dashes corresponding to external pattern are visible within aperture, clouded by a thin whitish callus. Columella and parietal callus dark purple, occasionally white in palest shells; columella pillar whitish in all individuals.

ANIMAL. *Colour*. Pigmentation grey to black; sides of foot darkly mottled; head darkest; tentacles banded, unpigmented stripe each side of base.

Penis (Fig. 9.62a–c). Length to 6.1 mm. Base simple, incorporating glandular disc. Filament long, tapering. Sperm groove open. Base and filament fawn, glandular disc pale brown.

Sperm. Eupyrene sperm 308–344 μm. Nurse cells (Fig. 9.62g–i) 35–51 μm, elongate oval or fusiform, usually with mucronate or papillose apex; basal flagellum to 250 μm; rods 1(2), basal, lozenge shaped to rounded oval; yolk granules small, becoming larger towards base.

Pallial oviduct (Fig. 9.62d–f). Length to 7.6 mm. Spiral section to 5.7 mm diam., $5\frac{1}{2}$ or $6\frac{1}{2}$ whorls; opaque albumen gland $\frac{1}{4}$ whorl, white; translucent albumen gland off white; opaque capsule gland 1 whorl, pale pink; translucent capsule gland pink to red brown; spiral usually distinct externally; egg groove darkly pigmented. Straight section to 4.0 mm, pale brown; no terminal

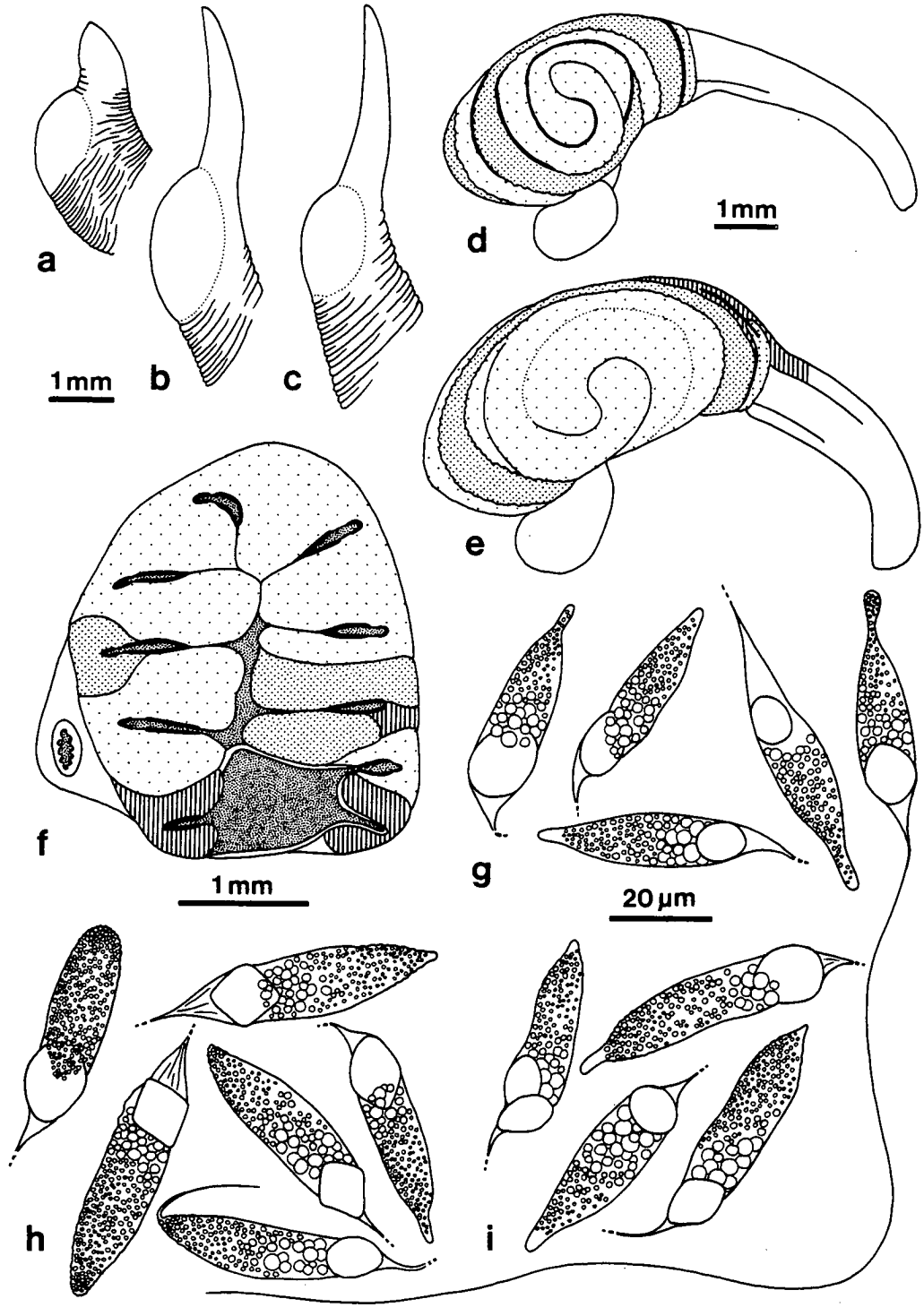


Fig. 9.62 *Littoraria (Palustorina) conica*: (a–c) penes, Santubong, Sarawak; (a) contracted; (b,c) relaxed; (d–f) pallial oviducts, with transverse section; (d) Santubong, Sarawak; (e,f) Penang, Malaysia; (g–i) sperm nurse cells, flagellum shown on one only; (g) Penang, Malaysia; (h,i) Santubong, Sarawak.

papilla. Bursa posterior, extending into spiral section. Development assumed oviparous.

Radula (Fig. 9.61b). Length to 28 mm; relative length 1.21–1.53. Chisel-toothed type; central rachidian cusp wide, same length as 2 small flanking cusps, giving almost continuous cutting edge; cusps of paired teeth extremely obliquely triangular, minor cusps reduced; lateral with gap anterior to main cusp.

Alimentary system. Anterior pair of oesophageal pouches large, to 1.9 mm diam., dark red and glandular. Mid-oesophagus also dark red and glandular.

DISTRIBUTION. *Habitat*. Occasional in *Bruguiera* and *Ceriops* zones, but typically found in the landward fringe, on trunks and leaves of *Avicennia, Excoecaria, Acanthus, Nypa* and others, 0.2–2.0 m above the ground. A continental species.

Range (Fig. 9.63). Southern Burma, west coast of Malay Peninsula, north-eastern Sumatra, Java, Borneo and southern Vietnam.

Records. BURMA: King I., Mergui Arch. (BMNH); MALAYSIA: PENINSULA: Batu Maung, Penang (DGR); 10 km N. of Port Kelang (DGR); SARAWAK: Santubong (DGR); SABAH: Po Bui I., Sandakan (USNM); SINGAPORE: Ubin I. (DGR); Kranji (ANSP); INDONESIA: SUMATRA: Belawan R., Deli (RNHL); JAVA (Philippi, 1846); KALIMANTAN: Boeloengan (MCZ); VIETNAM: Chilins, Vung Tau district (ANSP).

REMARKS. *L. conica* is a distinctive species which has in the past been well known, despite its restricted range and infrequent occurrence in museum collections. The species is a typical member of the subgenus *Palustorina*. Noteworthy anatomical features include the chisel-toothed radula, like that of *L. melanostoma*, and the anterior pair of oesophageal pouches which, like those of *L. cartnifera*, are red and glandular. The form and sculpture of the shell are constant, but colouration shows considerable variation. Shells from leaves and

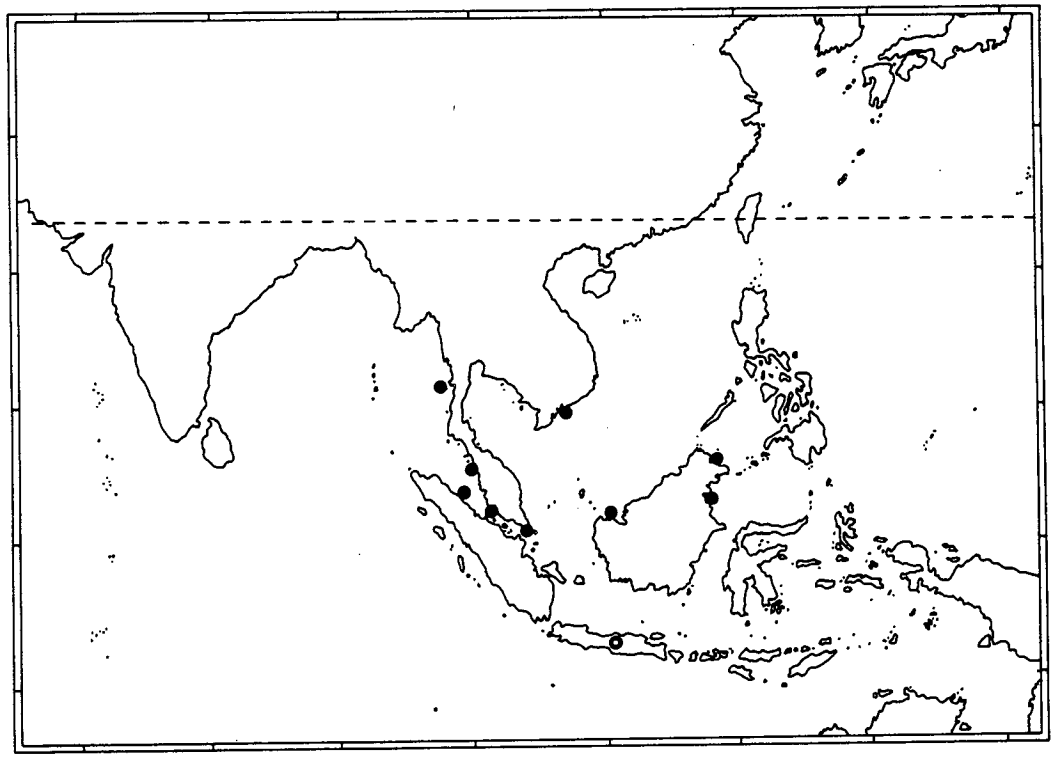


Fig. 9.63 Distribution of *Littoraria* (*Palustorina*) *conica*.

trunks of *Avicennia* and *Excoecaria* are often the palest in colour. Together with *L. carinifera*, this species is characteristically found in the landward fringe of the mangrove forest.

SIMILAR SPECIES. *L. carinifera* shares the strong peripheral keel of this species, but colour pattern and shell sculpture are at once diagnostic of each. Small specimens may be confused with *L. delicatula*, but in *L. conica* the protoconch projects as a papilla from the large first whorl of the teleoconch, the shell is broader, the columella wider and varices are absent. The animal of *L. delicatula* is unknown, but if placement of the species in the subgenus *Littorinopsis* is correct, then anatomical features should readily separate it from *L. conica*. Despite Tryon's synonymy, confusion with *L. undulata* should never occur.

9.2.4.4 *Littoraria* (*Palustorina*) *carinifera* (Menke, 1830)

Phasianella carinifera Menke, 1830: 51,141 [lectotype figure (Rosewater, 1970) Philippi, 1847, vol. 2: *Litorina* pl. 5, fig. 22; type locality Negros Occidental, Philippines]

Litorina carinifera - Philippi, 1847, vol. 2: 227, *Litorina* pl. 5, figs 22-24; Weinkauff, 1882: 48-49, pl. 6, figs 2,3

Littorina carinifera - Reeve, 1857: *Littorina* pl. 6, figs 29a-c; Nevill, 1885: 151; Frith *et al.*, 1976 [zonation]; Nielsen, 1976 [note on habitat]

Littorina (*Littorinopsis*) *carinifera* - von Martens, 1897: 198 [in part]; Prashad, 1921: 484; Oostingh, 1927; Rosewater, 1970: 464-465, pl. 325, fig. 5, pl. 355, figs 5-9,12,13 [in part]

Littorina (*Melaraphe*) *scabra* var. *carinifera* - Melvill & Standen, 1901: 363

Littorinopsis carinifera - Kuroda & Habe, 1952: 64; Brandt, 1974: 55-56

Littoraria carinifera - Higo, 1973: 46

Littorina carinifera subvar. *pyramidalis* Nevill, 1885: 151 [*nomen nudum*]

Littorina carinifera var. *laevior* Nevill, 1885: 151 [*nomen nudum*]

Littorina rubropicta von Martens, 1887: 170, pl. 16, figs 2a,b [King I., Mergui [Burma]; lectotype (Rosewater, 1970) BMNH 1887.3.10.140-4]

Littorina (*Melaraphe*) *scabra* var. *filosa* - Tryon, 1887: 244, pl. 42, fig. 28 [in part; not Sowerby, 1832]

Littorina scabra var. *filosa* - Pilsbry, 1895: 62 [not Sowerby, 1832]

Littorina (*Malaraphe*) *filosa* - Casto de Elera, 1896: 310 [in part; not Sowerby, 1832]

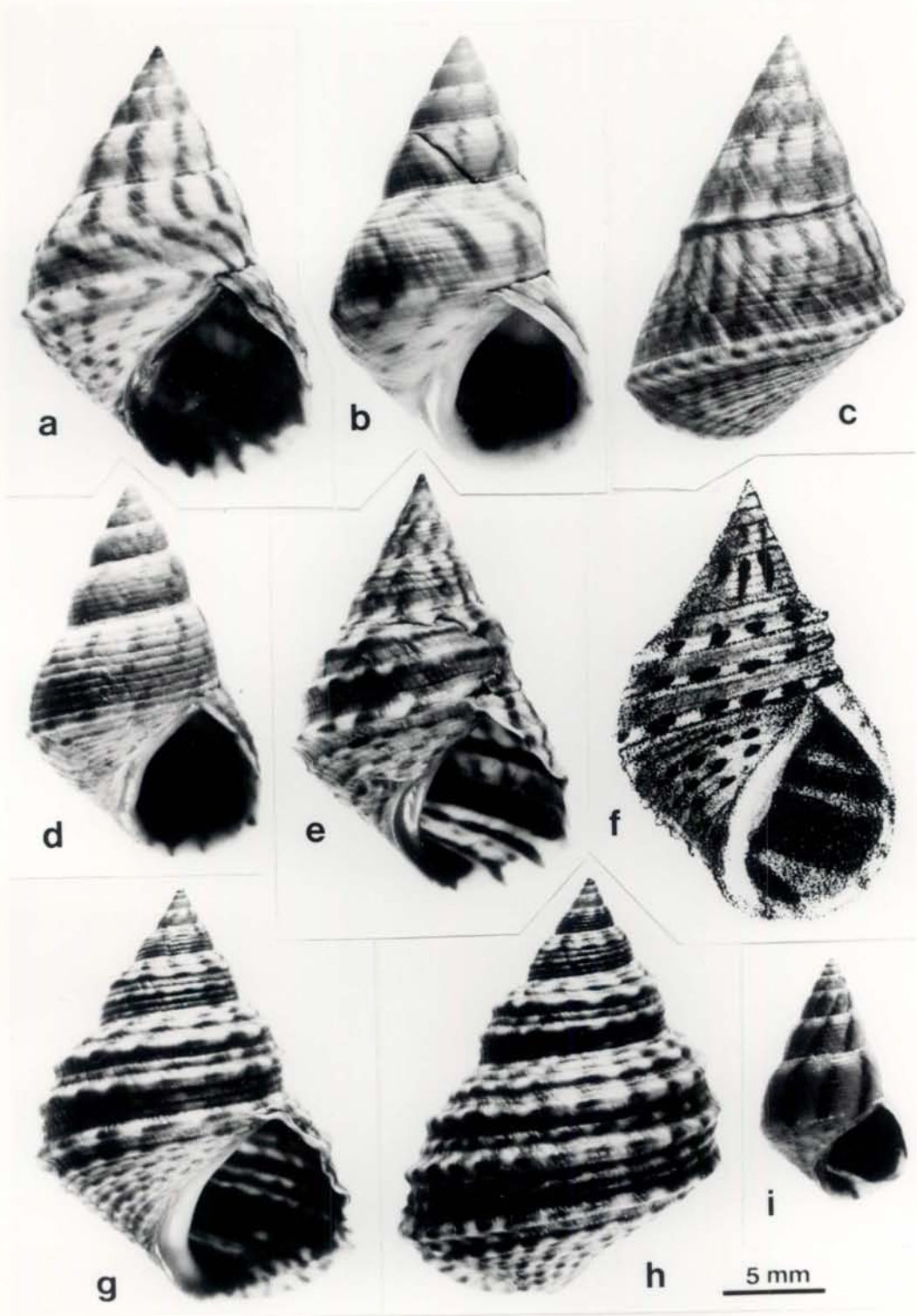
Littorinopsis scabra - Brandt, 1974: 53-54, pl. 4, fig. 61 [in part; not Linnaeus, 1758]

NOMENCLATURE. This well known species has usually been correctly determined in the literature, although occasionally it has been united with other carinate species such as *L. filosa*. Several authors have listed *Littorina perdix* King & Broderip (1832) in the synonymy of *L. carinifera*, apparently following Philippi (1847). No type specimen or figure of *Littorina perdix* is known to exist, but the original description, although brief, could not apply to *L. carinifera*; no locality was given.

