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AUSTRALIAN GASTROPODS OF THE FAMILY BURSIDAE. PART 1.

THE FAMILIES OF TONNACEA, THE GENERA OF BURSIDAE, AND REVISION OF SPECIES PREVIOUSLY ASSIGNED TO *TUTUFA* JOUSSEAUME, 1881

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SUMMARY

In a brief anatomical survey of the Tonnacea, family groups recognised are Tonnidae (subfamilies Tonninae and Oocorythinae), Ficidae, Cassidae (subfamilies Cassinae and Phaliinae), Cymatiidae (subfamilies Cymatiinae, Ranellinae, Distorsioninae) and Bursidae.

In a generic classification of the Bursidae based on opercular, penial, and stomach anatomical features, variceal position is considered to have little taxonomic significance. Genera recognised are *Bursa* Röding, 1798 (with subgenera *Lampadopsis* Jousseume, 1881; *Bufonariella* Thiele, 1929 [= *Dulcerana* (Iredale, 1931, unavailable) Oyama, 1964 = *Annaperenna* Iredale, 1936 = *Tritonoranella* Oyama, 1964]; *Colubrellina* Fischer, 1884; *Crossata* Jousseume, 1881 (with (?) subgenus *Olequahia* Stewart, 1926); *Tutufa* Jousseume, 1881 (with subgenus *Tutufella*, new name for *Lampas* Schumacher, 1817, not of Montfort, 1808); *Bufonaria* Schumacher, 1817 [= *Buffo* Montfort, 1810, not of Lacépède, 1788, = *Marsupina* Dall, 1904, = *Chasmotheca* Dall, 1904, = *Bursina* Oyama, 1964, = *Gyrineum* of authors, not of Link, 1807] (with subgenus *Aspa* H. and A. Adams, 1853); and *Bechtelia* Emerson and Hertlein, 1964.

The species and subspecies placed in *Tutufa* and its "subgenus" *Tritonoranella* Oyama, 1964 (shown to be a synonym of *Bursa* (*Bufonariella*)) are classified as: *Bursa* (*Bufonariella*) *latitudo latitudo* Garrard, 1961, Queensland; *B. latitudo natalensis* Coelho & Matthews, 1970, W. Atlantic; *B. latitudo wolfei* n. subsp., Hawaii; *B. (Bufonariella) ranelloides ranelloides* (Reeve, 1844), southern Japan; *B. ranelloides tenuisculpta* Dautzenburg and Fischer, 1906, E. & W. Atlantic to South Africa; *B. ranelloides humilis* n. subsp., Western Australia; *Tutufa (Tutufa) bardeyi* (Jousseume, 1894), N. Indian Ocean; *T. (Tutufa) bubo* (Linnaeus, 1758), Indo-West Pacific; *T. (Tutufa) bufo* (Röding, 1798), Indo-West Pacific; *T. (Tutufella) rubeta* (Linnaeus, 1758), Indo-West Pacific; *T. (Tutufella) n. subgen.) oyamai* Habe, 1973, E. Indian Ocean and W. Pacific; *T. (Tutufella?) tenuigranosa* (E. A. Smith, 1914), South China Sea; and *T. aff. rubeta*, Mocambique. A neotype is designated for *Murex rana* var. *bubo* Linnaeus, 1758, and lectotypes are designated for several other species.

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INTRODUCTION

Large bursids of the genus *Tutufa* Jousseaume are conspicuous members of the Indo-West Pacific molluscan fauna, and have been recorded in northern New Zealand and around northern Australia from Sydney to Fremantle. The second largest species, *T. bubo* (Linnaeus), is a source of trumpets for the people of the central and southern Indian and Pacific oceans. All but two are relatively common species, but despite detailed investigations by E. A. Smith (1914) and Hedley (1916a) their nomenclature and systematics have troubled all molluscan taxonomists since Linnaeus (1758). Although many recent reviews and shell books have used what is here concluded to be largely correct nomenclature, several species names are stabilised here and all available information brought together on the species of *Tutufa*. Recent examination of the collections and libraries of the Australian Museum, Sydney, the National Museum of Victoria, Melbourne and the Western Australian Museum, Perth, the loan of much tonnagean spirit material by these institutions, the gradual acquisition of a small spirit collection of Tonnacea by the N.Z. Geological Survey, and the loan of two of E.A. Smith's figured specimens of *Tutufa* by the British Museum (Natural History) have enabled me to undertake this initially brief anatomical survey of the Tonnacea and of the Bursidae and *Tutufa* in particular, and to offer my conclusions on the valid species of *Tutufa*.

