

A REVIEW OF THE GENERA OF THE IRAVADIIDAE
(GASTROPODA: RISSOACEA) WITH AN ASSESSMENT
OF THE RELATIONSHIPS OF THE FAMILY

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ABSTRACT

The family Iravadiidae is defined and shown to have a close relationship with the Hydrobiidae, not the Rissoidae as previously thought. Nine genera and five subgenera (of *Iravadia*) are provisionally recognised. Iravadiids live mainly in the Indo-West Pacific region in brackish-waters, or are marine. Seven new species, two new genera and one new subgenus are described.

The Iravadiidae have a slit-like ventral opening to the pallial genital duct in the female. The bursal duct and, with one exception, the bursa copulatrix, is entirely in the pallial part of the genital tract, not posterior to the pallial cavity as in the Hydrobiidae and the Rissoidae. It also differs from these families in having a rudimentary oesophageal gland. In most other respects the Iravadiidae resemble the Hydrobiidae. The family is shown to have a wide range of shell, radular and opercular forms.

Previously-named genera recognised as valid in the family are *Iravadia* (with *Fluviocingula*, *Fairbankia* and *Pseudonoba* as subgenera), *Rissopsis*, *Hyala*, *Ceratia*, *Nozeba*, *Chevallieria* and *Rhombostoma*.

Key words: Gastropoda; Rissoacea; Iravadiidae; taxonomy; systematics; anatomy; mangroves.

INTRODUCTION

Several of the genera considered here to be iravadiids have been regarded as members of the Rissoidae (Cossmann, 1921; Thiele, 1929; Wenz, 1939; Coan, 1964; Ponder, 1967) by most revisers. This revision has grown out of a survey of the genera of the Rissoidae currently being undertaken by the writer. During this work several genera, which previously had no suspected phyletic relationships, were tentatively grouped together principally because all possessed a peculiar, flat-topped, smooth protoconch with a very small initial whorl. Examination of the radula and anatomy of representative species has confirmed their relationship and suggested their separation into a family within the Rissoacea. This family grouping shares shell characters with the Rissoidae but in many anatomical characters resembles the Hydrobiidae.

In the last major revision of the mesogastropods (Wenz, 1939), the genera here regarded as iravadiids were included in 6 different families (Iravadiidae, Micromelaniidae, Rissoidae, Aclididae, Thiaridae and Eu-

limidae). The purpose of this paper is to outline the distinctive features of the Iravadiidae, define the genera and discuss the relationships of the family.

The genus *Iravadia* Blanford was proposed for a small, spirally-sculptured, brackish-water gastropod from India. The usage of this name has been restricted to a few species of similar appearance, mainly from estuarine habitats. Thiele (1928) proposed new family-group names for *Iravadia* and for *Fairbankia* Stoliczka, both genera being based on species found in mangroves in southern Asia. Brandt (1968) showed that, on the basis of their shells, radulae, opercula and external features of the head-foot, *Fairbankia* and *Iravadia* are closely related. This relationship has been confirmed by anatomical studies during this work.

Johansson (1950) described the female reproductive system of a European marine species, *Hyala vitrea* (Montagu), and showed it to have an anterior bursa copulatrix and a slit-like opening near the posterior end of the glandular pallial duct. Golikov & Starobogatov

(1975) considered these differences sufficiently great to create a new family for *Hyala*.

Anatomical work on species of *Iravadia* s.l. shows that their anatomy is similar to that of *Hyala vitrea* and that the *Iravadia-Hyala* group can be distinguished anatomically from the Hydrobiidae and Rissoidae.

MATERIALS AND METHODS

The specimens used in this survey are housed in several museums (see list of abbreviations), although the majority of the observations are based on material held in The Australian Museum. Scanning electron micrographs were obtained from material prepared as described by Ponder & Yoo (1976). Anatomical work was carried out on material fixed in Bouin's fixative or 5%–10% neutral formalin. This was sectioned at 5–6 μm and stained with Mallory's triple stain.

The generic diagnoses are intended to encompass all species included in the genus but the detail of opercular, radular and head-foot description is based only on those species for which the information is available. These species are cited in the diagnoses except when the genus is monotypic or when only the type-species has been examined.

The species listed under "Distribution" are principally those examined and confirmed as belonging to the genus. Whenever possible, names of other species probably belonging to the genus are also given. A list of material examined is given under each genus to indicate the range available to the writer and to assist future confirmation.

ABBREVIATIONS USED IN FIGURES

ag	albumen gland
agr	accessory groove
ass	anterior sperm sac
bc	bursa copulatrix
bd	duct of bursa copulatrix
cg	capsule gland
co	coiling part of oviduct
df	dorsal fold
gle	glandular epithelium
gp	gonopore
hpg	hypobranchial gland
ibc	opening of bursa copulatrix to capsule gland
lf	longitudinal fold
log	lower oviduct gland
mf	muscular fold

obc	pallial opening of bursa copulatrix
og	rudimentary oesophageal gland
p	prostate gland
pd	pallial duct from prostate gland
pm	posterior limit of pallial cavity
pvd	pallial vas deferens
r	rectum
rgd	reno-gonidial duct
ro	renal oviduct
sg	sperm groove
sr	seminal receptacle
sv	seminal vesicle
uog	upper oviduct gland
vc	ventral channel
vd	vas deferens
vf	ventral (outer) fold of sperm groove

MUSEUM ABBREVIATIONS

AIM	Auckland Institute and Museum, New Zealand.
AMS	Australian Museum, Sydney, Australia.
ANSP	Academy of Natural Sciences of Philadelphia, U.S.A.
BMNH	British Museum (Natural History), London, U.K.
GIT	Geological Institute, University of Tokyo, Japan.
GNHM	Natural History Museum, Genoa, Italy.
HUM	Humboldt Universität Museum, E. Berlin, E. Germany
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium.
NHMP	Muséum National d'Histoire Naturelle, Paris, France.
NM	Natal Museum, Pietermaritzburg, South Africa.
NMNZ	National Museum, Wellington, New Zealand.
NMV	National Museum of Victoria, Melbourne, Australia.
NMW	National Museum of Wales, Cardiff, U.K.
NSMT	National Science Museum, Tokyo, Japan.
SAM	South Australian Museum, Adelaide, Australia.
SMF	Senckenberg Museum, Frankfurt, W. Germany.
TGM	Geological Museum, Turin, Italy.
USBF	United States Bureau of Fisheries.
USNM	National Museum of Natural History, Washington, D.C., U.S.A.
ZMR	Zoological Museum, Rome, Italy.

TAXONOMY

Family IRAVADIIDAE Thiele, 1928

Synonyms: Fairbankiinae Thiele, 1928; Hyalidae Golikov & Starobogatov, 1975.

Diagnosis. Shell narrowly-conic to ovate-conic, usually solid, lacking inner chitinous shell layer, usually nonumbilicate, smooth or with spiral sculpture predominant, axial sculpture present as growth-lines, lamellae or, rarely, ribs. Aperture oval, usually weakly to distinctly angled anteriorly and posteriorly; varix on outer lip broad and strong to absent. Protoconch small, smooth, of about $1\frac{3}{4}$ – $2\frac{1}{2}$ convex whorls, planorbid (coiled in one plane) to depressed dome-shaped; first whorl minute, terminated by a distinct varix in some species. Periostracum sometimes well developed, rarely bearing processes. Head-foot often pigmented, cephalic tentacles long, slender, usually with a few stationary cilia, sometimes with colour bands; eyes at their outer bases. Snout of moderate length, usually bilobed. Foot usually with anterior edge indented and expanded laterally. Posterior end of foot pointed, rounded, slightly indented or deeply bifurcate. No posterior pedal mucous gland except for a rich supply of subepithelial glands in some species; anterior pedal gland distinct, confined to pedal haemocoel. Foot lacking a metapodial tentacle in most species. No pallial tentacle in most species. Radula taenioglossan, central teeth with zero to four pairs of basal denticles. Operculum with eccentric, submarginal or marginal nucleus. Penis short, thick, bent double or partially coiled when at rest; with a single distal or lateral opening and with accessory, often glandular, processes on a flattened, broad distal end in most species. Female genital duct comprises a short, simple renal oviduct opening directly to albumen gland. One or two seminal receptacles (usual-

ly one) open at point where renal oviduct joins albumen gland. Capsule gland with ventral gonopore variable in position and length; usually opening slit-like, either posterior, in middle section, subterminal or (in one species) most of ventral side of anterior two-thirds of gland open. Bursa copulatrix variable in position, entirely pallial in most species; bursal duct, when present, pallial (i.e., opens to capsule gland) or bursa opens directly to pallial cavity by vertical opening. A sperm sac anterior to gonopore developed in some species. Long dorsal folds in anterior part of oesophagus; rudimentary oesophageal gland present. Crystalline style present in stomach. Nervous system similar to that of Hydrobiidae.

Remarks. The family name Iravadiidae was given precedence over Fairbankiidae by Brandt (1968) and this is upheld here as the action of the first reviser. Starobogatov (1970) has used Fairbankiidae to include both *Iravadia* and *Fairbankia*.

The main characters separating the Iravadiidae from the two closest families, the Rissoidae and the Hydrobiidae, are given in Table 1.

General Anatomical Description

No attempt has been made to fully describe the anatomy of any of the species examined. The species examined anatomically are *Iravadia ornata* (Blanford), *Iravadia quadrasi* (Boettger), *Iravadia (Fairbankia) bombayana* (Stoliczka), *I. (F.) australis* Hedley, *Iravadia (Pseudomerelina nov.) mahimensis* (Melvill), *Nozeba topaziaca* (Hedley), and *Hyalia vitrea* (Montagu).

The Pallial Cavity. There is a well-developed ctenidium reaching to the posterior end of the pallial cavity and a conspicuous osphradium half to two-thirds the length of the ctenidium. The osphradium consists of a

TABLE 1. The main features separating the Iravadiidae, Hydrobiidae and Rissoidae.

	Iravadiidae	Hydrobiidae (s.l.)	Rissoidae
<i>Shell</i>			
Aperture	With weak to strong anterior channel	Usually without anterior channel	With or without anterior channel
Sculpture	Smooth or spiral predominant	Smooth, spiral or axial predominant	Smooth, spiral or axial predominant
Protoconch	Planorbid to depressed-dome-shaped, about 2 whorls, smooth	Dome-shaped, about $1\frac{1}{2}$ whorls, often pitted	Dome-shaped to sub-conical, $1\frac{1}{2}$ to about 3 whorls, sculpture variable, rarely smooth

TABLE 1 (Continued)

	Iravadiidae	Hydrobiidae (s.l.)	Rissoidae
<i>Operculum</i>	Oval, nucleus eccentric or marginal. Without peg and calcareous material	Oval to circular, nucleus eccentric to central. Sometimes with calcareous peg or smear	Oval, nucleus eccentric. Sometimes with horny peg; without calcareous material
<i>Radula</i>			
Central teeth	0–4 pairs of basal cusps, rudimentary in some species	0 to several pairs of basal cusps	1–3 pairs of basal cusps
<i>Head-foot</i>			
Cephalic tentacles	Long, ciliated, pigmented to unpigmented	Long, ciliated or smooth, pigmented or unpigmented	Long to moderately short, usually ciliated, rarely pigmented
Pallial tentacle(s)	Rudimentary or absent	Rudimentary or absent	Present or absent
Metapodial tentacle(s)	Usually absent	Usually absent	Often present
Posterior pedal mucous gland	Absent	Absent	Present or absent
<i>Reproductive systems</i>	Yes	Yes	No
Ventral wall of pallial oviduct with fold enclosing ventral channel			
Ventral wall of pallial oviduct	Open, or closed except for posterior, subterminal or median opening	Closed except for small terminal or subterminal opening	Closed (open in <i>Mere-lina</i> Iredale), except for terminal or subterminal opening
Glandular oviduct	Single gland	Single gland	Two glands
Anterior sperm sac	Present or absent	Absent	Usually absent
Bursa copulatrix	Anterior or posterior, within roof of pallial cavity (with one exception)	Posterior, within visceral mass	Posterior, within visceral mass
Renal oviduct	Renal oviduct opens directly to albumen gland	Renal oviduct opens to narrow oviducal coil	Renal oviduct opens to upper oviduct gland or (rarely) oviducal coil
Penis	With swollen distal end and accessory glandular structures	Simple or with accessory glandular structures	Usually simple; <i>Rissoina</i> with swollen distal end and accessory glandular structures
Prostate gland	Half within roof of pallial cavity	Half within roof of pallial cavity or (rarely) entirely behind cavity	None, or half to entirely within roof of pallial cavity; rarely behind cavity
<i>Digestive system</i>			
Mid-oesophagus	With long dorsal folds; with rudimentary oesophageal gland	With long dorsal folds; no oesophageal gland	With short dorsal folds; no oesophageal gland
Spherules in secretory cells in digestive gland	Absent	Present	Present
<i>Nervous system</i>			
Left pleural- and sub-oesophageal ganglia	Abutting	Fused or with short connective	Very short connective to abutting
Right pleural-supra-oesophageal ganglia	With long connective	With long to short connective	With moderately long connective

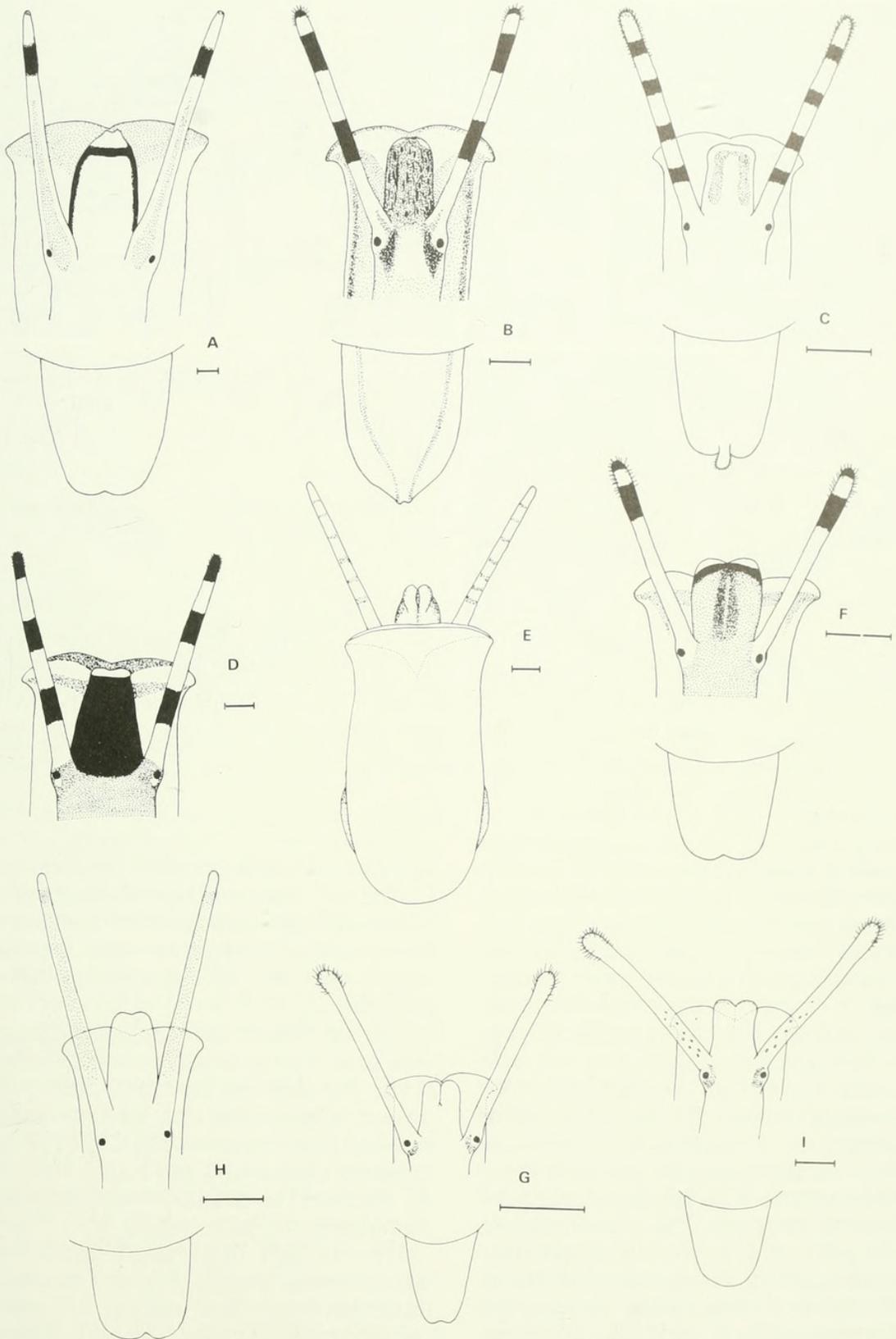


FIG. 1. Head-foot of some species of Iravadiidae drawn from living material. A. *Iravadia (Fairbankia) australis* (Hedley). Magnetic Island, Queensland, Australia. B. *Iravadia (Iravadia) quadrasi* (Boettger). Darwin, Northern Territory, Australia. C. *Iravadia (Pseudomerelina) mahimensis* (Melvill). Maningrida, Northern Territory, Australia. D. *Iravadia (Fairbankia) bombayana* (Stoliczka). Sembawang, Singapore. E. *Iravadia (Iravadia) ornata* (Blanford). Deep Bay, New Territories, Hong Kong. F. *Iravadia (Fluviocingula) resima* (Laseron). Darwin, Northern Territory, Australia. G. *Liroceratia sulcata* (Boettger). Taurama, near Port Moresby, Papua New Guinea. H. *Iravadia (Pseudonoba) bella* (Adams). Magnetic Island, Queensland, Australia. I. *Nozeba topaziaca* (Hedley). Port Hacking, New South Wales, Australia. Scales = 0.3 mm.

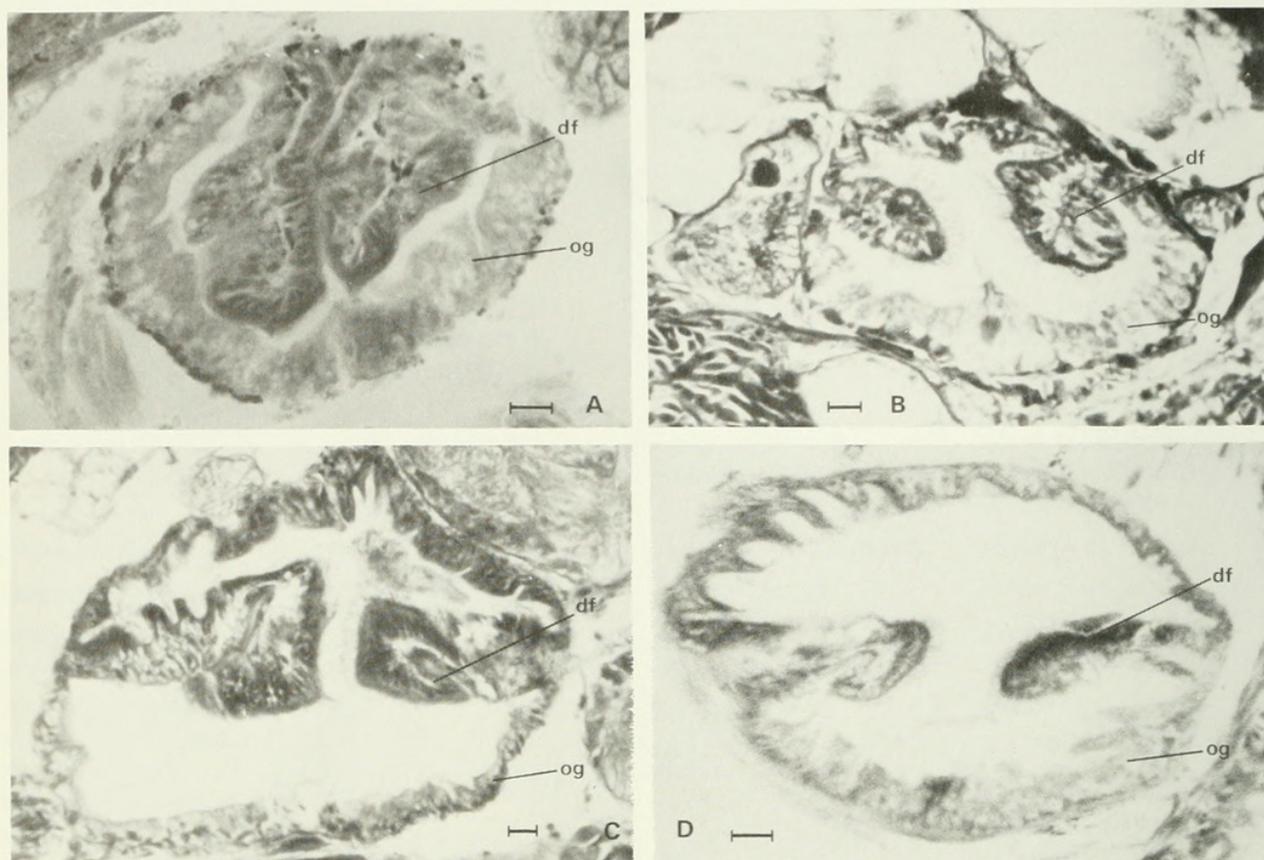


FIG. 2. Transverse sections of the mid-oesophagus of four species of the Iravadiidae. A. *Nozeba topaziaca* (Hedley). B. *Hyala vitrea* (Montagu). C. *Iravadia* (*Iravadia*) *ornata* (Blanford). D. *Iravadia* (*Fairbankia*) *australis* (Hedley). Scales = 0.01 mm.

broad, central sensory area bordered by narrow, ciliated ridges. A hypobranchial gland is also present.

Alimentary Canal. Generally similar to that of the Hydrobiidae. The buccal mass is large and there is a pair of jaws composed of chitinous rodlets. The salivary glands are tubular and pass dorsal to the circum-oesophageal nerve ring. The anterior part of the oesophagus is short to rather long, with a pair of long dorsal folds (Fig. 2, df) that coil upwards in the larger species (*Iravadia* spp., *I. (Fairbankia)* spp.) (Fig. 2C, D) but are simple in *Nozeba topaziaca* (Fig. 2A), *Hyala vitrea* (Fig. 2B) and *I. (Pseudomerelina) mahimensis*. All of these species have glandular tissue in the ventral wall of the mid-oesophagus (Fig. 2, og). This glandular epithelium is composed of irregular columnar cells and is interpreted as a remnant of an oesophageal gland. Comparison of the same region in rissoids and hydrobiids shows a simple, ciliated epithelium in which are scattered only a few gland cells. The stomach has a crystalline style in a well-developed style

sac. The rectum is looped in the dorsal wall of the mantle cavity and typically has the faecal pellets packed sideways. The digestive gland has two types of digestive cells and the excretory cells do not contain large refractive granules.

Female Reproductive System. This system was examined in detail, mainly by serial sections. Because of the brittle nature of the oviduct glands and the limited amount of material, some observations could not be confirmed and others are doubtful for particular species. The single female sectioned of *I. ornata* was not fully mature.

The narrow, thin-walled upper oviduct opens into a slightly thicker, ciliated, non-muscular, short renal oviduct. No gonopericardial or reno-gonidial duct was observed in any species except *I. ornata*, where there is a short, ciliated reno-gonidial duct. The glandular part of the oviduct consists of a posterior albumen gland (Figs. 4–7, ag) which partially displaces the kidney and which is continuous with the capsule gland lying in the roof of the pallial cavity. A seminal receptacle lies along-

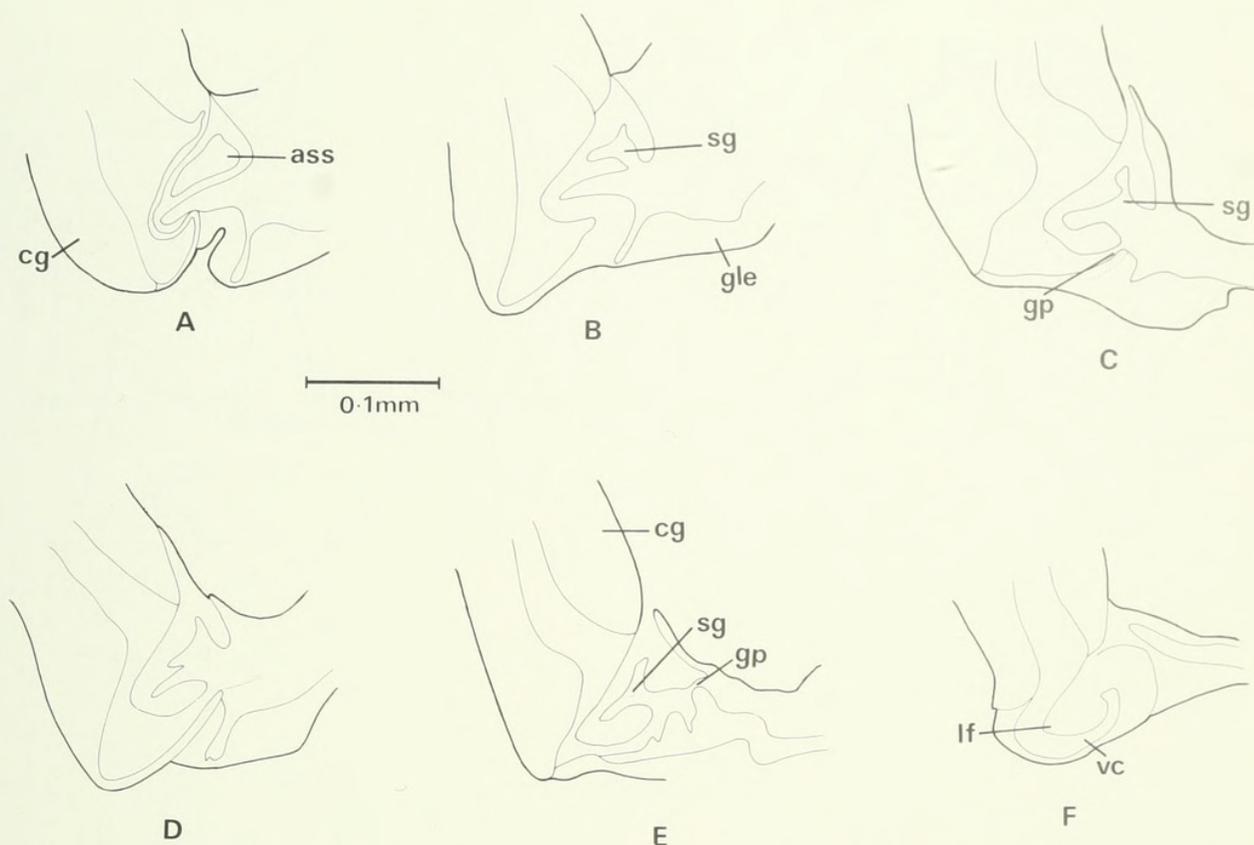


FIG. 3. A-F. Transverse sections through the ventral part of the female pallial genital duct of *Hyala vitrea* from near the anterior end to near the posterior end. All figures to same scale.

side the albumen gland and is partly embedded in it. *Hyala* has one (?) or two seminal receptacles and *Iravadia* (*Pseudomerelina*) *mahimensis* appears to have two. The other species appear to have only one (Figs. 4-7, sr). The seminal receptacle(s), together with a renal oviduct, opens into the oviduct just posterior to the capsule gland. This gland (Figs. 3-7, cg) opens to the pallial cavity by a long to short, slit-like ventral opening (gp) or gonopore. In *Nozeba topaziaca* and *Hyala vitrea* the oviduct aperture is in the posterior part of the capsule gland and the anterior part of the gland is blind (Fig. 21B). The oviduct opening extends along all of the anterior two-thirds of the ventral side of the capsule gland in *I. (Fairbankia) bombayana* (Fig. 7D) but is short and placed in the anterior part of the gland in *I. ornata* (Fig. 21G), *I. (Pseudomerelina) mahimensis* (Fig. 5) and *I. (Fairbankia) australis* (Fig. 6). It is long and in the middle of the gland in *I. quadrasi* (Fig. 4). There is a deep sperm groove (sg) on the lower, inner part of the inner (left) ventral wall of the capsule gland in the vicinity of the pallial opening in *I. (F.) australis*, *I. quadrasi* (Fig. 4B-D), *I. (P.) mahimensis* (Fig. 5B), *N. topaziaca* and