DIAGNOSIS. Shell: thick; spire whorls almost flat; peripheral keel strong, carinate; columella wide, excavated; primary grooves 7-9; secondary sculpture weak or absent; 15-30 ribs on last whorl, of which up to 9 may become carinate, or only peripheral rib may be carinate while others remain flat; grooves narrow; microsculpture of spiral striae on ribs, axial striae in grooves; colour grey with narrow orange or brown axial stripes, numbering 13-18 on last whorl; aperture pale with brown bands corresponding to external carinae. Animal: penis not bifurcate, filament small, tapering; oviparous.

SHELL (Fig. 9.64). *Shape*. Height 12-24 mm. Teleoconch 6-7 whorls. Shell thick, solid. Spire outline slightly convex; whorls almost flat, sometimes slightly turreted; sutures indistinct. Peripheral

Fig. 9.64 *Littoraria* (*Palustorina*) *carinifera*: (a) ♀, Santubong, Sarawak (DGR); (b) Bombay, India (BMNH); (c) ♀, Sungei Merbok estuary, Malaysia (DGR); (d) lectotype of *Littorina rubropicta* von Martens, King I., Mergui Arch., Burma (BMNH 1887.3.10.140–4); (e) ♀, Santubong, Sarawak (DGR); (f) lectotype figure of *Phastanella carinifera* Menke (Philippi, 1847, *Litorina* pl. 5, fig. 22); (g,h) Johore Strait (BMNH); (i) Tg. Rhu, Langkawi Is., Malaysia (WAM).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5 mm

keel strong, carinate. Adult lip not thickened or flared; varices absent. Columella wide, shallowly excavated; pillar straight or with a slight convex flexure at base. No sexual dimorphism.

Dimensions: Table 9.18.

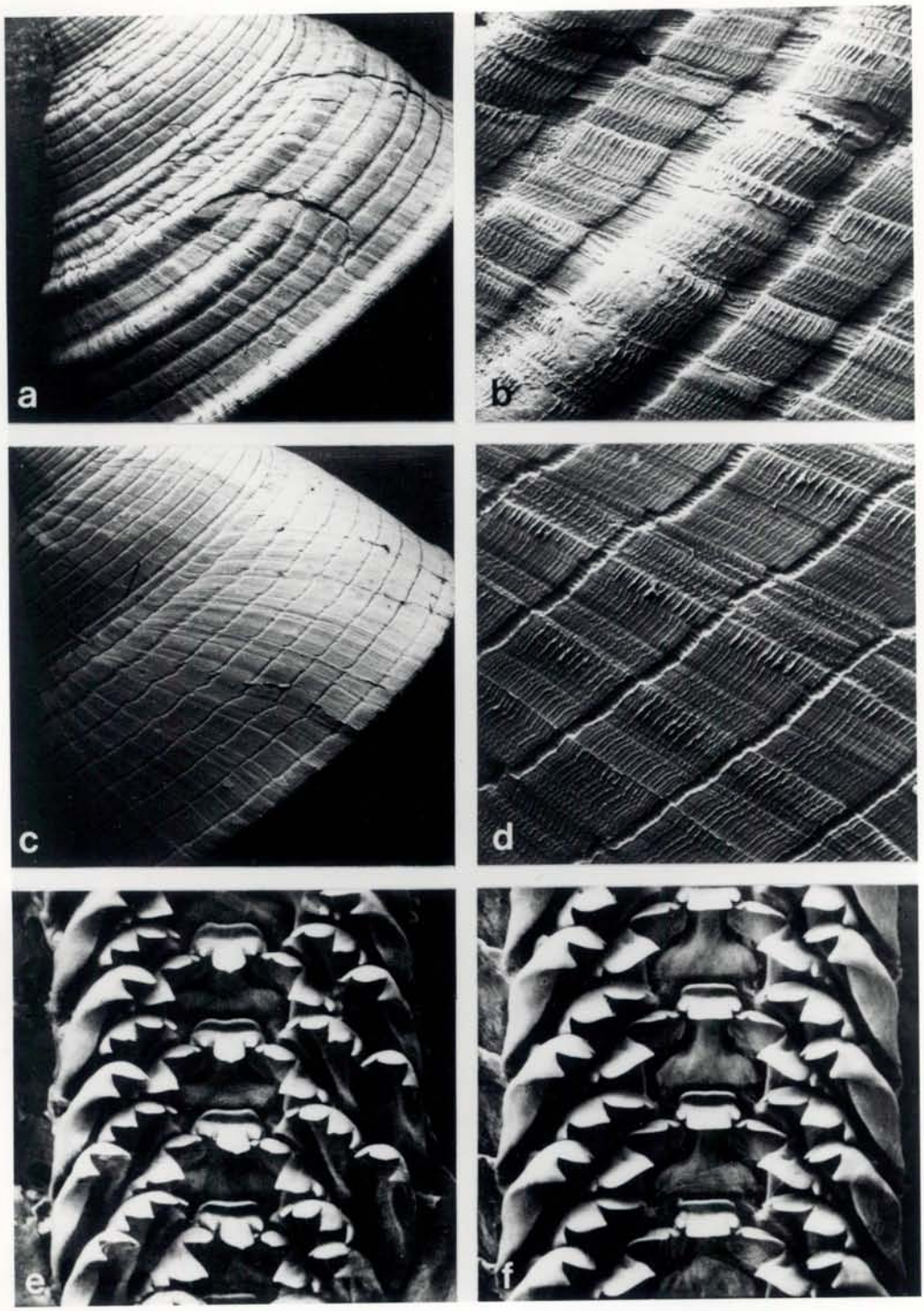
Sculpture (Fig. 9.65a–d). Protoconch normal. All teleoconch whorls sculptured. Primary grooves (6)7–9(10); spacing subequal, usually posterior 1–3 ribs narrowest, the following 1–2 ribs on shoulder widest. Secondary sculpture often absent, or confined to intercalation of a narrow riblet on the shoulder, sometimes as early as whorl 3, or division of a few primary ribs by faint secondary grooves on last whorl. In the most strongly sculptured carinate shells each primary rib may be divided at anterior $\frac{1}{3}$–$\frac{1}{2}$ of width on whorl 6, and on whorl 7 tertiary grooves may appear. Rib development on last whorl is variable: in smooth shells all 15–30 ribs remain low and flat except the prominent sharp peripheral carina; in carinate shells alternate ribs become more prominently rounded on whorl 6, developing into carinae on whorl 7, numbering up to 4 above and 4 below the large peripheral carina. Grooves remain narrow, less than $\frac{1}{4}$ rib width. Microsculpture of regular, fine, spiral striae on ribs; surface covered with fine, irregular, axial growth striae, strong and regular in grooves.

Colour. Rather constant. Ground colour blue grey, whitish or pale yellow, palest near suture and on carinae. Pattern of rusty orange or dark brown vertical, oblique or zigzag axial stripes, usually continuous over grooves, from suture to periphery, but on base broken into spots confined to ribs. Stripes narrow, numbering (10)13–18(25) on last whorl. Aperture with black or dark purple brown spiral bands corresponding to major carinae; usually the 3 bands at suture, periphery and around columella are widest, with lines and spots between; sometimes aperture is uniformly dark with a single pale band anteriorly. Columella pale pink, purple brown, grey or white.

Table 9.18 Dimensions of *Littoraria* (*Palustorina*) *carinifera*.

Specimen	Locality	Sex	Primary grooves	H (mm)	B (mm)	LA (mm)	WA (mm)	C (mm)	PR	S	SH
Phasianella carinifera lectotype figure (Philippi, 1847)	unknown			21.5	14.5	11.4	8.3		1.48	0.73	1.89
Littorina rubropicta lectotype, BMNH 1887.3.10.140-4	King I., Mergui, Burma		9	18.3	12.0	9.2	6.9		1.53	0.75	1.99
DGR	Santubong, Sarawak	♂	9	19.8	13.4	11.0	8.7	1.8	1.48	0.79	1.80
DGR	Santubong, Sarawak	♂	6	17.7	13.8	10.5	8.4	1.8	1.28	0.80	1.69
DGR	Santubong, Sarawak	♀	8	22.7	16.1	12.4	9.5	2.5	1.41	0.77	1.83
DGR	Santubong, Sarawak	♀	8	19.4	16.1	12.1	10.2	2.6	1.20	0.84	1.60
BMNH acc. 1838	Johore Strait		7	18.3	15.6	11.3	9.2	2.5	1.17	0.81	1.62
BMNH acc. 2176	Bombay, India		8	22.1	14.5	11.5	9.1	2.2	1.52	0.79	1.92
BMNH acc. 2176	Bombay, India		8	20.1	12.9	10.1	8.4	2.4	1.56	0.83	1.99
WAM 1037-81	Langkawi Is., Malaysia		8	12.1	7.8	6.0	4.6	0.8	1.55	0.77	2.02
WAM 1037-81	Langkawi Is., Malaysia		8	11.4	7.5	6.3	4.5	0.9	1.52	0.71	1.81
DGR, mean of 10	Sungei Merbok, Malaysia	♂		19.15					1.412	0.752	1.753
standard error				0.54					0.018	0.009	0.023
DGR, mean of 10	Sungei Merbok, Malaysia	♀		19.29					1.378	0.768	1.815
standard error				0.50					0.024	0.012	0.024
statistic t or U				0.189					64	69	69
probability				0.852					0.314	0.166	0.166

Fig. 9.65 *Littoraria* (*Palustorina*) *carinifera*: (a,b) Santubong, Sarawak; (a) last whorl (×10); (b) detail (×40); (c,d) Sungei Merbok estuary, Malaysia; (c) last whorl (×10); (d) detail (×40); (e) radula, Phuket I., Thailand (×275); (f) radula, Santubong, Sarawak (×220).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f

ANIMAL. *Colour*. Ground colour ochraceous to pale brown; pigmentation grey to black; sides of foot darkly mottled and speckled with opaque white flecks; head and tentacles darkly mottled, red buccal mass and oesophageal pouches visible within; tentacles sometimes conspicuously yellow ochre if dark pigment not too dense, pale stripes at base are indistinct.

Penis (Fig. 9.66a-e). Small, to 5.0 mm. Base simple, incorporating glandular disc. Filament small, tapering. Sperm groove open. Base and filament ochre, darkest around glandular disc; disc off white to cream.

Sperm. Eupyrene sperm 270-350 μm. Nurse cells (Fig. 9.66h-j) 30-46 μm; elongate-oval, tapering to basal flagellum up to 220 μm; rods 1(2-4), basal, shape variable, usually oval, occasionally narrow and elongate; yolk granules small, becoming larger towards base.

Pallial oviduct (Fig. 9.66f,g). Length to 8.0 mm. Spiral section to 5.7 mm diam., $5\frac{1}{2}$ whorls; opaque albumen gland $\frac{1}{4}$ whorl, cream yellow; translucent albumen gland ochre to fawn; opaque capsule gland 1-$1\frac{1}{2}$ whorls, cream to pale pink; translucent capsule gland orange brown to red; spiral distinct externally, but dark pigmentation of egg groove only visible in section. Straight section long, to 3.1 mm, orange brown, reddish translucent capsule gland extends around pigmented egg groove into straight section; no terminal papilla. Bursa posterior, extending into spiral section. Development assumed oviparous.

Radula (Fig. 9.65e,f). Length to 25 mm; relative length 0.99-1.36. Intermediate between saw- and chisel-toothed types; central rachidian cusp wide, usually with a straight edge; cusps of paired teeth obliquely triangular; lateral with gap anterior to main cusp.

Alimentary tract. Anterior pair of oesophageal pouches large (to

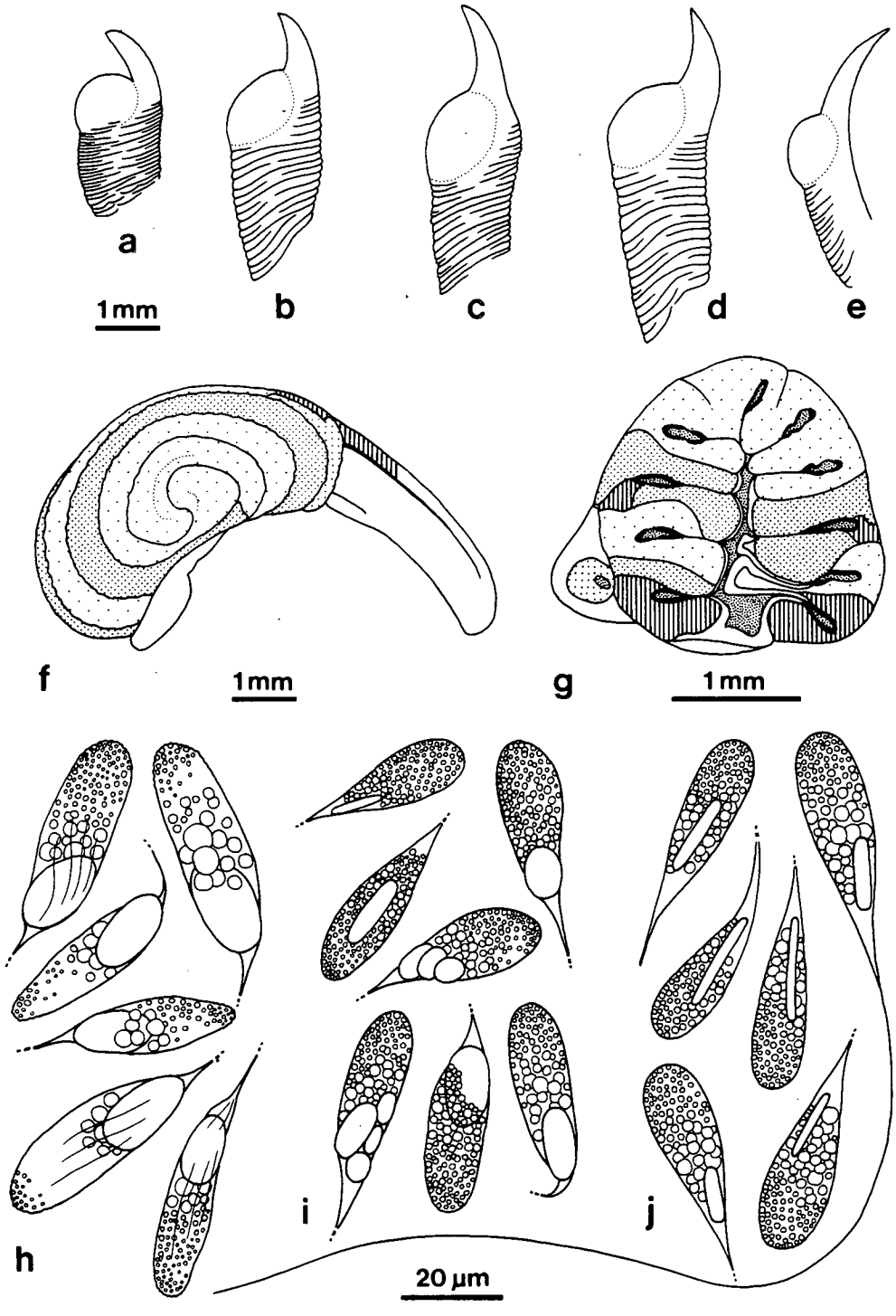


Fig. 9.66 *Littoraria* (*Palustorina*) *carinifera*: (a–e) penes; (a) contracted; (b–e) relaxed; (a–d) Santubong, Sarawak; (e) Phuket I., Thailand; (f,g) pallial oviduct, with transverse section, Santubong, Sarawak; (h–j) sperm nurse cells; (h) Santubong, Sarawak; (i,j) Phuket I., Thailand.

2.0 mm diam.), glandular, pink to dark red.

Pallial complex. Hypobranchial gland large, 1.5–2.2 mm wide, brown.

DISTRIBUTION. *Habitat*. At back of mangrove forests; in landward fringe on trunks and dead wood, also leaves of *Nypa*, 0–0.5 m above ground; extends into zones of *Bruguiera* and *Ceriops*; in marsh grass (von Martens, 1887).

Range (Fig. 9.67). Pakistan to Malaysia, Indonesia and Philippines.

Records. PAKISTAN: China Creek, Karachi (MCZ); INDIA: Bandra, N. of Bombay (USNM); Bombay (BMNH, RNHL, MCZ); Vingurla, N. of Goa (USNM); Netravati R., Mangalore (USNM, ANSP); Beypore estuary (BMNH); BURMA: King I., Mergui Arch. (BMNH); THAILAND: Ranong (MCZ); Ao Nam Bor, Phuket I. (DGR); Songkla (MCZ); Chonburi (USNM, ANSP); Ko Kut (USNM); MALAYSIA: PENINSULA: Tg. Rhu, Langkawi Is. (WAM); Sungei Merbok estuary, Kedah (DGR); Endau (AMS); Kuantan (NUS); SARAWAK: Santubong (DGR); SABAH: Labuan I. (RNHL); Tandjong Aru, Kota Kinabalu (ANSP); Po Bui I., Sandakan (USNM); SINGAPORE: Jelutong, Ubin I. (DGR); Loyang Besar (WAM); INDONESIA: SUMATRA: Weh I. (RNHL); Belawan R., Deli (RNHL); Belinju, Bangka I. (RNHL); JAVA: Tandjong Priok, Djakarta (RNHL); Madura I. (RNHL); SULAWESI: Makassar (RNHL); MOLUCCAS: Ternate I. (RNHL); IRIAN JAYA: Skroe, N.W. of Fakfak (RNHL); VIETNAM: Chilins, Vung Tau district (ANSP); PHILIPPINES: Pancol, Palawan I. (USNM, ANSP); Busuanga I. (RNHL); Viejo Victorias, Negros Occidental (USNM); Iloilo, Panay (USNM); Silanga, Samar (USNM); Medio I., Galera Bay, Mindoro (USNM); Alfonso XIII I., near Manila (ANSP).