As an introduction to what is intended to be two papers on the Bursidae of Australia, a brief anatomical survey of the Superfamily Tonnacea is given to differentiate the families, and a classification of the Bursidae is outlined.

THE FAMILIES OF TONNACEA

Superfamily **TONNACEA**

This group of large, carnivorous, pseudo-muricæan mesogastropods includes the families Tonnidae, Cassidae, Ficidae, Cymatiidae, and Bursidae. The major shell, opercular, radular and anatomical features of the families are set out here. Important references for opercula, radulae and genera, apart from the writer's personal observations, are Abbott (1968), Turner (1948), Oyama (1964), and Bayer (1971).

Family *Tonnidae*: Shell large, thin, with very inflated last whorl, short siphonal canal, low spire, and sculpture of relatively weak spiral cords only. Outer lip not thickened, or thickened in adult only. Periostracum a thin, smooth sheet. Two subfamilies can be recognised:

Subfamily *Tonninae*: Operculum lacking in adult. Radula with a low, broad central tooth having small interlocking basal processes similar to the relatively larger ones of Bursidae; lateral teeth elongate and massive with large rectangular bases. Jaw plates large. Proboscis extremely large, relatively short and not coiled in the proboscis sheath, but relatively very broad and extremely extendible, with a circular, transversely flattened anterior end. Oesophageal gland represented by glandular area of mid-oesophagus wall, not a discrete sac. Only two accessory salivary glands. Stomach having both digestive gland ducts in a deep pocket in the cardiac arm; the pyloric arm and intestine follow a twice reflected, strongly W-shaped path to the rectum (based on New Zealand specimens of *Tonna variegata cerevesina* Hedley, Fig. 1n). Unfortunately the large and fundamental work on the anatomy of *Tonna* by Weber (1927) has not been available to me, but much of

Weber's information is repeated by Hyman (1967).

Included genera: *Tonna* Brunnich, 1772; *Eudolium* Dall, 1889; *Malea* Valenciennes, 1883, and subgenus *Quimalea* Iredale, 1929.

Subfamily *Oocorythinae*: Operculum present in adult, unique in Tonnacea in being paucispiral with nucleus near adaxial edge of abapical end (see Turner 1948, pl. 75, fig. 8, 9, 11). Radula with central teeth lacking interlocking projections, otherwise similar to that of *Tonna*. Anatomical features not described.

Included genera: *Oocorys* Fischer, 1884, and subgenus *Benthodolium* Verrill and Smith, 1884; *Dalium* Dall, 1889.

Family *Ficidae*: Shell of medium size, thin, with long, narrow pyriform last whorl, long siphonal canal, low spire, and weak spiral sculpture only, although bearing peripheral nodules in some genera; periphery evenly rounded, keeled, or with axial folds. Outer lip not thickened. Periostracum a thin, furry sheet. Operculum absent in *Ficus*, relatively very small, black, and irregularly circular in the only other living genus, *Thalassocyon* (see Beu 1969). Radula with a low, broad, multicuspate central tooth lacking basal interlocking processes, similar to centrals of *Oocorythinae* and *Cymatiidae*; lateral teeth relatively large, with long rectangular bases. Jaw plates large. Proboscis exceedingly long and relatively narrow, much coiled in the wide proboscis sheath when not everted. Oesophageal gland a discrete sac. Salivary glands and the two accessory salivary glands relatively solid spongy structures at the rear of the floor of the cephalic cavity. Stomach not seen (based on two incomplete New South Wales specimens of *Ficus filus* Sowerby).

Ficidae show similarities on the one hand to *Tonna* in the large, enveloping last whorl and dominantly spiral sculpture of the shell and in the absence of an operculum in *Ficus* and, on the other hand, to *Distorsioninae* in the extremely long narrow proboscis that is much coiled and folded within its wide sheath, in the form of the lateral radular teeth, and in the similarity of the small, black, irregular operculum of *Thalassocyon* to that of *Distorsio*.

Some included genera: *Ficus* Röding, 1798; *Thalassocyon* Barnard, 1960; and the extinct Upper Cretaceous and Tertiary genera *Proficus* Finlay and Marwick, 1937; *Ficopsis* Conrad, 1866; *Trophosycon* Cooper, 1894; *Priscoficus* Conrad, 1866; *Fulguroficus* Sacco, 1890.