H. vitrea (Fig. 3B-E). This gutter runs forward and closes over to form an anterior sperm sac (Figs. 3-6, ass) which appears to function as a bursa copulatrix. In *I. (F.) bombayana* there is a sperm sac on the outer (left) side of the inner (left) wall of the posterior third of the capsule gland and it is wholly within the roof of the pallial cavity (Fig. 7, bc). This sac opens by way of a vertical slit (Fig. 7, obc), the outer edge of which represents the outer fold of the sperm groove, and its internal walls are heavily folded. In *I. (F.) australis* (Fig. 6) there is a similar sperm sac (bc), the opening (obc) of which lies in the anterior second quarter of the capsule gland, but there is also a small anterior sperm sac (ass) anterior to the oviducal opening. To enable these sperm sacs to be distinguished, the structure external to the capsule gland seen in *I. (Fairbankia)* species is hereafter called the bursa copulatrix and the sperm sac anterior to the oviducal opening is referred to as the anterior sperm sac. Both structures appear to function as a bursa copulatrix but no evidence of sperm ingestion was observed in sections of either structure. They both store sperm, although the bursa copulatrix was empty in most speci-

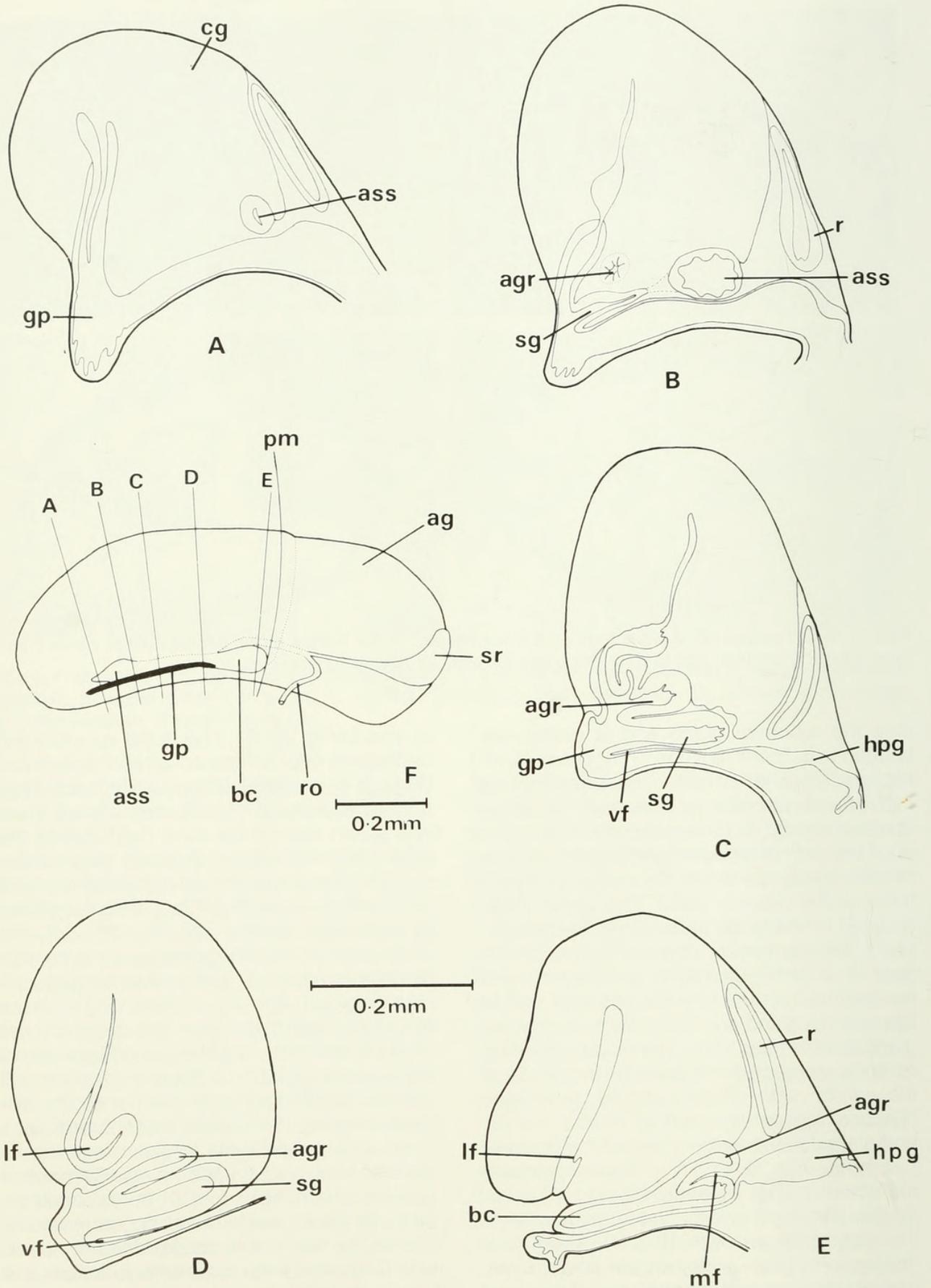


FIG. 4. Female reproductive system of *Iravadia (Iravadia) quadrasii*. A-E. Sections through the pallial genitalia at the positions marked on Fig. F. F. Lateral view of female genital system (excluding upper oviduct and ovary). Figs. A-E to same scale.

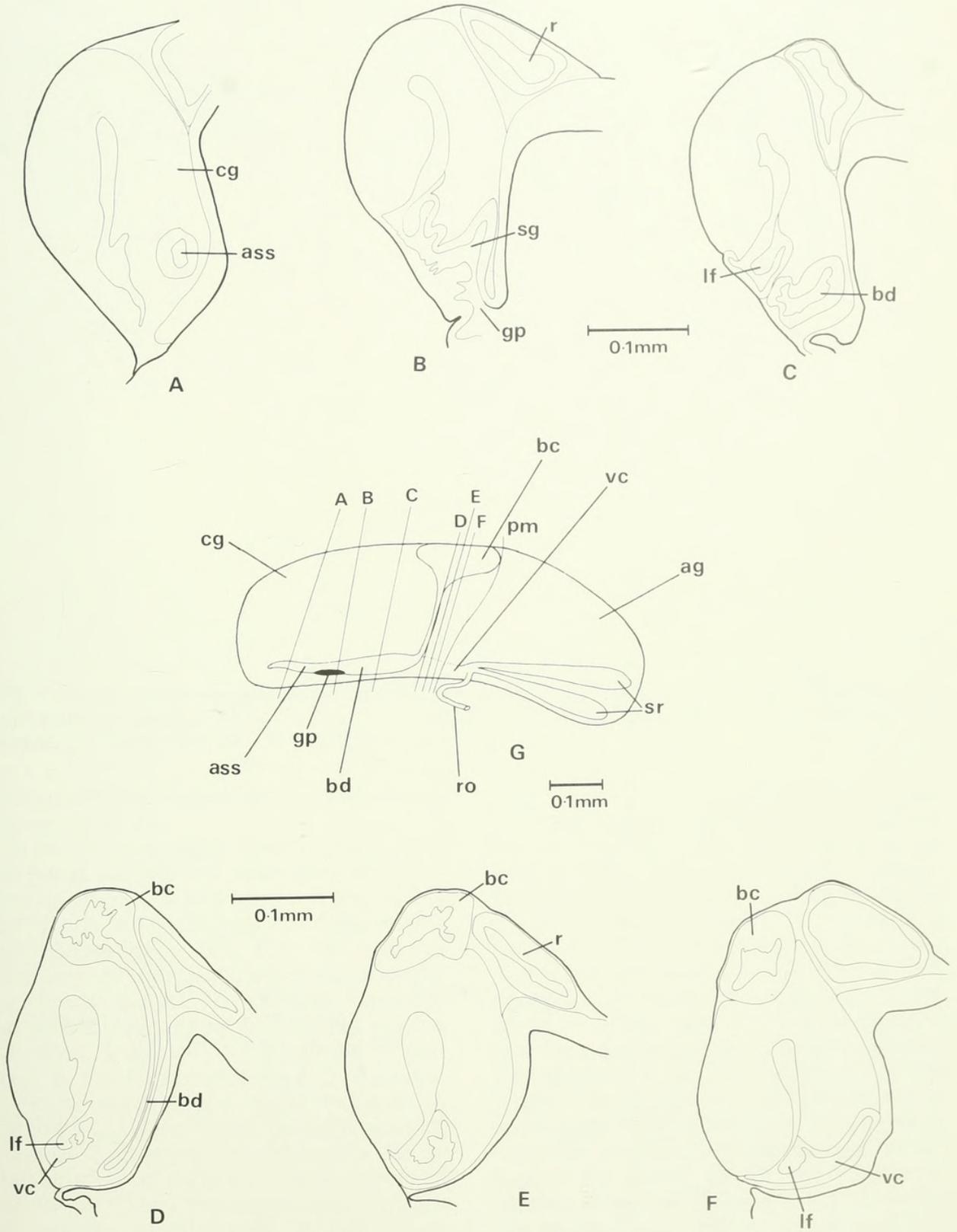


FIG. 5. Female reproductive system of *Iravadia* (*Pseudomerelina*) *mahimensis*. A-F. Transverse sections of the pallial genitalia at the positions marked on Fig. G. G. Lateral view of female reproductive system, excluding the upper oviduct and ovary. Figs. A-F to same scale.

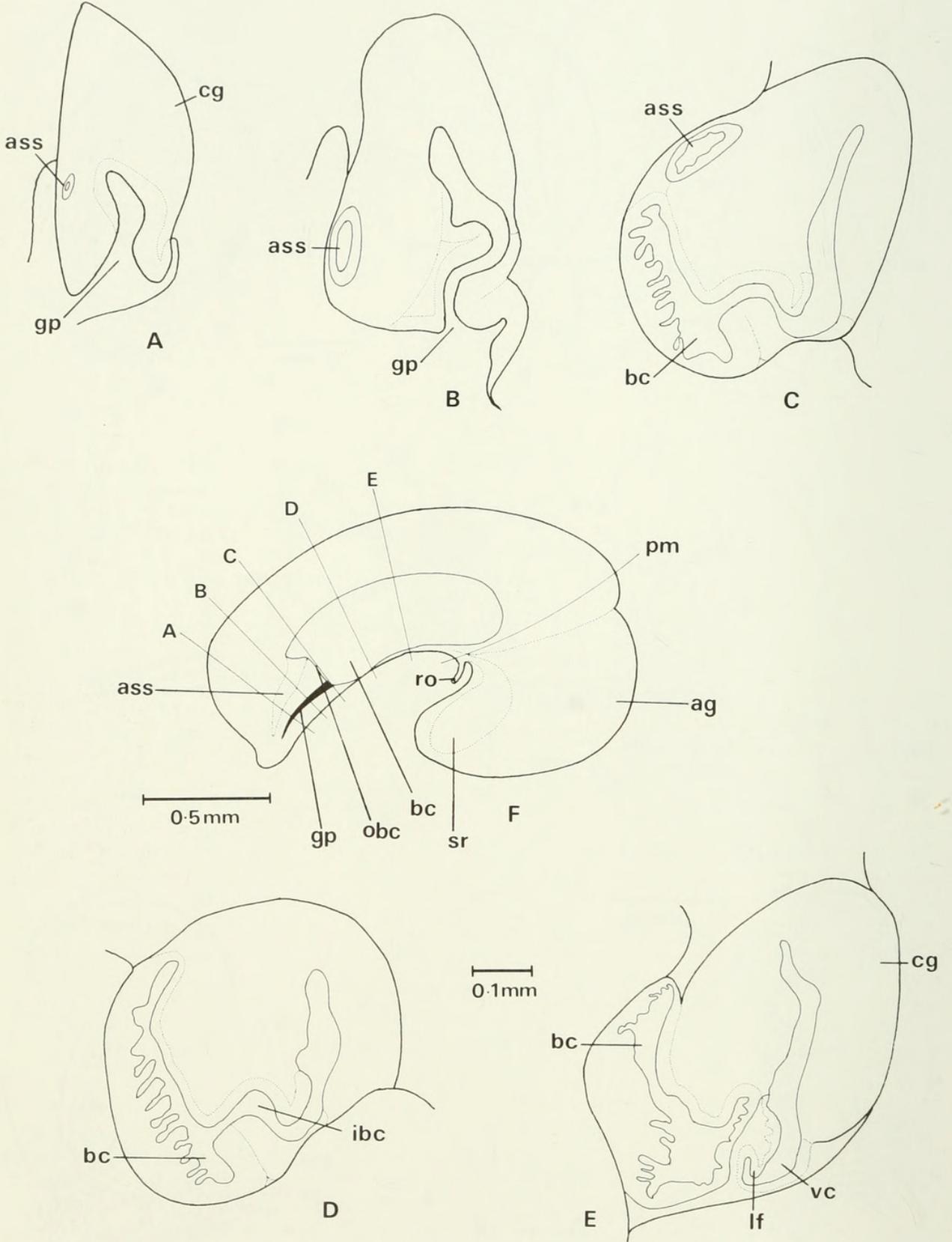


FIG. 6. Female reproductive system of *Iravadia (Fairbankia) australis*. A-E. Section through the pallial genitalia at the positions marked in Fig. F. F. Lateral view of female reproductive system, excluding the upper oviduct and ovary. Figs. A-E to same scale.

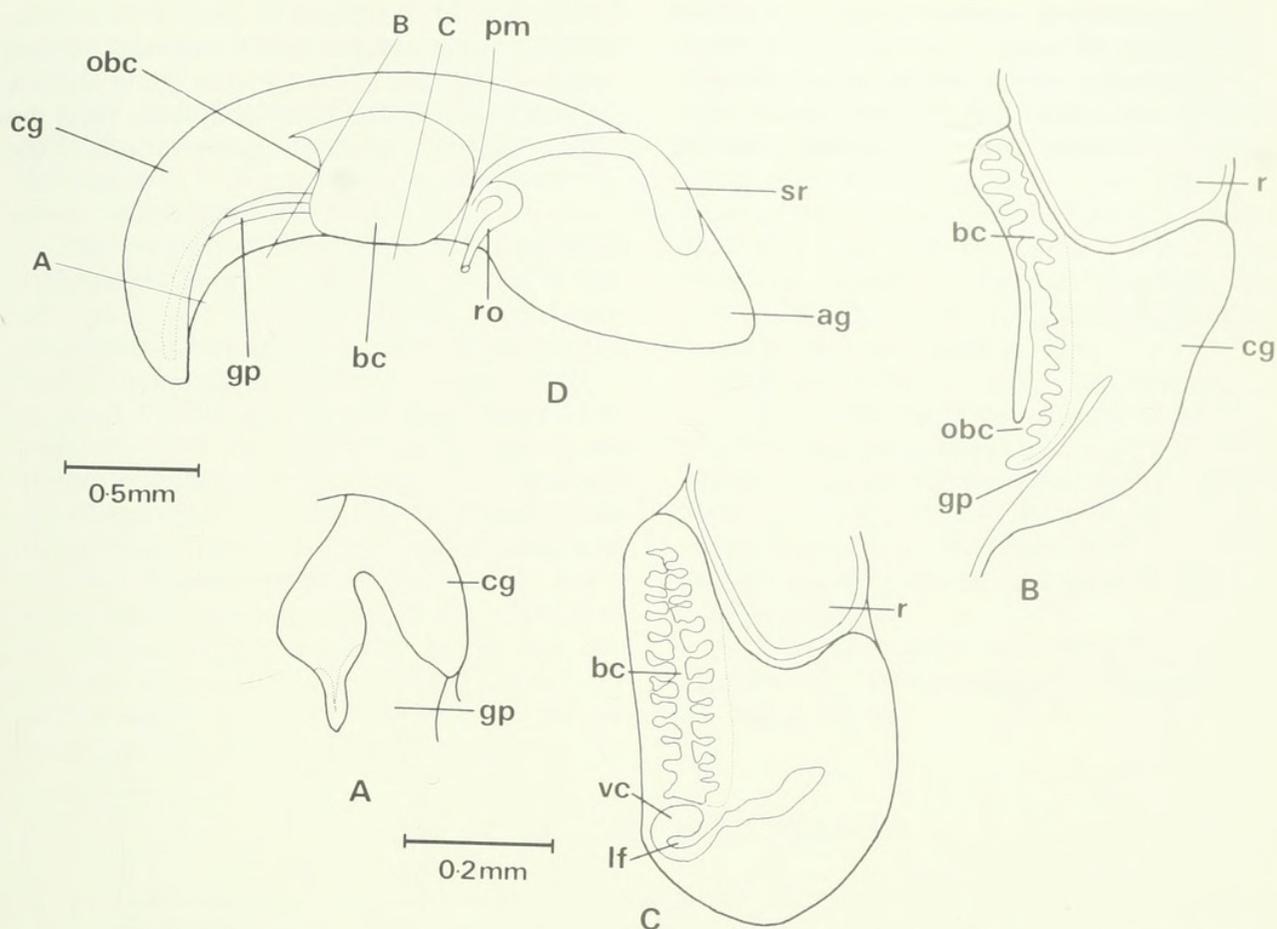


FIG. 7. Female reproductive system of *Iravadia (Fairbankia) bombayana*. A–C. Sections through the pallial genitalia at the position marked in Fig. D. D. Lateral view of female genital system, excluding the upper oviduct and ovary. Figs. A–C to same scale.

mens sectioned, suggesting a very temporary storage function.

In the two species of *Iravadia (Fairbankia)* the bursa copulatrix is open laterally to the capsule gland for a short distance (Fig. 6, ibc) and is then separated from it and becomes a blind pocket (Fig. 6E, 7C). The seminal receptacle (sr) opens into the posterior end of the ventral channel. The posterior section of the ventral channel has, as in all the species examined, a ciliated fold (lf) similar to that seen in the Hydrobiidae (see Discussion). *Iravadia quadrasi* (Fig. 4) has a ventral bursa copulatrix (bc) behind the oviducal opening extending back to the end of the pallial cavity. This structure is formed from the closure of the ventral (outer) fold of the sperm groove (vf), but the pallial opening of the capsule gland is closed slightly in front by the merger of the inner ventral edge of the ventral channel of the capsule gland and the upper edge of an accessory fold on the upper side of the sperm groove (Fig. 4C, D). This accessory fold is the dorsal edge of a glandular groove

(Fig. 4, agr) containing distinctive, blue-staining, cuboidal gland cells in its anterior section. Anteriorly, the groove is blind and merges with the capsule gland after forming a tubular structure. Posteriorly, it continues into the bursa copulatrix where its epithelium is similar to that of the remainder of the bursa. The prominent muscular fold (Fig. 4E, mf) separating the sperm groove and the groove dorsal to it, continues through the bursa. It was not possible to determine from the available material if the fold continued the full length of the bursa. In *I. (Pseudomerelina) mahimensis* (Fig. 5) the duct of the bursa copulatrix (bd) has been formed by the closure of the sperm groove just behind the opening to the capsule gland (Fig. 5, B–C). The tubular bursal duct runs posteriorly and then dorsally into the dorsally placed bursa copulatrix (bc) which lies above the posterior end of the capsule gland (Fig. 5, D–G). The type-species of *Iravadia*, *I. ornata* (Fig. 21G), shows a similar arrangement to that seen in the Hydrobiidae in possessing an anterior

oviducal opening, a ciliated fold in the ventral channel of the capsule gland and no anterior sperm sac. The bursal duct opens immediately behind the short, slit-like, muscular, sub-terminal opening and runs dorsally over the

inner wall of the gland to open to the long, tubular bursa which lies latero-dorsally on the outer (right) side of the capsule gland and the anterior half of the albumen gland. Thus the bursa extends behind the posterior end of the

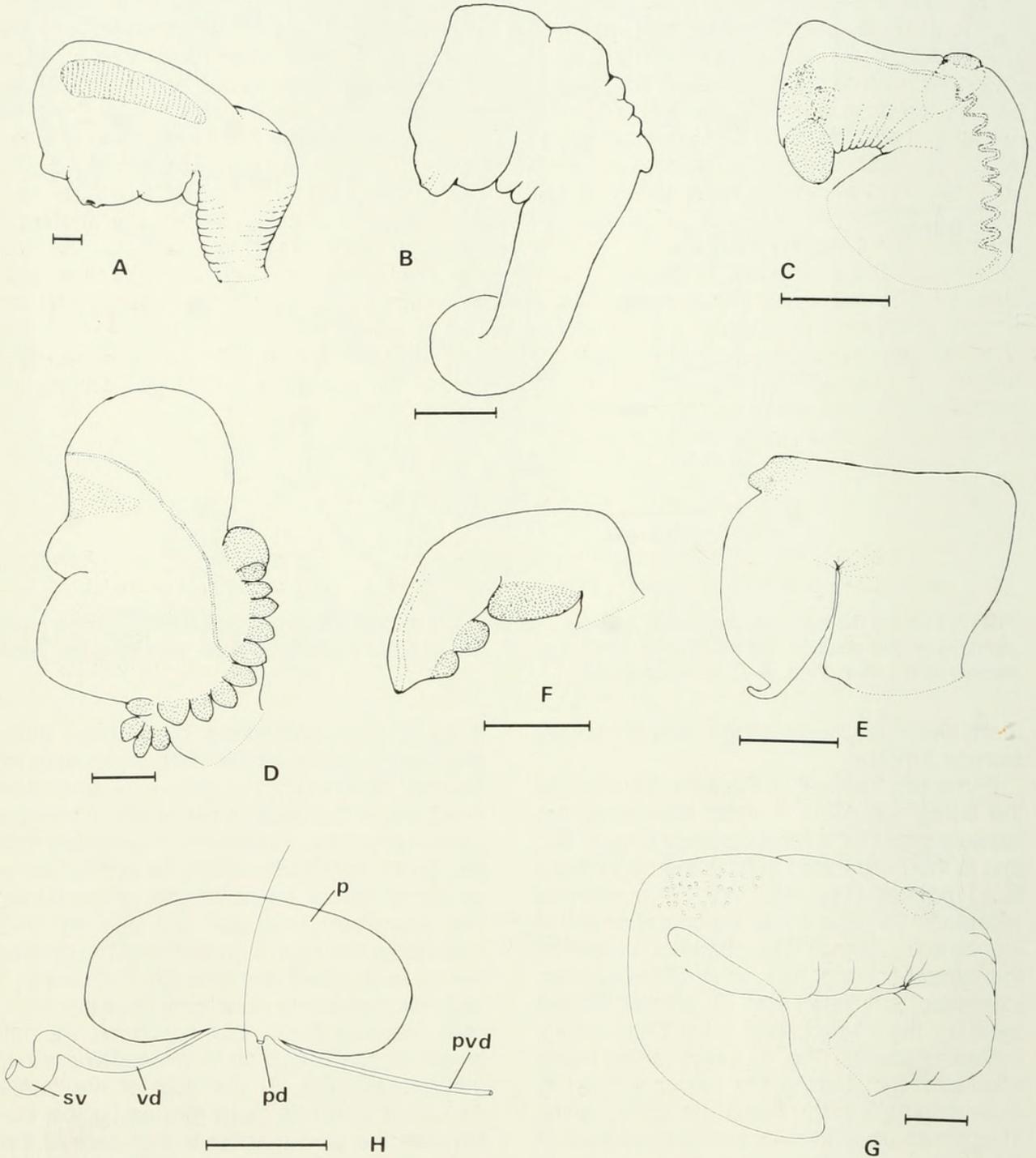


FIG. 8. A–G. Penes of some species of Iravadiidae. In Figs. C–F glandular areas are represented by stipple. A. *Iravadia (Iravadia) ornata* (Blanford). Deep Bay, New Territories, Hong Kong. B. *Iravadia (Iravadia) quadrasii* (Boettger). Hervey Bay, Queensland, Australia. C. *Iravadia (Pseudomerelina) mahimensis* (Melvill). Magnetic Island, Queensland, Australia. D. *Iravadia (Fairbankia) australis* (Hedley). Magnetic Island, Queensland, Australia. E. *Hyala vitrea* (Montagu). Ten km W of Strömstad, W Sweden, 35 m. F. *Nozema topaziaca* (Hedley). Port Hacking, New South Wales, Australia. G. *Iravadia (Fairbankia) bombayana* (Stoliczka). Sembawang Estuary, Singapore. H. Diagrammatic representation of the prostate gland and vas deferens of *Iravadia (Iravadia) ornata* (Blanford). Scales = 0.2 mm.

pallial cavity in this species. A thin-walled vestibular region may function as an anterior sperm sac.

Male Reproductive System. Examined in *Iravadia ornata*, *I. quadrasi*, *I. (Fairbankia) bombayana*, *I. (F.) australis*, *I. (Pseudomereлина) mahimensis* and *Hyala vitrea*.

The vas deferens forms a long, coiled seminal vesicle (Fig. 8H, sv) and the renal vas deferens is short and ciliated. The bean-shaped prostate gland (p) lies half within the pallial roof and has a median lumen except in a short middle section which is thin-walled ventrally. This section receives the renal vas deferens behind the posterior pallial wall and the pallial vas deferens (pvd) emerges in front of this wall. There is a very short, ciliated duct (pd) in *I. (Pseudomereлина) mahimensis* and *I. ornata* which emerges next to the junction of the prostate gland and the pallial vas deferens, and opens to the pallial cavity. No similar pallial opening was observed in the other species, although the sections were not

sufficiently good to positively exclude the presence of such a duct. The thin-walled, ciliated pallial vas deferens runs along the right side of the body wall and is not contained within it. The penis is large, with an expanded distal portion bearing one or more glandular processes (Fig. 8, A–G). There are both epithelial and internal glands. The single, muscular, ciliated penial duct is completely enclosed in the penis and lacks any epithelial connection to the exterior.

Nervous System. This has not been studied in detail but the nervous systems of *Iravadia (Fairbankia) bombayana* and *I. (F.) australis* appear to be generally similar to that of most Hydrobiidae. There is a long supraoesophageal connective and the suboesophageal ganglion lies against the left pleural ganglion.

The Renal System. The kidney is a simple sac with a thin lining except for a cluster of cells on the outer wall.

Key to the genera of the Iravadiidae

1. Shell elongate, sub-cylindrical, translucent, with expanded outer lip *Rissopsis*
- Shell elongate to ovate, opaque to semitranslucent, without expanded outer lip 2
- 2(1) Shell elongate, smooth or with spiral sculpture, outer lip without varix, sinuate, columella more-or-less vertical *Rhombostoma*
- Shell elongate to ovate, variously sculptured or smooth, outer lip with or without varix, more-or-less straight, columella concave in most species 3
- 3(2) Operculum with submarginal to marginal nucleus and concentric to sub-spiral growth 4
- Operculum with eccentric nucleus and spiral growth 5
- 4(3) Shell with spiral sculpture, well-developed in some species, operculum with marginal nucleus *Iravadia*
- Shell with spiral sculpture very weak or absent, operculum with submarginal nucleus *Chevallieria*
- 5(3) Shell with strongly prosocline outer lip 6
- Shell with approximately orthocline outer lip 8
- 6(6) Shell with fine spiral threads 7
- Shell smooth or almost so *Hyala*
- 7(6) Shell with peripheral ridge *Acliceratia* nov.
- Shell lacking peripheral ridge *Ceratia*
- 8(5) Shell with strong spiral lirae and a prominent varix at outer lip *Liroceratia* nov.
- Shell with weak spiral threads or smooth, without varix at outer lip *Nozeba*

Genus *Iravadia* Blanford, 1867: 56–58

Type-species: *Iravadia ornata* Blanford, 1867 (? = *Pyrgula clathrata* A. Adams, 1853); monotypy. Recent. India.

Synonym: *Iravadia*, *err. auct.*

Diagnosis. Shell. Elongately ovate-conic to ovate-conic, non-umbilicate to nar-

rowly-umbilicate, with predominantly spiral sculpture, a few species with conspicuous axials or with sculpture reduced to spiral rows of pits. Protoconch planorbid to depressed dome-shaped, of about 2–2½ smooth, convex whorls, usually terminated by a distinct varix. Periostracum often well-developed. **Head-foot.** Cephalic tentacles often banded

or spotted. Snout of moderate length, bilobed. Foot and head pigmented dorsally in most species. Anterior edge of foot usually indented, produced laterally. No pallial tentacles and usually no metapodial tentacle. **Penis.** With broad flattened head and accessory glandular areas. **Oviduct.** With long to short ventral pallial opening; bursa copulatrix present; anterior sperm sac present or possibly absent. **Operculum.** Oval, nucleus on columellar edge, with close, concentric growth lines; some species with weak internal ridge(s). **Radula.** Central teeth wide, each with a usually wide cutting edge bearing one to several, small, sharp cusps; lateral edges unthickened; zero to four basal denticles, weak in most species. Lateral teeth with narrow cutting edge, rather short cusps and long outer portion. Marginal teeth long, curved, with several small cusps.