REMARKS. Although the colour of the shell is rather constant, *L. carinifera* shows geographical variation in shape and sculpture. The form described by von Martens (1887) as *Littorina rubropicta*, with a rather smooth shell and single conspicuous peripheral carina, occurs

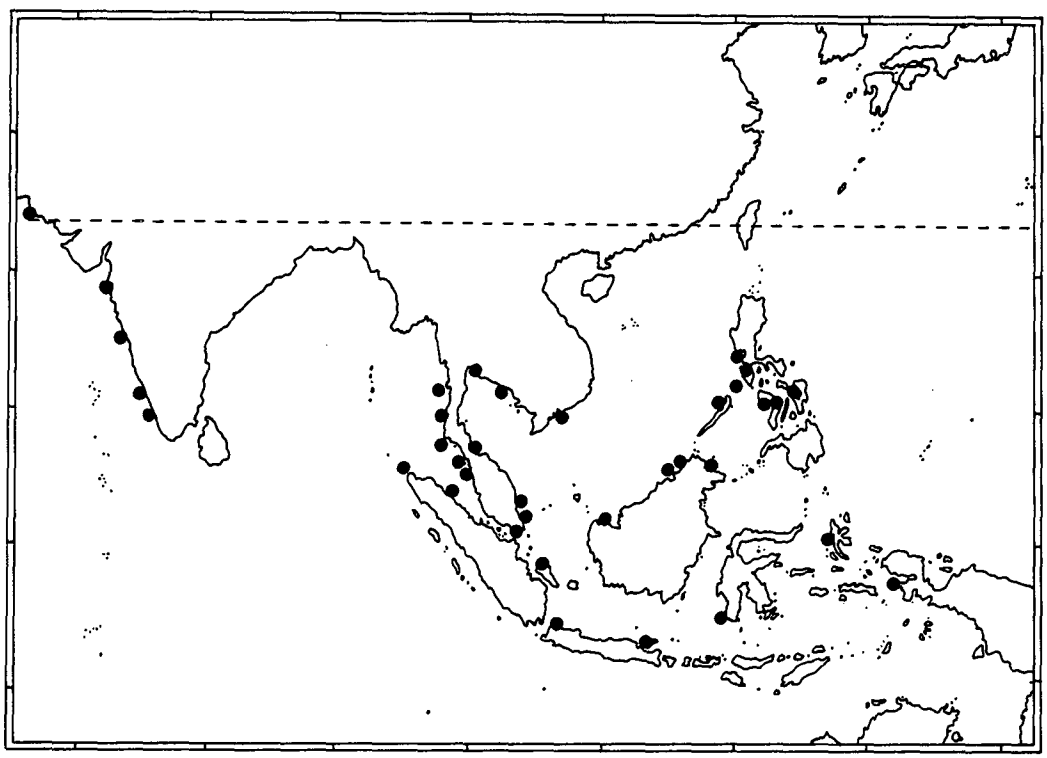


Fig. 9.67 Distribution of *Littoraria (Palustorina) carinifera*.

in north-eastern Sumatra, the west coast of the Malayan Peninsula and India. At Singapore and to the south and east the shells are of the typical, broad, strongly carinate form. Shells from Borneo and the Philippines are variable and include intermediates, so that taxonomic recognition of the two main forms is not justified. In a collection from the Langkawi Islands, western Malaysia (WAM) the shells are small, less than 14 mm in height, the periphery is merely angular, not carinate, the spiral grooves are shallow and occasionally obsolete, and the axial colour stripes are narrow (Fig. 9.64i). Intermediates link this unusual form with the more common '*rubropicta*' variety. The animal of *L. carinifera* is unusual in the large, red, glandular oesophageal pouches, found also in *L. conica*.

SIMILAR SPECIES. *L. carinifera* is highly distinctive, the combination of carinate shell, red brown axial stripes, banded aperture and wide columella distinguishing it immediately from the strongly ribbed or carinate species *L. filosa*, *L. cingulata*, *L. pallescens* and *L. sulculosa*. Only *L. conica* shows such a sharp angulation at the periphery, but is a thinner shell with more numerous ribs.

9.2.4.5 *Littoraria* (*Palustorina*) *sulculosa* (Philippi, 1846)

Littorina sulculosa Philippi, 1846: 142 [north coast of Australia; lectotype (Rosewater, 1970) BMNH 1968279]; Reeve, 1857: *Littorina* pl. 8, figs 39a,b; von Martens, 1889: 193

Litorina sulculosa - Philippi, 1847, vol. 3: 18, *Litorina* pl. 6, fig. 10; Weinkauff, 1882: 55, pl. 7, figs 5,8

Littorina (*Melaraphe*) *sulculosa* - Tryon, 1887: 247, pl. 43, fig. 52

Melaraphe sulculosa - Hedley, 1916: 38

Melarhaphe sulculosa - Hedley, 1918b: 275

Littorina filosa - Nevill, 1885: 148 [in part; not Sowerby, 1832]

Littorina (*Littorinopsis*) *scabra scabra* - Rosewater, 1970: 456-461,

pl. 352, figs 17,18 [in part; not Linnaeus, 1758]

NOMENCLATURE. The species was described by Philippi (1846) from material in the Cuming Collection. Only one lot in the BMNH corresponds with Philippi's description and Rosewater (1970) designated as lectotype the shell closest in appearance to Philippi's (1847) figure. No original label exists and a label written by Tomlin erroneously records the type locality as Java.

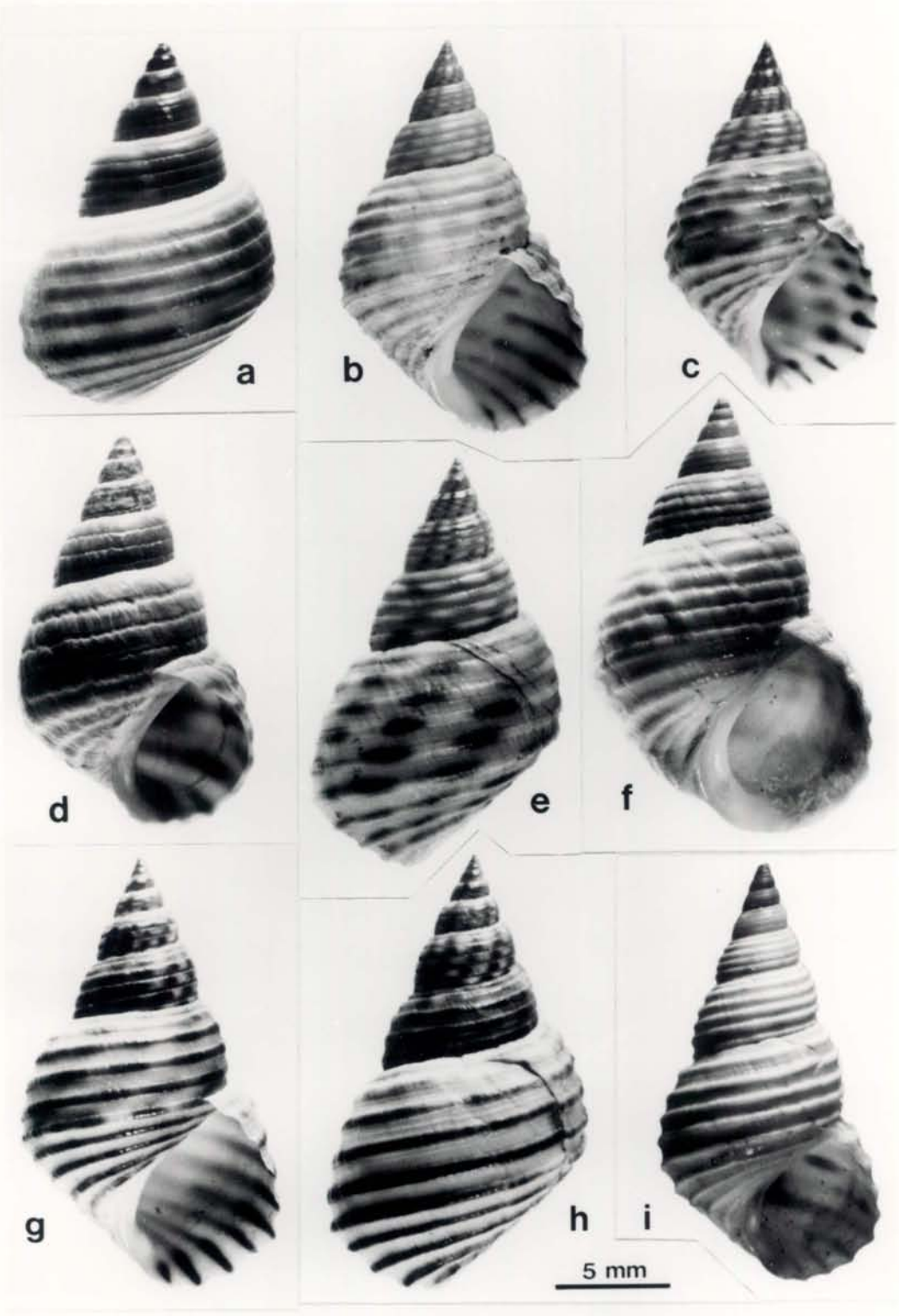
DIAGNOSIS. Shell: very thick; whorls rounded or turreted; columella wide, scarcely excavated, white; primary grooves 5–6; secondary sculpture usually absent; ribs rounded and prominent, numbering 9–11 on last whorl, with wide grooves between; microsculpture of faint spiral striae on ribs, strong axial striae in grooves; colour cream, ribs pale brown, unicolorous or marked with long dashes. Animal: penis not bifurcate, filament long, tapering; oviparous.

SHELL (Fig. 9.68). *Shape*. Height 14–23 mm. Teleoconch 7–8 whorls. Shell of relatively great thickness (to 1.5 mm) when large. Spire outline straight; whorls gently rounded, often somewhat turreted; sutures impressed. Peripheral keel moderately developed, marked by the most prominent of the primary ribs. Adult lip sharp, not flared; varices absent. Columella wide, scarcely excavated; pillar concave, with small constriction at base, producing a low, rounded knob. Sexual dimorphism: males smaller.

Dimensions: Table 9.19.

Sculpture (Fig. 9.69a–d). Protoconch normal. First 0.5–1 whorl of teleoconch smooth. Primary grooves (4)5–6(7), almost equidistant, but posterior rib usually narrowest; occasionally posterior groove does not form until whorl 4–5, then posterior rib is the widest on earlier whorls. Secondary sculpture usually absent, but on whorl 8 of largest shells 1–3 narrow riblets may be intercalated in each primary groove. Primary ribs become rounded and prominent on whorls 7–8, numbering 9–11 on last whorl. Primary grooves at first narrow,

Fig. 9.68 *Littoraria* (*Palustorina*) *sulculosa*: Broome, W.A. (NMV); (b,c) Broome, W.A. (DGR); (b) ♂; (c) ♂; (d) lectotype of *Littorina sulculosa* Philippi, N. Australia (BMNH 1968279); (e) ♀, Broome, W.A. (DGR); (f) Broome, W.A. (NMV); (g,h) ♀, Broome, W.A. (DGR); (i) Derby, W.A. (AMS).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b
c
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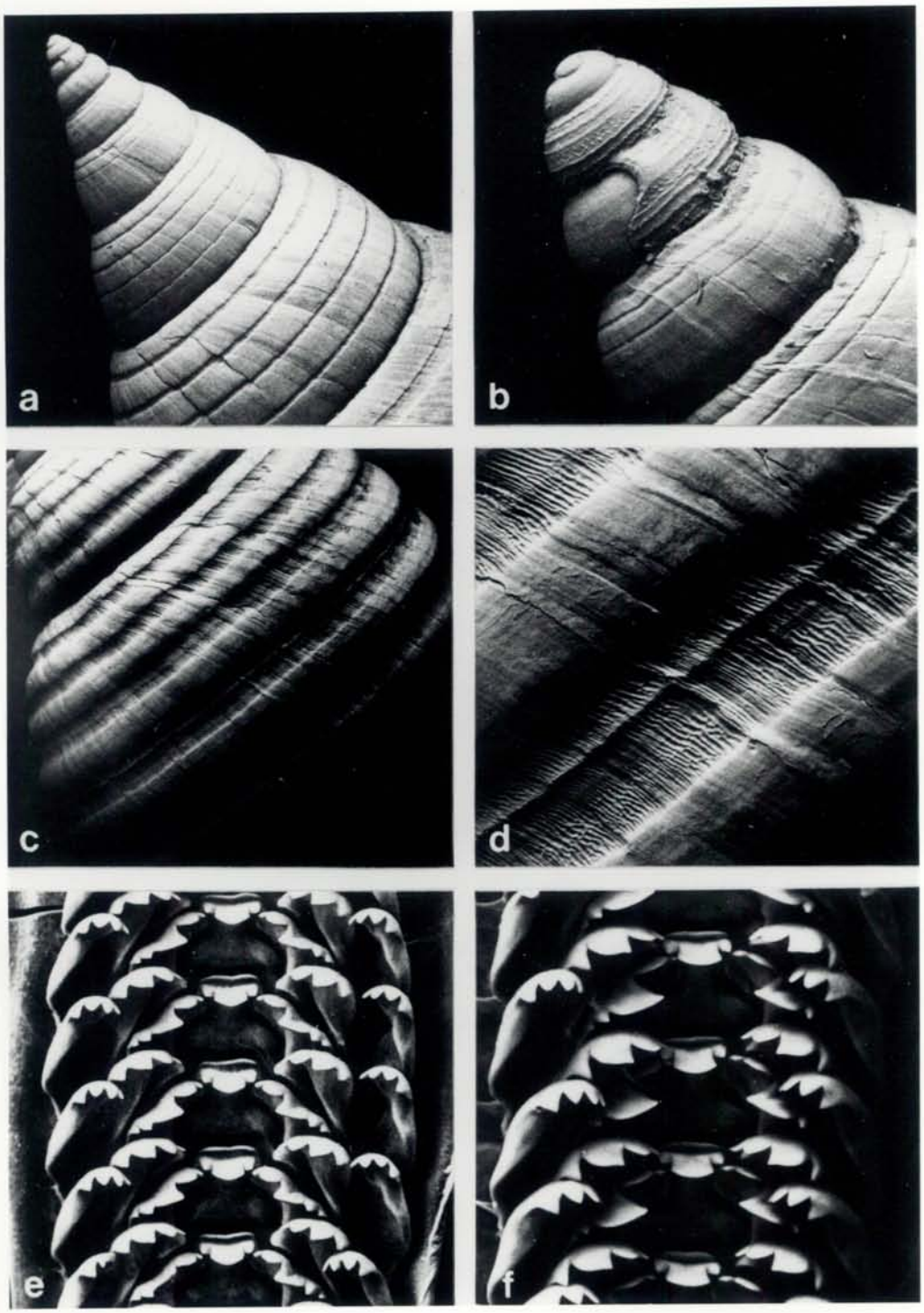
5 mm

Table 9.19 Dimensions of *Littoraria (Palustorina) sulculosa*.

Specimen	Locality	Sex	Primary grooves	H (mm)	B (mm)	LA (mm)	WA (mm)	C (mm)	PR	S	SH
Littorina sulculosa lectotype, BMNH 1968279	North coast of Australia		4	17.2	10.4	8.7	6.2	1.6	1.65	0.71	1.98
DGR	Broome, W.A.	♂	5	17.4	11.4	9.2	7.0	1.6	1.53	0.76	1.89
DGR	Broome, W.A.	♂	6	15.9	10.1	8.1	5.9	1.2	1.57	0.73	1.96
DGR	Broome, W.A.	♀	5	22.5	15.3	12.5	8.6	1.9	1.47	0.69	1.80
DGR	Broome, W.A.	♀	6	18.5	11.4	9.4	7.0	1.2	1.62	0.74	1.97
AMS C.131743	Derby, W.A.		5	18.0	9.9	7.7	5.7	0.8	1.82	0.74	2.34
AMS C.131743	Derby, W.A.		5	15.0	8.2	6.6	4.7	0.8	1.83	0.71	2.27
DGR, mean of 10	Broome, W.A.	♂		14.01					1.531	0.715	1.837
standard error				0.58					0.008	0.010	0.018
DGR, mean of 10	Broome, W.A.	♀		17.75					1.560	0.733	1.874
standard error				0.41					0.011	0.008	0.018
statistic t or U				5.250					75	67	73
probability				<.001					0.064	0.218	0.090

Fig. 9.69 (a–e) *Littoraria* (*Palustorina*) *sulculosa*, Broome, W.A.: (a) spire (×19); (b) protoconch (×90); (c) last whorl (×9); (d) detail (×35); (e) radula (×210). (f) *Littoraria* (*Palustorina*) *articulata*: radula, Kanchanadit, Thailand (×325).


a
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almost equal to rib width on whorl 7, but 1–3 times rib width on whorl 8. Microsculpture of faint spiral striae on ribs, sometimes indistinct; surface covered by irregular axial growth lines; grooves sculptured by fine, strong, axial striae.