Family *Cassidae*: Shell medium to large, moderately to highly inflated, thick and solid, with large last whorl and low spire, short, moderately to very strongly twisted anterior canal, and moderately coarse to very weak spiral and axial sculpture (usually dominantly of relatively weak spiral cords). Outer lip strongly thickened, varices remaining at preadult growth pauses in many genera. Periostracum very weakly developed or absent. Operculum always present. Radula similar to those of *Charoniinae* and *Oocorythinae*, but with smaller basal limbs on the lateral teeth. Jaw plates large. Proboscis relatively narrow and short, not coiled in the narrow sheath. Oesophageal gland a discrete sac, usually large and firm, black, lying well to posterior of cephalic cavity. Two large accessory salivary glands present. Stomach a relatively simple, thin-walled tube, intestine straight from stomach to anus. Two subfamilies can be recognised.

Subfamily *Cassinae*: Anterior canal weakly twisted, lacking prominently margined fasciole of *Phaliinae*; operculum narrowly oval to subrectangular, with nucleus approximately central, or near abapical end; accessory salivary glands firm and of

much-folded, broadly tubular structure, lying one behind the other so that the oesophagus is initially central but passes gradually to the right around the left (posterior) accessory salivary gland, and the oesophageal gland is at posterior right (based on *Cassis* [*Hypocassis*] *fimbriata* (Quoy & Gaimard) from Blanche Pt., near Adelaide, South Australia). Shells of most species are relatively elongate and heavily callused, and almost all have more prominent sculpture than those of species in subfamily Phaliinae. *Morum* lacks a radula (Beu, 1976a). Reynell (1905, 1906) has given a good general account of the anatomy of *Galeodea echinophora* (Linnaeus), under the name *Cassidaria rugosa* (*Galeodea* is not preoccupied, as frequently supposed, the cited earlier name being spelled *Galeodes*).

Some included genera and subgenera: *Cassis* Scopoli, 1777, and subgenus [*Hypocassis*] *fimbriata* (Quoy & Gaimard) from Blanche Pt., near Adelaide, South, 1847; *Sconsia* Gray, 1847; *Morum* Röding, 1798, and subgenera *Herculea* Hanley in H. & A. Adams, 1858, and *Oniscidia* Mörch, 1852 (= *Cancellomorum* Emerson and Old, 1963, = *Pulchroniscia* Garrard, 1961); *Galeodea* Link, 1807, and subgenus *Galeocorys* Kuroda & Habe, 1957.

Subfamily *Phaliinae* nov.: shells relatively short and rounded, with weak callusing and usually with weak sculpture, almost entirely spiral; anterior canal very strongly twisted, with a prominently margined fasciole; operculum obtusely fan-shaped, with nucleus at angle between the two straight adaxial edges. Accessory salivary glands thin-walled and sacular, as in Tonnidae, Cymatiidae and Bursidae; salivary glands and accessory salivary glands lateral and clasped on either side of oesophagus well behind proboscis; oesophagus passes down central floor of cephalic cavity so that oesophageal gland is at posterior centre. Stomach a narrow, thin-walled tube with sphincter at anterior end but not at posterior, with finely and closely pleated walls; a prominent typhlosole commences obliquely at the relatively broadly open fold between cardiac and pyloric arms, and gradually reduces in height as it runs along left edge of pyloric arm. Anterior digestive gland duct beneath typhlosole on left edge at bend of stomach, posterior digestive gland duct halfway along left edge of pyloric arm (based on New Zealand specimens of *Semicassis pyrum* (Lamarck)).

Some included genera and subgenera: *Phalium* Link, 1807; *Semicassis* Mörch, 1852 (= *Xenophalium* Iredale, 1927, = *Xenogalea* Iredale, 1927, = *Tylocassis* Woodring, 1928; see Beu, 1976b) and subgenus *Antephalium* Iredale, 1927; *Echinophoria* Sacco, 1890 (= *Mauicassis* Fleming, 1943); *Casmaria* H. & A. Adams, 1853.