Distribution and habitat. Indo-Pacific; in brackish-water or in shallow-water, sheltered marine environments to the continental shelf.

Remarks. The genus *Iravadia* possesses a peculiar operculum with a lateral nucleus and concentric growth rings. Although no satisfactory explanation can be offered for the development of this type of operculum, it is assumed that it arose early in the Tertiary, probably from the *Chevallieria* lineage. Evidence for this assumption is the existence of an operculum intermediate in structure in a Recent species attributed to *Chevallieria* and described below. Thiele (1928), on the basis of the structure of the operculum, created two new subfamilies, one for *Fairbankia* in the Micromelaniidae and the other for *Iravadia* in the Hydrobiidae. His placement of these genera in two different families was based on the presence of lateral (basal) denticles on the central teeth of the radula in *Iravadia* and the assumed absence of these in *Fairbankia*. The virtually identical opercular characters and the general similarity of the radula led Brandt (1968, 1974) to include both genera in

the Iravadiidae. Because a continuum in shell and radular characters can be observed between typical species of *Iravadia* and *Fairbankia* these two groups are regarded here as being congeneric. There are, however several important differences in the female genitalia of the type-species of these two groups. Examination of an additional species of *Iravadia* s.s., *I. quadrasi*, indicates that considerable differences in the female genitalia may exist within the groupings as here recognised. Similarly, differences between *I. (Fairbankia) australis* and *I. (F.) bombayana* are also marked, although not so radically.

The taxonomy adopted is conservative in that some traditional characters (especially the operculum) are given considerable weight. There are too many gaps in the available information for genital characters to be used in a primary way at the genus-group level at this time, although, undoubtedly they will ultimately be extremely valuable in refining the classification.

Several subgenera are used because these appear to be recognisable groupings, although difficult to define clearly at a higher level. No doubt, when more anatomical information is available, some will be discarded and others may be elevated to generic rank.

The five subgenera recognised show a wide diversity of shell sculpture but are generally similar in other shell features and in their radular and opercular characters as well as in the external appearance of the head-foot. *Iravadia* appears to have diversified from a marine group (subgenus *Pseudonoba*) which has an ancestry traceable at least to the Miocene, and possibly to the Eocene, of Europe. Several species here included in *Iravadia (Pseudonoba)* live in brackish waters or in sheltered, shallow coastal waters; others live on the continental shelf. The incursion into brackish water by members of this genus possibly took place on more than one occasion (Fig. 22).

Key to subgenera of *Iravadia*

1. Shell ovate-conic, with heavy spiral cords (two to six on penultimate whorl); operculum with nucleus in middle of columellar edge 2
- Shell ovate-conic to narrowly-elongate, smooth or with weak to moderate spiral sculpture (more than four cords on penultimate whorl); operculum with nucleus in middle of columellar edge or displaced from middle 3
- 2(1) Shell with distinct axial ribs; operculum without internal ridges ... *Pseudomerelina* nov.
- Shell with axial ribs or threads; operculum with two internal ridges radiating from nucleus in middle of columellar edge *Iravadia* s.s.

- 3(1) Shell smooth or with weak to moderate spiral cords and fine axial threads or lamellae 4
 Shell with spiral rows of punctures *Fluviocingula*
- 4(3) Outer lip of aperture evenly prosocline, base of shell without distinct fold ... *Fairbankia*
 Outer lip of aperture slightly prosocline, orthocline, or weakly opisthocline, with shallow anterior and posterior channels, base of shell with distinct fold in most species *Pseudonoba*

Subgenus *Iravadia* s.s.

Diagnosis. Shell. Of moderate to small size, ovate-conic to elongate-conic, non-umbilicate, with strong spiral cords and weak axial threads to axial ribs. Aperture oval, sub-angled posteriorly and anteriorly, peristome usually thick; outer lip with heavy varix, slightly prosocline. Protoconch (Figs. 9F, 10B) as for genus. Periostracum well developed. Figs. 9A, F, H; 10A, B. **Head-foot.** Cephalic tentacles with narrow, black bands (in *I. ornata* and *I. quadrasi*) and white spots. Foot with almost straight to indented anterior edge, indented (*I. angulata*), rounded (*I. ornata*) or pointed (*I. quadrasi*) posterior end. No metapodial tentacle. Figs. 1B, E. (*I. ornata*, Hong Kong (New Territories), *I. quadrasi*, Singapore and Darwin, *I. angulata*, Darwin). Figs. 1B, E. **Penis.** (Not examined in *I. angulata*) Bent forwards on itself when at rest, with aperture on inner edge in middle of broad distal half. Outer portion of distal half lamella-like, inner part thick, rugose (*I. ornata*, Fig. 8A) or both sides rugose (*I. quadrasi*, Fig. 8B). **Oviduct.** Known for *I. quadrasi* (Fig. 4) and *I. ornata* (Fig. 21G). Anterior sperm sac present and long oviducal opening in middle of capsule gland in *I. quadrasi*; bursa copulatrix a posterior, ventral sac. Bursa copulatrix on right side and latero-dorsal to capsule gland and albumen gland in *I. ornata* and bursal duct opens immediately behind short subterminal opening on left side. A single seminal receptacle in both species. **Operculum.** As for genus, with nucleus midway on columellar edge. Two low radial folds emerge from nucleus and cross about two-thirds of inner surface of operculum (*I. ornata*, *I. angulata*, *I. quadrasi*). Figs. 9B, G; 10D, E. **Radula.** Central teeth wide, low, each with short, tongue-like projection in middle of ventral edge and a single, short, weak denticle just inside each unthickened lateral edge (absent in *I. angulata*); a second pair of weak denticles on some central teeth of some specimens of *I. quadrasi*. Lateral and marginal teeth as for genus; lateral teeth with only a long, primary cusp and a small cusp inside

this in *I. angulata*; multicuspate in the other two species examined (*I. ornata*, *I. quadrasi*). Figs. 9C-E; 10C.

Distribution. Southeast Asia as far N as Hong Kong (New Territories) (*Iravadia ornata* Blanford, 1867 ? = *Pyrgula clathrata* A. Adams, 1853, = *Iravadia princeps* Preston, 1915 ? = *I. funera*, *I. ennurensis* and *I. anandalei* Preston, 1916). Central Indo-Pacific (*Alvania quadrasi* Boettger, 1893 = *Rissoa garretti* Tate, 1899, *nom. nov. pro R. venusta* Garrett, 1873, *non* Philippi, 1844 = *Rissoa (Alvania) alveata* Melvill & Standen, 1901 = *Merelina humera* Laseron, 1956 = *Merelina goliath* Laseron, 1956 = *Merelina reversa* Laseron, 1956 = *Planapexia quadrina* Laseron, 1956 = *Iravadia reticulata* Brandt, 1968). Northern and NE Australia (*Rissoina carpentariensis* Hedley, 1912 = *Pellamora amplexa* Laseron, 1956 = *Pellamora truncata* Laseron, 1956); *Pellamora capitata* Laseron, 1956 = *Pellamora spiralis* Laseron, 1956; *Pellamora angulata* Laseron, 1956).

Habitat. *Iravadia ornata* was collected under stones in the lower littoral, in an estuarine situation, but not associated with extant mangroves. *Iravadia angulata* and *I. quadrasi* have been found in mangroves under objects in shallow pools. Brandt (1974) records *I. ornata* and *I. quadrasi* (= *reticulata* Brandt) as living in brackish water in the drainages of mud flats, nipa palm and mangrove swamps, and in the estuarine area of rivers. They were found partly buried in mud, feeding on decaying organic material.

Material Examined. *I. ornata*. Specimens ex Blanford and several other lots (AMS). *R. carpentariensis*. Holotype, paratypes and several other lots (AMS). *Pellamora* species of Laseron, 1956. Types (AMS) and other lots of *P. capitata* and *P. angulata* (AMS). *A. quadrasi*. Lectotype, paralectotypes (SMF) and many other lots (AMS). *P. quadrina*. Holotype (AMS). *M. goliath*. Holotype and paratypes (AMS). *R. garretti*. Holotype (ANSP). *R. (A.) alveata*. Holotype (BMNH). *M. humera*. Holotype AMS). *M. reversa*. Holotype and paratypes (AMS).

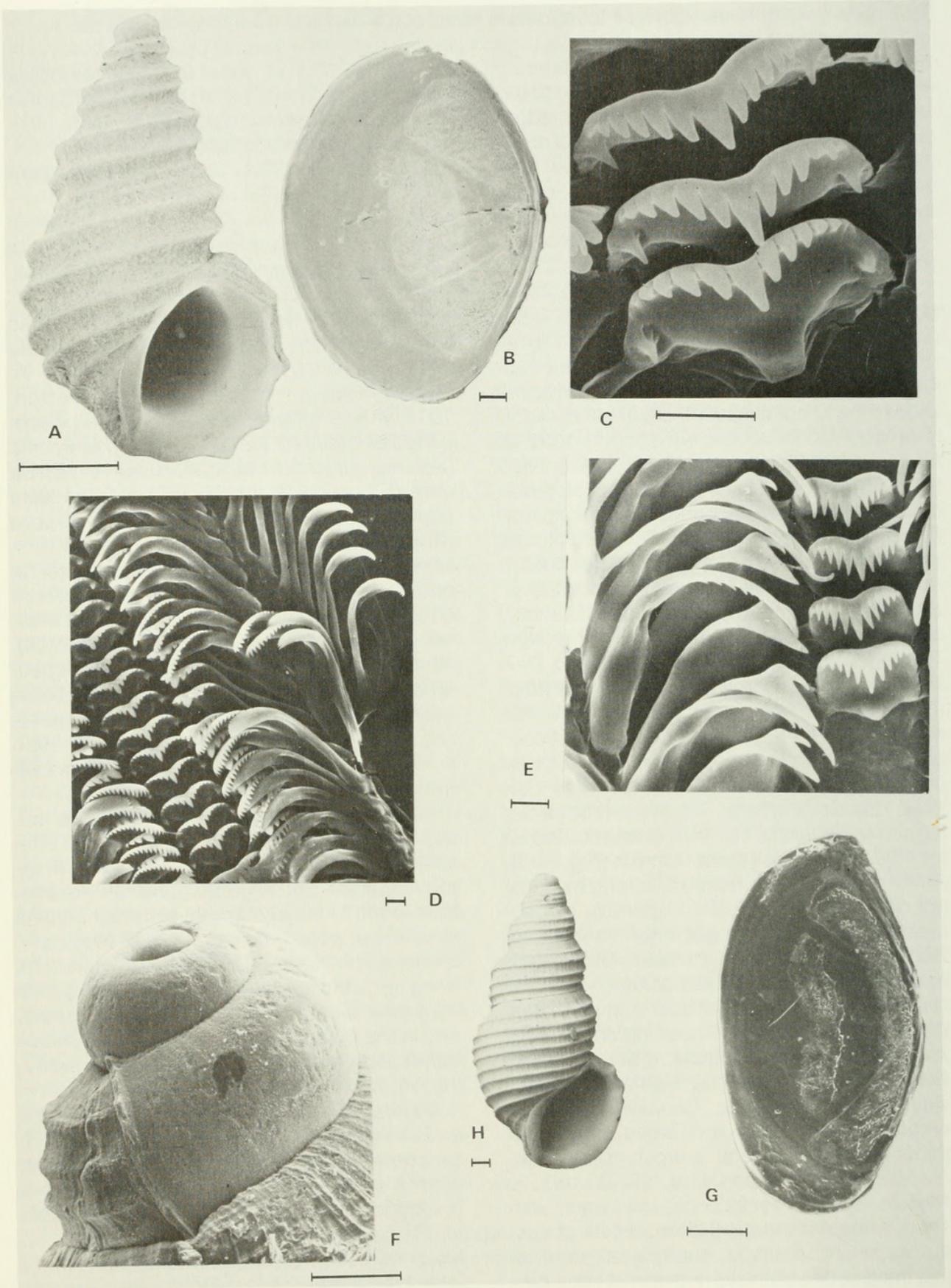


FIG. 9. A–D. *Iravadia (Iravadia) ornata* (Blanford), type-species of *Iravadia*. Deep Bay, New Territories, Hong Kong (AMS). A. Shell. B. Operculum, inner side. C, D. Radula. C. Central teeth only. E–H. *Iravadia (Iravadia) angulata* (Laseron). Norman River, Gulf of Carpentaria, Queensland, Australia (AMS). E. Radula. F. Protoconch. G. Operculum, inner side. H. Shell. Scales: shells = 1 mm; opercula and protoconchs = 0.1 mm; radulae = 0.01 mm.

Remarks. The type-species, *I. angulata* and *I. quadrasi* are estuarine and, whereas the other two Australian species apparently have not been collected alive, they probably have a similar habitat.

Iravadia angulata differs from *I. ornata* in shell characters (compare Figs. 9A and H), the shell being more like that of species of *Iravadia* (*Fairbankia*) in its tall spire, relatively weak spiral cords, thin peristome and weak varix. The angulated whorls are, however, atypical of the subgenus *Fairbankia*. The operculum (Fig. 9G) is nearly identical to that of *Iravadia ornata* (Fig. 9B) and it is mainly because of the similarity in this structure that *I. angulata* is tentatively included in *Iravadia* s.s. The radula of *I. angulata* has central teeth (Fig. 9E) lacking any basal denticles and the lateral teeth are virtually unicuspid and differ from other species examined in the genus in this respect, except for two new species of *I. (Pseudonoba)* described in the Appendix and discussed below. *Iravadia quadrasi* (Fig. 10A) has more pronounced axial sculpture than *I. ornata* but agrees in other respects.

The differences in the female genitalia of *I. ornata* and *I. quadrasi* are considerable but other species of *Iravadia* should be examined to determine the limits of variation of the female genitalia before further subdivision of this group is proposed.

Subgenus *Pseudomerelina* Ponder,
n. subgen.

Type-species: *Alvania mahimensis* Melvill, 1893. Recent, Bombay, India.

Diagnosis. Shell. Ovate-conic, with oval aperture, anterior subangulation of aperture absent; sculpture of axial ribs and spiral cords, gemmate at points of intersection. Aperture oval, not markedly subangled posteriorly, rounded anteriorly; outer lip prosocline, varix strong. Protoconch (Fig. 10J) as for genus. Periostracum thin. Figs. 10I, J. **Head-foot.** With conspicuous pigmentation on snout and bands on tentacles. Cephalic tentacles with short 'setae' distally and active cilia in spiral series along rest of tentacles. Foot weakly cleft anteriorly. Posterior end of foot with a weak indentation and a very short, flattened tentacle bearing short, stationary cilia. (Specimens examined from Darwin and Magnetic Island, Australia and Singapore). Fig. 1C. **Penis.** Flat-

tened, with two protuberances, one small, glandular swelling at about half-length on outer side and a flattened section near distal end on outer side. Penial duct in rounded, distal lobe on inner side. Fig. 8C. **Oviduct.** With small anterior bursa copulatrix and pallial, dorsal, posterior bursa copulatrix with narrow, vertical duct. Oviducal opening short, anteriorly placed. Two seminal receptacles (Fig. 5). **Operculum.** As in *Iravadia* s.s. but without internal ridges. An irregular, thickened area inside columella edge in a few specimens. Fig. 10F, G. **Radula.** As in *Iravadia* s.s., with one basal denticle on central tooth. Lateral teeth (1-3) + 1 + (3-4). Fig. 10H.

Distribution. Southeast Asia, India, and central Indo-Pacific to tropical Australia. (*Alvania mahimensis* Melvill, 1893 = *Merelina sucina* Laseron, 1956 = *Merelina solida* Laseron, 1956 = *Iravadia tuberculata* Brandt, 1974).

Habitat. Seaward edge of mangroves, especially on the edge of creeks, on weed, etc., and objects in small pools. Usually abundant when present.

Material Examined. *A. mahimensis.* Two syntypes (BMNH) and several other lots (AMS). *M. sucina.* Holotype and paratypes (AMS). *M. solida.* Holotype (AMS).

Remarks. This subgenus is proposed for a single species, the shell of which is distinguished from those included in *Iravadia* s.s. by its gemmate sculpture, relatively weak spiral cords, two purple spiral bands on the body whorl, and more evenly-oval aperture. The radula is almost identical to that of *Iravadia ornata* but the operculum, although similar in shape, lacks any internal ridges. *Iravadia (Pseudomerelina) mahimensis* is the only species of the Iravadiidae known to possess a metapodial tentacle (Fig. 1C). It has presumably disappeared in the other species of the family examined alive, although there is a low ridge on the posterior end of the foot in *I. quadrasi* (Fig. 1B). In addition, the penis is of simpler construction than in the other subgenera of *Iravadia*; it has a less swollen distal portion and only two small accessory protuberances; and there are two seminal receptacles in the female genital system, not one as in other members of the genus.

Iravadia (Pseudomerelina) mahimensis lives in an estuarine habitat and in the sheltered waters of enclosed bays and appears to have a wide distribution through the central Indo-Pacific.

The shells of *Iravadia (Pseudomerelina)*

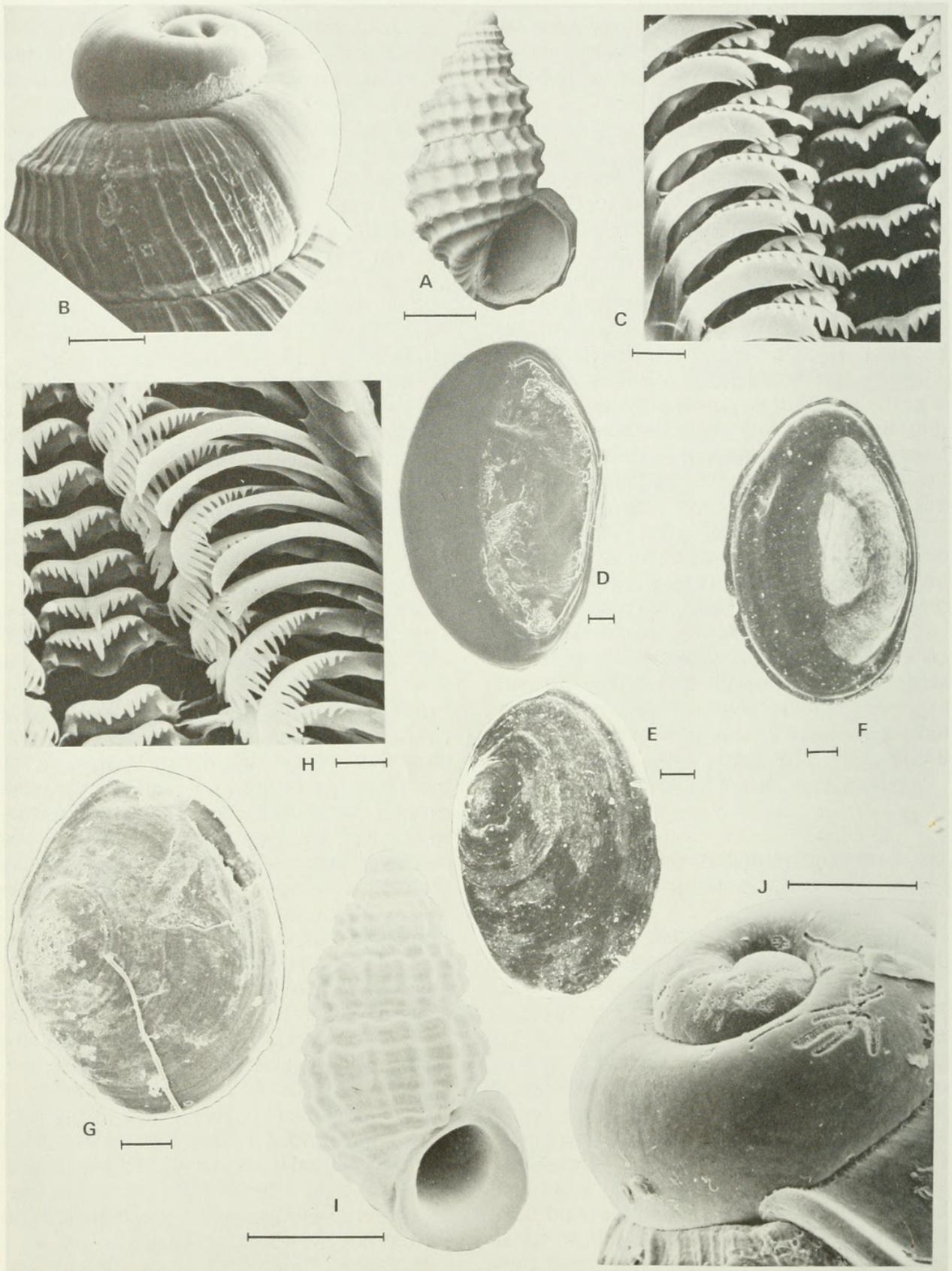


FIG. 10. A–E. *Iravadia (Iravadia) quadrasi* (Boettger). A. Shell. B. Protoconch. C. Radula. D–E. Operculum, inner (D) and outer (E) sides. A, B, D. Proserpine River estuary, Wilson, Queensland, Australia. C. Gatakers Bay, Hervey Bay, Queensland. E. Mouth of Brisbane River, Queensland. All AMS. F–J. *Iravadia (Pseudomerelina) mahimensis* (Melville). Type-species of *Pseudomerelina* nov. F, G. Operculum, inner (F) and outer (G) sides. H. Radula. I. Shell. J. Protoconch. F. Magnetic Island, Queensland, Australia. G–J. Maningrida, Arnhem Land, Northern Territory, Australia. Both AMS. Scales: shells = 1 mm; opercula and protoconchs = 0.1 mm; radulae = 0.01 mm.

mahimensis (Fig. 10I) and *Iravadia* (*Iravadia*) *quadrasi* (Fig. 10A) are superficially very similar to species of *Alvania* and *Merelina* (Rissoiidae) but can be distinguished by their prosocline outer lips and their small, smooth, flattened protoconchs.

Subgenus *Fairbankia* (Blanford MS)
Stoliczka, 1868 (July): 274

Type-species: *Fairbankia bombayana* (Blanford MS) Stoliczka, 1868, original designation. Recent, Bombay, India.

Synonyms: *Pellamora* Iredale, 1943: 206. Type-species: *Iravadia australis* Hedley, 1900; original designation. Recent, NE Australia.

Wakauraia Kuroda & Habe, 1954: 75. Type-species: *Fairbankia* (*Wakauraia*) *sakaguchii* Kuroda & Habe, 1954. Recent, Japan.

Diagnosis. **Shell**. Elongately-conic, non-umbilicate, solid, with weak to moderate spiral sculpture and weak axial threads or lamellae. Aperture relatively small, weakly to distinctly angled anteriorly, very weakly channelled posteriorly, outer lip slightly to moderately prosocline. Protoconch as for genus. Periostracum moderately well-developed, with short processes in some species. Fig. 11A, F.

Head-foot. Cephalic tentacles very slightly 'setose' distally, with or without a few darkly pigmented bands or black spots. Head and foot pigmented dorsally. Anterior edge of foot indented, posterior end blunt, with shallow indentation. No metapodial tentacle. (*I. (F.) australis*, *I. (F.) bombayana*). Fig. 1A, D. *I. (F.) cochinchinensis* and *I. (F.) rohdei* appear to be similar according to Brandt's (1974) description.

Penis. (*I. (F.) australis*). Short, compressed, with a row of accessory glandular swellings below an expanded distal portion on which penial duct opens subterminally. Fig. 8D., *I. (F.) bombayana* with broad, simple head; only one glandular area apparent in middle region (Fig. 8G).

Oviduct. Anterior sperm sac absent (*I. (F.) bombayana*) or very reduced (*I. (F.) australis*); bursa copulatrix with vertical opening separated from oviducal opening. Oviducal opening short and anteriorly placed (*I. (F.) australis*) or occupying anterior two-thirds of capsule gland (*I. (F.) bombayana*). A single seminal receptacle present. Figs. 6, 7. **Operculum**. Oval, with nucleus approximately two thirds along columellar edge, growth-lines concentric, a more-or-less longitudinal, low, internal ridge

present (*I. (F.) bombayana* and *I. (F.) australis*). *I. (F.) sakaguchii* is similar (Kuroda & Habe, 1954, text fig. 12). Fig. 11D, E, G. H. **Radula**. Similar to that of *Iravadia* s.s. but central teeth with two or three weak, basal denticles placed against upper lateral margins and just beneath outer, dorsal cutting edge (*I. (F.) bombayana* and *I. (F.) australis*). *I. (F.) sakaguchii* is similar but no basal denticles are shown in the illustration of the central tooth (Kuroda & Habe, 1954, text fig. 11). Fig. 11B, C, I, J.

Distribution. South and SE Asia, Sumatra, S China, Philippines (*F. bombayana* = *Fairbankia quadrasi* Boettger, 1893; *Fairbankia cochinchinensis* Bavay & Dautzenberg, 1940; *Fairbankia rohdei* Brandt, 1968; *Onoba tenuilirata* Boettger, 1893). Northern and NE Australia (*Iravadia australis*). Red Sea (?*Onoba elongata* Hornung & Mermod, 1928). Japan (*F. (W.) sakaguchii*).

Habitat. Mangroves, under objects in shallow pools (*I. (F.) australis*) or on the surface of mud in standing water (*I. (F.) bombayana*). Drainage system of mudflats, nipa palm and mangrove swamps (*I. (F.) bombayana*, *I. (F.) rohdei*, Brandt, 1974).

Material Examined. *F. bombayana*. A few lots (AMS, BMNH). *F. quadrasi*. One lot (AMS). *F. cochinchinensis*. Three lots, ex Brandt (USNM). *I. australis*. Holotype, paratypes and several other lots (AMS). *F. rohdei*. Four lots (USNM). *O. tenuilirata*. Holotype (SMF). *O. elongata*. Holotype (GNHM). *F. (W.) sakaguchii*. Paratypes (USNM).

Remarks. The species in this subgenus differ from those in *Iravadia* s.s. in their more elongate shells with weaker spiral sculpture, more oval apertures, and the bursa copulatrix has a vertical opening separate from that of the capsule gland. The central teeth of the radula have only weak, dorso-laterally placed basal denticles and the nucleus of the operculum is displaced from the middle of the columellar edge. The species of *Iravadia* (*Fairbankia*) live in an estuarine habitat, usually amongst mangroves, like those of *Iravadia* s.s.