Colour. Rather constant. Ground colour cream, whitish or pale fawn. Ribs fawn, pale orange pink or grey brown, often unicolorous, or marked with long, indistinct dashes. Spire whorls coloured like rest of shell, but usually with dashes discrete and aligned into axial series; spire whorls sometimes grey, paler at sutures. Aperture white, with dark lines and dashes corresponding to external pattern, glazed within by a cream callus. Columella and parietal callus usually white, sometimes tinged pink.

ANIMAL. *Colour*. Pigmentation pale grey; sides of foot pale, mottled and lined; head pale grey, red buccal mass visible internally; tentacles banded, unpigmented stripe each side of base.

Penis (Fig. 9.70e–g). Length to 4.4 mm. Base simple, incorporating small glandular disc. Filament long, tapering. Sperm groove open. Penis cream.

Sperm. Eupyrene sperm 205–240 μm. Nurse cells (Fig. 9.70h–j) 36–55 μm, elongate oval, tapering at base, slightly constricted at mid-length; basal flagellum to 205 μm; rods 1–4, basal, rectangular; yolk granules small, becoming larger towards base.

Pallial oviduct (Fig. 9.70a–d). Length to 5.7 mm. Spiral section to 5.2 mm diam., $5\frac{1}{2}$ whorls; opaque albumen gland $\frac{1}{4}$ whorl, white; translucent albumen gland white to pale grey; opaque capsule gland $1\frac{1}{2}$ whorls, white or pale pink; translucent capsule gland orange brown to red; spiral distinct externally, egg groove usually darkly pigmented. Straight section to 2.4 mm, grey to pale brown, brown translucent capsule gland visible posteriorly; no terminal papilla. Bursa posterior, extending into spiral section. Development assumed oviparous.

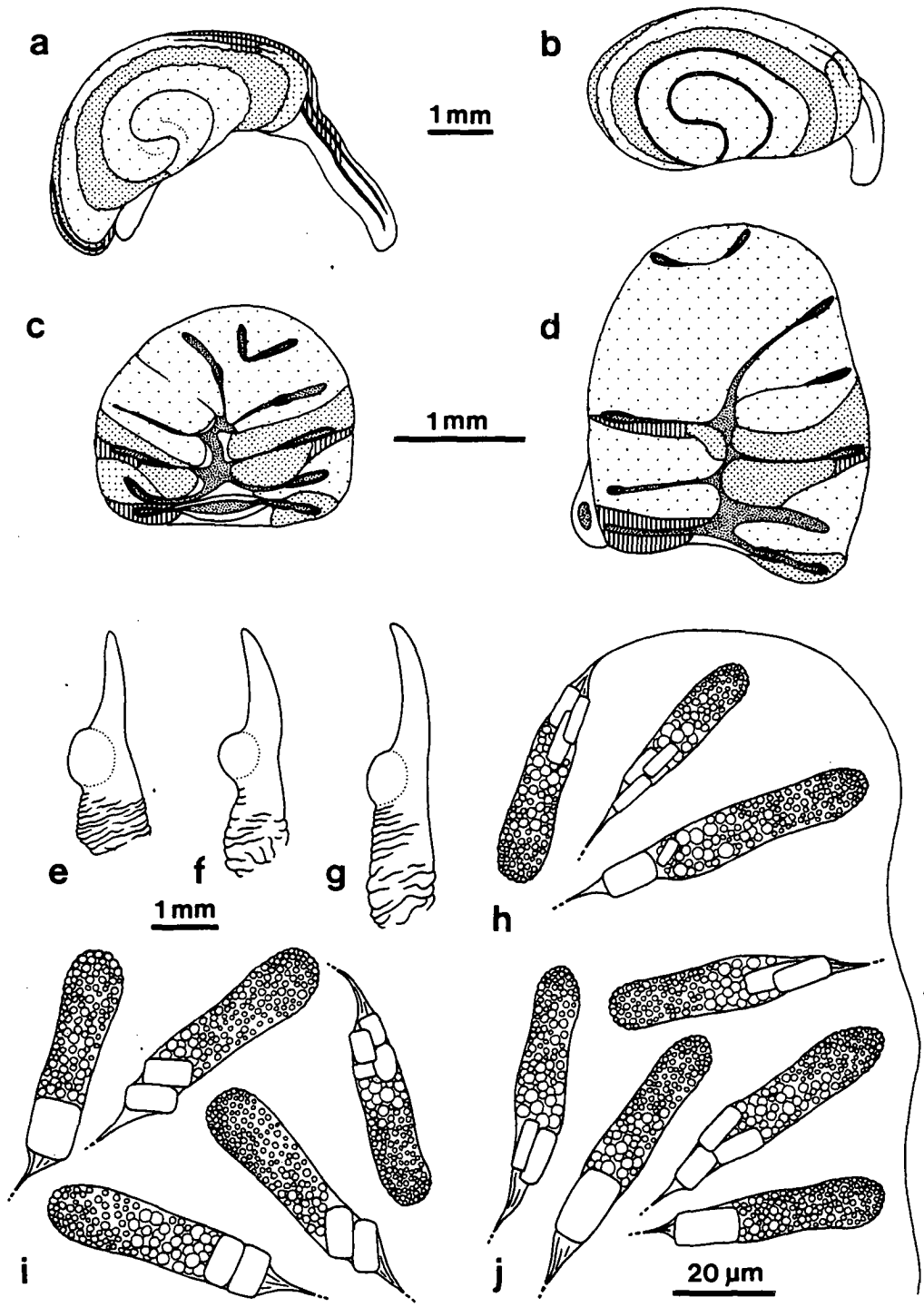


Fig. 9.70 *Littoraria* (*Palustorina*) *sulculosa*, Broome, W.A.: (a-d) pallial oviducts, with transverse sections; (e-g) penes; (h-j) sperm nurse cells.

Radula (Fig. 9.69e). Length to 17 mm; relative length 0.78–0.89. Intermediate between saw- and chisel-toothed types; central rachidian cusp broad, edge slightly pointed; cusps of paired teeth rather obliquely triangular; lateral with gap anterior to main cusp.

DISTRIBUTION. *Habitat*. At Broome, W.A., occurs from middle almost to landward side of a forest entirely of *Avicennia* trees, on trunks and also on leaves, 0–1.4 m above ground; sometimes under logs at back of forest. Also seen occasionally on *Rhizophora* roots. Fairly frequent on and under rocks on sheltered shores.

Range (Fig. 9.71). north-western Australia, from Exmouth Gulf to Vansittart Bay.

Records. AUSTRALIA: W.A.: Bay of Rest, Exmouth Gulf (WAM); Onslow (AMS); Antonni Mia, Point Sampson (WAM); Cossack (BMNH); Port Hedland (AMS); False Cape Creek, La Grange Bay (AMS, ANSP); Broome (DGR, AMS, NMV); Derby (AMS, WAM); Port Warrender, Admiralty Gulf (WAM); Vansittart Bay (AMS, WAM).

REMARKS. Because of the restricted and remote distribution of *L. sulculosa*, it is rare in museum collections outside Australia. Anatomical features of this species are typical of the genus *Palustorina*, but the shell bears a superficial resemblance to that of the sympatric *L. (Littorinopsis) cingulata cingulata*, from which separation may be difficult in the field. In mangrove forests the habitats of these two species overlap, but *L. sulculosa* occurs at lower levels and is less common towards the landward side of the forest. The shell of *L. sulculosa* is rather constant in form and colour, although in a collection from Derby, W.A., (AMS) all specimens have unusually tall spires (Fig. 9.68i). Typical shells of this species are remarkable for their extreme thickness (1.5 mm at the outer apertural lip in a shell 18.7 mm in height).

SIMILAR SPECIES. *L. sulculosa* is unlike any other member of the subgenus *Palustorina*. Although the penis and oviduct are immediately

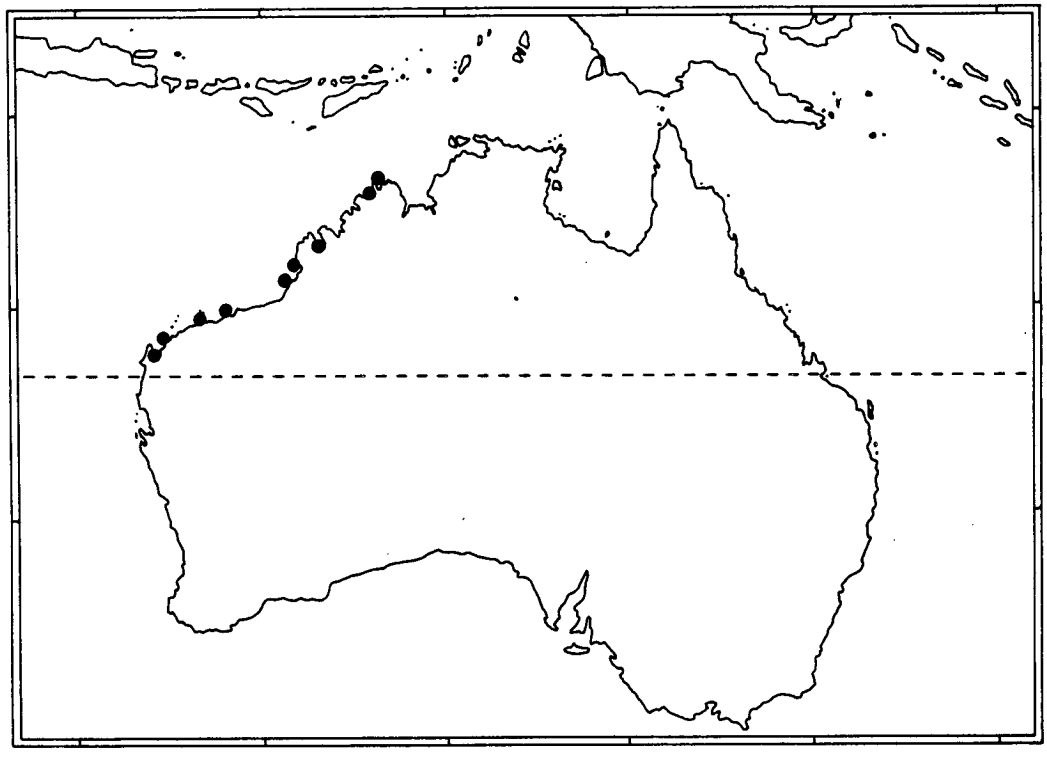


Fig. 9.71 Distribution of *Littoraria* (*Palustorina*) *sulculosa*.

diagnostic, the shells of *L. sulculosa* and *L. cingulata cingulata* are similar in form and colour. *L. sulculosa* is most reliably distinguished by the strong axial microsculpture in the spiral grooves, but in addition there are fewer primary ribs on the last whorl, the colour pattern is of long dashes or continuous spiral lines, and the columella is usually white.

9.2.4.6 *Littoraria (Palustorina) articulata* (Philippi, 1846)

Littorina intermedia var. *articulata* Philippi, 1846: 141 [Swan Point [W.A., Australia]; neotype here designated BMNH 198348, just S. of Lookout Hill, Broome, W.A., Australia; additional specimens from neotype lot AMS, WAM, USNM; not *Litorina scabra* var. *articulata* Philippi, 1847]

Litorina intermedia var. *articulata* - Philippi, 1847, vol. 2: 223

? *Litorina intermedia* var. *strigata* - Philippi, 1847, vol. 2: 223, *Litorina* pl. 5, fig. 7 [in part; not Philippi, 1846; original citation of figures of var. *strigata* corrected to pl. 5, figs 7,8,9]

Littoraria strigata ('Philippi') - Habe, 1964: 29, pl. 9, fig. 31 [not Philippi, 1846]

Littorina (Melaraphe) scabra var. *intermedia* - Tryon, 1887: 224, pl. 42, fig. 23 [in part; not Philippi, 1846]

Littorina (Malaraphe) intermedia - Casto de Elera, 1896: 309-310 [in part; not Philippi, 1846]

Littorina (Littorinopsis) intermedia - von Martens, 1897: 197 [in part; not Philippi, 1846]

Littorina intermedia - Yen, 1933: 93; Fischer, 1970: 99 [both not Philippi, 1846]

Melarhaphe intermedia - Yen, 1942: 196 [not Philippi, 1846]

Litorina sinensis Philippi, 1847, vol. 3: 16-17, *Litorina* pl. 6, fig. 23 [China; lectotype here designated MNHNP, 13.4 mm]; Lischke, 1871b: 71-72; Weinkauff, 1882: 83-84, pl. 11, figs 9,12

Littorina intermedia var. *sinensis* - Nevill, 1885: 147

Littorina sinensis - Pilsbry, 1895: 62

Melaraphe (Litt.) blanfordi Dunker, 1871: 150 [Rockhampton [Qld., Australia]; location of type unknown, not in Museum für Naturkunde, E. Berlin, R. Kilias, pers. comm.]

Melarapha blanfordi - Iredale & McMichael, 1962: 38

Litorina strigata Lischke, 1871a: 148–149 [Nagasaki, Japan; type in Academy of Sciences, Leningrad? (Rosewater, 1970)]; Lischke, 1871b: 73, pl. 5, fig. 22 [both not *Littorina intermedia* var. *strigata* Philippi, 1846]

Littorina strigata Lischke - Pilsbry, 1895: 62 [not Philippi, 1846]

Littorina (Melaraphe) strigata Lischke - Tryon, 1887: 245, pl. 43, fig. 33 [not Philippi, 1846]

Littorinopsis strigata (Lischke) - Kuroda & Habe, 1952: 64; Oyama & Takemura, 1961: fig. 10 [both not Philippi, 1846]

Littoraria strigata (Lischke) - Kojima, 1958c [egg capsule]; Azuma, 1960: 10; Higo, 1973: 46 [both not Philippi, 1846]

Littoraria strigata ('Dunker') - Yoo, 1976: 56, pl. 7, figs 18,19 [not Philippi, 1846]

Melaraphe scabra - Hedley, 1916: 37 [in part; not Linnaeus, 1758]

Littorina (Littorinopsis) scabra scabra - Rosewater, 1970: 456–461, pl. 352, figs 28,29 [in part; not Linnaeus, 1758]

Littorina undulata - Berry, 1963 [in part; not Gray, 1839]

Littorinopsis undulata - Brandt, 1974: 54 [in part; not Gray, 1839]

NOMENCLATURE. Philippi (1846) described *Littorina intermedia* var. *articulata* in a work based upon material in the Cuming Collection, now in the BMNH. Although the types of other species described by Philippi in the same article are located in the BMNH, that of var. *articulata* is lost. From the original descriptions and from the figures published by Philippi in the following year, it is evident that his concept of *Littorina intermedia* embraced the species here defined as *L. strigata* (Philippi; not Lischke), *L. articulata* and possibly also *L. subvittata*, in addition to *L. intermedia s. s.* Of these four, only *L. articulata* occurs at Swan Point, W.A., the type locality of var. *articulata*, and shells from north-western Australia

fit the original description: '*testa interstitiis sulcorum regulariter albido et fusco articulatis* . . . only 6 lin. [13.2 mm] high'. The var. *articulata* was not figured as such by Philippi, but his *Litorina* pl. 5, fig. 7, cited in the text as *Litorina intermedia* var. *strigata* (see Section 9.2.3.5 for a discussion of the error in the original citation) resembles specimens of *L. articulata* from north-western Australia. This resemblance is also seen in one of the paralectotypes of var. *strigata*, which was probably the original of the figure. In view of several known errors in the citations of the figures in Philippi's text, it is not impossible that the figure does indeed represent var. *articulata*, and that the specimen is its type, which has become mixed with the type collection of var. *strigata*. However, in the absence of an original label and because of the variability of *L. strigata*, there is insufficient evidence for the designation of shell or figure as lectotype of var. *articulata*. Although there is no reasonable doubt as to the identity of var. *articulata*, a neotype with preserved animal has been designated. This is necessary in view of confusion in the literature between this species and *L. intermedia*, and because of its close relationship with *L. strigata*, from which unequivocal separation is only possible on the basis of anatomical features. No material is available from Swan Point, but the neotype lot was collected from Broome, only 200 km to the south.

In 1847 Philippi described and figured *Litorina sinensis* from a collection from China received from Largilliert. In the MNHNP there are three shells from the Largilliert Collection housed in the Natural History Museum of Rouen (P. Bouchet, pers. comm.) and one of these is here designated as lectotype. Although Lischke (1871b) distinguished his new species *Litorina strigata* from *L. sinensis* on the basis of shell shape, sculpture and pattern, the form seems to fall within the range of specimens of *L. articulata* from Japan. Since *L. strigata* (Philippi) is not known from China or Japan, *Litorina sinensis* and *Litorina strigata* Lischke are placed in the synonymy of *L. articulata*. *Melaraphe blanfordi* was described by Dunker (1871) from Rockhampton, Queensland, but even in the absence

of a type specimen or a figure, can be determined as *L. articulata* since *L. strigata* (Philippi) is not recorded from Australia.