Family *Cymatiidae*: shell small to extremely large, thick and solid, varied in shape but generally resembling muricean neogastropods in most features except that there are only two varices per whorl, rather than three or more; last whorl of most genera relatively small, siphonal canal short to long, spire short to tall; sculpture of most genera of prominent spiral and axial cords and nodules. Outer lip prominently variced in all genera, varices remaining at preadult growth pauses in almost all genera. Periostracum prominent, bearing numerous short to long bristles in most genera. Operculum always present, with central, adaxial, subcentral, or abapically terminal nucleus. Anatomical features varied; only two accessory salivary glands; oesophageal gland a discrete sac; stomach unpleated, with both digestive gland ducts in the pyloric arm, a prominent typhlosole along left edge of pyloric arm, and intestine straight from stomach to anus (in an Australian specimen of *Charonia lampas rubicunda* (Perry); Fig. 1 h). Three subfamilies can be recognised.

Subfamily *Cymatiinae*: Protoconch tall and narrowly conical in almost all genera; periostracum bearing luxuriantly bristled, prominent, thin axial blades; central radular

tooth markedly wider than high, with many small, similar denticles on each side of the main cusp; jaw plates large; proboscis relatively short, not coiled within sheath when contracted. These are the Cymatiidae of the tropics, and all have long planktonic larval lives.

Included genera and subgenera: *Cymatium* Röding, 1798; *Ranularia* Schumacher, 1817 and subgenera *Lotoria* Emerson & Old, 1963 and *Gutturium* Mörch, 1852; *Septa* Perry, 1810 (= *Monoplex* Perry, 1811, = *Cabestanimorpha* Iredale, 1936) and subgenera *Cymatriton* Clench & Turner, 1957, and *Reticutriton* Habe & Kosuge, 1966; *Linatella* Gray, 1857, and subgenus *Gelagna* Schaufuss, 1869.

Subfamily *Ranellinae*: Protoconch low and turbinate; periostracum smooth, furry or with large, evenly spaced bristles, lacking axial blades; central radular tooth approximately equidimensional, with only a few denticles on each side; jaw plates large; proboscis as in Cymatiinae. These are the Cymatiidae of western America, Europe and, above all, the Southern Ocean, with few Indo-West Pacific or Caribbean species. Most have only short planktonic larval lives, and long larval lives are found only in *Ranella olearia*, *Fusitriton cancellatus*, *Argobuccinum pustulosum*, *Charonia*, and presumably *Sassia* (sensu stricto) and *Cabestana* (*Turritriton*) *labiosa*.

Included genera and subgenera: *Charonia* Gistel, 1847; *Cabestana* Röding, 1798, and subgenus *Turritriton* Dall, 1904 (= *Tritoniscus* Dall, 1904); *Cymatiella* Iredale, 1929 (= *Vernotriton* Iredale, 1936); *Cymatona* Iredale, 1929; *Sassia* Bellardi, 1873 (= *Phanozesta* Iredale, 1936) and subgenera *Austrosassia* Finlay, 1931, *Austrotriton* Cossmann, 1903 (= *Negyriina* Iredale, 1929) and *Proxicharonia* Powell, 1938; *Haurokoa* Fleming, 1955; *Fusitriton* Cossmann, 1903; *Argobuccinum* Hermannsen, 1846, and subgenera *Mediargo* Terry, 1970 and *Priene* H. & A. Adams, 1858; *Ranella* Lamarck, 1816 (= *Mayena* Iredale, 1917, = *Gyrinopsis* Dall, 1925); *Gyrineum* Link, 1807 (= *Apollon* Montfort, 1810) and subgenus *Biplex* Perry, 1811.

Subfamily *Distorsioninae* Kuroda, Habe & Oyama, 1971 (emend.): protoconch and periostracum as in most Ranellinae, but radula distinctive, with down-curved corners of the broad central tooth, and large lateral teeth resembling those of *Ficus*; jaw plates extremely small; shell very distorted, with prominently plicate inner-lip calluses retained at pre-adult growth pauses; proboscis extremely long and narrow and much folded and coiled in the proboscis sheath when contracted, as in *Ficus*. Lewis (1972) has figured many of the anatomical features of *Distorsio*.

The genitive form of *torsio* (Latin, a wringing or griping) is *torsionis*, so that the subfamily name formed from *Distorsio* should be spelled Distorsioninae.

The single included genus is *Distorsio* Röding, 1798, and its subgenera *Rhysema* Clench and Turner, 1957 (synonymised with *Distorsio* by Lewis, 1972), *Personella* Conrad, 1865, and *Distorsionella* Beu, 1978.