Brandt (1968) described the radula, operculum and animal of his new species *F. rohdei* from Thailand and Thiele (1928) described the radula and operculum of *F. bombayana*. These species have radulae and opercula very similar to those of *Iravadia ornata*; Blanford (1868) and Brandt (1968, 1974) recognised them as closely related genera. Brandt (1974) pointed out the similar-

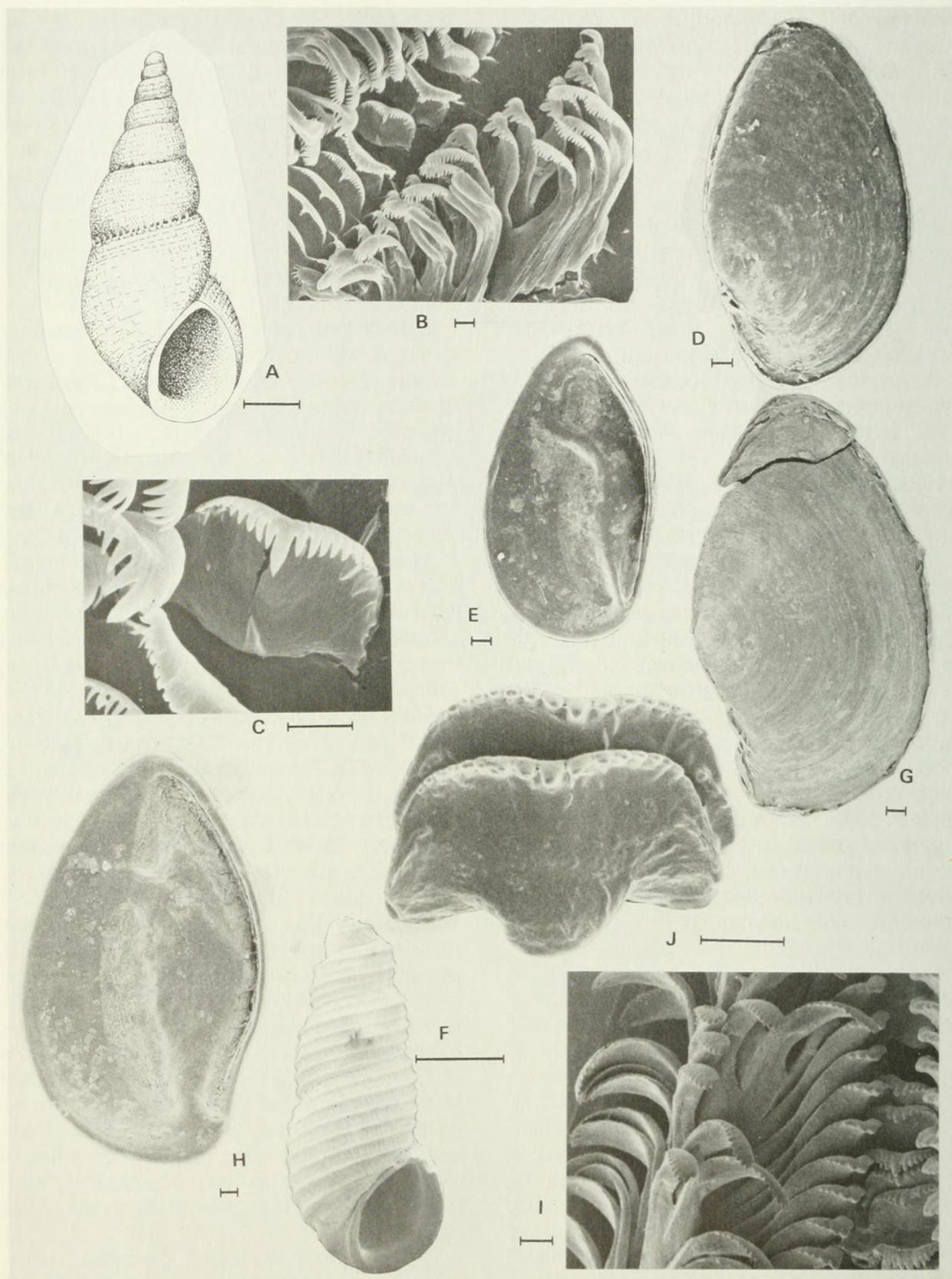


FIG. 11. A–E. *Irvadia (Fairbankia) bombayana* (Stoliczka), type-species of *Fairbankia*. A. Shell. B, C. Radula, central tooth. D–E. Operculum, outer (D) and inner (E) sides. A, D, E. Bombay, India (ex Blanford) (BMNH). B, C. Sembawang Estuary, Singapore (AMS). F–I. *Irvadia (Fairbankia) australis* (Hedley), type-species of *Pellamora*. F. Shell. Paratype, Bowen, Queensland, Australia (AMS). G, H. Operculum, outer (G) and inner (H) sides. I, J. Radula. G–J. Magnetic Island, Queensland, Australia (AMS). Scales: shells = 1 mm; opercula = 0.1 mm; radulae = 0.01 mm.

ity of the shells of *Fairbankia bombayana* to *Mainwaringia* Nevill, 1884 (type-species *Melania (Mainwaringia) paludomoidea* Nevill, 1884) but the radula as figured by Annandale & Prashad (1919) is dissimilar and the operculum is described as "horny, extremely thin, paucispiral, with the nucleus eccentric." Certainly the characters of the radula and operculum remove *Mainwaringia* from any close association with *Fairbankia*.

The shells of the type-species of *Pellamora* and *Fairbankia* differ in the relative strength of the spiral sculpture. A gradation is seen, however, in three SE Asian species, from weak spiral sculpture in *I. (F.) bombayana* to distinct spirals in *I. (F.) cochinchinensis* to moderately strong spirals in *I. (F.) rohdei*. The spiral sculpture of this last species approaches that of *I. (F.) australis* (Fig. 11F). *Iravadia angulata* is, on the other hand, very similar in shell characters (Fig. 9H) to *I. (F.) australis*. The type-species of *Wakauraia* is, as admitted by its authors, very similar to other species of *Fairbankia*. The main difference appears to be in the degree of angulation of the anterior end of the aperture. As this character alone is not considered to be of subgeneric importance, *Wakauraia* is regarded here as a synonym of *Fairbankia*.

Blanford (1868) published the description of his new genus (*Fairbankia*) in December, 1868. In his discussion he cites the Stoliczka (1868) reference in which his genus name was inadvertently introduced in July, 1868. Because Stoliczka gives a full description of the genus and species, he should be regarded as the author of *Fairbankia*.

Subgenus *Fluviocingula* Kuroda & Habe, 1954: 73

Type-species: *Fluviocingula nipponica* Kuroda & Habe, 1954; original designation. Recent, Japan.

Synonym: *Mesodestea* Laseron, 1956: 451. Type-species: *Mesodestea resima* Laseron, 1956; original designation. Recent, northern Australia.

Diagnosis. **Shell**. Small, ovate-conic, rather thin, usually narrowly-umbilicate with evenly-convex whorls, sculptured with very weak, scarcely-raised spiral cords and axial threads, interspaces forming shallow pits (Fig. 12D). Aperture oval, with very weak anterior and posterior angulations, peristome thin, varix weak, outer lip prosocline. Protoconch as for genus. Periostracum rather thin. Fig. 12A, B,

D. **Head-foot**. Head pigmented, cephalic tentacles with a broad band of pigmentation and stationary 'setae' distally. Foot cleft anteriorly and posteriorly. No metapodial tentacle (*F. resima*, Darwin, N Australia). Fig. 1F. **Penis** and **oviduct** not known. **Operculum**. Similar to that of species of *Iravadia* (*Iravadia*) but without internal ridges (*I. (F.) nipponica*, *I. (F.) resima*). Fig. 12C, H. **Radula**. Central teeth similar to those in *Iravadia* s.s. and *I. (Fairbankia)*, with central teeth showing from none to two laterally placed basal denticles on each side (none or one in *I. (F.) resima*, two in *I. (F.) nipponica*). Fig. 12E-G.

Distribution. Inland Sea of Japan and Sea of Japan (*F. nipponica*). Northern Australia (*M. resima*).

Habitat. Associated with mangroves but at their inshore edge in damp areas (*I. (F.) resima*). Saltwater lagoons and estuaries on mud and *Zostera*, up to 1 m in depth from negative temperatures to 33°C (summer); salinity 4-7‰ (*I. (F.) nipponica*, Golikov & Kussakin, 1978).

Material Examined. *F. nipponica*. One lot ex Golikov (AMS); paratypes (USNM). *M. resima*. Holotype and a few other lots (AMS).

Remarks. The type-species of *Fluviocingula* and *Mesodestea* are very similar, although the Australian species has a more elongate shell (Fig. 12A, B) and a slightly different radula (compare Figs. 12E, F with G). This subgenus differs from the others included in *Iravadia* by its curious shell sculpture, a series of minute spiral pits (Fig. 12D) between the weak spiral cords. The narrow umbilicus also sets the shell of this group of species apart from the remainder of the genus, although in an undescribed Australian species the umbilicus is absent. The operculum resembles that of species of *Iravadia* (*Pseudomerelina*), in lacking any internal ridges.

Golikov & Kussakin (1978) report probable viviparity in *I. (F.) nipponica*.

Subgenus *Pseudonoba* Boettger, 1902: 145

Type-species: *Pseudonoba peculiaris* Boettger, 1902; original designation. Middle Miocene, Rumania.

Synonyms: *Sinusicola* Kuroda & Habe, 1950 (Jan. 15): 16. Type-species: *Turbonilla (Careliopsis) filiola* Yokoyama, 1927 (= *Rissoina yendoii* Yokoyama, 1927), original designation. Upper Pleistocene, Koyasu, Japan.

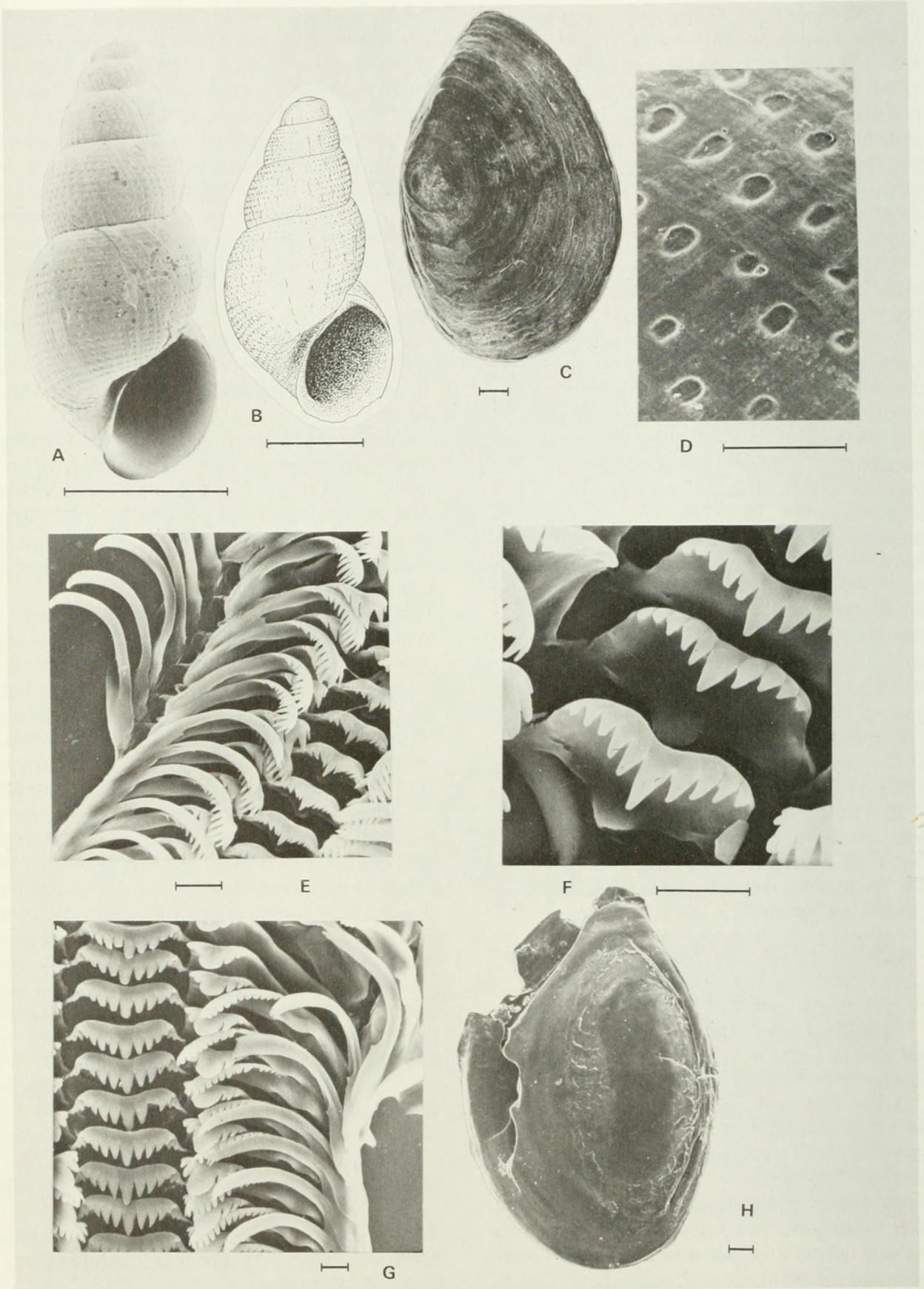


FIG. 12. A-F. *Iravadia (Fluviocingula) resima* (Laseron), type-species of *Mesodestea*. A, B, D: Shell; B, holotype (AMS), D, microsculpture of teleoconch. C. Operculum, outer side. E-F. Radula; F, central teeth. A, C-F. Diana Beach, Darwin, Northern Territory, Australia (AMS). G, H. *Iravadia (Fluviocingula) nipponica* (Kuroda & Habe), type-species of *Fluviocingula*; Posyet Bay, U.S.S.R. (AMS) G. Radula, H. Operculum, inner side. Scales: shells = 1 mm except Fig. D scale = 0.1 mm; opercula = 0.1 mm; radulae = 0.01 mm.

Paronoba Laseron, 1950 (Jan. 27): 283. Type-species: *Paronoba subquadrata* Laseron, 1950; original designation. Recent, SE Australia.

Dipsotoma Laseron, 1956: 416. Type-species: *Rissoa mercurialis* Watson, 1886 (= *Rissoa bella* A. Adams, 1851, ? = *Onoba delicata* Philippi, 1849); original designation. Recent, tropical Indo-Pacific.

Lucidinella Laseron, 1956: 427. Type-species: *Lucidinella conicera* Laseron, 1956 (= *Rissoa (Amphithalamus) densilabrum* Melvill, 1912); original designation. Recent, tropical Indo-Pacific.

Iraqirissia Dance & Eames, 1966: 39. Type-species: *Rissoa (Amphithalamus) aristaei* Melvill, 1912; original designation. Recent, India.

Diagnosis. Shell. Elongately-ovate to narrowly-elongate, nonumbilicate or with shallow umbilical chink; most species with distinct basal fold; sculptured with weak to moderate spirals and weak axial threads. Aperture not much expanded, with thick to moderate varix; outer lip slightly to moderately prosocline, orthocline or weakly opisthocline, usually with distinct but shallow anterior excavation and posterior subangulation. Protoconch as for genus. Periostracum thin, often covered with a reddish brown coating. Figs. 13A–D, I, J; 14A, B, G; 15A, B, E, H; 16A, B, G. **Head-foot.** Cephalic tentacles unpigmented, with spiral bands of cilia. Posterior end of foot slightly indented, anterior end indented. No metapodial tentacle. (*I. (P.) bella*, Magnetic Island, Queensland; *I. (P.)* cf. *aristaei*, Singapore; *I. (P.)* sp., cf. *bella*, Singapore). Fig. 1H. **Penis** and **oviduct** not known. **Operculum.** Elongately-oval, usually with columellar margin indented towards lower end, nucleus in middle of columellar margin or displaced slightly. A weak, longitudinal internal ridge sometimes present (several species examined). Figs. 14C, D, H; 15C, G; 16C, H, I. **Radula.** Similar to other members of the genus except central teeth with more pronounced lateral extensions in some species; one to four small to very large denticles on lateral edges of central teeth. Cutting edge of central teeth broad with numerous denticles, to very narrow, with only three. Lateral teeth with one to several cusps (several species examined—see Remarks). Figs. 14E, F, I; 15D, F; 16D, E, F.

Distribution. Tropical Indo-Pacific (*R. (A.) aristaei*, *Rissoa (Scrobs) ictriella* Melvill, 1910, = *Rissoa (Amphithalamus) alphisiboei*

Melvill, 1912; *Aclis atemeles* Melvill, 1896; ? *Onoba delicata* Philippi, 1849 ? = *Rissoa bella* A. Adams, 1851 = *Rissoa vitrea* Garrett, 1873 = *Rissoa (Onoba) mercurialis* Watson, 1886 = *Onoba philippinica* Boettger, 1893 = *Rissoina oscitans* Preston, 1905 = *Amphithalamus psomus* Melvill, 1918; *Chevallieria padangensis* Thiele, 1925; *Rissoa (Amphithalamus) densilabrum* Melvill, 1912 = *Onoba quadrasi* Boettger, 1893 (secondary homonym of *Iravadia quadrasi* (Boettger, 1893)) = *Lucidinella conicera* Laseron, 1956 = *Lucidinella conicera patruelis* Laseron, 1956; *Lucidinella sublaevis* Laseron, 1956). Late Miocene, western Pacific (Eniwetok Atoll) (*Cingula (Peringiella) parryensis* Ladd, 1966). Southeastern Australia (*P. subquadrata*). Japan (*R. yendoi* = *T. (C.) filiola* Yokoyama, 1927). New Zealand (*Dipsotoma inflata* Ponder, 1968). Middle Miocene, Rumania (*P. peculiaris*). Eocene, France (? *Ceratia (?) allixi* Cossmann, 1922).

Habitat. Marine to estuarine. *I. (P.) bella* and *I. (P.)* sp. cf. *aristaei* were found living in mangroves under objects on the mud or in shallow pools. *Iravadia (P.) padangensis*, and the three new species described in the Appendix are fully marine and live in relatively deep water. *Iravadia (P.) densilabrum* was collected alive under coral blocks at low tide in a fully marine situation.

Material Examined. *P. peculiaris*. Lectotype and many paralectotypes (SMF), one lot, ex Cossmann (NHMP). *C. (P.) parryensis*. Holotype (USNM). *O. delicata*. One specimen so named (BMNH). *O. bella*. Two probable syntypes ex Adams (NMW) and several other lots (AMS). *R. vitrea*. Five syntypes (ANSP). *R. (O.) mercurialis*. Holotype (BMNH). *O. philippinica*. Lectotype and paralectotype (SMF). *R. oscitans*. Three syntypes (BMNH); two "paratypes" (ANSP). *A. psomus*. Holotype (BMNH). *P. subquadrata*. Six syntypes and several other lots (AMS). *C. padangensis*. Holotype and 11 paratypes (HUM). *O. quadrasi*. Lectotype and one other specimen (SMF). *R. (A.) densilabrum*. Two syntypes (BMNH) and several other lots (AMS). *L. conicera* and *L. conicera patruelis*. Holotypes and paratypes (AMS). *L. sublaevis*. Holotype (AMS). *D. inflata*. Holotype (AIM). *T. (C.) filiola*. Holotype (GIT). *R. yendoi*. Holotype (GIT) and one other lot (NSMT). *R. (A.) aristaei*. Lectotype and two paralectotypes (BMNH). *C. (?) allixi*. One lot (topotypes), ex Le Renard.

Remarks. At least some of the species of

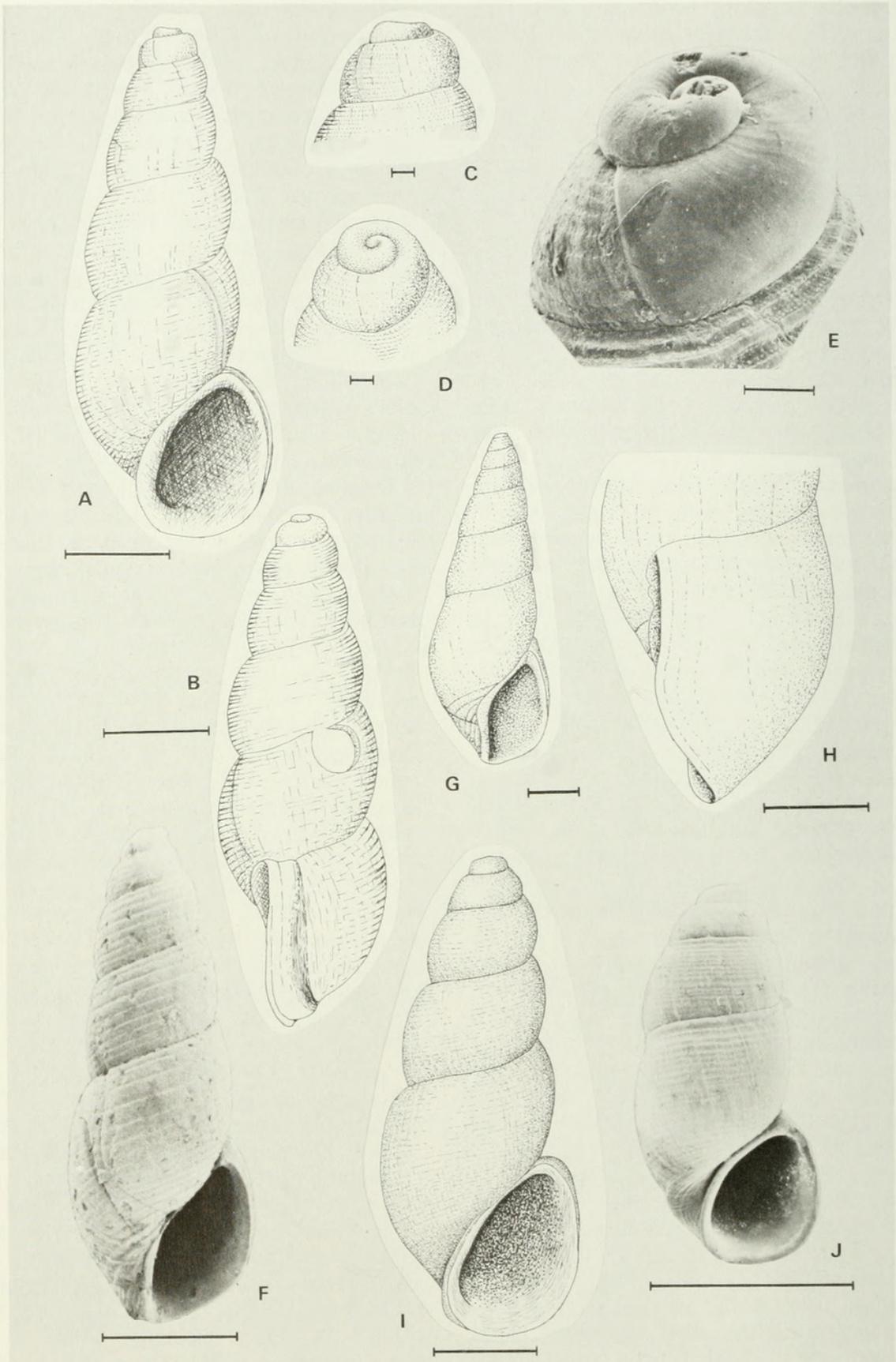


FIG. 13. A-D. *Iravadia (Pseudonoba) peculiaris* (Boettger), type-species of *Pseudonoba*; topotype, Kostej, Rumania (ex Cossmann Colln.) (NHMP). A, B. Shell, front and side views. C, D. Protoconch. E-F. *Rhombostoma imperforatum* (Sacco). Ozciano, Italy, (ZMR). E. Protoconch, F. Shell. G, H. *Rhombostoma carmelae* (Brugnone), syntype (ZMR); type-species of *Rhombostoma*; G, H. Shell. H. side view of aperture. I, J. *Iravadia (Pseudonoba) subquadrata* (Laseron), type-species of *Paronoba*. I, J. Shells; I. holotype. Port Stephens, New South Wales, Australia (AMS). J. Port Hacking, New South Wales (AMS). Scales: shells = 1 mm; protoconchs = 0.1 mm.

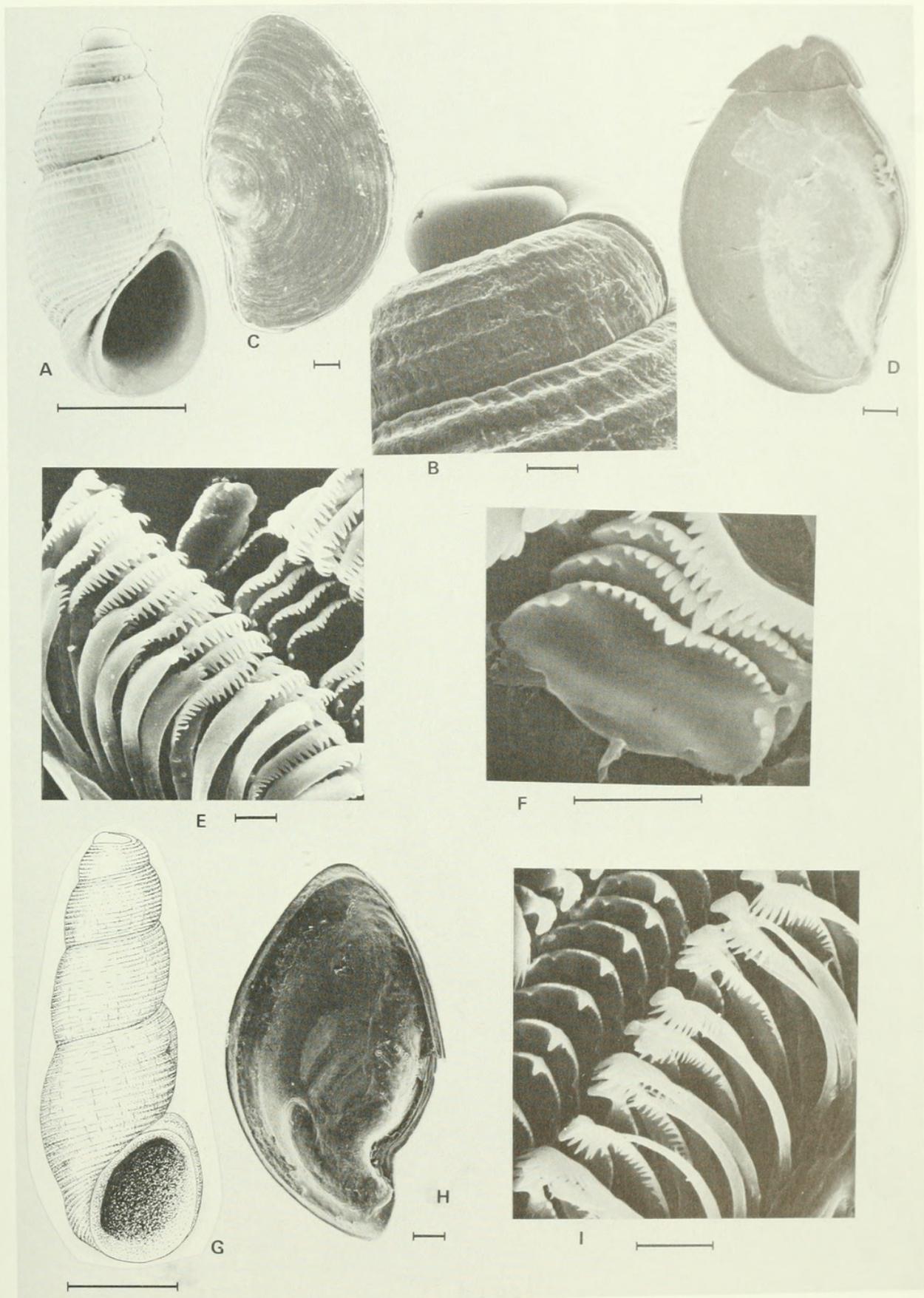


FIG. 14. A-F. *Iravadia (Pseudonoba) densilabrum* (Melvill), type-species of *Lucidinella*. A. Shell. Paratype of *Lucidinella conicera* Laseron, Whitehaven Beach, near Bowen, Queensland, Australia (AMS). B. Protoconch. C, D. Operculum, outer (C) and inner (D) sides. E, F. Radula, F, central teeth. B, C, E. Lindeman Is., Queensland (AMS); D, E. Norsup, Malekula, New Hebrides (AMS). G-I. *Iravadia (Pseudonoba) profundior* sp. nov. G. Shell of holotype. H. Operculum (inner side). I. Radula. H and I from paratype. Scales: shells = 1 mm; opercula and protoconchs = 0.1 mm; radulae = 0.01 mm.