L. articulata (and probably also *L. strigata*) has sometimes been misidentified as *L. undulata*, particularly in recent ecological studies in South East Asia (Section 11.5) and also in museum collections. *L. undulata* does not occur in mangrove habitats.

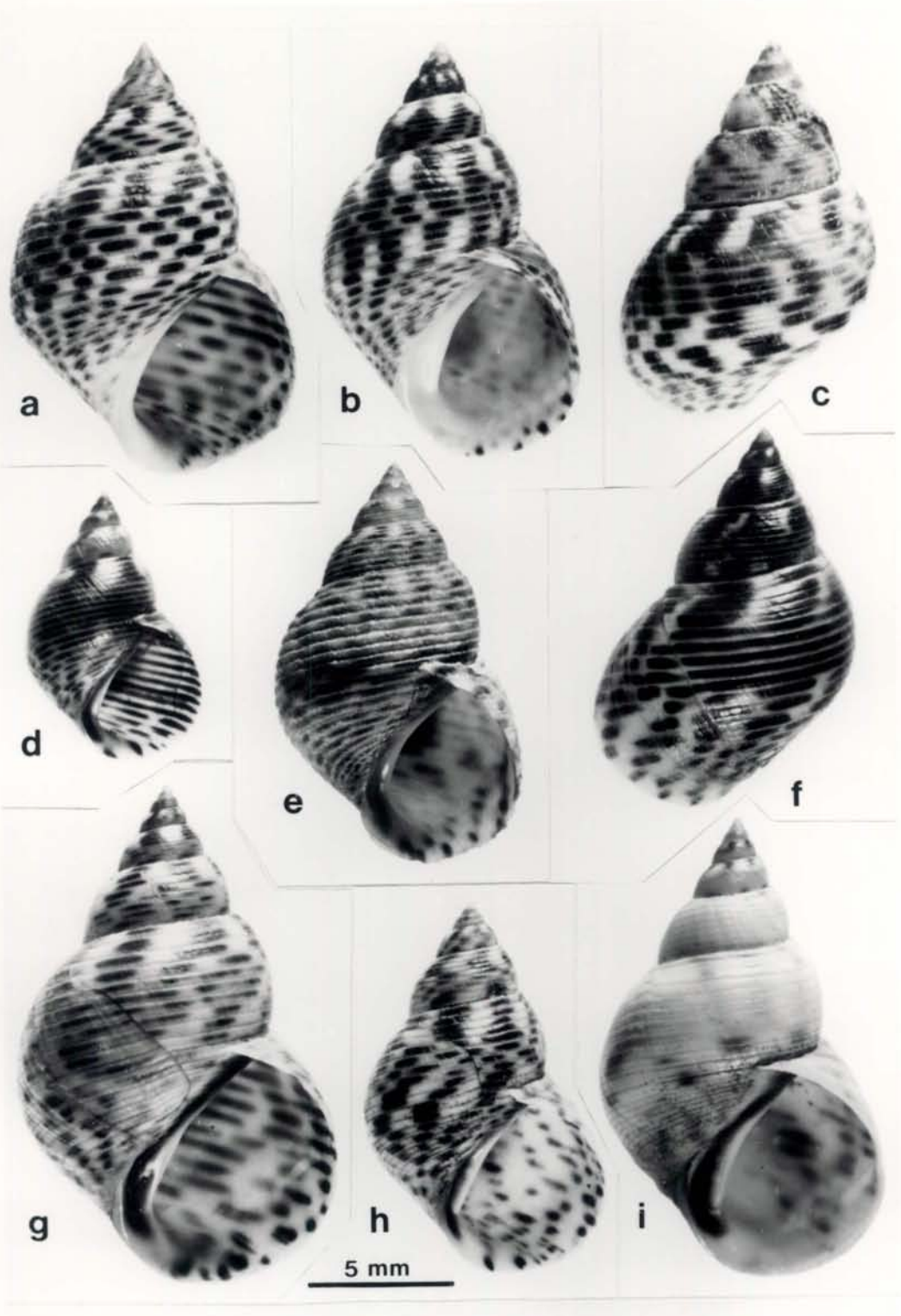
DIAGNOSIS. Shell: small (less than 20 mm); solid; spire relatively low, whorls rounded; peripheral keel absent; columella wide, excavated; primary grooves 8–10; secondary sculpture often weak or absent; total of 20–33 flat ribs on last whorl; grooves usually impressed lines only; microsculpture indistinct; colour variable, cream yellow to white, with pattern of brown or black dashes on ribs, dashes usually aligned at suture and periphery to form short axial stripes numbering 8–11 on last whorl. Animal: penis not bifurcate, base broad, filament less than half length of base; oviparous.

SHELL (Fig. 9.72). *Shape*. Height 6–20 mm. Teleoconch 5–6 whorls. Shell of moderate thickness, solid. Spire relatively low, outline slightly convex; whorls rounded, sutures impressed. Peripheral keel absent, but 1–2 ribs at periphery may be slightly enlarged, and pattern also emphasizes periphery. Adult lip not thickened or flared; varices absent. Columella wide, deeply excavated; pillar straight, strongly pinched at base. Sexual dimorphism: males smaller.

Dimensions: Table 9.20.

Sculpture (Fig. 9.73). Protoconch normal, usually eroded smooth; first whorl of teleoconch relatively large. All teleoconch whorls sculptured by spiral grooves. Primary grooves 8–10 by whorl 4, usually equidistant, but posterior 1–3 ribs may be a little wider and posterior groove deepest. Secondary sculpture often absent; on whorl 6 some ribs, or all but posterior rib, may be divided by a

Fig. 9.72 *Littoraria* (*Palustorina*) *articulata*: (a) ♀, Broome, W.A. (DGR); (b) neotype of *Littorina intermedia* var. *articulata* Philippi, ♂, Broome, W.A. (BMNH 198348); (c) lectotype of *Littorina sinensis* Philippi, China (MNHNP); (d) ♂, Magnetic I., Qld. (DGR); (e) ♂, Tolo Harbour, Hong Kong (AMS); (f) ♀, Magnetic I., Qld. (DGR); (g) ♀, Karumba, Qld. (BMNH); (h) ♂, Kanchanadit, Thailand (DGR); (i) ♀, Magnetic I., Qld. (DGR).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g
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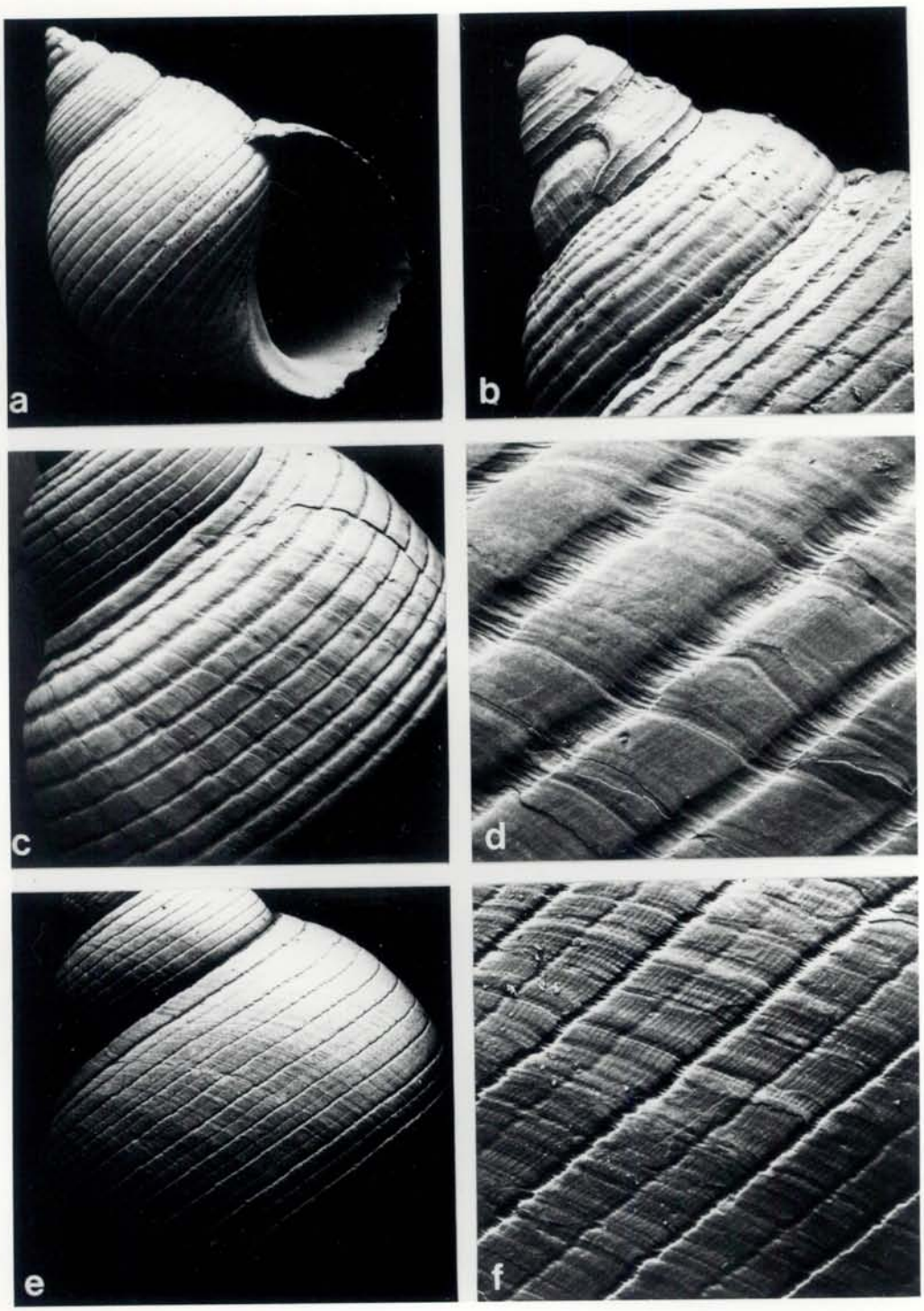
5 mm

Table 9.20 Dimensions of *Littoraria* (*Palustorina*) *articulata*.

Specimen	Locality	Sex	Primary grooves	H (mm)	B (mm)	LA (mm)	WA (mm)	C (mm)	PR	S	SH
Littorina intermedia var. *articulata* neotype, BMNH 198348	Broome, W.A.	♂	9	14.4	9.6	8.3	6.3	2.0	1.50	0.80	1.73
Litorina sinensis lectotype, MNHNP	China		8	13.4	9.5	7.4	5.5	1.1	1.41	0.74	1.81
DGR	Broome, W.A.	♂	10	13.9	9.8	8.2	6.1	1.5	1.42	0.74	1.70
DGR	Broome, W.A.	♂	9	14.5	10.1	8.9	6.9	1.9	1.44	0.78	1.63
DGR	Broome, W.A.	♀	9	15.6	11.1	9.1	6.9	1.8	1.41	0.76	1.71
DGR	Broome, W.A.	♀	9	15.9	10.4	9.2	6.8	1.9	1.53	0.74	1.73
DGR	Magnetic I., Qld.	♂	8	12.3	8.9	7.4	5.3	1.2	1.38	0.72	1.66
DGR	Magnetic I., Qld.	♀	9	15.5	11.2	9.4	7.5	1.6	1.38	0.80	1.65
DGR	Ubin I., Singapore	♂	9	10.8	7.2	6.4	4.9	1.2	1.50	0.77	1.69
DGR	Ubin I., Singapore	♀	9	12.4	8.6	7.3	5.6	1.3	1.44	0.77	1.70
DGR, mean of 10	Broome, W.A.	♂		12.92					1.430	0.756	1.677
standard error				0.39					0.007	0.009	0.014
DGR, mean of 10	Broome, W.A.	♀		14.77					1.419	0.768	1.715
standard error				0.20					0.007	0.009	0.013
statistic t or U				4.189					62	61.5	72
probability				0.001					0.394	0.415	0.106

Fig. 9.73 *Littoraria* (*Palustorina*) *articulata*: (a,b) Magnetic I., Qld.; (a) young shell (×18); (b) protoconch (×85); (c,d) Broome, W.A.; (c) last whorl (×9); (d) detail (×36); (e,f) Magnetic I., Qld.; (e) last whorl (×10); (f) detail (×42).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small secondary groove at $\frac{1}{2}$ width. Tertiary sculpture seldom developed. Total of primary and secondary ribs on last whorl (16)20-33, up to 50 ribs if tertiary sculpture is present; ribs of approximately equal width, low and flattened but for posterior rib which is usually rounded and prominent; in strongly sculptured shells 1-2 peripheral ribs may also be somewhat raised and rounded. Grooves usually impressed lines only, but up to $\frac{1}{4}$ rib width in shells with strongest sculpture; primary grooves occasionally become obsolete on shoulder of last whorl. Microsculpture of faint, regular, spiral striae confined to ribs, but sometimes indistinct or absent; irregular axial growth striae cover surface; strong, regular, axial striae are visible in wider grooves.

Colour. Variable. Ground colour usually cream yellow, sometimes pale grey or white (very rarely orange pink), with pattern of black or dark brown dashes on ribs. Typically, dashes aligned across the 3-4 posterior ribs to form axial stripes, numbering 8-11 at suture of body whorl, dashes aligned also at peripheral 4 ribs; these zones of alignment separated by a band of dense non-aligned dashes, which may merge to form continuous spiral stripes; on the base dashes are sparse and not conspicuously aligned. Degree of pigmentation is variable: shells may be black with pale grooves and yellow spots at suture and periphery; pattern may be pale and confined to suture and periphery, but is never absent; dashes may be roughly aligned over whole whorl from suture to base, but remain discrete, separated by pale grooves. Aperture yellow or cream, with purple black dashes corresponding to external pattern, glazed by whitish callus within. Columellar pillar white, parietal callus and columellar excavation dark purple, but occasionally merely tinged pink or entirely white.

ANIMAL. *Colour*. Pigmentation dark grey to black; sides of foot darkly mottled; head black, sometimes with pale central streak; tentacles darkly banded, unpigmented stripe each side of base.

Penis (Fig. 9.74a-k). Length to 5.0 mm. Base simple, incorporating glandular disc. Filament small, less than half length

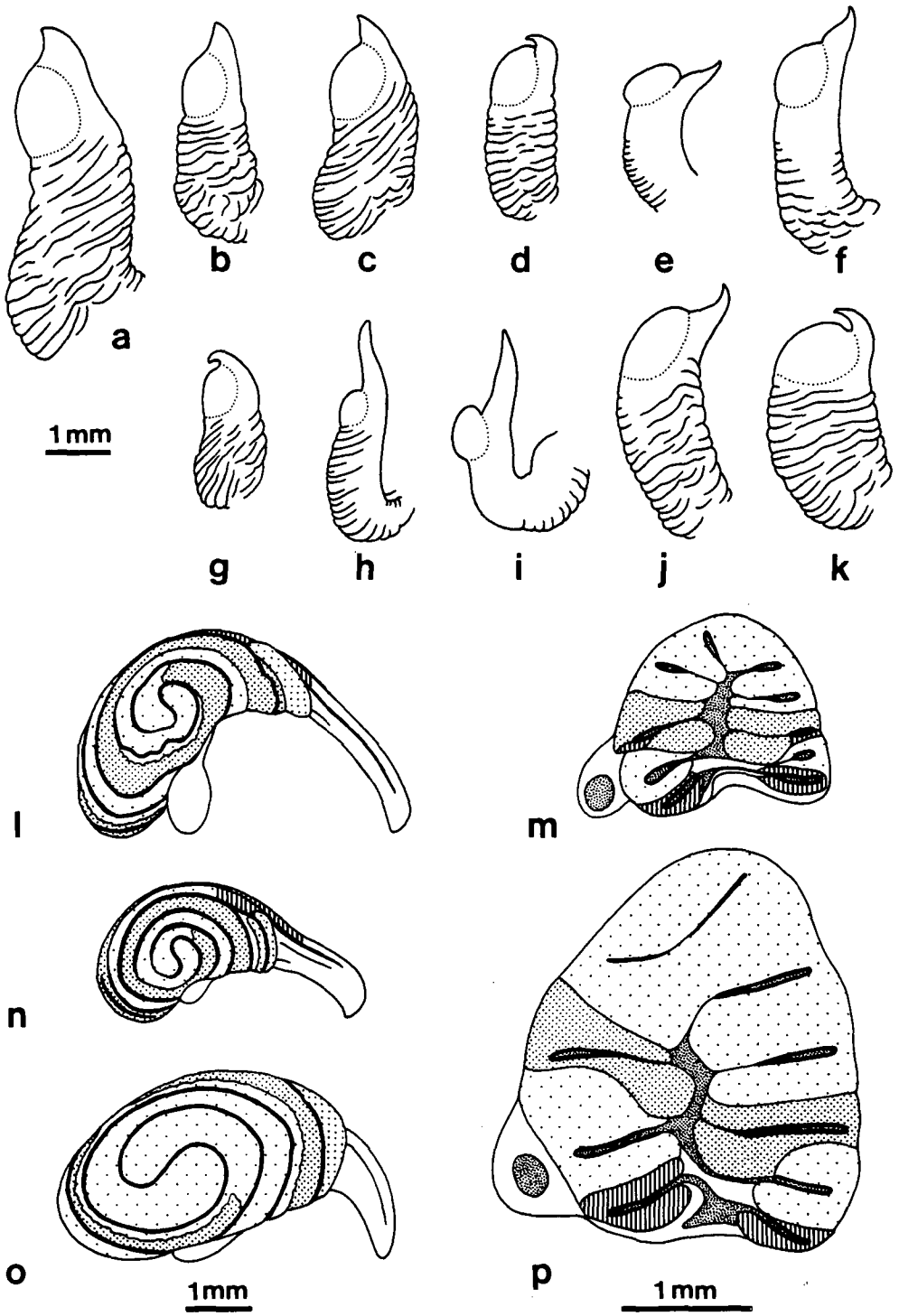


Fig. 9.74 *Littoraria* (*Palustorina*) *articulata*: (a-k) penes; (a-c) Broome, W.A.; (d-f) Magnetic I., Qld.; (g) Tolo Harbour, Hong Kong; (h) Iso, Kagoshima Bay, Japan; (i) Sanchun-Kun, Kyongsang-Namdo, S. Korea; (j,k) Kanchanadit, Thailand; (l-p) pallial oviducts, with transverse sections; (l,m) Broome, W.A.; (n) Magnetic I., Qld.; (o,p) Kanchanadit, Thailand.

of base, tapering. Sperm groove open. Base and filament off white to pale ochre; glandular disc opaque white to cream.