Family *Bursidae*: Shell small to large, extremely thick and solid, similar in shape to Cymatiidae but even more coarsely sculptured; unique anal canal present in outer lip at posterior end of aperture; spire low to moderately tall and siphonal canal short; varices as in Cymatiidae but aligned up sides of spire (as in some genera of Ranellinae) in most genera. Periostracum weakly developed or absent. Operculum always present, with adaxial, abaxial, central, or abapically terminal nucleus. Radula with relatively small, narrow-armed, shallowly \wedge -shaped central tooth; near the extremity of each basal arm is a small downward-projecting process (present also in Tonninae) that interlocks adjacent centrals; lateral teeth large, with relatively small, narrow bases and long, strongly hooked cusps. Jaw plates minute in *Tutufa* (s.s.), absent in all other genera and subgenera.

Proboscis relatively short and broad, not folded in sheath when contracted, as in Tonnidae and Cymatiidae, in some genera having a circular, transversely flattened anterior end as in *Tonna*. Oesophageal gland a discrete sac. A third small accessory salivary gland is attached to the right salivary gland. Stomach with one digestive gland duct near posterior end of each arm; path of intestine to rectum straight in most genera examined, but in *Bursa* (*Bufonariella*) *granularis* (Röding) it has a small sharp flexure similar to the much larger flexure in *Tonna*. A classification of the family is given below.

Family **Bursidae**: generic classification

Kuroda, Habe & Oyama (1971, p.133-4) classified the Bursidae of Sagami Bay in two subfamilies, Bursinae (including "*Gyrineum*" = *Bufonaria*, and *Bursa*) and Tutufinae nov. including *Tutufa* and *Bufonariella* [containing *Triton ranelloides* Reeve, 1844, and therefore = *Bursa* (*Bufonariella*) of this paper] but the only feature *B.* (*Bufonariella*) *ranelloides* has in common with *Tutufa* is its variceal position and, as noted below, variceal position is not a useful guide to relationships in the Bursidae. Study of the anatomy, described below, shows that the Bursidae is an extremely homogeneous group in which no subfamilies can be recognised.

Vokes (1973) has offered valuable comments on the classification and taxonomic criteria of the Bursidae, reaching the same conclusion as the writer, that variceal position has little taxonomic significance in Bursidae. Most of her conclusions on relationships agree with those of the writer, but her classification ignores the criteria of the radula, the anatomy and, in particular, the operculum. Her excellent figured Chipola Formation (Lower Miocene) specimen of *Bursa* ("*Tutufa*") *pelouatensis* (Cossman and Peyrot) (Vokes 1973, Figs 2a, 6) has close affinities with the recent *B. caelata* (Broderip) and *B. granularis* (Röding), species shown here to belong in *Bursa* (*Bufonariella*), which has an abapically terminal opercular nucleus. The figured shell has varices aligned on early spire whorls, becoming unaligned on the last few whorls only, whereas species of *Tutufa* have all varices placed as in cymatiids all down the spire. The resemblance of *B.* (*Bufonariella*) *pelouatensis* to *Tutufa* (*Tutufella*) *rubeta* is as superficial as are many of the other superficial resemblances in the family cited by Vokes, as *T. rubeta* has an operculum with the nucleus situated near the centre of the height, and a short distance in from the abaxial edge. *B. amphitrites* Maury (Vokes 1973, Fig. 1a, b) also belongs in *Bufonariella*.

Especially characteristic features of the family are the permanent anal siphon in the mantle edge, accommodated in the shell by a deep posterior canal in the outer lip that is produced into the spout which may be short to very long. The accessory salivary glands are very large, and thin-walled. The left salivary gland has attached one long, narrow accessory gland that fills two-thirds of the cephalic cavity, and the right one has attached two smaller accessory glands, the left filling most of the remainder of the cephalic cavity and the right one relatively small and filling the extreme right anterior corner of the cephalic cavity. Prominent processes on each side of the two narrow basal limbs of the central radular teeth interlock all the central teeth. The periostracum is very weakly developed, whereas it is very prominent in the superficially similar Cymatiidae.

According to observed oesophageal, stomach and rectal contents and the report by Houbriek and Fretter (1969, p.424), the prey of Bursidae studied seems to be polychaetes. The extendible proboscis, in many genera with a broad, flat tip and lateral lips, and the large salivary glands are apparently adaptations to anaesthetising tubicolous polychaetes, removing them from their tubes, and swallowing them whole. Many species (in *Bursa* and subgenera) are found on tropical shallow water coral reefs and rocks, and others (in *Tutufa* and *Bufonaria*) are more commonly taken in deeper water on the

continental shelf from sand and mud substrates, but habitats vary greatly within one genus.