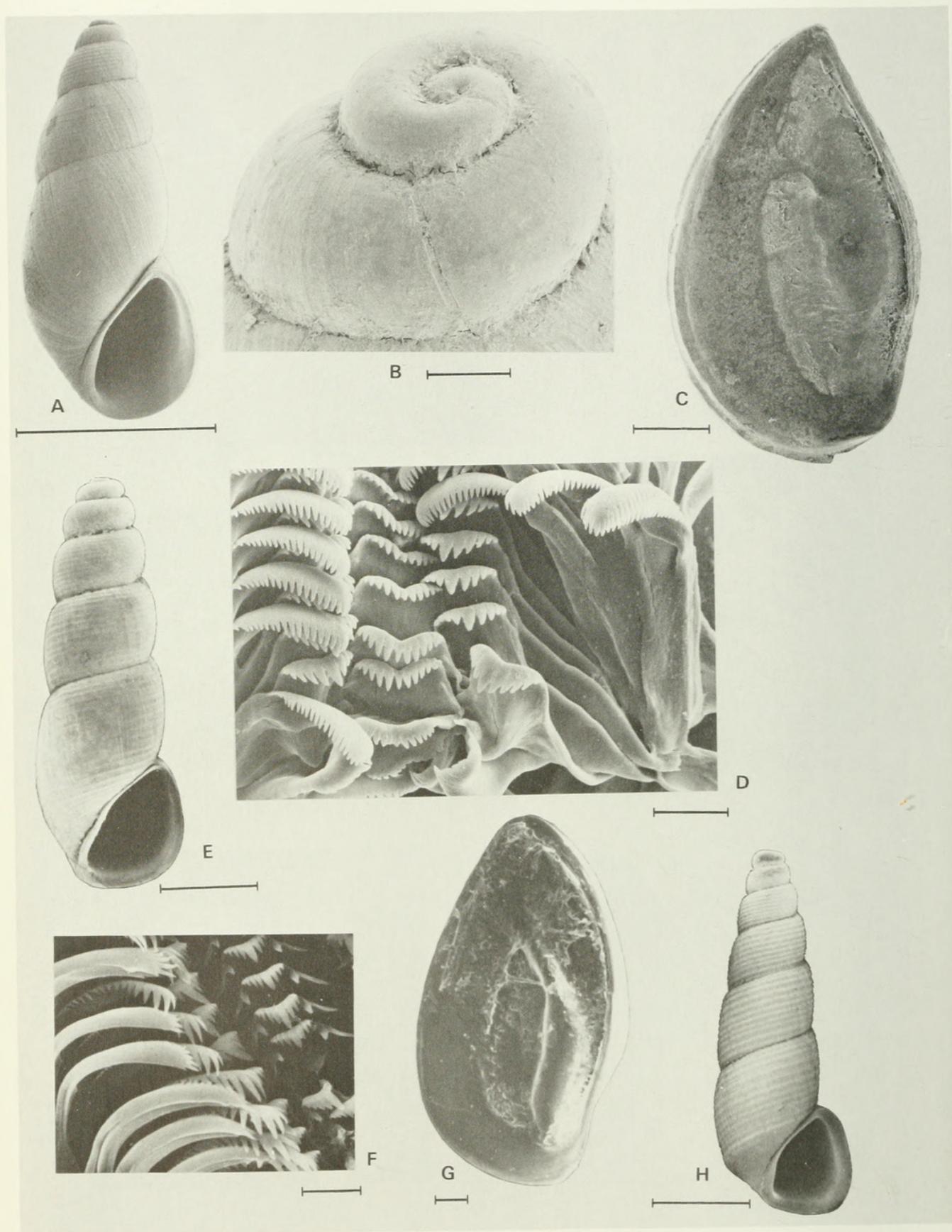


FIG. 15. A–D. *Iravadia* (*Pseudonoba*) *bella* (Adams), type-species of *Dipsotoma* Laseron. Magnetic Island, Queensland, Australia (AMS). A. Shell. B. Protoconch, C. Operculum, inner side. D. Radula. E. *Iravadia* (*Pseudonoba*) *filiola* (Yokoyama), type-species of *Sinusicola*, Tomioka, Amakusa, Kyushu, Japan (NSMT). Shell. F–H. *Iravadia* (*Pseudonoba*) sp. Sembawang, Singapore (AMS). F. Radula. G. Operculum, inner side. H. Shell. Scales: shells = 1 mm; opercula and protoconchs = 0.1 mm; radulae = 0.01 mm.

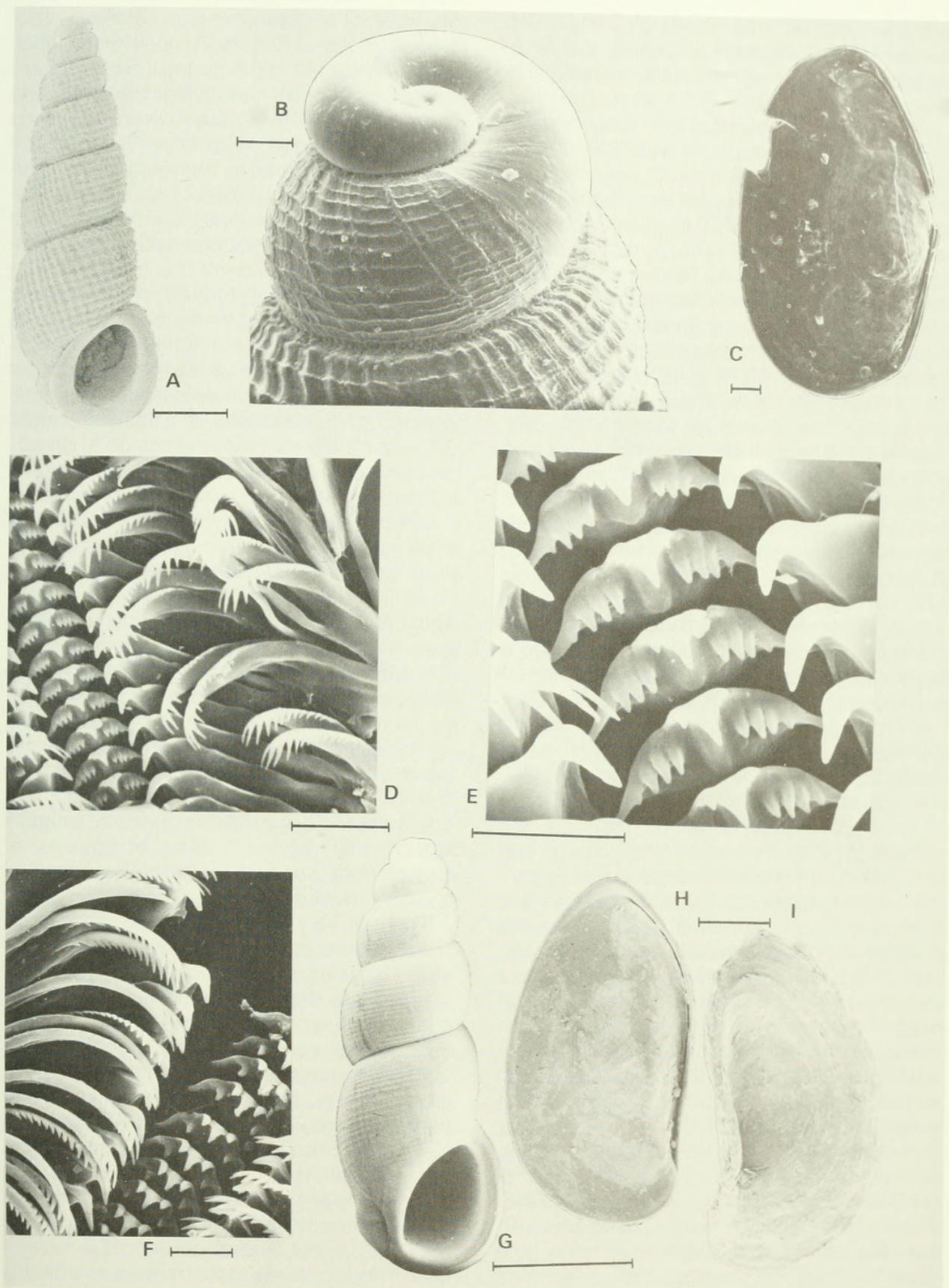


FIG. 16. A-E. *Iravadia (Pseudonoba) gemmata* sp. nov. A. Shell of holotype. B. Protoconch. C. Operculum, D, E. Radula; E, central teeth. B-E, from paratypes. F-I. *Iravadia (Pseudonoba) expansilabrum* sp. nov. F. Radula. G. Shell of holotype. H, I. Operculum, inner (H) and outer (I) sides. F, H, I. from paratype. Scales: shells = 1 mm; opercula and protoconchs = 0.1 mm; radulae = 0.01 mm.

this subgenus are fully marine and range from shallow coastal waters to relatively deep water. The type-species of *Dipsotoma*, *Sinusicola* and *Iraqirissoa* probably normally live in estuarine conditions.

The shells of species of this subgenus encompass a considerable range of form. There appears to be a gradation from very elongate shells (as in the type-species of *Iraqirissoa* and *Sinusicola* (Fig. 15E)) to others with moderate spires, the latter usually having much less-impressed sutures and flatter whorls than the former. The spiral ornament usually consists of rather weak spiral threads but some species are sculptured with close spiral lirae. Species included in *Lucidinella* by Laseron (1956) have shells with prominent axial threads and a rather strong basal fold. The lower part of the inner lip is separated from this basal fold and an umbilical chink is formed between them. This style of shell is very similar to a relatively weakly and spirally sculptured species of *Iravadia* s.s., *I. capitata* (Laseron), and to some species of *Iravadia* (*Fairbankia*). *Paronoba subquadrata* (Figs. 13I, J) is somewhat intermediate in the basal features of the shell in sometimes having a basal fold and thus forms a link between *Lucidinella conicera* (= *densilabrum*) (Fig. 14A), which always has a basal fold and *Dipsotoma mercurialis* (= *bella*) (Fig. 15A), which lacks one. This last species resembles the type-species of *Pseudonoba* (Fig. 13A, B) in all essential shell features.

Habe (1958) described the radula and operculum of *Sinusicola endoi* (*sic!*, = *yendoi*), which agree closely with those of the type-species of *Fairbankia*, *Pseudomerelina* and species of *Lucidinella*, although the structure of the inner side of the operculum was not noted. The shell of this species (Fig. 15E) is smaller than most of the type-species included in the synonymy of *Pseudonoba* but agrees generally with them in shape and sculpture. It is also similar to species in the subgenus *Fairbankia* in shape but is smaller in size and has an orthocline, not prosocline, outer lip. A very similar species, *Rissoa aristaei* Melvill, from Bombay, is the type-species of *Iraqirissoa*. Specimens from Singapore of a possibly undescribed species similar to both *R. aristaei* and *T. filiola* (Fig. 15H) differ in the characters of the central teeth of the radula from the figure of the radula of *S. yendoi* (= *T. filiola*) (Habe, 1958), but have an operculum like that of species of *Fairbankia* and *Pseudonoba* (Fig. 15G). These species appear to fall

between *Fairbankia* and *Dipsotoma* in shell features but are here included somewhat tentatively in *Pseudonoba*. The common shell features outlined in the generic diagnosis are a combination of characters which tie the type-species of the genera listed in synonymy together. Further support for their close relationship is gained by the very similar opercular characters seen in the species examined, which encompass the majority of the observed shell variations within the subgenus.

Unfortunately, the radular and opercular characters of some of the type-species of the genus-group names included in the synonymy are not known, so this grouping must be considered somewhat tentative. The type-species of *Pseudonoba* is a Miocene fossil but the radula and operculum of a closely similar new species (see Appendix) have been examined (Fig. 14G-I). *Paronoba subquadrata* is also known only from its shell which is, as noted above, similar to *P. peculiaris* and also to *Dipsotoma mercurialis* in all essential features. The shell of the type-species of *Iraqirissoa* is similar but more elongate than the shells of the type-species of *Pseudonoba* and *Dipsotoma*. It also has a rather weak basal fold and weak spiral sculpture.

Pseudonoba is probably more closely related to *Fairbankia* than to *Iravadia*, as far as can be judged from the shell, radula and operculum. The probable greater antiquity and mainly marine habitat of species of *Pseudonoba* suggest that it is the ancestral group within the genus *Iravadia*.

There is very considerable variation in the radular teeth, particularly in the central teeth, in the species examined in this group. This may indicate that the group is polyphyletic but it is also possible that because it is of some antiquity and considerable geographic spread this is divergence within a single phyletic group. The 'normal' *Iravadia* radula is seen in some species (Figs. 14E, F, I; 15D) but *I. (P.) cf. aristaei* from Singapore has central teeth with well-defined, long, lateral margins that show some thickening and there is a prominent basal denticle on each side of each tooth (Fig. 15F). This type of central tooth is very similar to that seen in the genera *Liroceratia* nov., *Hyala* and *Nozeba* and it is similar to the central teeth of many rissoids and hydrobiids. It is thus probable that this type of tooth can be regarded as "primitive" and that the "typical" *Iravadia* central tooth is derived from it by a

loss of lateral thickening, a widening of the cutting edge and a reduction in the size of the basal denticles. This condition can be seen in *I. (P.) yendoi* (see Habe, 1958), a species almost indistinguishable from *I. (P.) aristaei*, in *I. (P.) densilabrum* (Fig. 14E, F) and in *I. (P.) bella* (Fig. 15D). A deep-water species from the Indian Ocean is closer to the type-species of *Pseudonoba* in shell features than *I. (P.) bella* and has a radula (Fig. 16F) in which the lateral edges of the central teeth are thickened and the cutting edge is narrow, giving the tooth a sub-triangular outline. There is a prominent basal denticle on the central tooth of this species but in a new species from the Philippines there are three to four large basal denticles (Fig. 16D, E). Both of these species are described in the Appendix. *I. (P.) densilabrum* has one to three rudimentary denticles, so that multiple basal denticles are not unique in the subgenus. The radula of two of the new species is also unusual in having a very prominent cusp on the lateral teeth and zero or one secondary cusp.

In view of the general similarity in the shell and opercular features, and the existence of intermediate radular types, the species are tentatively grouped into a single subgenus, *Pseudonoba*. It is probable, however, that when additional information is available, further division will be required.

Genus *Chevallieria* Cossmann, 1888: 244

Type-species: *Chevallieria labrosa* Cossmann, 1888; original designation. Eocene, Paris Basin, France.

Synonym: *Nanadoma* Laseron, 1956: 447. Type-species: *Nanadoma imitoris* Laseron, 1956; original designation. Recent, N Australia.

Diagnosis. **Shell**. Subcylindrical, thin, non-umbilicate, with convex whorls, basal fold weak to absent, smooth or with extremely fine spiral striae and, in some species, distinct axial growth lines. Aperture pyriform, angled and weakly channelled posteriorly, rounded to weakly angled anteriorly, outer lip orthocline to slightly opisthocline, varix strong to absent. Protoconch relatively large, flattened, smooth, of about 1¾–2 whorls. Fig. 17A–D, G, H. **Head-foot, penis** and **oviduct** unknown. **Operculum**. Elongate, with spiral form apparent; columellar edge slightly indented, transparent, a weak internal ridge along columellar edge (*C. australis* sp. nov.).

Fig. 17E. **Radula**. Central teeth rather large, each with four small cusps on either side of a small median cusp; lateral margins unthickened, with a small denticle; basal margin with tongue-like projection. Lateral teeth with small, sharp cusps 5 + 1 + (?6); marginal teeth with numerous small, sharp cusps (*C. australis* sp. nov.). Fig. 17F.

Distribution. Tropical Indo-Pacific (*N. imitoris*; *Rissoina columen* Melvill, 1904 = *Rissoina (Scrobs) elspethae* Melvill, 1910). New species from South Australia and the Miocene and Pliocene of Victoria, Australia are described in the Appendix. Eocene, Paris Basin (*C. labrosa* and *Chevallieria cylindroides* Cossmann, 1907). There have been several additional species attributed to *Chevallieria* from the Eocene of the Paris Basin, but these species have not been examined.

Habitat. The only species found alive (see Appendix) was collected under stones in a marine situation. *Chevallieria imitoris* also probably lives in a fully marine habitat.

Material Examined. *C. labrosa*. One specimen ex Cossmann colln. (NHMP), three specimens ex J. Le Renard (AMS). *N. imitoris*. Holotype, two paratypes and several other lots (AMS). *R. columen*. Holotype (BMNH). *R. (S.) elspethae*. Three syntypes (BMNH). *C. cylindroides*. One lot (AMS).

Remarks. The shell of the type-species of *Chevallieria* (Fig. 17A) differs from that of the type-species of *Nanadoma* (Fig. 17G) in having a weak basal fold and a strong varix on the outer lip. Another congeneric species found in the Eocene of the Paris Basin, *C. cylindroides*, lacks a basal fold and agrees extremely closely with a Miocene species from Victoria, Australia (Fig. 17B), which is described in the Appendix. This Australian species differs from *C. labrosa* mainly in having a weaker varix on the outer lip. The Recent *C. imitoris* has a very weak to absent varix.

Chevallieria labrosa closely resembles some species of *Iravadia* (*Pseudonoba*) in shell features and this genus is probably the group from which *Pseudonoba* evolved. Species of *Chevallieria* differ from those of *Pseudonoba* by their smaller, thinner shells and extremely delicate spiral sculpture, or smooth surface. The only operculum examined is similar to that of species of *Iravadia* (*Pseudonoba*) in shape but is more nearly spiral in construction, the nucleus being placed away from the margin (Fig. 17E). This type of operculum is intermediate between

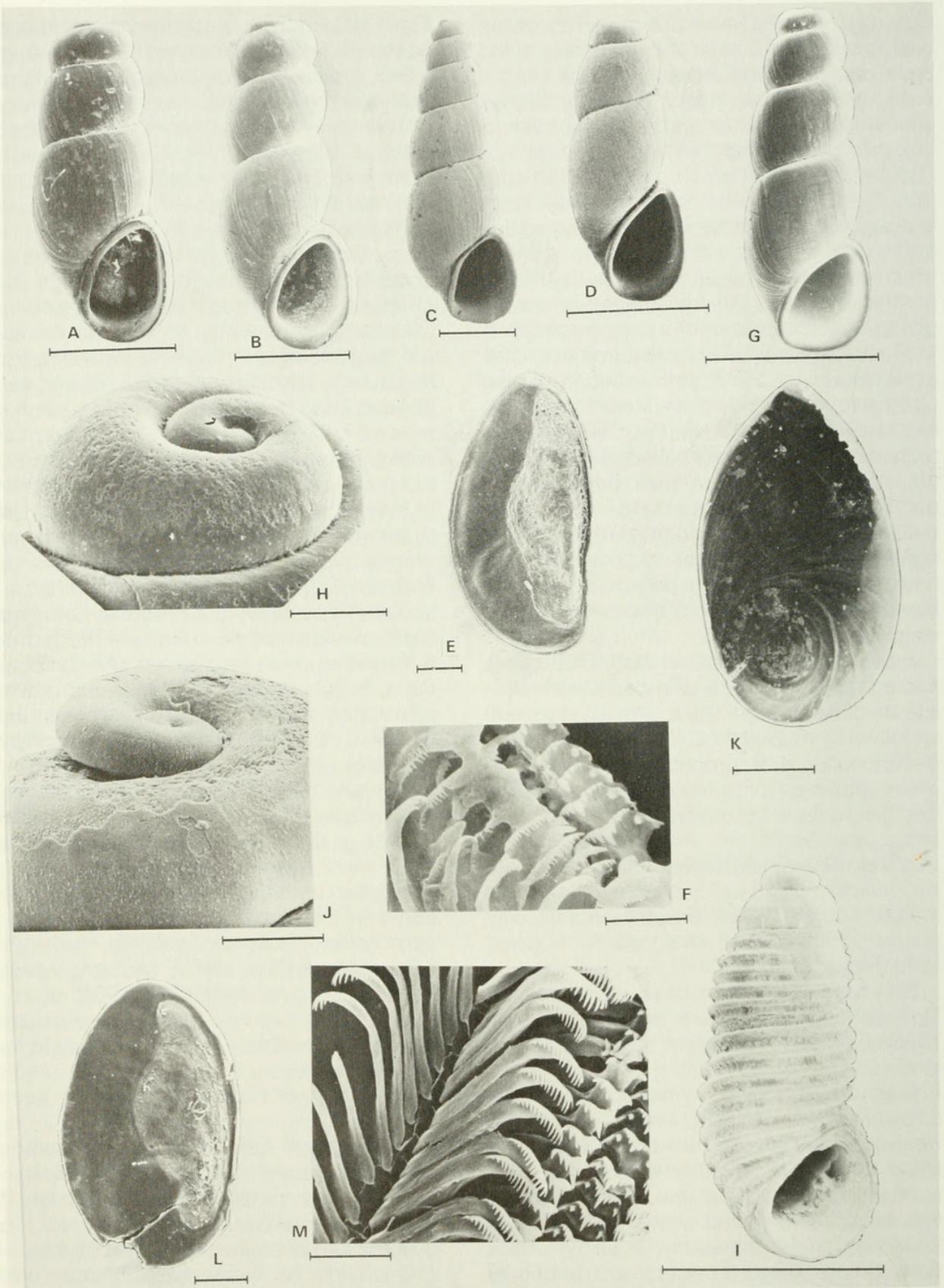


FIG. 17. A. *Chevallieria labrosa* Cossmann, type-species of *Chevallieria*; La Ferme de L'Orme, Yvelines, France (AMS). Shell. B. *Chevallieria balcombensis* sp. nov. Shell of holotype. C. *Chevallieria gippslandica* sp. nov. Shell of holotype. D-F *Chevallieria australis* sp. nov. Holotype. D. Shell. E. Operculum, inner side. F. Radula. G-H. *Chevallieria imitoris* (Laserson), type-species of *Nanadoma*, Shoal Bay, Mackay, Queensland, Australia (AMS). G. Shell. H. Protoconch. I-M. *Liroceratia sulcata* (Boettger), type-species of *Liroceratia* nov., Taurama, near Port Moresby, Papua, New Guinea (AMS). I. Shell. J. Protoconch. K, L. Operculum, outer side (K) and inner side (L). M. Radula. Scales: shells = 1 mm; opercula and protoconchs = 0.1 mm; radulae = 0.01 mm.

the normal spiral operculum seen in *Hyala*, *Nozeba* and *Liroceratia* and the typical *Iravadia* operculum. It is closer in form to the operculum of species of *Iravadia* (*Pseudonoba*) than to any of the other subgenera of *Iravadia*.

Genus *Rhombostoma* Seguenza, 1876: 14

Type-species: *Eulima carmelae* Brugnone, 1873; subsequent designation Sacco, 1892: 19. Pliocene, Sicily.

Synonym: *Eulimopsis* Brugnone, 1881: 120. Type-species: *Eulima carmelae* Brugnone, 1873; monotypy. Pliocene, Sicily.

Diagnosis. Shell. Small, elongate-conic, smooth or spirally sculptured, with weakly-convex whorls. Aperture elongately-ovate, angled and weakly channelled posteriorly; distinctly and rather deeply-channelled anteriorly; outer lip sinuate, with middle and uppermost (adapical) section advanced (see Fig. 13H). Inner lip thin, narrow; columella vertical, narrow. No external varix. Protoconch relatively small, of about two whorls, the first 1½ whorls flat, the last half whorl rapidly descending. Figs. 13E–H. **Animal** unknown.

Distribution. Pliocene and Miocene of Italy (*E. carmelae*; *Ondina imperforata* Sacco, 1892 = *Ondina pliobliqua* Sacco, 1892 = *striata* auct.). ?Miocene of Austria (*Chemnitzia striata* Hörnes, 1856).

Material Examined. *E. carmelae*. Syntypes (ZMR). *O. pliobliqua*. Sacco material (TGM), six specimens (ZMR). *C. striata*. Photograph of holotype ex A. Warén.

Remarks. Pavia (1975) has discussed this genus and describes in some detail one of the fossil species it contains. The shell of these species has a protoconch typical of the Iravadiidae (Fig. 13E) and a broad anterior notch in the aperture similar to that seen in some other genera in the family. The spiral cords of *R. imperforata* (Fig. 13E) also suggest a relationship with *Iravadia*. The weak varix and rather narrow aperture combined with the solid, tall-spired shell set the species included in this genus somewhat apart from the other genera in the family, although the overall apertural features resemble those of *Iravadia* (*Fairbankia*) *sakaguchii*. *Chemnitzia striata* Hörnes possibly belongs to this group although its aperture shows some similarity to that of species of *Iravadia* (*Pseudonoba*) in being less distinctly angled anteriorly.

Probably this group represents an off-shoot from an early *Pseudonoba* lineage but, because of its rather distinctive shell characters and the impossibility of confirming a close relationship with *Iravadia*, it is tentatively separated. Wenz (1940) and Pavia (1975) included this genus in the Eulimidae.

Genus *Liroceratia* Ponder, gen. nov.

Type-species: *Cingula sulcata* Boettger, 1893. Recent, Philippines.

Diagnosis. Shell. Small, solid, elongately-ovate, sculptured with strong spiral cords. Aperture oval, subangled posteriorly, rounded anteriorly, with weak, broad, anterior excavation; outer lip orthocline, with strong, broad varix. Protoconch similar to that of *Iravadia*. Periostracum yellow to brown, conspicuous. Fig. 17I, J. **Head-foot**. Cephalic tentacles long, strap-like, unpigmented, with stiff 'setae' distally; eyes at outer bases in small bulges. Snout of moderate length, bilobed. Foot weakly-cleft anteriorly, very weakly-indented posteriorly, anterior mucous gland indistinct. No posterior pedal mucous gland, no pallial tentacles and no metapodial tentacle. (*L. sulcata*, Taurama, near Port Moresby, Papua New Guinea). Fig. 1G. **Penis** and **oviduct** unknown. **Operculum**. Oval, coiled, thin, simple, nucleus eccentric, last whorl large. Fig. 17K, L. **Radula**. Very similar to that of *Hyala vitrea*, but with cutting edge of each lateral tooth raised on a neck-like extension from the base of the tooth. Fig. 17M.

Distribution. Tropical central Indo-Pacific from the Philippines to Fiji and Papua New Guinea (*C. sulcata*, = *Pellamora minutura* Laserson, 1956). *Rissoa truncata* Garrett, 1873 from Fiji is probably related.

Habitat. The seaward edge of mangroves under stones in the mid-littoral.

Material Examined. *C. sulcata*. Holotype (SMF), one lot Philippines and several other lots (AMS). *P. minutura*. Holotype and paratypes (AMS). *R. truncata*. Three syntypes (ANSP).

Remarks. This genus is based on a species which has a shell very like a miniature *Iravadia*, particularly in its protoconch characters and in having strong spiral cords. Its radula and operculum, however, resemble those of *Hyala vitrea*. The shell also superficially resembles that of marine species placed in rissoid genera such as *Lironoba* Iredale, 1915

but is easily distinguished by its protoconch characters (Fig. 17J), the rissoids having dome-shaped, sculptured protoconchs.

Species of *Chevallieria* are very similar to *Liroceratia sulcata* in their general shell features. They differ in their weak to absent spiral sculpture and in the details of the radular and opercular features of the one species for which these characters are known.

An Eocene species, *Ceratia* (?) *allixi* Cossmann, tentatively included in *Iravadia* (*Pseudonoba*) above, has similarities with this genus in most shell characters.

Genus *Hyalia* H. & A. Adams, 1852: 359

Type-species: *Hyalia vitrea* (= *Turbo vitreus* Montagu, 1803); monotypy. Recent, Europe.

Diagnosis. Shell. Small, thin, smooth, or with microscopic spiral threads. Aperture simple, oval, outer lip strongly prosocline, lacking a varix; weak posterior angulation present but no posterior sinus; shallowly but broadly excavated anteriorly. Protoconch smooth, of 2½ whorls, lacking a distinct terminal varix, first whorl rising slightly above level of nucleus. Fig. 18E–G. **Head-foot.** Animal unpigmented. Cephalic tentacles strap-like, long, having six to eight stationary cilia proximally, with eyes in the centre of their bases. Snout rather long, bilobed. Foot indented in front, rounded posteriorly. No accessory tentacles (*H. vitrea*, Clark, 1852 and A. Warén *in litt.*, 1981). Fretter & Graham (1978), apparently incorrectly, state that the posterior end of the foot is bifid.

Penis. U-shaped when at rest, with short filament distally and small glandular bulge about two-thirds of length from base. Fig. 8E.

Oviduct. With large anterior sperm sac, no bursa copulatrix and posterior oviducal opening. There are either one or two seminal receptacles. Fig. 3 and Johansson (1950).

Operculum. Oval, thin, simple, spiral, with eccentric nucleus, last whorl very large (*H. vitrea*). Fig. 18H. **Radula.** Lateral and marginal teeth typical of family, central teeth with cutting edge relatively narrower than in *Iravadia*, cusps few, sharp, median cusp rather long; lateral margins spread outwards, slightly thickened; each tooth with a denticle on each side of face (*H. vitrea*). Fig. 18I, J.

Distribution. Coast of Europe and Mediterranean Sea (*H. vitrea* = *H. mediterranea* Nordsieck, 1972). Sea of Japan (? *H. adamsi* Golikov & Kussakin, 1971). Upper Oligocene,

North Sea Basin (*Rissoa dissoluta* Wiechmann, 1874).

Habitat. Marine, sublittoral and on the continental shelf (15–100 m in deep burrows made by other animals on muddy bottoms (A. Josefson, personal communication, *vide* A. Warén *in litt.*) (*H. vitrea*). *Hyalia adamsi* lives on *Zostera* in an enclosed bay with fluctuating salinity (Golikov & Kussakin, 1978).

Material Examined. *H. vitrea*. Several lots (BMNH, AMS and other museums). *R. dissoluta*. One lot (NMV).

Remarks. Thorson (1946) described a free-swimming larva from Denmark which he identified as "*Onoba vitrea*." It had fine spiral striae on the only whorl of the teleoconch that had developed. He surmised that the smooth shell of specimens of *Hyalia vitrea* was due to wear and that his larva belonged to that species. The shells examined in this study show no trace of spiral striae but Jeffreys (1867) and A. Warén (*in litt.*) state that very fine microscopic spiral striae are present in perfect specimens.