Sperm (Fig. 5.3e,f). Eupyrene sperm 236–252 μm. Nurse cells (Fig. 9.75d–f) 30–42 μm, elongate oval to fusiform; basal flagellum to 170 μm; rods 1–2(4), basal, elongate oval; yolk granules small, becoming larger towards base.

Pallial oviduct (Fig. 9.74l–p). Length to 5.7 mm. Spiral section to 4.8 mm diam., $5\frac{1}{2}$ whorls; opaque albumen gland $\frac{1}{3}$ whorl, white; translucent albumen gland white to grey or fawn; opaque capsule gland $1–1\frac{1}{2}$ whorls, cream, ochre or pale pink; translucent capsule gland red brown; spiral distinct externally; egg groove darkly pigmented. Straight section to 2.0 mm, fawn; no terminal papilla. Bursa posterior, extending into spiral section. Development oviparous.

Egg capsules (Fig. 9.75a–c). Capsules 248–268 μm diam., transparent, biconvex discs, convexity usually more pronounced on one side, with broad circumferential flange; containing single ova; egg covering 76–82 μm diam. (pers. obs. at Magnetic I., Qld.). At Amakusa, Kyushu, Japan, Kojima (1958c) reported symmetrically biconvex capsules 350 μm in diam., lacking circumferental flange, and with egg covering 100 μm diam. (Fig. 9.75c).

Radula (Fig. 9.69f). Length to 14 mm; relative length 0.85–1.18. Intermediate between saw- and chisel-toothed types; central rachidian cusp square to broadly rectangular, edge rounded or slightly pointed; cusps of paired teeth obliquely triangular; lateral with gap anterior to main cusp.

DISTRIBUTION. *Habitat*. Most abundant in *Avicennia* fringe, less so in *Sonneratia* fringe, common also on outermost *Rhizophora* trees. On trunks at outer edge of forest, 0.3–1.2 m above ground, up to 2.0 m if tidal range is great. Frequent at lower levels on roots in *Rhizophora* forests, but does not extend further than the back of

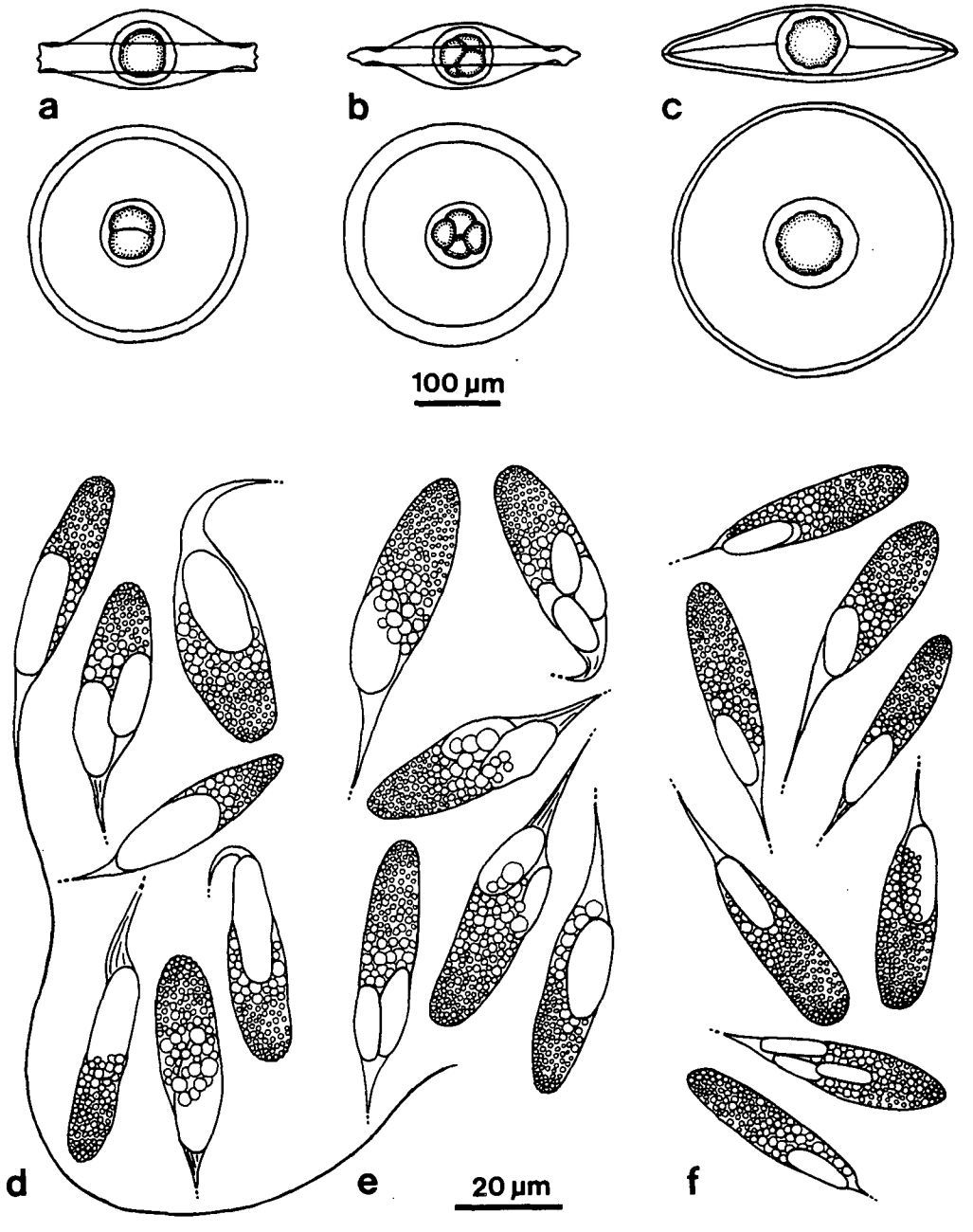


Fig. 9.75 *Littoraria* (*Palustorina*) *articulata*: (a–c) egg capsules; (a) normal form, Magnetic I., Qld.; (b) abnormal form, Magnetic I., Qld.; (c) Amakusa, Kyushu, Japan (after Kojima, 1958c); (d–f) sperm nurse cells; (d,e) Magnetic I., Qld.; (f) Kanchanadit, Thailand.

this zone. Sometimes abundant on sheltered rocks and wooden pilings, at and above water level. A continental species.

Range (Fig. 9.76). Known range (determination based on anatomy, indicated by 'A' in list of records below) extends from Moreton Bay, Qld., around northern coast of Australia to Exmouth Gulf, W.A.; elsewhere Singapore, Sarawak, Gulf of Thailand, Vietnam, Hong Kong, southern Japan. Based on identification of shells alone, the range is extended to central Indonesia; occurence in India is doubtful.

Records. INDIA: Bombay (BMNH); Mandapam (ANSP); Madras (BMNH); Waitair, Vishakhapatnam (ANSP); Diamond Harbour, Bengal (BMNH); SRI LANKA: Trincomalee (BMNH); BURMA: near Cape Negrais, Arakan (BMNH); Salween R. (BMNH); King I., Mergui Arch. (BMNH); ANDAMAN IS. (BMNH); THAILAND: Songkhla (MCZ); Kanchanadit, near Surat Thani (DGR, A); Hua Hin (WAM, A); Bang Saen, 14 km S.W. of Chon Buri (ANSP, A); MALAYSIA: PENINSULA: Batu Maung, Penang (DGR, A); Sungei Merbok estuary, Kedah (DGR, A); 10 km N. of Port Kelang (DGR, A); Kuantan (AMS); SARAWAK: Santubong (DGR, A); SABAH: Po Bui I., Sandakan (USNM); SINGAPORE: Jelutong, Ubin I. (DGR, A); Loyang Besar (WAM); INDONESIA: SUMATRA: Weh I. (RNHL); Bangka I. (RNHL); JAVA: Tandjong Priok, Djakarta (RNHL, MCZ); Rembang (RNHL); S. coast Madura I. (RNHL); Paternoster I. (RNHL); KALIMANTAN: Balikpapan (RNHL); SULAWESI: Makassar (RNHL); IRIAN JAYA: Merauke (AMS, RNHL); VIETNAM: Ben Dinh, Vung Tau district (ANSP, A); Ile de la Table, Tonkin (MCZ); CHINA: Hainandao I. (ANSP); Amoy (USNM, RNHL); mouth of Yangtze R. (BMNH); Tsingtao, Shantung (Academia Sinica; BMNH); HONG KONG: Tolo Channel (BMNH, A); Deep Bay, New Territories (AMS, A); S. KOREA: Sachun-Kun, Kyongsang-Namdo (ANSP, A); JAPAN: Ryukyu Is. (AMS); Iso, Kagoshima Bay, Kyushu (NSMT, A); Hirado, Hizen, Kyushu (AMS); Amakusa, Kyushu (USNM; NSMT, A); Ehime Pref., Shikoku (USNM); AUSTRALIA: W.A.: Bay of Rest, Exmouth Gulf (WAM); Onslow (AMS); Broome (DGR, A; AMS; NMV); Derby (AMS); Port Warrender, Admiralty Gulf (WAM, A); Wyndham (AMS); N.T.: Ludmilla Creek, Darwin (DGR, A); Port Essington (AMS, A); Woolen R., Arnhemland (AMS); QLD.: Sweers I. (AMS); Karumba (AMS); Thursday I. (DGR, A): Boigu I. (WAM);

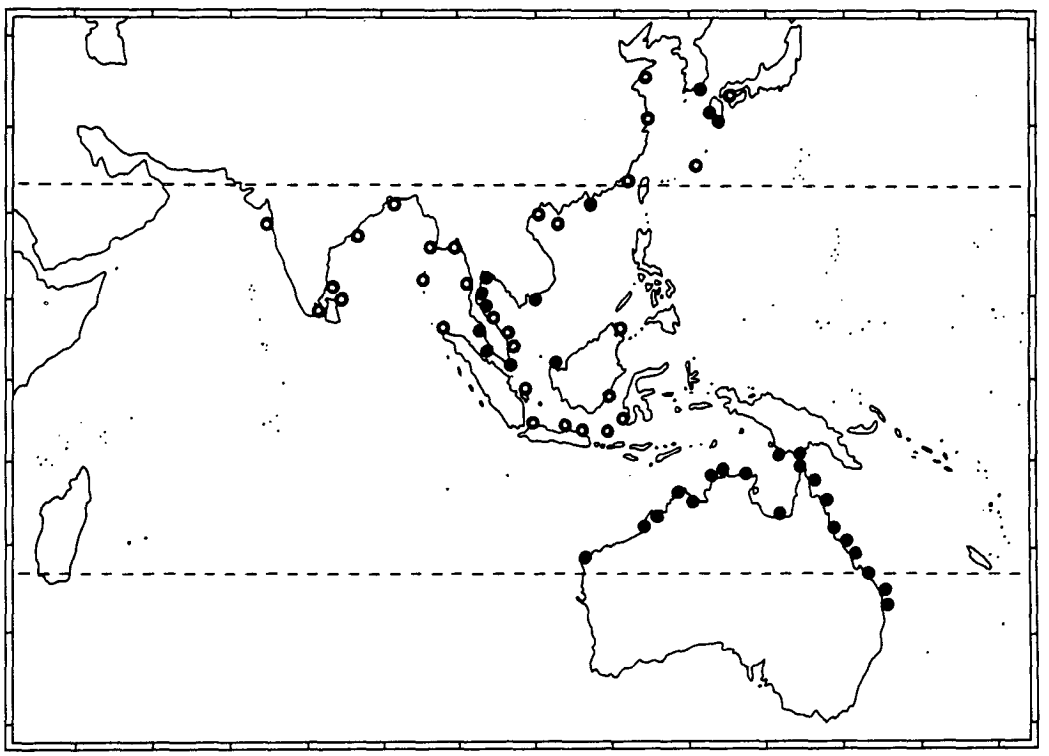


Fig. 9.76 Distribution of *Littoraria* (*Palustorina*) *articulata*. Closed circles, records confirmed by anatomical data; open circles, records based on shells alone.

Quintell Beach, Iron Range (QM); Low Is. (QM); Missionary Bay, Hinchinbrook I. (DGR, A; USNM); Magnetic I. (DGR, A): Bowen (WAM); Mackay (WAM); N. Keppel I. (AMS); Yeppoon (AMS); Gladstone (AMS); Urangan (AMS); Sandgate, Moreton Bay (QM, NMV).

REMARKS. Shells of *L. articulata* and *L. strigata* (Philippi) are often indistinguishable and anatomical characters are required for their separation. The close relationship between these two species is discussed in the remarks upon *L. strigata*. The distribution map (Fig. 9.76) is compiled largely from museum collections of shells so that determinations are often doubtful. In particular, occurence of the species in India has not been confirmed by preserved material and it is possible that only *L. strigata* occurs there.

Amongst preserved specimens, shell characters are fairly constant, varying only in prominence of the spiral grooves and in details of colour pattern. A rather well defined geographical form (Fig. 9.72a,b) occurs in north-western Australia, from Admiralty Gulf to Exmouth Gulf; the neotype is of this form, as, presumably, was the specimen on which Philippi based this species. In this region the shells are more strongly sculptured, with wider grooves, the columella is white as opposed to purple, and the shell colouration is characteristic, the ground colour white with a pattern of discrete black or brown dashes. There are no anatomical differences, however, and the form is not considered worthy of taxonomic recognition.

In specimens from China and Japan, the colour pattern is sometimes diffuse and the sculpture may be strong (Fig. 9.72c,e). In addition the penial filament of such shells is sometimes relatively longer than in specimens from South East Asia and Australia. The egg capsule of the Japanese form has been illustrated by Kojima (1958c; reproduced Fig. 9.75c herein), and is larger than that of the species at Magnetic I., Queensland (Fig. 9.75a), and lacks the circumferential flange. However, ever at the latter locality there is some variation in capsule shape, and an unusual form (Fig. 9.75b)

is more similar to that drawn by Kojima. The eastern Asian form is tentatively assigned to *L. articulata*. Further work is necessary on the forms of *L. articulata* and also on their relationship with the form here recognized as a separate species, *L. strigata*.

Of the many thousands of specimens seen, only 4 have been found in which the ground colour of the shell is orange pink. This colour form is known elsewhere in the subgenus only in *L. melanostoma* and is rare in that species also, although pink shells are not infrequent in the subgenus *Littorinopsis*. The species occupies a wide range of habitats and zones. At the seaward edge of continental mangrove forests it occurs in great numbers, often closely packed on trunks at and just above the water level.

SIMILAR SPECIES. Differentiation of *L. articulata* from the two similar species *L. strigata* and *L. vespacea* is discussed in the remarks upon these two. Anatomically, *L. intermedia* and *L. articulata* are perfectly distinct, belonging to different subgenera. THe shells are usually easily separated, but in doubtful cases the following characters can be used: that of *L. articulata* is smaller, the whorls more rounded and the spire lower; spiral sculpture is usually less pronounced; the ground colour is white or yellow, not grey; the pattern of dark dashes (except in the N.W. Australian form) is less discrete and regular than in *L. intermedia*, and there are fewer axial colour stripes at the suture of the last whorl. The shell of *L. undulata* (Fig. 9.81a-c) is rarely at all similar to that of *L. articulata*; in the former the spiral sculpture is usually obsolete, the columellar pillar relatively longer, straight and lilac in colour, and if darkly coloured the shell pattern is of uninterrupted axial zigzag stripes. Anatomically, *L. undulata* is distinguished by a penial glandular disc of unusually large size (Fig. 5.2e). The West African *L. cingulifera* (Fig. 9.81h,i) can be extremely similar to *L. articulata*, but the spire is usually lower and the aperture more patulous, the columellar pillar relatively longer, straight and not so sharply pinched at the base, the shell pattern more often of spiral lines than dashes; anatomically the

species are separated by the form of the penis, for in *L. cingulifera* the glandular disc is borne on a small projection of the base and the filament is broad and blunt (Fig. 5.2g).