Genera of the Bursidae have been reviewed only by Jousseau (1881), Cossman (1903, pp.85-119, in Tritonidae), Dall (1904), Cooke (1916) and Oyama (1964). The latter author regarded almost all recognisable taxa as full genera, and did not consider fossils. As a background setting within which *Tutufa* is treated as a genus and several species previously assigned to *Tutufa* are placed in other genera, a summary is presented here of what the writer considers is a meaningful classification of the Bursidae, expressing relationships in the family as clearly as is possible in Linnaean nomenclature.

Genus **Bursa** Röding, 1798

Bursa Röding, 1798: 128. Type species (by subsequent designation, Jousseau, 1881, p.174): *Murex bufonius* Gmelin, 1791 (in synonymy of *Bursa monitata* Röding, 1798), Recent, Indo-West Pacific.

Pseudobursa Rovereto, 1899: 6. Unnecessary replacement for *Bursa* Röding, 1798.

The designation by Jousseau (1881, p.174) of *Murex bufonius* Gmelin, 1791, as type species of *Bursa* Röding, 1798 is valid, as Röding (1798, p.128) cited *Murex bufonius* Gmelin as a synonym of his species *Bursa monitata* (International Commission on Zoological Nomenclature, 1964, Article 69(a)i). Recently Beu (1978, p.23) incorrectly attributed the first valid type designation for *Bursa* to Oyama (1964).

Shell small to moderate-sized, dorsoventrally compressed, thick and solid, coarsely sculptured, with short to tall spire; operculum lanceolate, with abapically terminal nucleus. Stomach with the two digestive gland ducts close together near bend between cardiac and pyloric arms. Seminal groove closed.

Subgenus **Bursa** sensu stricto

Shell small to moderately large for genus, sculptured with large, coarsely rugose, rounded nodules; varices aligned up spire sides; aperture of uniform colour, black or red to white; posterior canal very deep, in most species produced into a long, tubular spine, and spines of previous outer lips remaining prominent on spire.

Some included species: *Bursa (Bursa) bufonia* (Gmelin, 1791) (= *B. luteostoma* Pease, 1861) (Pease 1861, p.397), Indo-West Pacific; *B. (Bursa) mammata* (Röding, 1798) (= *rosa* Perry, 1811, = *siphonata* Reeve, 1844), Indo-West Pacific; *B. (Bursa) tuberosissima* (Reeve, 1844), Indo-West Pacific; *B. (Bursa) xantostoma* (Tapparone-Canefri, 1878) (Tapparone-Canefri 1878, p.249), West Pacific; *Bursa* species with black aperture (Cernohorsky 1967b, p.46, pl. 1, Fig. 2; Reeve 1844b, pl. 5, Fig. 23a).

Almost all male specimens of *Bursa* and its subgenera examined had the seminal groove closed for the whole of its length. The large adult specimen (shell 69 mm high) from Flying Fish Cove, Christmas Island, Indian Ocean (Western Australian Museum, WAM 835-71) dissected in this study (Fig. 1a, 21) had the groove completely closed, as demonstrated by probing and sectioning. The only exception was a small shell with a white aperture, strongly plicate inner lip, long posterior canal spines, and external coarsely rugose sculpture, judged to be a juvenile specimen of *B. bufonia*, from Batangas Province, Luzon, Philippines (Western Australian Museum, WAM 500-69) in which the small narrowly tapering penis bore a clearly open seminal groove. Probe examination under stereoscope enlargement demonstrated that the groove was open for all its length exposed in the mantle cavity. It appears that this specimen (shell 29 mm high) is an

immature *B. bufonia* in the early stages of developing its external reproductive system, and that the seminal groove is fully open when first developed, even in genera where it is normally closed when mature.

The stomach of *B. bufonia* (Fig. 1a) has moderately thickened walls, an irregularly plicate, sacular cardiac arm, a straight tubular pyloric arm, both digestive gland ducts near the bend between the two arms, and a typhlosole running from the anterior digestive gland duct into the intestine, more prominent in the intestine than in the stomach.

Subgenus **Lampadopsis** Jousseau, 1881

Lampadopsis Jousseau, 1881:175. Type species (by original designation): *Ranella rhodostoma* G. B. Sowerby II, 1841, ex Beck MS; Indo-West Pacific.