The type-species of the genus has a thin, smooth shell lacking a varix on the outer lip and has a paucispiral operculum. The somewhat flattened protoconch is similar to that of *Iravadia* and *Hyalia* and also lacks a posterior mucous gland and accessory tentacles. In addition, the female reproductive system (Johansson, 1950) has a posterior slit in the glandular pallial duct, an anterior sperm sac, and lacks both a separate upper oviduct gland and a coiled oviduct, features also observed in *Iravadia* (herein).

The apertural features and general texture of the shell recall those of *Nozeba* and it is probable that these two genera are closely related. *Hyalia vitrea*, however, differs from species of *Nozeba* in having a narrower shell, a strongly prosocline (not orthocline) outer lip and a weaker posterior angulation of the aperture.

Hyalia adamsi has a much broader shell than *H. vitrea*. As I have not been able to examine specimens, the generic location of this species has not been confirmed. If it is a *Hyalia*, a member of this genus can survive in waters of low salinity.

Genus *Ceratia* H. & A. Adams, 1852: 359

Type-species: *Rissoa proxima* (Alder MS) Forbes & Hanley, 1850; monotypy. Recent, Europe.

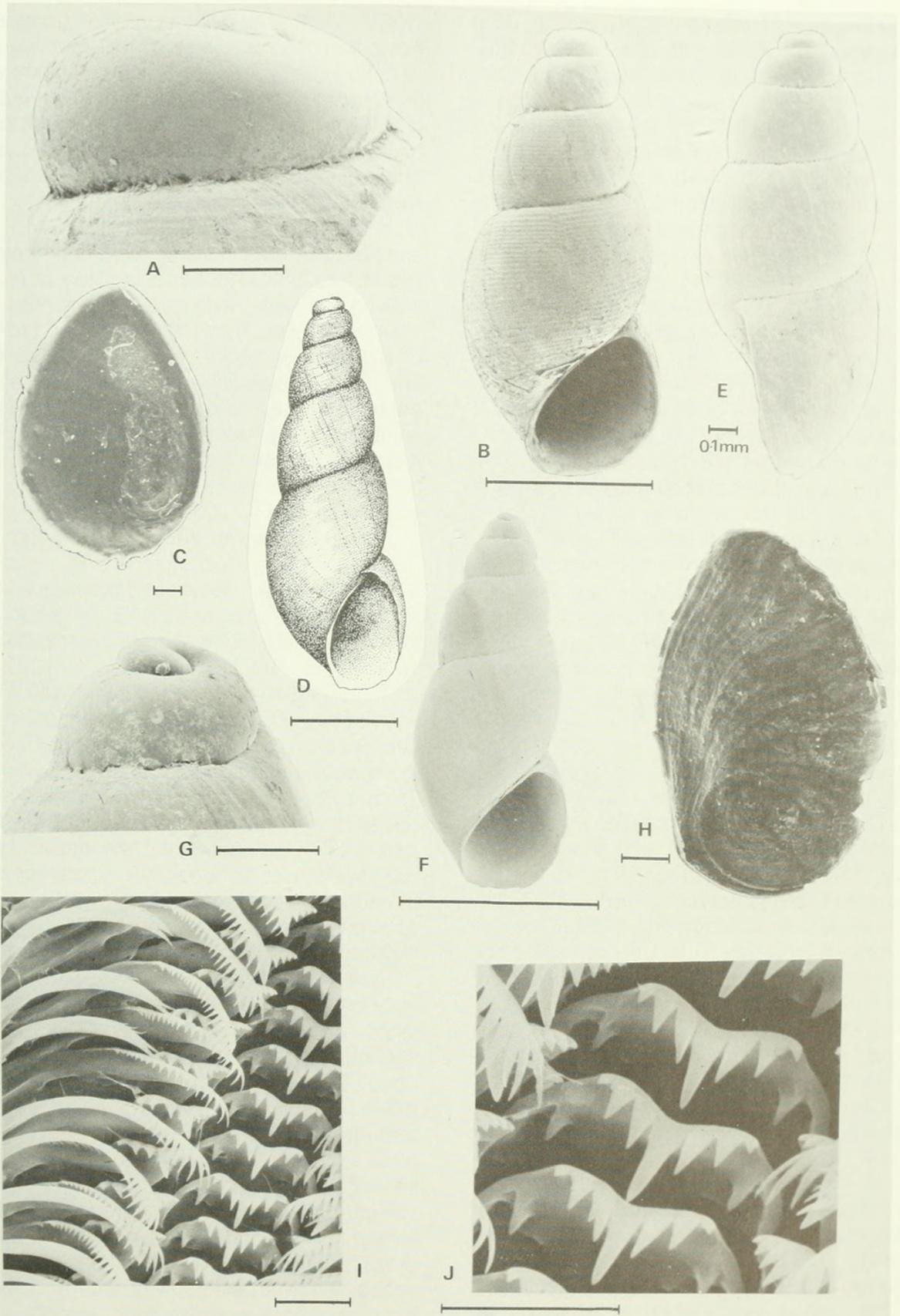


FIG. 18. A-C. *Ceratia proxima* (Forbes & Hanley), type-species of *Ceratia*. A. Protoconch. B. Shell. C. Operculum, inner side. A, B. Torbay, Devon, England (BMNH), C. Bay of Biscay, France (AMS). D. *Ceratia alta* (Gabb), type-species of *Hebeteaclis*; holotype (ANSP). E-J. *Hyala vitrea* (Montagu), type-species of *Hyala*. E, F. Shell, Vigo Bay, Spain, 36 m (AMS). G. Protoconch, H. Operculum, outer side. I, J. Radula, J, central teeth. G-J. Horns Reef, Danish North Sea coast, 50 m (ZMC). Scales: shells = 1 mm; opercula and protoconchs = 0.1 mm; radulae = 0.01 mm.

Synonym: Hebetaclis Pilsbry, 1922: 389. Type-species: *Auriculina alta* Gabb, 1873; original designation. "Miocene," Dominican Republic.

Diagnosis. Shell. Very similar to that of *Hyalia* but with fine spiral striae. Protoconch of about two whorls, first whorl slightly elevated, nucleus depressed, similar to that of *Hyalia*; smooth (except for "some fine spiral lines" according to Fretter & Graham, 1978). Fig. 18A, B, D. **Head-foot.** Pigmented white. Cephalic tentacles flat, rather short, smooth, gently attenuating and becoming minutely claviform at distal ends, which have a few stationary 'cilia'; eyes large, on minute swellings at outer bases of tentacles. Snout short but extendible, not bilobed. Foot large, fleshy, anterior edge deeply indented and produced into two long, lateral processes. Posterior end of foot divided into two long, widely divergent 'tails.' No accessory tentacles (Clark, 1852). **Penis and oviduct** unknown. **Operculum.** As in *H. vitrea* (*C. proxima*). Fig. 18C. **Radula.** The only radula of *C. proxima* available was accidentally mounted upside down but the shape of the central tooth is more nearly square than in that of *H. vitrea*. Lateral teeth finely cusped.

Distribution. Southern British Isles to the Mediterranean Sea (*Rissoa striatula* Jeffreys, 1847 (preocc.) = *C. proxima*). *Ceratia proxima* has been recorded from the Pliocene of England (Jeffreys, 1867) and the Pliocene and Pleistocene of Italy (Pavia, 1975). Miocene, Dominican Republic (*A. alta*). *Ceratia minutissima* Cossmann, 1888 from the Eocene of the Paris Basin, is possibly congeneric but no specimens have been available for examination.

Habitat. Marine, subtidal and on the continental shelf (*C. proxima*).

Material Examined. *R. striatula*. Neotype (USNM). *C. proxima*. A few lots (BMNH, USNM). *A. alta*. Holotype and paratypes (ANSP).

Remarks. *Ceratia* is only tentatively regarded as a genus distinct from *Hyalia* on the basis of the differences in the shape of the posterior end of the foot. Clark's (1852) description of the animal of *C. proxima* is based on the careful examination of at least two specimens. He observed this species together with *Hyalia vitrea* and commented at length as to the distinctiveness of the animals. Certainly the deeply cleft posterior end of the foot of *C. proxima* appears to be unique and has been confirmed by Fretter & Graham

(1978). Most species of *Iravadia* do, however, have the posterior end of the foot weakly-indented. Only one specimen containing a dried animal was available for examination and the mount of the radula was unsuccessful. The resuscitated dried remains did show that the posterior end of the foot was deeply cleft and that the operculum is identical to that of *H. vitrea*. Thus the familial position of this species is based mainly on shell features (which are almost identical to those of *Hyalia*) and on the lack of accessory tentacles.

Dr. A. Warén (*in litt.*) first examined the type of *A. alta* (Fig. 18D) and suggested its relationships. An examination of the type-material confirmed his assessment that *Hebetaclis* is a synonym of *Ceratia* as far as it is possible to judge from shell characters.

Genus *Nozeba* Iredale, 1915: 453

Type-species: *Rissoa emarginata* Hutton, 1885; original designation. Plio-Pleistocene and Recent, New Zealand. = *Neozeba*, *err. auct.*

[? = *Pasithea* Lea, 1833: 99, 207. Type-species: *Pasithea claibornensis* Lea, 1833; subsequent designation Gray, 1847: 160. Eocene, Alabama, North America. Synonym: ?*Pasitheola* Cossmann, 1896: 26. Unnecessary replacement name for *Pasithea* Lea, 1833, *non Pasythea* Lamouroux, 1812].

Synonyms: *Antinodulus* Cossmann, *in* Cossmann & Peyrot, 1919: 568. Type-species: *Bulimus globulus* Grateloup, 1827; original designation. Lower Miocene, France.

Syntharella Laseron, 1955: 100. Type-species: *Eulima topaziaca* Hedley, 1908; original designation. Recent, SE Australia.

Diagnosis. Shell. Ovate to elongately-conical, surface glossy, non-umbilicate, rather solid, smooth or with spiral threads, sometimes spirals moderately strong on base. Aperture rounded to distinctly-excavated anteriorly, sharply-angled posteriorly but not channelled. Posterior corner of aperture turned forward slightly, rest of outer lip approximately orthocone; inner lip partially disconnected from parietal wall in some species. No external varix. Protoconch smooth, of 2-2¼ convex whorls, flattened on top, last whorl descending, apex partially immersed. Periostracum thin. Fig. 19A, C-E, I. **Head-foot.** Cephalic tentacles long, strap-like, non-pigmented, with the eyes in small bulges at their outer bases; a few stiff "setae" distally.

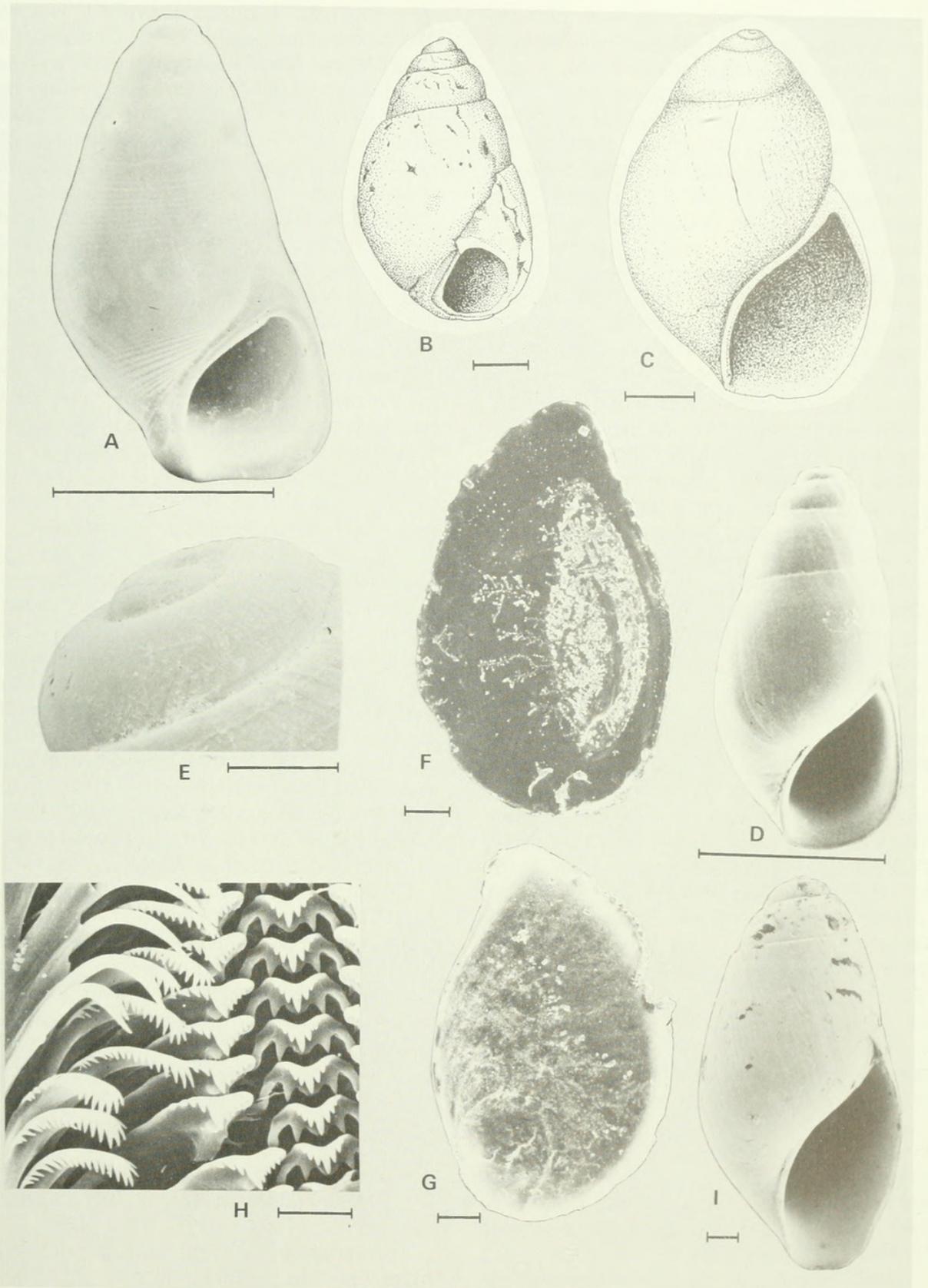


FIG. 19. A. *Nozeba emarginata* (Hutton), type-species of *Nozeba*. Outer Bay of Islands, New Zealand, 80 m (NMNZ). Shell. B. *Pasithea claibornensis* Lea, type-species of *Pasithea*. Shell of holotype. C. *Nozeba globulus* (Grateloup), type-species of *Antinodulus*; St. Paul-les-Dax, France (AMS). Shell. D–H. *Nozeba topaziaca* (Hedley), type-species of *Syntharella*. D. Shell. E. Protoconch. F, G. Operculum, inner (F) and outer (G) sides. H. Radula. D, F–H, Fisherman's Bay, Port Hacking, New South Wales, Australia (AMS); E. The Spit, Sydney, New South Wales (AMS). I. *Nozeba guttula* (Lea). Claiborne Sand Bed, Claiborne, Alabama, U.S.A. (USNM). Shell (subadult). Scales: shells = 1 mm; opercula and protoconch = 0.1 mm; radula = 0.01 mm.

Snout moderately long, extensile, bilobed. Foot slightly pigmented dorsally, with weakly-cleft anterior edge onto which opens a conspicuous, triangular anterior mucous gland; no posterior mucous gland present. Posterior pallial tentacle very short; no anterior pallial tentacle or metapodial tentacle. Postero-dorsal side of foot simple. (*N. topaziaca*, Port Hacking, New South Wales). Fig. 11. **Penis.** When at rest, bent double behind right cephalic tentacle, slightly to right of mid-line of head; wide, rather short, with enclosed duct opening at distal end, with three glandular swellings on inner edge. Fig. 8F. **Oviduct.** As for *Hyala*. **Operculum.** Oval, thin, simple, spiral, nucleus eccentric, last whorl large (*N. emarginata* Ponder, 1967; *N. mica*, *N. topaziaca*). Fig. 19F, G. **Radula.** Central teeth relatively large, cutting edge about equal to $\frac{1}{2}$ total width, cusps small; lateral edges at about 45° to cutting edge, thickened, free from rest of base for most of their length. A pair of prominent denticles on face of each central tooth overlap tooth in front; a tongue-like extension of the base between. Lateral teeth elongate, cutting edge rather long, with many small cusps; a small protuberance on face of tooth below cutting edge. Marginal teeth long, curved, with many small cusps (*N. mica* Ponder, 1967; *N. topaziaca*). Fig. 19H.

Distribution. New Zealand, Recent (*R. emarginata* = *Rissoina coulthardi* Webster, 1908; *Nozeba mica* Finlay, 1930), Tertiary (Pliocene-Miocene) (four species—see Fleming, 1966). Temperate Australia (*Eulima topaziaca* Hedley, 1908 = *Estea amblycorymba* Cotton, 1944); Lower Miocene, Victoria (*Rissoa gatliffiana* Chapman & Gabriel, 1914). Eocene of France (*Amphimelania lucida* Cossmann, 1886; *Balanocochlis eulimoides* Cossmann, 1888). Eocene of Alabama, North America (*Pasithea guttula* Lea, 1833). Miocene of France (*B. globulus*).

A new species from the Philippine Islands is tentatively assigned to this genus and is described in the Appendix. Undescribed species have been seen from the Eocene of New Zealand and Upper Cretaceous (Ripley Formation) of the U.S.A.

Habitat. Marine, on the continental shelf (*N. mica*, *N. emarginata*) and living on sea grasses in estuaries and embayments in the lower littoral and sublittoral (*N. topaziaca*).

Material Examined. *P. claibornensis*. Holotype (ANSP). *R. emarginata*. A few lots (NMNZ, AMS). *N. mica*. A few lots (NMNZ). *E. topaziaca*. Holotype, paratypes and many

other lots (AMS). *E. amblycorymba*. Holotype and other material identified by Cotton (SAM). *R. gatliffiana*. Three paratypes (NMV). *A. lucida* and *B. eulimoides*. One lot of each species, ex J. Le Renard (AMS). *P. guttula*. Holotype (ANSP) and two other lots (ANSP, USNM). *B. globulus*. One lot ex J. Le Renard (AMS).

Remarks. This genus has a long Tertiary history. The two Recent New Zealand species are marine but *N. topaziaca* from Australia lives in estuaries. A new species (see Appendix) tentatively referred to *Nozeba* was found in deep water in the Philippines. (Fig. 20G–J).

Pasithea may possibly be an earlier name for *Nozeba* but, unfortunately, that genus name is based on a very poorly preserved specimen which, according to Palmer (1937), may be a gerontic form of *P. guttula* (Fig. 19I). The type specimen (Fig. 19B) is, however, much larger than available material of *P. guttula* and may not be congeneric or even con-familial. *Pasithea guttula* is, together with some European Eocene species, included in *Pasitheola* by Cossmann (1921) and these certainly appear to be congeneric with *Nozeba*. An undescribed Eocene species from New Zealand is also a *Nozeba*. Gougerot & Le Renard (1977) have revised the Eocene species from the Paris Basin. Several specimens in the USNM from the Upper Cretaceous (Ripley Formation, SE U.S.A., USGS 25923, 28440, 27924) appear to be an undescribed species of *Nozeba*.

Cossmann, in several publications, considered the species he included in *Pasitheola* to be members of the Thiaridae. Other authors have placed this genus in the Eulimidae. *Nozeba topaziaca* (Fig. 19E–H), the type-species of *Syntharella* Laseron, agrees with *Nozeba emarginata* in essential shell characters and can be included in the genus *Nozeba*. *Syntharella* was regarded as a genus in the Eulimidae by Laseron (1955).

Genus *Rissopsis* Garrett, 1873: 228

Type-species: *R. typica* Garrett, 1873; monotypy. Recent, Fiji.

Diagnosis. Shell. Of moderate size, sub-cylindrical, thin, translucent, surface smooth and glossy, with flat whorls and pyriform aperture. Inner lip rather broad, thin; outer lip expanded slightly, orthocone to prosocline, aperture broadly excavated anteriorly; varix absent. Protoconch of about two whorls, very

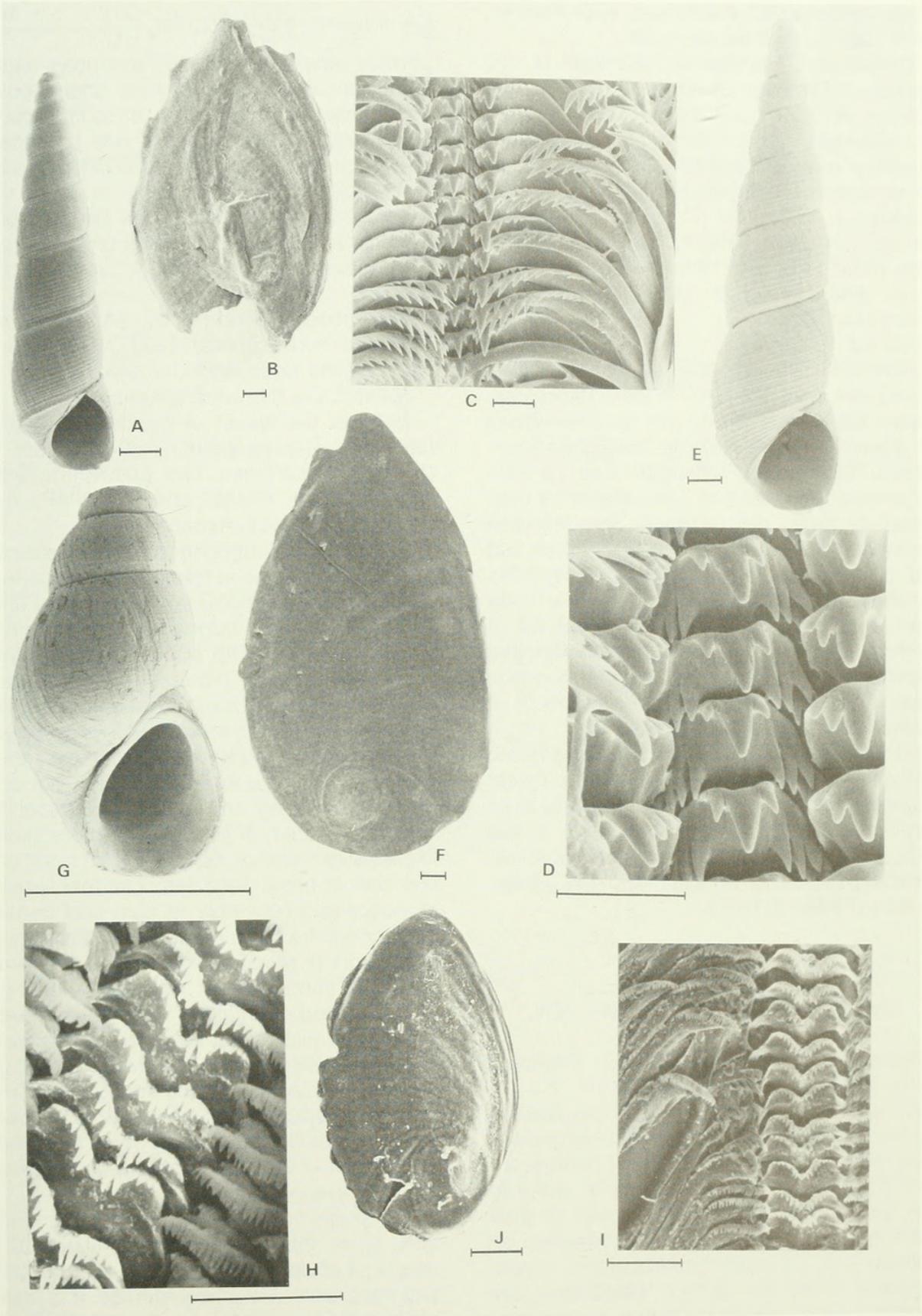


FIG. 20. A–D. *Acliceratia beddomei* (Dautzenberg), type-species of *Acliceratia* nov.; off Abidjan, Ivory Coast (NHMP). A. Shell. B. Operculum, inner side. C, D. Radula, D, central teeth. E–F. *Acliceratia carinata* (Smith); off Abidjan, Ivory Coast (NHMP). E. Shell. F. Operculum, inner side. G–J. *Nozeba* (?) *striata* sp. nov., holotype. G. Shell. H–I. Radula, H, central teeth. J. Operculum, inner side. Scales: shells = 1 mm; opercula = 0.1 mm; radulae = 0.01 mm.

small, tightly coiled, planorboid. (See Ponder, 1974, fig. 1). **Animal** unknown.

Distribution. Fiji, Samoa, Marshall Is. (*R. typica*); Durban, South Africa (*Rissopsis tuba* Kilburn, 1977; *Fusus prolongata* Turton, 1932 ? = *Rissopsis ligula* Kilburn, 1975). Northern Australia (one undescribed species). Philippines (one undescribed species).

Material Examined. *R. typica*. Lectotype and paralectotype (ANSP). One other specimen (SAM). *R. tuba*. Holotype and six paratypes (NM). *R. ligula*. Holotype and three paratypes (NM).

Habitat. Unknown.

Remarks. The type-species and the genus have been discussed by Ponder (1974). *Rissopsis* appears to be related to *Chevallieria* or, possibly, *Hyala*, judging from shell characters. Species of *Rissopsis* can be distinguished from those of *Chevallieria* by their large, smooth, glossy shell, the broadly-excavated anterior edge of the aperture and the subcylindrical spire. *Rissopsis* species resemble *Hyala vitrea* in having a smooth shell of similar shape, and, in *R. tuba*, a strongly prosocline outer lip. A more detailed assessment of the relationships of this genus must, however, await the examination of at least the radula and operculum.

Of the two species of *Rissopsis* from South Africa, one is distinct but the other (*R. ligula*) is very similar to *R. typica*, differing only in its slightly larger size. Single specimens of two undescribed species are known from northern Australia (AMS, C.126209) and the Philippines (USNM, 281302).

Genus *Acliceratia* Ponder, gen. nov.

Type-species: *Aclis beddomei* Dautzenberg, 1912. Recent, West Africa.

Diagnosis. **Shell.** Large for family, elongate-conic, thin, with spiral sculpture and a peripheral angulation or keel. Aperture angled posteriorly, rounded anteriorly; outer lip thin, lacking a varix, prosocline, with no posterior sinus; inner lip a thin, narrow glaze on parietal wall. Protoconch of about two whorls, typical of family. Fig. 20A, E. **Head-foot.** Unknown. Faecal pellets in rectum aligned perpendicular to rectal wall as is typical of family (*A. carinata*). **Penis** and **oviduct** unknown. **Operculum.** Thin, oval, simple, spiral, with eccentric nucleus, last whorl very large (*A. beddomei*, *A. carinata*). Fig. 20B, F. **Radula.**

Central teeth sub-triangular, $\frac{(2)1 + 1 + 1(2)}{3}$;

primary cusp large, sharp; secondary cusps small; basal cusps prominent, sharp; outermost cusp on outer edge of tooth. Lateral teeth large, with long bases and prominent, pointed primary cusp; secondary cusps rather small, (3)2 + 1 + 5. Marginal teeth with sharp, rather large cusps, the largest about equal in size to primary cusps of central and lateral teeth (*A. beddomei*, *A. carinata*). Fig. 20C, D.

Distribution. West Africa (*A. beddomei*; *Aclis carinata* Smith, 1871). Paleocene, France (one undescribed species).

Habitat. On the continental shelf.

Material Examined. *A. beddomei*. One lot (identified Dautzenberg) and one other lot (NHMP). *A. carinata*. Two specimens Dautzenberg Colln.; IRSNB; one lot (NHMP). *A. n. sp.* One lot, ex Le Renard.

Remarks. Although the two Recent species of *Acliceratia* agree in opercular and apertural characters with *Ceratia* and *Hyala*, they differ in having a much larger shell (9–12 mm in length compared with about 3 mm for *Hyala vitrea* and *Ceratia proxima*) which bears a distinct peripheral ridge. The details of the central teeth of the radula of *C. proxima* are unknown but the very poor available mount shows them to be sub-rectangular, not sub-triangular as they are in *Acliceratia* species. The central teeth of *H. vitrea* are more similar in shape to those of *Acliceratia* but have only one pair of basal denticles. The two species of *Acliceratia* resemble in size and general shell characters some species included here in *Iravadia* (*Pseudonoba*) but they differ from all of the subgenera of *Iravadia* in having a simple, coiled operculum. The radula characters are similar to at least one species of *Iravadia* (*Pseudonoba*) in having multiple basal denticles on the central teeth. This character separates *Acliceratia* from the other genera (excluding *Ceratia* in which the details of the central teeth are not known) possessing a simple operculum.

The shells of the two Recent species (Figs. 20A, E) in this genus differ in size and in details of sculpture. They occur sympatrically and have almost identical radulae. It is possible that they represent morphs (sexual?) of a single species.