9.2.4.7 *Littoraria* (*Palustorina*) *strigata* (Philippi, 1846)

Littorina intermedia var. *strigata* Philippi, 1846: 141 [Jimamailan [Himamaylan], Negros I., Philippines; lectotype here designated BMNH 1968353]; Nevill, 1885: 146-147 [in part]

Litorina intermedia var. *strigata* – Philippi, 1847, vol. 2: 223, *Litorina* pl. 5, fig. 8 [in part; original citation corrected to figs 7,8,9]

Littorina intermedia – von Martens, 1887: 169-170; Hidalgo, 1904-5: 206 [both in part; not Philippi, 1846]

Littorina (*Melaraphe*) *scabra* var. *intermedia* – Tryon, 1887: 244 [in part; not Philippi, 1846]

Littorina (*Malaraphe*) *intermedia* – Casto de Elera, 1896: 309-310 [in part; not Philippi, 1846]

Littorina (*Littorinopsis*) *intermedia* – von Martens, 1897: 197 [in part; not Philippi, 1846]

Littorinopsis intermedia – Brandt, 1974: 54 [in part; not Philippi, 1846]

Littorina (*Littorinopsis*) *scabra scabra* – Rosewater, 1970: 456-461, pl. 352, fig. 8 [in part; not Linnaeus, 1758]

Littorina undulata – Berry, 1972 [in part; not Gray, 1839]

Littorinopsis undulata – Brandt, 1974: 54 [in part; not Gray, 1839]

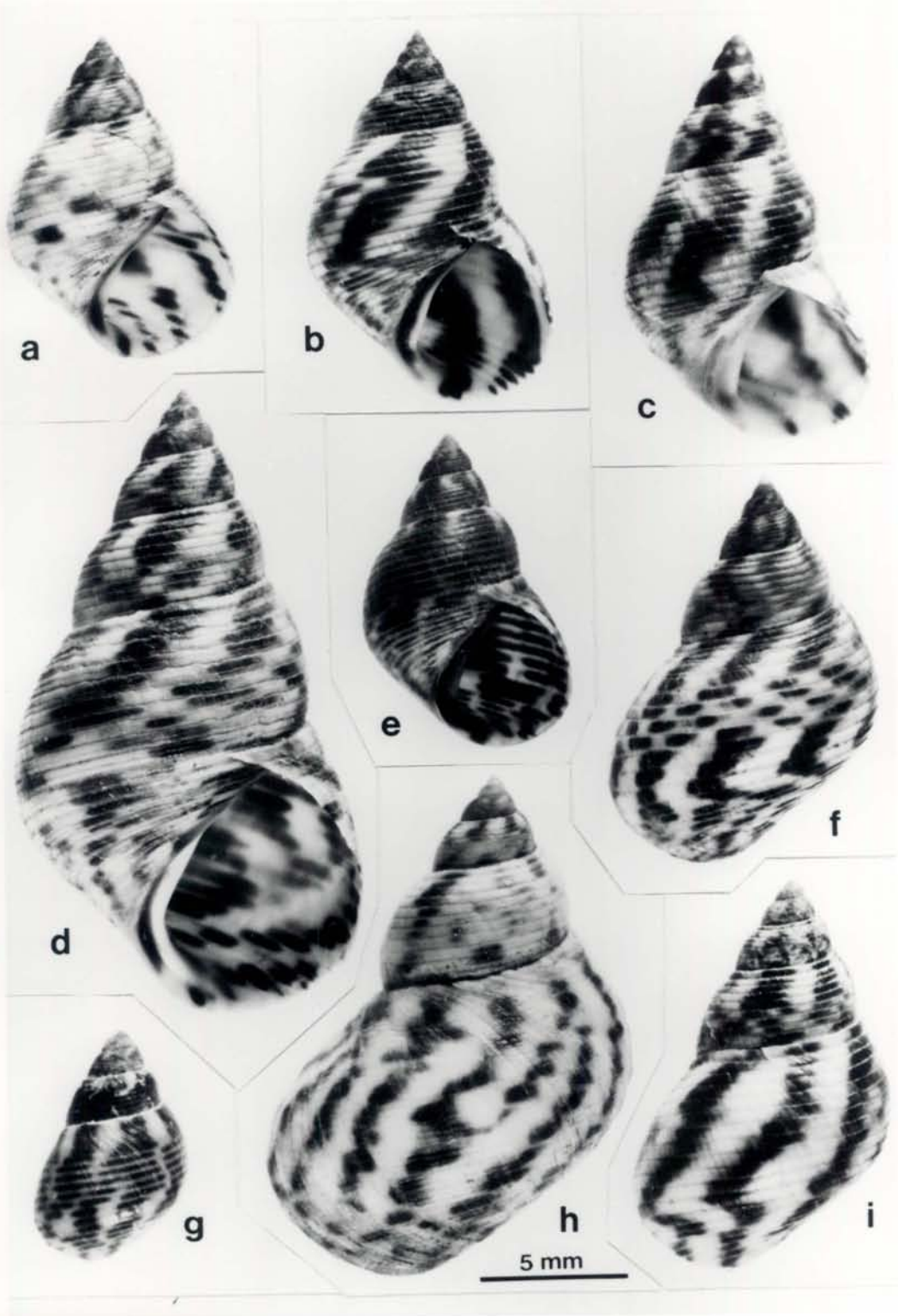
NOMENCLATURE. Since separation of *L. strigata* from *L. articulata* is dependent largely upon anatomical characters, type specimens, figures and descriptions based on shells alone are difficult to interpret. *Littorina intermedia* var. *strigata* was described by Philippi in 1846 from material in the Cuming Collection, and the variety was figured by the author the following year. Of the three

figures referred to in the text as var. *strigata* (see Section 9.2.3.5 for a discussion of the error in the original citation), figures 7 and 9 may represent respectively the species here recognized as *L. articulata* and *L. subvittata*. Only figure 8 is typical of the species to which the name *strigata* is here restricted. The origin of the figured specimens was not mentioned in the text, but there is little doubt that a lot from the type locality in the BMNH contains the original specimen of Philippi's figure 8, although no label in Cuming's hand remains. This figured specimen was recognized by Rosewater (1970), who designated it as lectotype of *Littorina intermedia*. However, this designation is not acceptable (Section 9.2.3.5) and the same specimen is here designated lectotype of *Littorina intermedia* var. *strigata*. The determination of this specimen is not in doubt, for the shell (Fig. 9.77c) is of the type most characteristic of *L. strigata* and not seen in *L. articulata*; furthermore, of these two species only the former is known to occur in the Philippines. It should be noted that *Litorina strigata* Lischke is apparently a synonym of *L. articulata*, and not of *L. strigata* (Philippi).

DIAGNOSIS. Shell: small (less than 21 mm); solid; spire whorls rounded; peripheral keel absent; columella of moderate width, excavated; primary grooves 8–10; secondary sculpture often weak or absent; total of 20–33 flat ribs on last whorl; grooves narrow; microsculpture indistinct; colour variable, cream yellow to white with black or brown pattern typically forming 6–8 broad, oblique, axial stripes, but pattern may be broken up into poorly aligned dashes on ribs. Animal: penis not bifurcate, base narrow, filament long, greater than length of base; oviparous.

SHELL (Fig. 9.77). *Shape*. Height 6–21 mm. Teleoconch 5–7 whorls. Shell of moderate thickness, solid. Spire outline slightly convex, whorls rounded; sutures impressed. Peripheral keel absent, but pattern may sometimes emphasize periphery. Adult lip not thickened or flared; varices absent. Columella of moderate width, excavated; pillar straight, pinched at base. Sexual dimorphism: males smaller,

Fig. 9.77 *Littoraria (Palustorina) strigata*: (a) ♂, Penang, Malaysia (DGR); (b) ♂, Kanchanadit, Thailand (DGR); (c) lectotype of *Littorina intermedia* var. *strigata* Philippi, Himamaylan, Negros I., Philippines (BMNH 1968353); (d) ♀, Kanchanadit, Thailand (DGR); (e,f) Penang, Malaysia (DGR); (e) ♂; (f) ♀; (g) ♂, Manila Bay, Philippines (AMS); (h) ♀, Penang, Malaysia (DGR); (i) ♀, Kanchanadit, Thailand (DGR).


a
b
c
d
e
f
g
h
i
5 mm

aperture narrower.

Dimensions: Table 9.21.

Sculpture (Fig. 9.78a,b). Protoconch not seen, usually eroded smooth; first whorl of teleoconch relatively large. All teleoconch whorls sculptured by spiral grooves. Primary grooves number 8–10 by whorl 4, approximately equidistant, posterior groove usually deepest. Secondary sculpture often absent, but on whorl 6 some ribs, or all ribs but the most posterior, may be divided by a small secondary groove at about $\frac{1}{2}$ width. A few tertiary grooves are formed in largest shells only. Ribs usually remain flattened, but for the rounded and prominent posterior rib; in the most strongly sculptured forms all ribs may be somewhat rounded. Total of primary and secondary ribs on body whorl 20–33, up to 60 on largest shells with tertiary sculpture. Grooves usually about $\frac{1}{5}$ rib width, but sometimes impressed lines only, and rarely up to $\frac{1}{2}$ rib width. Microsculpture of faint, regular spiral striae confined to ribs, occasionally indistinct or absent; surface covered by irregular axial growth striae; strong and regular axial striae visible in wider grooves.

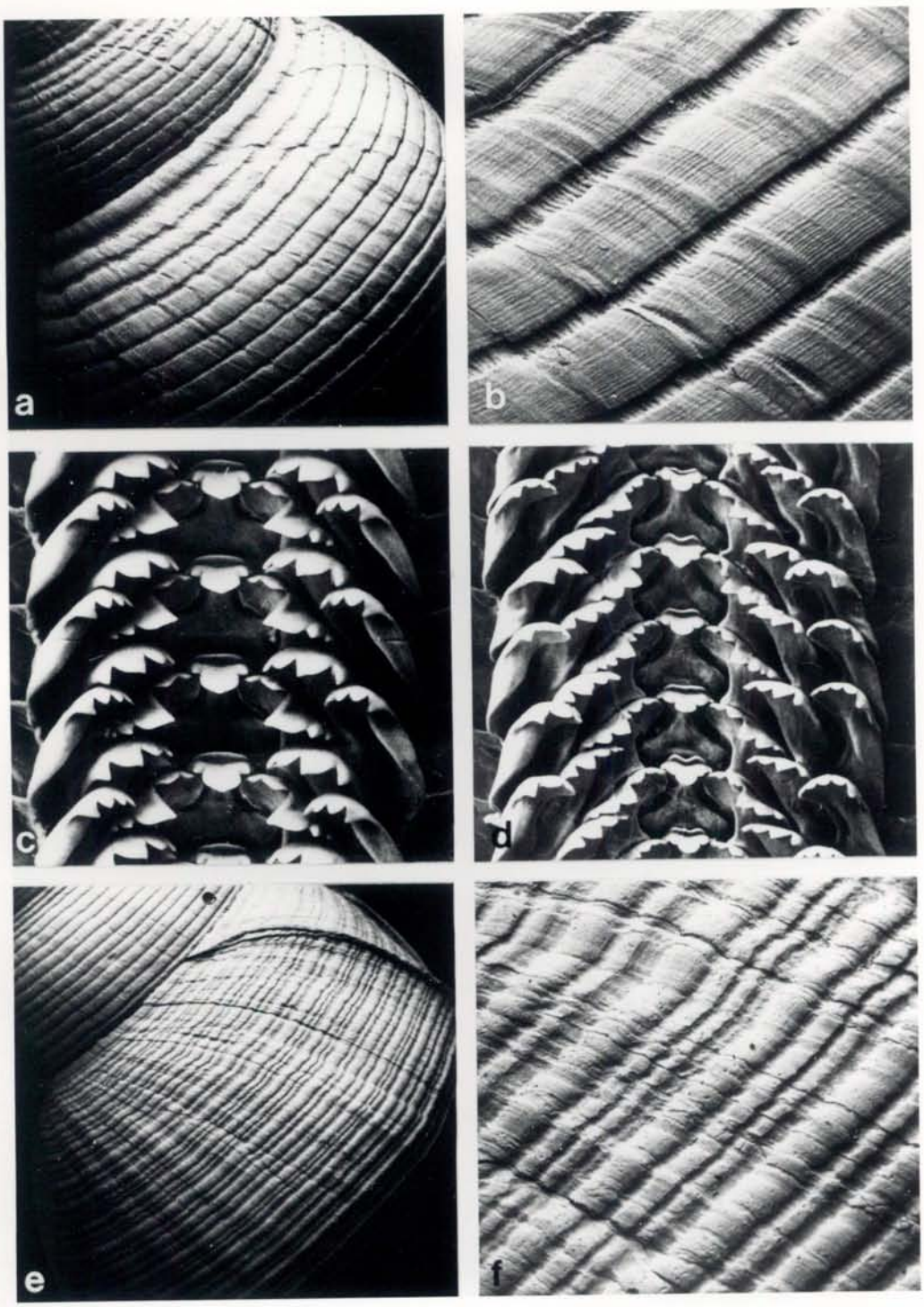
Colour. Variable. Ground colour cream yellow or white, with a black or dark brown pattern. Typically, pattern is conspicuously aligned from suture to base, to form 6–8 broad, oblique or zigzag, axial stripes, separated by an approximately equal width without pigment; stripes are continuous across grooves and may divide and anastomose. Pattern sometimes broken up into separate spiral dashes on ribs, aligned only at suture and periphery; shells may be sparsely or densely patterned. Aperture yellow or cream, with black lines and stripes corresponding to external pattern; in largest shells glazed by a thin whitish callus within. Parietal callus and columellar excavation dark purple, occasionally only tinged pink; columellar pillar white.

ANIMAL. *Colour*. Pigmentation black; sides of foot darkly mottled;

Table 9.21 Dimensions of *Littoraria* (*Palustorina*) *strigata*.

Specimen	Locality	Sex	Primary grooves	H (mm)	B (mm)	LA (mm)	WA (mm)	C (mm)	PR	S	SH
Littorina intermedia var. *strigata* lectotype, BMNH 1968353	Himamaylan, Negros I., Philippines		10	14.1	9.0	7.5	5.5	1.4	1.57	0.73	1.88
DGR	Kanchanadit, Thailand	♂	10	12.1	8.0	6.6	4.8	0.9	1.51	0.86	1.83
DGR	Kanchanadit, Thailand	♂	9	12.5	8.9	7.2	5.3	1.1	1.40	0.74	1.74
DGR	Kanchanadit, Thailand	♀	9	21.0	12.5	10.6	7.7	1.7	1.68	0.73	1.98
DGR	Kanchanadit, Thailand	♀	9	13.7	9.0	7.6	5.5	1.2	1.52	0.73	1.80
DGR	Penang, Malaysia	♂	9	13.4	8.4	7.5	5.4	1.0	1.60	0.72	1.79
DGR	Penang, Malaysia	♀	9	14.9	10.2	8.6	6.7	2.0	1.46	0.78	1.73
AMS C.131827	Manila, Philippines	♂	8	7.0	5.3	4.6	3.3	0.5	1.32	0.72	1.52
AMS C.131827	Manila, Philippines	♀	8	7.2	5.5	4.8	3.5	0.8	1.31	0.73	1.50
DGR, mean of 10	Penang, Malaysia	♂		11.20					1.422	0.737	1.655
standard error				0.31					0.022	0.007	0.022
DGR, mean of 10	Penang, Malaysia	♀		12.94					1.419	0.773	1.681
standard error				0.68					0.022	0.010	0.032
statistic t or U				2.321					51	83	56
probability				0.032					0.970	0.012	0.436

Fig. 9.78 (a–c) *Littoraria* (*Palustorina*) *strigata*: (a,b) Kanchanadit, Thailand; (a) last whorl (×11); (b) detail (×43); (c) radula, Penang, Malaysia (×260). (d–f) *Littoraria* (*Littorinopsis*) *ardouiniana*, Three Fathoms Cove, Hong Kong: (d) radula (×170); (e) last whorl (×7); (f) detail (×26).


a
b
c
d
e
f

head darkest; tentacles darkly banded, stripes at base often absent or indistinct.

Penis (Fig. 9.79a-h). Length to 6.0 mm. Base simple, rather narrow, incorporating small glandular disc. Filament long, greater than length of base, tapering. Sperm groove open. Penis white to cream.

Sperm. Eupyrene sperm 240 μm. Nurse cells (Fig. 9.79l-n) 34-47 μm; elongate oval, tapering to basal flagellum, sometimes slightly constricted at mid-length; basal flagellum to 175 μm; rods 1-4(6), small, basal, rectangular; yolk granules small, becoming larger towards base.

Pallial oviduct (Fig. 9.79i-k). Length to 5.0 mm. Spiral section to 4.2 mm diam., $4\frac{1}{2}$ whorls; opaque albumen gland $\frac{1}{4}$ whorl, white; translucent albumen gland white; opaque capsule gland $\frac{1}{2}$-$\frac{3}{4}$ whorl, pale pink or white; translucent capsule gland red brown; spiral distinct externally; egg groove darkly pigmented. Straight section short, to 1.4 mm, pale brown; no terminal papilla. Bursa posterior, extending into spiral section. Development assumed oviparous.