An undescribed Paleocene species from France came from shallow water deposits at Bachivillers, Oise. It agrees closely with the Recent species in shell characters.

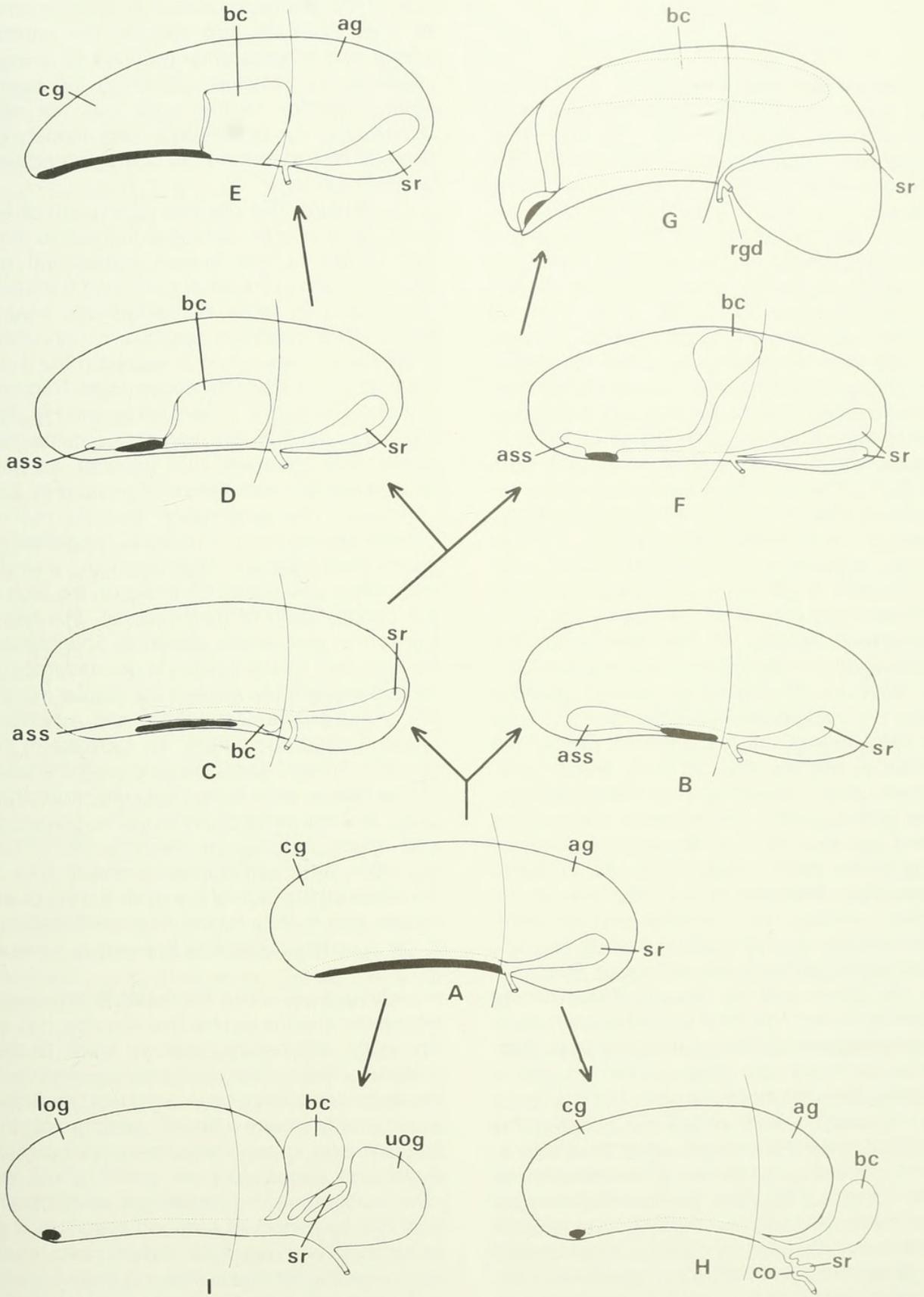


FIG. 21. Diagrams showing the types of female genitalia in the Iravadiidae and generalized examples of the Hydrobiidae and Rissoidae. The arrows indicate possible directions of evolutionary change in the genitalia and are not intended to indicate phylogenetic relationships. A. Hypothetical ancestral condition. B. *Hyala vitrea*. C. *Iravadia (Iravadia) quadrasi*. D. *Iravadia (Fairbankia) australis*. E. *Iravadia (Fairbankia) bom-bayana*. F. *Iravadia (Pseudomerelina) mahimensis*. G. *Iravadia (Iravadia) ornata*. H. Generalized Hydrobiidae. I. Generalized Rissoidae.

DISCUSSION

Evolution of the Iravadiidae

Female Genitalia. A hypothetical evolutionary scheme of the female genital system is schematically shown in Fig. 21. Here it is assumed, following Johansson (1968), that the ancestral condition was an open pallial oviduct (Fig. 21A). Closure of the originally open capsule gland from behind forwards, enclosing the sperm groove within the ventral channel, apparently occurred in the Hydrobiidae (Johansson, 1948) (Fig. 21H). It appears as though, in the Iravadiidae, closure of the ventral opening occurred differently, beginning anteriorly and moving backwards. This resulted in a slit-like opening in the posterior half of the capsule gland as seen in *Hyala vitrea* and *Nozeba topaziaca* (Fig. 21B). Further evolution appears to have resulted in the opening becoming secondarily anterior (as in *Iravadia ornata*) (Fig. 21G) or even, apparently secondarily, open over much of its length (as in *Iravadia (Fairbankia) bombayana*) (Fig. 21E). A sperm sac (ass) developed anterior to the opening by the sperm groove, closing over to become a tubular structure. Posteriorly, in *Iravadia quadrasi* (Fig. 21C), the deep, muscular sperm groove is open throughout the posterior part of the oviducal opening and contains unorientated sperm. Just posterior to the oviducal opening the sperm groove closes over, becoming a blind sac (bc) which extends to the posterior end of the pallial cavity. This sac, or bursa copulatrix, develops in a similar way in the other species of *Iravadia* investigated, although its relative position and its opening vary considerably. In the subgenus *Fairbankia* the bursa and its opening have swung dorsally to form a lateral pocket-like structure with a separate pallial opening. *Iravadia (Fairbankia) australis* (Fig. 21D) retains a rudimentary anterior sperm sac but this is lost in *I. (F.) bombayana* (Fig. 21E), in which the anterior two-thirds of the capsule gland is open ventrally. In *Iravadia (Pseudomerelina) mahimensis* (Fig. 21F), the bursal opening is enclosed immediately behind the oviducal opening. It appears as though the bursa (bc) in this species has migrated dorsally and the opening of the bursal duct has retained its original position. The bursal duct is developed from part of the sperm groove, whereas the bursa itself is probably an outgrowth from this groove. The bursal sac has migrated back behind the pallial cavity and lies on the outer

side of the glandular oviduct in *Iravadia ornata* (Fig. 21G). In that species the anterior sperm sac is apparently reduced to a small vestibule-like structure (although the sperm storing function of this area was not confirmed) and the bursal duct runs almost vertically from just behind the short, subterminal genital opening.

Operculum. The peculiar operculum of *Iravadia* (s.l.) is a considerable departure from that of the normal, coiled, paucispiral operculum seen in the other genera of the Iravadiidae and in most Rissoidae and Hydrobiidae. The modified operculum may have arisen in a *Chevallieria* ancestor in the early Tertiary as discussed above (see Remarks under *Iravadia* and *Chevallieria*, and Fig. 22). It is assumed that this type of operculum has arisen only once and that *Iravadia*, as here recognised, is a monophyletic group (Fig. 23).

Radula. The assumption that the marine genera are the most primitive is supported by species of *Hyala* and *Nozeba* having a single pair of well-developed denticles on the face of the central teeth of their radulae, this being the normal rissocean condition. This character is shared by the estuarine genus *Liroceratia* and these three genera are similar in having a non-pigmented animal and a normal, spirally-coiled operculum. An increase in the number of basal denticles on the central teeth of the radula may have occurred more than once, several pairs being found in *Acliceratia* and some species of *Iravadia* (s.l.). The reduction and, sometimes, eventual loss of denticles on the face of the central teeth of the radula, due to their lateral migration, appears to be a common trend in the genus *Iravadia* (s.l.).

Habitat. Species of *Chevallieria* appear to be marine and the genus, like *Nozeba*, has an ancestry extending back at least to the Eocene. *Chevallieria* is probably ancestral to *Iravadia (Pseudonoba)*, which is recorded from the Miocene. Some species of the *Pseudonoba* group migrated into brackish water and appear to have given rise to the other subgenera of *Iravadia*, all of which are confined to waters of reduced salinity. Other incursions into brackish water have been made by at least one species in both *Nozeba* and *Liroceratia* (Fig. 22) and, possibly, *Hyala*. This propensity for the iravadiids to move into low salinity areas might suggest that the ancestral group inhabited sheltered bays and estuaries and that the marine species in the family are derived from these. A detailed an-

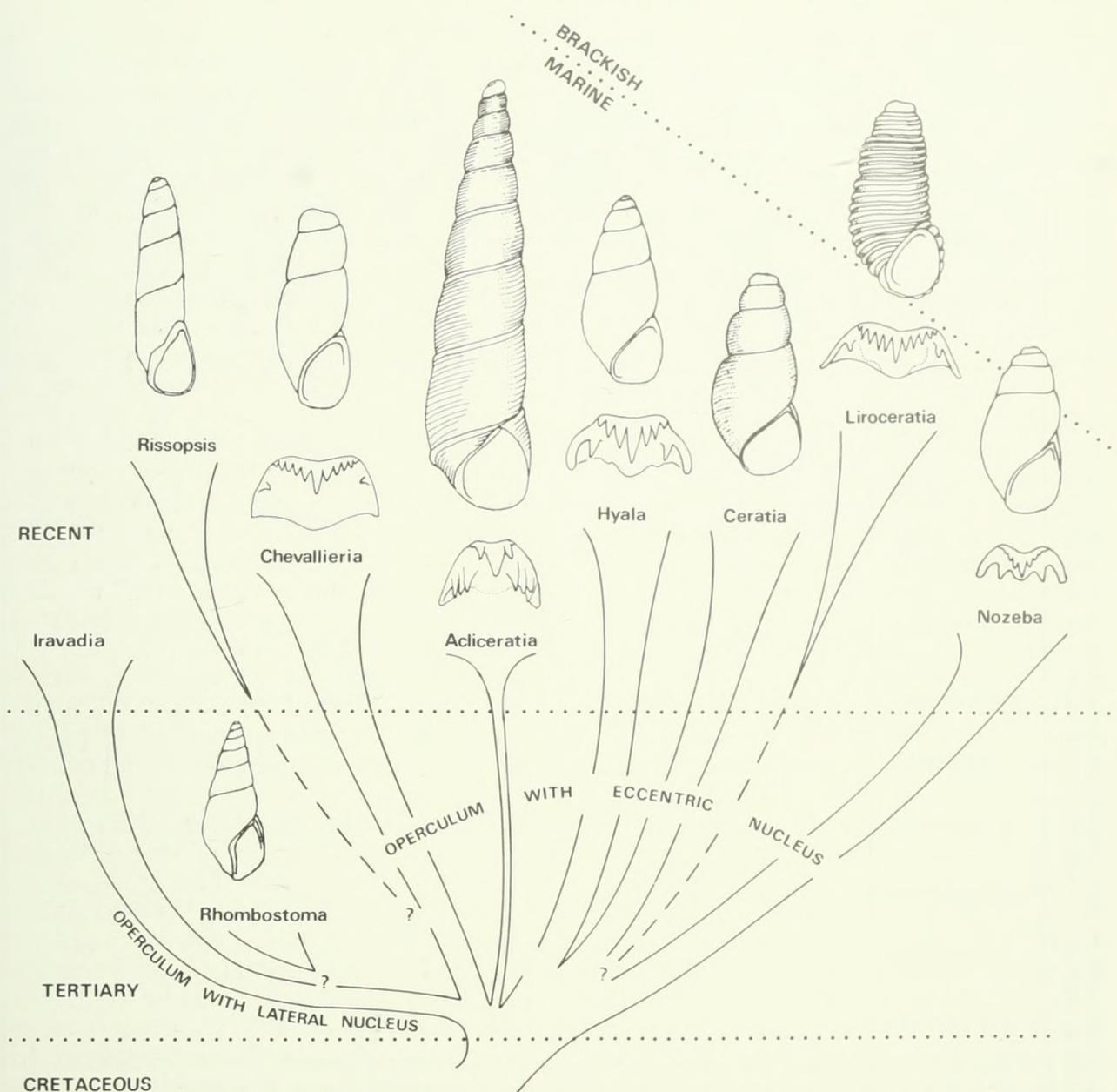


FIG. 22. A speculative interpretation of the evolution of genera of the Iravadiidae through time and their incursions into brackish water. The diagram is intended to indicate possible relationships and display shell diversity and the differences in the structure of the central teeth of the radula.

analysis of the habitats of the older fossil species has not been possible but the indications are that they are found together with typically marine species. The assumed movement into low salinity areas, mainly mangrove habitats, by the ancestral *Iravadia* stock appears to have been followed by a minor adaptive radiation resulting in a wide diversity of shell form and sculpture (Fig. 23). Species included here in the subgenus *Pseudonoba* range from brackish-water mangrove habitats to fully marine, relatively deep-water species.

Classification

In general, less is known about the genera possessing a spiral operculum than *Iravadia*.

They appear to be generally related and have many of the characters listed in Table 2 in common. There is, however, little justification or advantage, considering the available evidence, for merging them to any greater extent than has been done, until more about them is known. It is possible that at least *Hyala* and *Ceratia* may prove to be congeneric but the other groups probably represent lineages that have been long separated and are thus probably anatomically distinct. Fig. 22 is an attempt to indicate probable relationships and provide a summary of my concept of the evolution of the group. Two genera (*Rissopsis* and *Rhombostoma*) are known only from their shells, so that their detailed relationships are

TABLE 2. A list of some of the morphological and habitat features used to distinguish the fourteen genus-group taxa of the Iravadiidae (+, present in all species; ±, present in some species; -, absent in all species; ++ very strongly developed; (+), very strongly developed).

	<i>Iravadia</i>	<i>Iravadia</i> s.s.	<i>Pseudomerelina</i>	<i>Fairbankia</i>	<i>Fluviocingula</i>	<i>Pseudonoba</i>	<i>Rhombostoma</i>	<i>Chevallieria</i>	<i>Hyalia</i>	<i>Ceratia</i>	<i>Alliceratia</i>	<i>Liroceratia</i>	<i>Nozeba</i>	<i>Rissopsis</i>
1. Pallial tentacle present	+	-	-	-	-	-	?	?	-	-	?	-	+	?
2. Metapodial tentacle present	-	-	+	+	-	-	?	?	-	-	?	-	-	?
3. Cephalic tentacles pigmented	+	+	+	+	+	-	?	?	-	-	?	-	-	?
4. Posterior end of foot	-	-	-	-	-	-	?	?	-	-	?	-	-	?
A. Bifid	-	-	-	-	-	-	?	?	-	-	?	-	-	?
B. Rounded or weakly indented	+	+	+	+	+	+	?	?	+	+	?	+	+	?
5. Basal cusps on central radular teeth	+	+	+	+	+	+	?	?	+	+	+	+	+	?
A. One pair	+	+	+	+	+	+	?	?	+	+	+	+	+	?
B. 2-4 pairs	+	+	-	-	+	+	?	?	-	-	-	-	-	?
C. None	+	+	-	-	+	+	?	?	-	-	-	-	-	?
6. Operculum	+	+	+	+	+	+	?	?	-	-	-	-	-	?
A. Nucleus marginal	-	-	-	-	-	-	?	?	-	-	-	-	-	?
B. Nucleus submarginal	-	-	-	-	-	-	?	?	-	-	-	-	-	?
C. Nucleus eccentric	-	-	-	-	-	-	?	?	+	+	+	+	+	?
7. Shell sculpture	+	+	+	+	+	+	±	±	-	-	+	+	+	±
A. Spirals predominant	+	+	+	+	-	-	±	±	-	-	+	+	+	±
B. Smooth or with weak spiral threads	+	+	+	+	-	-	±	±	-	-	+	+	+	±
C. Axials prominent	+	+	+	+	-	-	±	±	-	-	+	+	+	±
D. With weak axial and spiral threads	+	+	-	-	+	+	±	±	-	-	+	+	+	±
8. Aperture of shell with anterior angulation	+	+	-	-	+	+	±	±	-	-	+	+	+	±
9. Outer lip of aperture	(+)	-	-	-	-	(+)	-	(+)	-	-	-	-	-	-
A. Opisthocline	+	-	-	-	-	+	±	±	-	-	+	+	+	±
B. Orthocline	+	+	+	+	+	±	±	±	+	+	+	+	+	±
C. Prosocline	+	+	+	+	+	±	±	±	+	+	+	+	+	±
10. Bursa copulatrix	+	+	+	+	?	?	?	?	-	-	?	?	-	?
A. Dorsal and pallial	+	+	+	+	?	?	?	?	-	-	?	?	-	?
B. Dorsal, behind pallial cavity	+	+	-	-	?	?	?	?	-	-	?	?	-	?
C. Ventral and pallial	+	+	-	-	?	?	?	?	-	-	?	?	-	?
D. Lateral and pallial	+	+	-	-	?	?	?	?	-	-	?	?	-	?
E. Absent	-	-	-	-	?	?	?	?	+	+	?	?	+	?
11. Anterior sperm sac	+	+	-	-	?	?	?	?	+	+	?	?	+	?
A. Well-developed	+	+	-	-	?	?	?	?	+	+	?	?	+	?
B. Poorly-developed	+	+	+	+	?	?	?	?	-	-	?	?	-	?
C. Absent	+	+	-	-	?	?	?	?	-	-	?	?	-	?
12. Habitat	+	+	-	-	-	±	±	±	+	+	+	-	±	+
A. Marine	+	+	-	-	-	±	±	±	+	+	+	-	±	+
B. Estuarine	+	+	-	-	+	±	±	±	(+?)	(+?)	+	+	±	-

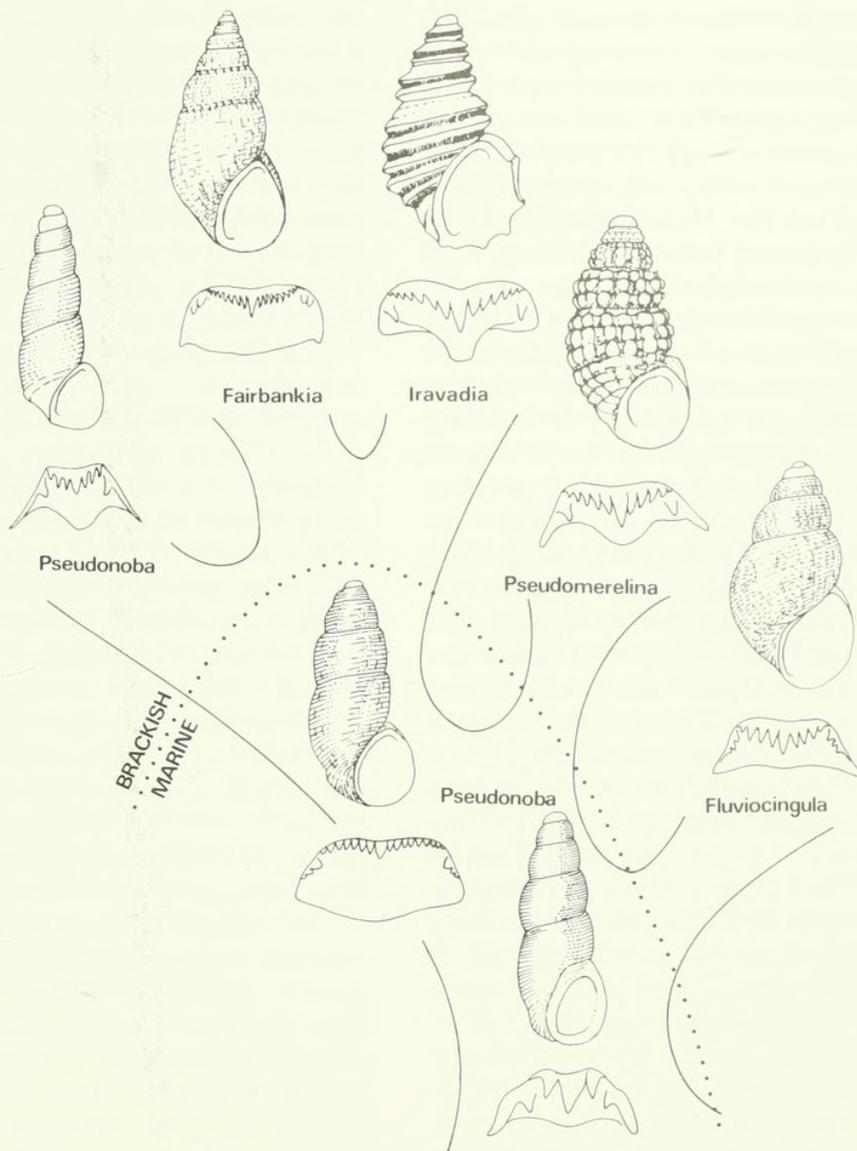


FIG. 23. Diagram showing diversity of shell morphology and the shape of the central teeth of the radula in the genus *Iravadia*. In addition, speculative evolutionary relationships and incursions into brackish water are indicated.

impossible to assess. *Hyalia vitrea* is known in reasonable detail and only one, possibly atypical, species of *Nozeba* has been investigated anatomically. The head-foot of the type-species of *Liroceratia* and *Ceratia* is known and only the radula and operculum of one species of *Chevallieria* have been available for examination. Thus, the conclusions made about the relationships of these genera must be considered tentative.

The subdivision of *Iravadia* is more conservative than that of previous classifications because of the considerable similarity of the observed characters, with the exception of the shell characters in some cases. The genitalia also show differences but there are limitations in the knowledge of the structure of the female genital system, in particular, for some of the groups. The grouping within *Ira-*

vadia assumed to be the most primitive (*Pseudonoba*), contains species showing a wide diversity of radular structure and habitat and may be subdivisible. Any refinement of the classification, however, seems inadvisable until more evidence is available.

Familial Relationships

Anatomically the Iravadiidae are very similar to the Hydrobiidae (as defined by Davis, 1980) but the shells have more resemblance to those of rissoids. Both the Rissoidae and an expanded concept of the Hydrobiidae (see below) are contrasted in Table 1 with the Iravadiidae.

Radoman (1973) has defined nine families in his "superfamily" Hydrobioidea. On the available information these all appear to be

closer to the Hydrobiidae than to the Rissoidae, Iravadiidae or Pomatiopsidae. For this reason the table of characters comprising the Rissoidae, Hydrobiidae and Iravadiidae includes the characters of all Radoman's Hydrobioidea, as defined by him, combined with the definition of the Hydrobiidae of Davis (1980). This grouping is loosely referred to as Hydrobiidae *sensu lato*.

The considerable similarity in the structure of the head-foot, the nervous system, the alimentary canal and the male genital system in the Iravadiidae and the Hydrobiidae (s.l.) may be due to convergence but there is also a strong possibility that the two groups may have a common ancestry.

The peculiar, flattened, glossy protoconch is the only uniform and distinctive shell feature which characterises the Iravadiidae. The iravadiids investigated apparently lack a distinct posterior pedal gland and, in most species, a metapodial tentacle and pallial tentacles. The peculiar penes seen in this group are reminiscent of some Hydrobiidae in having accessory, glandular swellings. This feature is also seen in some species of *Rissoina* (Kosuge, 1965; Ponder, 1968) but is otherwise unknown in the Rissoidae. The long, coiled dorsal folds in the anterior section of the oesophagus are other structures which are shared with the Hydrobiidae.

Johansson (1950) described the female reproductive system of *Hyala vitrea* (Montagu) and showed that it had an anterior sperm sac and that the slit-like opening to the female genital duct was near the posterior end of the glandular pallial duct. Johansson doubted that *Hyala vitrea* should be included in the Rissoidae but, in the latest revision of the European rissoids (Fretter & Graham, 1978), *H. vitrea* is, along with *Ceratia proxima*, included in *Onoba* Adams, the type-species of which (*O. semicostata* (Montagu)) is known to have a normal rissoid female genital system (Fretter & Patil, 1961).

The Iravadiidae and Hydrobiidae (s.l.) agree in most anatomical features except for the lack of spherules in the digestive gland of the Iravadiidae and in the structure of the female genital duct. They also differ from each other in their protoconchs; most hydrobiids having dome-shaped protoconchs of about 1½ whorls with an irregularly pitted surface. This is in sharp contrast to the small, somewhat planorboid, smooth protoconchs of species of the Iravadiidae.

The protoconch differences may, however,

be partly due to the assumed different developmental modes in the two families. The veliger larvae of *Hyala vitrea* are known to be planktonic (Thorson, 1946) and, although there are no direct observations on the other species in the family, the morphology of their protoconchs strongly supports the view that they all have planktotrophic larvae. Hydrobiids, on the other hand, are probably all direct developers.

The lack of spherules in the digestive gland is unusual in the Rissoacea and seems to be a constant feature, as determined histologically. These spherules have been consistently observed in other rissoacean families (my own observations, Fretter & Graham, 1962) except the Assimineidae.

The female reproductive system of *Iravadia ornata* superficially resembles that of members of the Hydrobiidae. Common features include the small, subterminal genital opening and the bursa copulatrix lying, in part, behind the pallial cavity. *Iravadia ornata* differs from the hydrobiids in having a pallial bursal duct, in much of the bursa lying along the capsule gland, in lacking a narrow, coiled section of the oviduct between the renal oviduct and the oviduct gland, and in having a large seminal receptacle which opens at the junction of the ventral channel and the renal oviduct. It is conceivable that the female genitalia characteristic of the Hydrobiidae evolved from an iravadiid similar to *I. ornata*. This would have to occur by the posterior migration of the opening to the bursal duct because the bursa copulatrix of the hydrobiids, and its duct, lie behind the pallial cavity where they enter an extension of the ventral channel beneath the albumen gland. This sequence of events, however, is unlikely because of the specialized opercula in *Iravadia* species and the lack of an oviducal coil.

The longitudinal fold in the ventral channel of the posterior end of the capsule gland and the anterior part of the albumen gland of the iravadiids is probably homologous to the almost identical fold in the ventral channel of the capsule gland of the Hydrobiidae. In that family, however, the albumen gland lacks a ventral channel, this continuing posteriorly from the capsule gland as a closed, separate tube. The ventral channel in the Rissoidae lacks a fold (Johansson, 1948; Fretter & Graham, 1962). The homology of this fold is clear in *Hyala vitrea* (Fig. 3, lf) where the sperm groove (sg) lies behind the fold and continues posteriorly to the opening of the seminal

receptacle. The situation in the genus *Iravadia* (Figs. 4–7) is somewhat complicated by the formation of a secondary fold and groove to a greater or lesser extent within the sperm groove and the derivation of the bursa copulatrix from the sperm groove. The fold persisting to the entrance of the seminal receptacle in *Iravadia* species appears to be derived from the upper inner edge of a "greater sperm groove" (i.e., the secondary grooves are apparently derivatives of the originally single sperm groove) and can thus be regarded as homologous with the fold in *Hyalia* and the hydrobiids.

The bursa copulatrix (as here recognised) of the Iravadiidae is possibly not homologous with that of the Hydrobiidae and Rissoidae. The bursa in these families agrees in position with the iravadiid seminal receptacle and may be homologous with it. The seminal receptacle(s), in the Hydrobiidae, in particular, usually opens into the coiled section of the oviduct and may be a new structure.

The Pomatiopsidae have been described and defined by Davis (1979, 1980) and show a wide variety of shell characters. All of the members of this family have two openings to the female genital system, a distal oviducal opening and a spermathecal opening. A narrow spermathecal duct leads to the bursa copulatrix, which lies behind the pallial cavity. The radula also differs; the innermost basal cusps on the central teeth are larger than the outer ones, the opposite condition to that seen in the Iravadiidae.

An anterior sperm sac (or bursa copulatrix) is known in two other rissoacean families, the Caecidae (Marcus & Marcus, 1963), which have uncoiled shells, and the Vitrinellidae (Fretter, 1956), which have depressed-helicoid shells and animals with well developed pallial and metapodial tentacles.