Radula (Fig. 9.78c). Length to 17 mm; relative length 1.07-1.32. Intermediate between saw- and chisel-toothed types; central rachidian cusp broad, edge straight or slightly pointed; cusps of paired teeth obliquely triangular; lateral with gap anterior to main cusp.

DISTRIBUTION. *Habitat*. Most common on trunks in *Avicennia* fringe, 0.3-1.8 m above ground; also on *Sonneratia* trunks and roots of outermost *Rhizophora* trees, but scarce in *Rhizophora* forest. Sometimes abundant on sheltered rocks and wooden pilings.

Range (Fig. 9.80). Known range (determination based on anatomy, indicated by 'A' in list of records below) south-western Thailand, Singapore, Gulf of Thailand, Java, Sarawak, Philippines. Based on

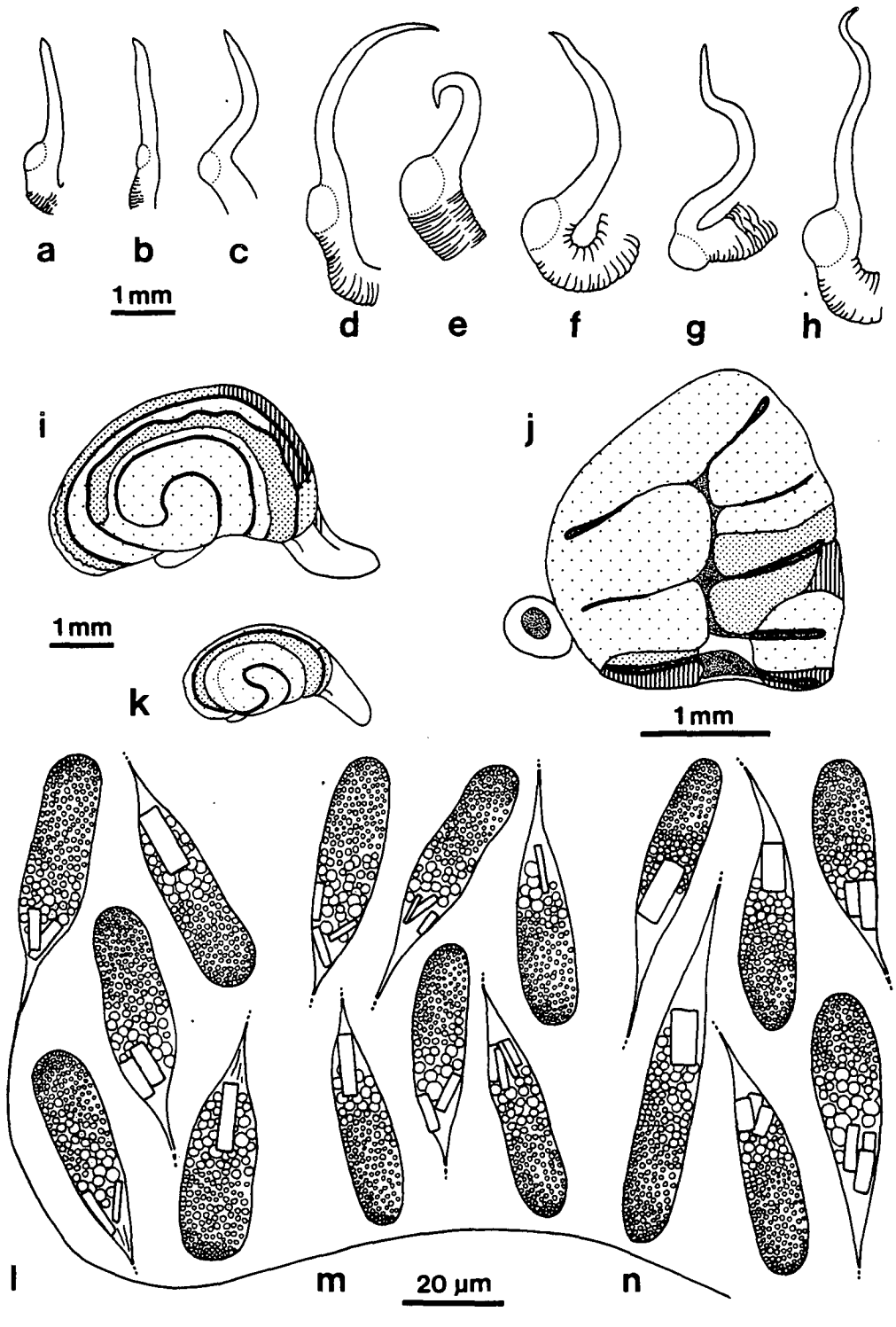


Fig. 9.79 *Littoraria (Palustorina) strigata*: (a–h) penes; (a,b) Manila Bay, Philippines; (c) Phuket I., Thailand; (d–f) Kanchanadit, Thailand; (g,h) Penang, Malaysia; (i–k) pallial oviducts, with transverse section; (i,j) Kanchanadit, Thailand; (k) Manila Bay, Philippines; (l–n) sperm nurse cells; (l) Kanchanadit, Thailand; (m) Penang, Malaysia; (n) Phuket I., Thailand.

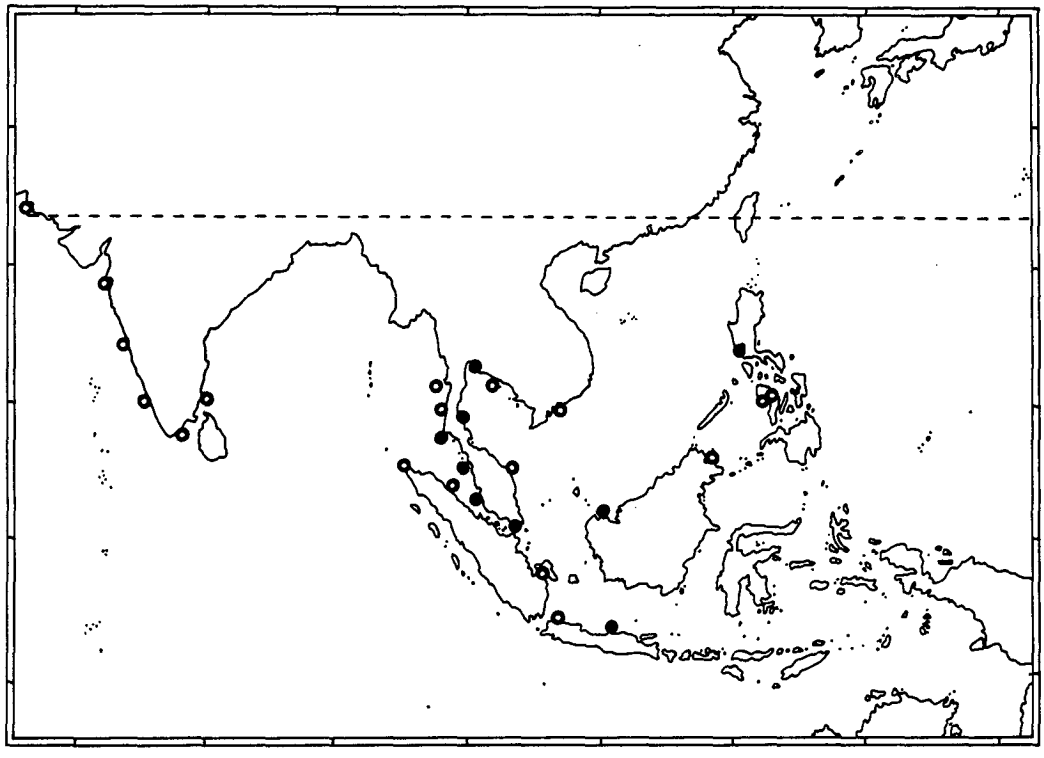


Fig. 9.80 Distribution of *Littoraria* (*Palustorina*) *strigata*. Closed circles, records confirmed by anatomical data; open circles, records based on shells alone.

identification of shells, range is extended west to India and Pakistan.

Records. PAKISTAN: west wharf, Karachi (MCZ); INDIA: Bombay (BMNH, MCZ, USNM); Vingurla, N. of Goa (USNM); Netravati R., Mangalore (USNM); Gulf of Mannar (USNM); Adyar R. estuary, Madras (USNM); BURMA: Elphinstone I., Mergui Arch. (BMNH); Victoria Point (MCZ); THAILAND: Tanga I., Butang Group (USNM); Ao Nam Bor, Phuket I. (DGR, A); Kanchanadit, near Surat Thani (DGR, A); Bang Saen, 14 km S.W. of Chon Buri (ANSP, A); Ko Kut (USNM); MALAYSIA: PENINSULA: Batu Maung, Penang (DGR, A); Sungei Merbok estuary, Kedah (DGR, A); 10 km N. of Port Kelang (DGR, A); Trengganu (ANSP); SARAWAK: Santubong (DGR, A); SABAH: Po Bui I., Sandakan (USNM); SINGAPORE: Jelutong, Ubin I. (DGR, A); VIETNAM: Chilins, Vung Tau district (ANSP); INDONESIA: SUMATRA: Weh I. (RNHL); Belawan R., Deli (RNHL); Tandjong Njioer, Bangka I. (RNHL); JAVA: Tandjong Priok, Djakarta (RNHL); Djepara (USNM, A); PHILIPPINES: Viejo Victorias, Negros I. (USNM); Iloilo, Panay (USNM); S.E. Bataan, Luzon (ANSP); Cavite, Manila Bay (AMS, A).

REMARKS. This species is clearly very closely related to *L. articulata* and shells alone are often indistinguishable. That the two are probably distinct was first suggested by the observation that in several South East Asian populations of supposed *L. 'articulata'* the penis was dimorphic. The dimorphism was not associated with reproductive condition, since all males examined were mature, nor with obvious parasitic infection. Furthermore, from observations on *L. articulata* throughout the year at Magnetic Island, Queensland, it was known that penial form did not show seasonal change. The narrow penial type with long filament was found to be correlated with a shell pattern of broad axial stripes, and all sperm nurse cells examined (from localities: Kanchanadit, S.E. Thailand; Phuket I., S.W. Thailand; Penang, Malaysia; Manila Bay, Philippines) contained small, rectangular rods, in contrast with the larger, oval rods of *L. articulata*. Males are immediately separable by penial and sperm characters, but determination of females is more

difficult. Usually the pallial oviduct consists of $4\frac{1}{2}$ whorls and the opaque capsule gland of $\frac{1}{2}$-$\frac{3}{4}$ whorl ($5\frac{1}{2}$ and 1-$1\frac{1}{2}$ respectively in *L. articulata*), but the number of whorls visible depends upon the plane of the transverse section and the opaque capsule gland is somewhat variable in extent. At certain localities (e.g. those on the Malayan Peninsula listed above) shells of *L. strigata* can usually be distinguished by their stronger sculpture and by the fewer and uninterrupted axial black stripes. However, shells of *L. strigata* from Manila Bay (Fig. 9.77g) and some from Java, Singapore and the Gulf of Thailand, fall within the range of typical *L. articulata*. Other examples of separate species of littorinids with closely similar shells have been reported (Sacchi & Rastelli, 1967; Hannaford Ellis, 1979; Murray, 1979), but further research is necessary to verify that *L. articulata* and *L. strigata* are indeed distinct species.

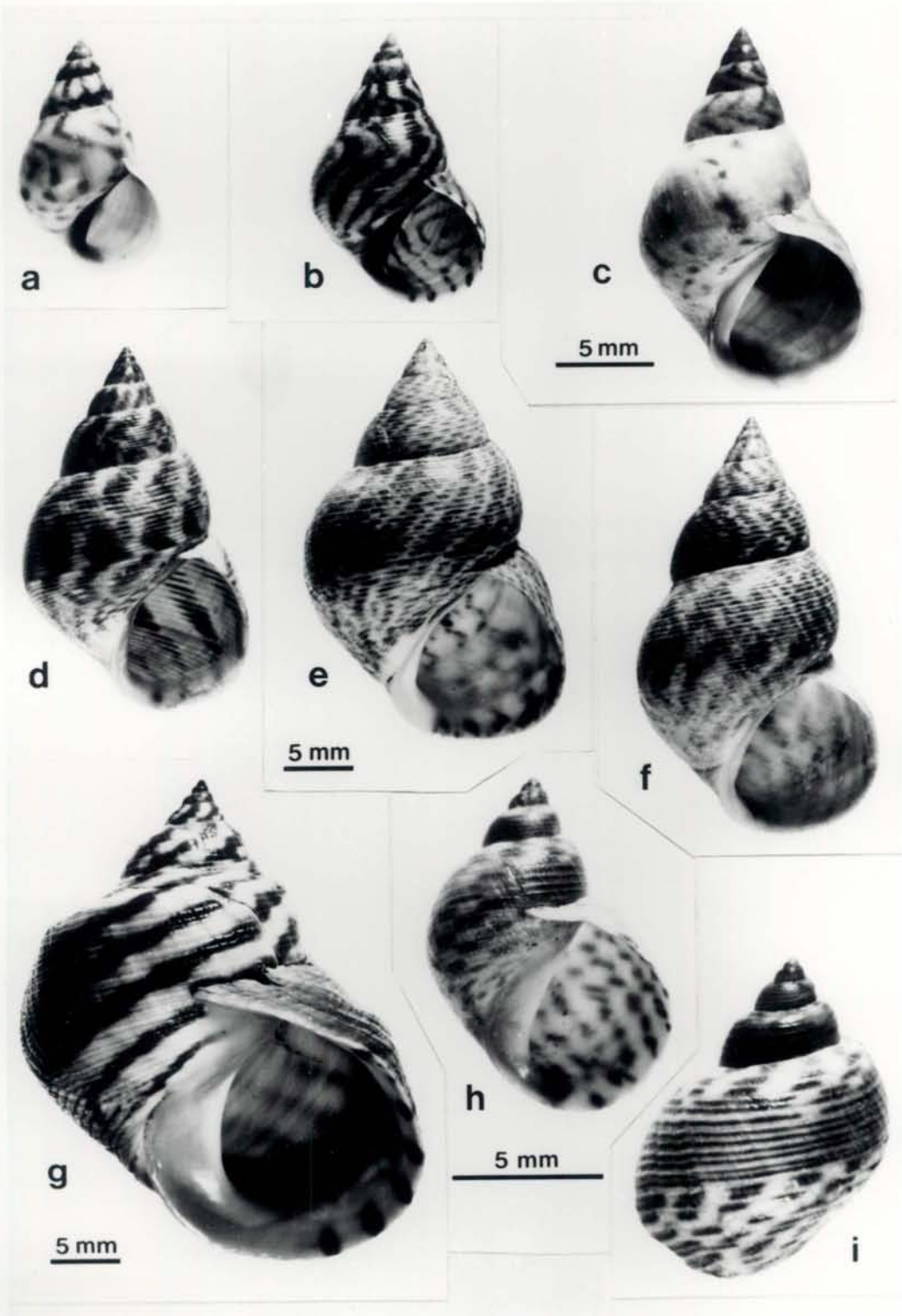
There is no clear habitat difference between *L. strigata* and *L. articulata*. Both occur commonly at similar levels on the trunks of the outermost trees of mangrove forests. However, at the South East Asian localities where the ranges overlap, either one or other species is dominant (*L. strigata* at: Phuket I., S.W. Thailand; Batu Maung, Penang; Sungei Merbok estuary, Kedah; near Port Kelang, Malaysia; *L. articulata* at: Singapore; Santubong, Sarawak; all DGR). The only localities at which both species are abundant are in the Gulf of Thailand (Kanchanadit, S.E. Thailand, DGR, *L. strigata* 30%; and near Chon Buri, ANSP). There is a suggestion that *L. strigata* is dominant in the somewhat less turbid and more oceanic situations.

The geographical distribution of *L. strigata* is imperfectly known, since many records are based upon shells alone. No preserved material has been seen from India, but shells from this area often resemble typical *L. strigata* rather than *L. articulata*, and it is possible that only the former occurs there.

SIMILAR SPECIES. Separation from *L. articulata* is discussed above. Other similar species include *L. intermedia*, *L. undulata* and *L.*

cingulifera, as discussed in the remarks on *L. articulata* (Section 9.2.4.6). *L. vespacea* is superficially similar even in anatomical features; the penis of *L. strigata* lacks a constriction at the base of the filament and is more slender, the sperm nurse cells are flagellate, the bursa copulatrix is posterior and the oviduct of only $4\frac{1}{2}$ whorls; the shell of *L. strigata* is more narrow, the columella less deeply excavated and the axial stripes are fewer than in *L. vespacea*.

Fig. 9.81 (a–c) *Littoraria* (*Littoraria*) *undulata*: (a,b) Green I., Qld.; (a) ♂; (b) ♀; (c) Sula Arch., Indonesia (BMNH). (d–f) *Littoraria* (*Littorinopsis*) *angulifera* : (d) Gabon (AMS); (e) Banana, Zaire (BMNH); (f) Colon, Panama (AMS). (g) *Littoraria* (*Littoraria*) *zebra*, Panama (BMNH). (h,i) *Littoraria* (*Littoraria*) *cingulifera*, Lagos, Nigeria (BMNH).


a
b
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