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REFERENCES CITED

- ADAMS, H. & ADAMS, A., 1852, On a new arrangement of British Rissoae. *Annals & Magazine of Natural History*, (2)10: 358–359.
- ANNANDALE, N. & PRASHAD, B., 1919, Some gastropod molluscs from the Gangetic delta. *Records of the Indian Museum*, 16: 241–257, 1 pl.
- BLANFORD, W. T., 1867, Contributions to Indian malacology No. 8. List of estuary shells collected in the Irawadi in Pegu, with descriptions of new species. *Journal of the Asiatic Society of Bengal*, 36: 51–72.
- BLANFORD, W. T., 1868, Descriptions of *Fairbankia*, a new genus and species of Rissoidae from Western India. *Annals & Magazine of Natural History*, (4)2: 399–401.
- BOETTGER, O., 1902, Zur Kenntnis der fauna der mittelmiozänen Schichten von Kostež im Krasso-Szorényer Komitat. II. *Verhandlungen und Mitteilungen des Siebenburgischen Vereins für Naturwissenschaften in Hermannstadt*, 51: 1–200.

- BRANDT, R. A. M., 1968, Description of new non-marine mollusks from Asia. *Archiv für Molluskenkunde*, 98: 213–289.
- BRANDT, R. A. M., 1974, The non-marine aquatic Mollusca of Thailand. *Archiv für Molluskenkunde*, 105: i–iv, 1–423.
- BRUGNONE, G., 1881, Le conchiglie Plioceniche delle vicinanze di Caltanissetta. *Bullettino della Società Malacologica Italiana*, 6: 83–157, 1 pl.
- CLARK, W., 1852, On some undescribed animals of the British Rissoae. *Annals & Magazine of Natural History*, 10: 254–264.
- COAN, E., 1964, A proposed revision of the Rissoacean families Rissoidae, Rissoinidae, and Cingulopsidae (Mollusca: Gastropoda). *Veliger*, 6: 164–171.
- COSSMANN, M., 1888, 1896, Catalogue illustré des Coquilles Fossiles de l'Eocène des environs de Paris. *Annales de la Société royale malacologique de Belgique*, 23(1888): 1–328, pl. 1–12; 31(1896): 1–94, pl. 1–3.
- COSSMANN, M., 1921, *Essais de Paléoconchologie Comparée*. Livr. 12: 1–336, pl. 1–11. Paris.
- COSSMANN, M. & PEYROT, A., 1916–1919, Conchologie néogénique de l'Aquitaine. Tome III (Gastropodes). *Actes de la Société Linnéenne de Bordeaux*, 69: 157–365; 70: 5–212.
- DANCE, S. P. & EAMES, F. E., 1966, New molluscs from the Recent Hammar Formation of south-east Iraq. *Proceedings of the Malacological Society of London*, 37: 35–43.
- DAVIS, G. M., 1979, The origin and evolution of the gastropod family Pomatiopsidae, with emphasis on the Mekong River Triculinae. *Academy of Natural Sciences of Philadelphia, Monograph* 20: 1–120.
- DAVIS, G. M., 1980, Snail hosts of Asian *Schistosoma* infecting man: evolution and coevolution. *In The Mekong Schistosoma; Malacological Review, Supplement 2*: 195–238.
- FLEMING, C. A., 1966, Marwick's illustrations of New Zealand shells with a checklist of New Zealand Cenozoic Mollusca. *New Zealand Department of Scientific & Industrial Research, Palaeontological Bulletin*, 173: 1–456.
- FRETTER, V., 1956, The anatomy of the pro-sobranche *Circulus striatus* (Philippi) and a review of its systematic position. *Proceedings of the Zoological Society of London*, 126: 369–381.
- FRETTER, V. & GRAHAM, A., 1962, *British Pro-sobranche Molluscs, their functional anatomy and ecology*. Ray Society, London, xvi + 755 p.
- FRETTER, V. & GRAHAM, A., 1978, The pro-sobranche molluscs of Britain and Denmark. Part 4—Marine Rissoacea. *Journal of Molluscan Studies, Supplement 6*: 151–241.
- FRETTER, V. & PATIL, A. M., 1961, Observations on some British rissoaceans and a record of *Setia inflata* Monterosato, new to British waters. *Proceedings of the Malacological Society of London*, 34: 212–223.
- GARRETT, A., 1873, Descriptions of new species of marine shells inhabiting the South Sea Islands. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 1873: 209–231, 233–237.
- GOLIKOV, A. N. & KUSSAKIN, O. G., 1978, *Shell bearing littoral gastropods of the seas of the U.S.S.R.* Leningrad, 256 p., 33 pl. (in Russian).
- GOLIKOV, A. N. & STAROBOGATOV, Ya. I., 1975, Systematics of prosobranche gastropods. *Malacologia*, 15: 185–232.
- GOUGEROT, L. & LE RENARD, J., 1977, Clefs de détermination des petites espèces de gastéropodes de l'Eocène du Bassin Parisien. VIII. Le genre *Graphis*; IX. Le genre *Pasitheola*. *Cahiers des Naturalistes. Bulletin des Naturalistes Parisiens*, 30: 37–54.
- GRAY, J. E., 1847, A list of the genera of Recent Mollusca, their synonyma and types. *Proceedings of the Zoological Society of London*, 15: 129–219.
- HABE, T., 1958, On the radulae of Japanese marine gastropods (4). *Venus, Japanese Journal of Malacology*, 20: 43–60.
- IREDALE, T., 1915, A commentary on Suter's "Manual of the New Zealand Mollusca." *Transactions & Proceedings of the New Zealand Institute*, 47: 417–497.
- IREDALE, T., 1943, A basic list of the fresh water Mollusca of Australia. *Australian Zoologist*, 10: 188–230.
- JEFFREYS, J. G., 1867, *The Mollusca*. Vol. IV. *Marine shells, British Conchology*, London, p. 1–486, pl. 1–4.
- JOHANSSON, J., 1948, Über die Geschlechtsorgane der Hydrobiiden und Rissoiden und den ursprünglichen Hermaphroditismus der Pro-sobranche. *Arkiv för Zoologi*, 40A(15): 1–13.
- JOHANSSON, J., 1950, Über die weiblichen Geschlechtsorgane von *Hyala vitrea*, einer von dem Rissoa-Typus stark abweichenden Form der Gruppe Rissoacea. *Arkiv för Zoologi*, 42A(7): 1–6.
- KOSUGE, S., 1965, Anatomical study on Japanese Rissoacea (I). On the family Rissoidae (I). *Venus, Japanese Journal of Malacology*, 24: 130–151, pl. 15.
- KURODA, T. & HABE, T., 1950, Nomenclatural notes. *Illustrated Catalogue of Japanese Shells*, 2: 16.
- KURODA, T. & HABE, T., 1954, New aquatic gastropods from Japan. *Venus, Japanese Journal of Malacology*, 18: 71–79.
- LASERON, C. F., 1950, Review of the Rissoidae of New South Wales. *Records of the Australian Museum*, 22: 257–287.
- LASERON, C. F., 1955, Revision of the New South Wales eulimoid shells. *Australian Zoologist*, 12: 83–107.
- LASERON, C. F., 1956, The families Rissoinidae and Rissoidae (Mollusca) from the Solanderian and Dampierian Zoogeographical Provinces. *Australian Journal of Marine & Freshwater Research*, 7: 384–484.
- LEA, I., 1833, *Contributions to Geology*. 227 p., 6 pl.
- MARCUS, E. & MARCUS, E. du B.-R., 1963, Meso-

- gastropoden von der Küste São Paulos. *Akademie der Wissenschaften und der Literatur, Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse*, 1: 1–105.
- NEVILL, G., 1884, *Hand list of Mollusca in the Indian Museum, Calcutta. Part II. Gastropoda. Prosobranchia-Neurobranchia* (contd.). Government Printer, Calcutta. x + 306 p.
- PALMER, K. v. W., 1937, The Claibornian Scaphopoda, Gastropoda and Dibranchiate Cephalopoda of the southern United States. *Bulletins of American Paleontology*, 7(32)1: 1–548; 2: 549–730. 90 pl.
- PAVIA, G., 1975, I Molluschi del Pliocene inferiore di Monteu Roero (Alba, Italia NW). *Bollettino della Società Paleontologica Italiana*, 14: 99–175, 14 pl.
- PILSBRY, H. A., 1922, Revision of W. M. Gabb's Tertiary Mollusca of Santo Domingo. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 73: 305–435, pl. 16–47.
- PONDER, W. F., 1967, The classification of the Rissoidae and Orbitestellidae with descriptions of some new taxa. *Transactions of the Royal Society of New Zealand, Zoology*, 9: 193–224.
- PONDER, W. F., 1968, The morphology of some small New Zealand Prosobranchs. *Records of the Dominion Museum*, 6: 61–95.
- PONDER, W. F., 1974, A review of the Australian species assigned to *Rissopsis* Garrett with a description of a new species of *Rissopsetia* (Mollusca: Gastropoda). *Journal of the Malacological Society of Australia*, 3: 25–35.
- PONDER, W. F. & YOO, E. K., 1976, A revision of the Australian and tropical Indo-Pacific Tertiary and Recent species of *Pisinna* (= *Estea*) (Mollusca: Gastropoda: Rissoidae). *Records of the Australian Museum*, 30: 150–247.
- RADOMAN, P., 1973, New classification of brackish water Prosobranchia from the Balkans and Asia Minor. *Prosebná Izdanja. Museum d'Histoire Naturelle de Beograd. Edition hors serie*, 32: 1–30.
- SACCO, F., 1892, I molluschi dei terreni terziarii del Piemonte e della Liguria, parte 11. Eulimidae e Pyramidellidae (parte). *Memorie della R. Accademia delle Scienze di Torino*, ser. 2, 42: 1–100, 2 pl.
- SEGUENZA, G., 1876, Studii stratigraphici sulla formazione pliocenica dell'Italia meridionale. *Bollettino del R. Comitato geologica d'Italia*, 7: 7–15, 91–103, 179–189, 260–271, 355–359 (part of series 1873–77).
- STAROBOGATOV, Ya. I., 1970, Molluscan fauna and zoogeographical partitioning of continental water reservoirs of the world. *Akademiya Nauk SSSR. Zoologicheskii Institut Nauka, Leningrad*, 372 p. (in Russian).
- STOLICZKA, F., 1867–1868, Cretaceous fauna of Southern India. 2. The Gastropoda. *Memoirs of the Geological Survey of India Palaeontologia indica*, Series V, 2, xiii + 500 p., 28 pl.
- THIELE, J., 1928, Revision des Systems der Hydrobiiden und Melaniiden. *Zoologische Jahrbücher. Systematik, Ökologie und Geographie der Tiere*, 55: 351–402.
- THIELE, J., 1929, *Handbuch der systematischen Weichtierkunde*. Jena. Part 1: 1–376.
- THORSON, G., 1946, Reproduction and larval development of Danish marine bottom invertebrates. *Meddelelser fra Kommissionen for Danmarks Fiskeri- og Havundersøgelser, serie: Plankton*, 4(1): 1–523, figs. 1–199.
- WENZ, W., 1938–1944, Gastropoda. *Handbuch der Paläozoologie*. 6(1): Lief. 1–7. 1639 p. Berlin.

APPENDIX. DESCRIPTIONS OF NEW SPECIES OF IRAVADIIDAE

Genus *Iravadia*

Subgenus *Pseudonoba*

Iravadia (*Pseudonoba*) *profundior* Ponder, sp. nov.

Fig. 14G–I

Description. **Shell.** Small, elongately pupoid, rather solid, non-umbilicate. Protoconch small, smooth, glossy, of about two whorls, flat-topped, sharply-terminated. Teleconch of four convex whorls, sutures impressed. Fifteen spiral threads on penultimate whorl, 18 primary spirals on body whorl together with a few, weak secondary spiral threads and several weak spirals on basal fold. Axial sculpture of indistinct growth lines. Lower base with broad, rounded basal fold. Aperture rather large, oval, very weakly-excavated posteriorly, not angled, broadly and shallowly-excavated anteriorly. Outer lip slightly prosocline with sharp edge, thickened within, with broad, prominent varix. Inner lip thickened, narrow, attached to parietal area. Colour yellowish-white, periostracum yellow to brown, with ferruginous deposit in one of the two paratypes (Fig. 14G).

Dimensions.	length	diameter
Holotype	3.86 mm	1.47 mm
Paratype	4.24	1.51
	3.86	1.48

Operculum. Oval, columellar edge indented just beyond nucleus, which is displaced from middle of edge. A low, broad, internal fold parallel to columellar edge (Fig. 14H).

Radula. Central teeth broadly-triangular, median cusp short, with several (six to nine) minute cusps on either side. A pair of weak denticles near lateral margins of central teeth. Lateral teeth with prominent primary cusp and

several (three to five) small cusps on outer side. Marginal teeth multicuspate (Fig. 14I).

Type-locality. Off Lusaran Light, Guimaras, Philippines, USBF Stn. 5183, in 96 fathoms (175 m), in soft mud.

Types. Holotype and two paratypes (USNM, 281302). All specimens collected alive.

Other material examined. Off Adyagan Is., E. Masbate, Philippines, USBF Stn. 5392, 135 fathoms (247 m): two shells (USNM, 281897).

Remarks. This new species is superficially similar to *Paronoba subquadrata* Laseron, 1950 (= *Iravadia (Pseudonoba) subquadrata* herein) in shell features but differs in being larger, in having a relatively thicker peristome with a much stronger varix, and in having stronger spiral sculpture. *Iravadia (Pseudonoba) bella* also has a similar shell but this differs in being larger, more inflated, with relatively weaker spiral sculpture and no basal fold.

The two additional specimens (USNM, 281897) referred to this species have smaller shells (maximum length 3.19 mm) than the type-series, the outer lip is orthocone, the aperture is weakly subangled posteriorly and the teleoconch consists of only 3½ whorls. They agree in most other details and consequently are regarded as a variety of *I. (P.) profundior*. Two lots in the USNM from Daram Channel, W. Samar, 32 fathoms (59 m) (USNM, 280751) and N of Marinduque, 50 fathoms (95 m) (USNM, 276116), have still smaller shells (maximum length 3.01 mm), with relatively stronger spiral sculpture and an orthocone to opisthocline outer lip. They are more similar to the two atypical specimens of *I. (P.) profundior* (USNM, 281897) than to the type series and are not considered to be the same species. These specimens also have some similarity to *I. (P.) densilabrum*.

Iravadia (Pseudonoba) expansilabrum

Ponder, sp. nov.

Fig. 16F-I

Description. Shell. Small, elongately-pupoid, thin, non-umbilicate. Protoconch small, smooth, glossy, with two whorls, flat-topped, sharply-terminated. Teleoconch of about 4¼ convex whorls, with moderately-impressed sutures. Sculpture of close, fine spiral threads (approximately 26 on penultimate whorl) and inconspicuous axial growth lines. Lower base with prominent fold sculp-

tured with a few weak, spiral threads. Aperture oval, very weakly-subangled and excavated posteriorly; convex and broadly and shallowly excavated anteriorly. Outer lip slightly opisthocline, thickened within, with sharp edge, a thick varix behind. Inner lip broadly-expanded over parietal area as a thin callus, not expanded over basal fold. Colour yellowish-white, periostracum yellowish but with a thick, ferruginous coating in the two specimens collected alive (Fig. 16G).

Dimensions.	length	diameter
Holotype	3.18 mm	1.18 mm
Paratypes	2.95	1.10
	3.21	1.24
	3.03	1.14
	3.06	1.16

Operculum. Oval, columellar edge flattened, twisted outwards with a weak, internal, longitudinal fold parallel to it. Nucleus marginal, slightly displaced from middle of edge (Fig. 16H, I). *Radula.* Central teeth broadly-triangular, with strong cusps on narrow cutting edge $\frac{1 + 1 + 1}{1 \quad 1}$, a single pair of prominent denticles on face of each tooth. Lateral teeth with large primary cusps and possibly a small cusp on inside edge. Marginal teeth multicuspate (Fig. 16F).

Type-locality. c. 40 miles (64 km) WSW off Tulear, Malagasy Republic, 23°19'S, 43°36'E, 82 m. 6 August, 1964. A. Bruun Str. 363W.

Types. Holotype and five paratypes (USNM, 717549). Holotype coated with gold.

Remarks. This species is closest to *I. (P.) subquadrata* but its shell differs from that species and all others in the genus by its broadly expanded inner lip. The radular features, especially those of the central teeth, are unusual for *Iravadia*, and are discussed in the remarks on *Pseudonoba* above.

Iravadia (Pseudonoba) gemmata Ponder,

sp. nov.

Fig. 16A-E

Description. Shell. Small, very elongately-conic, solid, non-umbilicate. Protoconch small, smooth, glossy, of 2-2½ whorls, flat-topped, sharply-terminated (Fig. 16B). Teleoconch of about six convex whorls, with deeply-impressed sutures. Sculpture of about 17 nodulous spiral ribs on body whorl, 12-14

on penultimate whorl, crossed by weak, close, prosocline axial riblets with small, rounded gemmules at points of intersection. Lower base with prominent, sharp fold, smooth or with weak spiral striae, partly overlaid by inner lip. Aperture rather large, oval, with weak angulation and excavation posteriorly, shallowly and broadly excavated anteriorly; inner lip broad, thickened, attached to parietal area, its outer edge convex; outer lip thickened at edge and behind, slightly prosocline, with a wide, flat-topped varix immediately behind. Colour white, periostracum yellow to brown, thin. Some specimens coated with a ferruginous deposit which stains shell orange-brown to nearly black (Fig. 16A).

Dimensions.	length	diameter
Holotype	5.52 mm	1.85 mm
Paratypes (277683)	5.33	1.78
	4.95	1.62
	5.27	1.80
	5.12	1.65
	(283016) 4.73	1.65

Operculum. Oval, columellar edge convex, nucleus near middle of edge. No internal ridges (Fig. 16C). **Radula.** Central teeth broad, dorsal margin convex, cutting edge narrow, with one or two weak lateral cusps and a long, sharp median cusp; lateral margins widely flared, thickened. Three pairs of strong, closely-spaced denticles arise from face of tooth just below lateral margin; fourth pair of weak denticles below outer part of lateral margin. Middle of face of central tooth with a vertical, thickened band; ventral edge of tooth convex. Lateral teeth elongate, with a single, long, sharp cusp at inner edge and very weak cusp outside this cusp; otherwise simple. Marginal teeth with numerous sharp cusps (Fig. 16D, E).

Type-locality. Off Limbancauayan Is., W. Samar, Philippines; 50 fathoms (91.4 m), fine, grey sand, USBF Stn. 5210.

Types. Holotype (USNM, 283016a) and three paratypes (two juveniles) (USNM, 283016b); 16 paratypes (one juvenile) (USNM, 177683). Holotype coated with gold.

Other material examined. Buton Strait, Celebes (Sulawesi), 37 fathoms (68 m), USBF Stn. 5642: ten specimens (USNM, 279749), one specimen (USNM, 290829). Philippines: S of Corregidor Lt., 35 fathoms (64 m), USBF Stn. 5100: two specimens (USNM, 257398), two specimens (USNM

257397). North off Marinduque, 50 fathoms (91 m), USBF Stn. 5220: 17 specimens (USNM, 276115). North off Marinduque, 193 fathoms (353 m), USBF Stn. 5221: one specimen (USNM, 277065). Lagonoy, East Luzon, 47 fathoms (86 m), USBF Stn. 5448: one specimen (USNM, 289018). Off Tacbuc Point, East Leyte, 62 fathoms (113 m), USBF Stn. 5479: four specimens (USNM, 283016). Off Magabao Is., East Mindanao, 494 fathoms (903 m), USBF Stn. 5236: one specimen (USNM, 276875).

Remarks. The radula of this species differs from all others known in the genus by the characters of the central teeth, as discussed in the remarks on the subgenus *Pseudonoba* above. The shell is readily separated from other species of *Pseudonoba* by its gemmate sculpture. The operculum is closest to that of *Iravadia* (*Pseudomerelina*) *mahimensis* in morphology.

This species probably represents a separate grouping within, or close to, *Iravadia* s.l. but, until the radulae of more species of *Iravadia* (*Pseudonoba*) are known, allowing its relationships to be more accurately assessed, it can be tentatively retained in *Pseudonoba*.

The denticles on the face of the central teeth appear to have increased in size and number to take over the scraping function of the lateral cusps, the original cutting edge being reduced in size. Species of *Iravadia*, typically have several small cusps and weaker (i.e., less thickened) teeth.

Genus *Chevallieria*

Chevallieria australis Ponder, sp. nov.

Fig. 17D-F

Description. **Shell.** Minute, pupoid, thin, non-umbilicate. Protoconch relatively large, of $1\frac{3}{4}$ whorls, flat on top, terminated abruptly, smooth. Teleoconch of about $2\frac{1}{3}$ convex whorls, sutures lightly impressed. Surface smooth except for indistinct axial growth lines. Aperture rather large, oval, subangled and very slightly channelled posteriorly, broadly and very shallowly excavated anteriorly. Outer lip orthocline, slightly thickened within, no external varix. Inner lip thickened, narrow upper half attached to, or free from, parietal wall, lower half free. Periostracum thin, yellowish-brown (Fig. 17D).

Dimensions.	length	diameter
Holotype	1.50 mm	0.68 mm
Paratype	1.64	0.75

Dimensions.	length	diameter
Holotype	1.98 mm	0.79 mm
Paratypes	2.24	0.83
	1.98	0.79
	1.62	0.73
	1.90	0.79
Bird Rock Cliffs	2.20	0.92

Operculum. (Fig. 17E) and **radula** (Fig. 17F) as described under generic diagnosis for *Chevallieria*.

Type-locality. Emu Bay, N.E. Kangaroo Is., South Australia, on sheltered, rocky shore under rocks at low water neap; 7 March 1978. Collected by I. Loch, E. K. Yoo and K. Handley.

Types. Holotype (C.126181) and paratype (C.126182), AMS.

Other material examined. Point Sinclair, S. Australia, two shells (AMS, C.126183); Largs Bay, S. Australia, one shell (SAM); Tumbay Bay, S. Australia, one shell (AMS, C.126184); Bathurst Point, Rottnest Is., Western Australia, one shell (AMS, C.126185).

Remarks. This species is closest to *Chevallieria columen* (Melvill) but the shell of that species is larger (greater than 2.5 mm in length), relatively narrower and the teleoconch consists of about 3½ whorls. The new species and *C. columen* differ from the other Recent species described from Australia, *C. imitoris* (Laserson), in lacking fine spiral striae on the surface of the shell. *Chevallieria imitoris* also has a relatively narrower shell than *C. australis*. It is known from Darwin, N Australia (the type-locality) and Queensland. Other specimens of *Chevallieria* from the tropical Indo-Pacific appear to include unnamed species, but insufficient material is available to describe these.

Chevallieria balcombensis Ponder, sp. nov.
Fig. 17B

Description. Shell. Minute, pupoid, thin, non-umbilicate. Protoconch relatively large, of two whorls, flat on top, terminated abruptly. Teleoconch of about three convex whorls, sutures slightly impressed. Surface smooth, shining, with weak axial growth lines the only sculpture. Aperture rather large, oval, weakly-subangled and very shallowly channelled posteriorly, broadly and shallowly-channelled anteriorly. Outer lip very slightly opisthoclinal to very slightly prosoclinal, thickened slightly within, with sharp edge and prominent, rounded external varix. Inner lip narrow, thickened, attached or partially free from parietal wall (Fig. 17B).

Type-locality. Fossil Beach, Balcombe Bay, Mornington, Victoria, Australia. Middle Miocene (Balcombian), J. Voorwinde Colln.

Types. Holotype (C.126186) and eight paratypes (C.126187), AMS; two paratypes NMV, P.62046.

Other material examined. Topotypes, W. J. Parr Colln., two specimens (NMV, P.62044, 62047); Bird Rock Cliffs, Torquay, Victoria, Lower Miocene-Upper Oligocene (Janjukian) one specimen (NMV, P.62045).

Remarks. Of the Australian species, the shell of *C. balcombensis* is closest to *C. australis* in lacking spiral striae, but it differs in its slightly larger size and prominent apertural varix.

Chevallieria gippslandica Ponder, sp. nov.
Fig. 17C

Description. Shell. Small, elongately-conical, rather solid, non-umbilicate. Protoconch small, smooth, of two whorls, flat-topped, sharply-terminated. Teleoconch of 4¼ convex whorls; sutures impressed. Sculpture of weak, axial growth lines only. Aperture oval, subangled and with shallow channel posteriorly, broadly and slightly excavated anteriorly. Outer lip slightly opisthoclinal, thickened within, with a sharp edge and flat, weak to prominent external varix. Inner lip narrow, attached to, or separated from, parietal wall (Fig. 17C).

Dimensions.	length	diameter
Holotype	3.82 mm	1.44 mm
Paratypes	3.58	1.41
	3.57	1.32
	3.18	1.18

Type-locality. Roadcutting, right bank of Meringa Creek, 100 m S of Kalimna-Nungerner Road, Gippsland, E. Victoria, Australia. In bed below Lower Jemmys Point shell bed, Jemmys Point Formation, Kalimnan, Lower Pliocene. Collected by W. F. Ponder, T. A. Darragh and P. H. Colman, 11 Jan. 1970.

Types. Holotype (C.126207) and three paratypes (C. 126208), AMS; two paratypes, NMV, P.62048 from type-locality, collected Dec. 1966.

Other material examined. Kalimnan: Ditch on E side of Meringa Creek, in lowest shell band four m above creek (NMV, P.62048, two paratypes); SW side of Bunga Creek, road cutting Princes Highway, Gippsland, E. Victoria, one specimen (NMV, P.62049); zero to two m above beach in cliff 50–100 m E of Kalimna Jetty, in lower shell bed, Gippsland, E. Victoria (NMV, P.62051). Cheltenhamian: NE side Bunga Creek, road cutting, Princes Highway, Gippsland, E. Victoria; one specimen (NMV, P.62050).

Remarks. This species is relatively large for the genus and resembles species of *Iravadia* (*Pseudonoba*) in general shell characters. It lacks, however, any trace of spiral sculpture and does not have a basal fold. It appears to be derived from *Chevallieria balcombensis*, which it closely resembles, except in size and number of whorls.

Genus *Nozeba*

Nozeba (?) *striata* Ponder, sp. nov.
Fig. 20G–J

Description. Shell. Small, elongately-ovate, rather thin, with dull surface. Protoconch smooth, of moderate size, of $1\frac{3}{4}$ whorls, nucleus very small, depressed. Teleoconch of $2\frac{1}{2}$ convex whorls, sutures impressed. Sculpture of fine, close, raised spiral lines with linear interspaces and weak axial growth lines. Aperture sub-oval with broad anterior notch and posterior subangulation. Outer lip orthocone, lacking external varix; inner lip narrow, slightly thickened, free in anterior half.

Umbilical chink small in holotype, more pronounced in paratype (Fig. 20G).

Dimensions.	length	diameter
Holotype	1.84 mm	1.05 mm
Paratype	1.69	1.03

Operculum. Thin, simple, spiral, nucleus eccentric (Fig. 20J). *Radula.* Central teeth broad, cutting edge concave, lateral wings only slightly thickened, at about 45° to vertical; median cusp very small, blunt, six to seven lateral cusps on each side, narrow, sharp, inner ones about twice length of median cusp; no basal denticles, lateral margins slightly thickened. Lateral teeth with narrow cutting edge, primary cusp moderately long, sharp, secondary cusps sharp, c. $3 + 1 + c.$ 6. Marginal teeth with broad, almost straight cutting edges and long bases, with numerous small, sharp cusps almost equal in length to secondary cusps on lateral and central teeth, but narrower (Fig. 20H, I).

Type-locality. Pujada Bay, E Mindanao, Philippines, 218 fathoms (399 m) USBF Stn. 5243.

Types. Holotype and paratype (USNM, 311059). Holotype coated with gold.

Remarks. This species differs from the two Australasian species of *Nozeba*, for which the radula is known, in not having a pair of basal denticles on the central tooth of the radula, and in the median cusp of the central teeth being relatively very small. The shell, however, has all the essential characters of *Nozeba* species as diagnosed herein, except that it lacks a glossy surface. It differs from the described species by the combination of the following characters: the relatively large aperture, the spiral sculpture, the dull surface, the rather solid shell and the umbilical chink. Only two other described species have distinct spiral sculpture: *N. emarginata* and *N. gatlifiana*.



Ponder, W. F. 1984. "A review of the genera of the Iravadiidae (Gastropoda: Rissoacea) with an assessment of the relationships of the family." *Malacologia* 25, 21-71.

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