As the genitive form of *lampas* (Latin, a torch) is *lampadis*, the emendation by Fischer (1884, p.656) of *Lampasopsis* Jousseau to *Lampadopsis* is justified, and has been followed by most authors.

Shell small to moderate-sized, sculptured with large, rounded nodules that are smooth or bear finely-dissected spiral cords; varices aligned up spire sides; aperture uniformly red to violet, or white with a red parietal blotch; posterior canal extremely short, and shallowly cut into outer lip beyond varix, not into varix.

Some included species: *Bursa (Lampadopsis) rhodostoma* (G. B. Sowerby II, 1841), Indo-West Pacific; *B. (Lampadopsis) venustula* (Reeve, 1844), Polynesia (Cernohorsky 1967a, p.315); *B. (Lampadopsis) cruentata* (G. B. Sowerby II, 1841), Indo-West Pacific; *B. (Lampadopsis) grayana* Dunker, 1863, Red Sea (Dunker 1863-4, p.58, pl. 19, Fig. 5, 6); *B. (Lampadopsis) asperrima* Dunker, 1863, "China" (Dunker, 1863-4, p.57, pl. 19, Fig. 3, 4); *B. (Lampadopsis) thomae* (d'Orbigny, 1842), Caribbean; *B. (Lampadopsis) bergeri* "Sowerby" Tapparone-Canefri, 1881, Mauritius (Tapparone-Canefri 1881, pl. 2, Fig. 1, 2); *B. (Lampadopsis) paulucciana* Tapparone-Canefri, 1876, Mauritius (Tapparone-Canefri 1881, pl. 2, Fig. 16, 17); *B. (Lampadopsis) consobrina* (Mayer, 1871), Upper Miocene of Italy (Bellardi 1873, p.239, pl. 15, Fig. 8), a species closely related to *B. cruentata*.

Specimens identified as *Bursa thomae* (d'Orbigny) sent on loan from the Museum of Comparative Zoology, Harvard University, are identical to Indo-West Pacific specimens of *B. (Lampadopsis) rhodostoma* (Sowerby) in all features, except that they all have a pale pinkish lavender inner lip rather than the pink to deep-red inner lip seen in Indo-West Pacific specimens. As several of the Caribbean shells were collected alive quite recently, this difference cannot be due to fading and is presumed to be significant, and probably *B. thomae* is another example of a Caribbean geographic subspecies of a species otherwise limited to the Indo-West Pacific or Panamic faunas, as so frequently occurs in Tonnacea.

Subgenus **Bufonariella** Thiele, 1929

Bufonariella Thiele, 1929:284. Type species (by monotypy): *Murex scrobilator* Linnaeus, 1758; Pliocene to Recent, Mediterranean.

Dulcerana Iredale, 1931:213. Type species (by original designation): *Ranella granifera* Lamarck, 1816 (= *Tritonium granulare* Röding, 1798); Recent, Caribbean and Indo-West Pacific (unavailable, no differentiation from related taxa).

Annaperenna Iredale, 1936:310. Type species (by original designation): *Ranella verrucosa* G. B. Sowerby I, 1825; southwest Pacific (Sydney Harbour; Lord Howe Is.; Norfolk

Is.; Kermadec Islands; northern New Zealand).

Dulcerana Oyama, 1964:332. Type species (by original designation): *Tritonium granulare* Röding, 1798.

Tritonoranella Oyama, 1964:332. Type species (by original designation): *Triton ranelloides* Reeve, 1844, Recent, southern Japan.

Oyama (1964, pp.330, 332) appears to have been the first author to publish the data required to make the name *Dulcerana* available in nomenclature.

Shell of relatively light build, with moderately tall spire, short anterior siphonal canal, posterior canal short and shallow, and sculpture of several rows of small to moderately large, rounded gemmae; varices aligned up spire sides, at least on earliest spire whorls, but either aligned or situated at every $\frac{2}{3}$ whorl on last few whorls. Stomach with both digestive gland ducts near bend between cardiac and pyloric arms.

Oyama (1964, p.332) described the operculum of *Bufonariella scrobilator* as having an abaxial nucleus, as in *Tutufa*, and therefore treated *Bufonariella* as a genus related to *Tutufa* and distinct from *Dulcerana* "Iredale" Oyama. However, other authors have described the operculum of *B. scrobilator* as having a terminal, abapical nucleus, and the specimen of *B. scrobilator* figured by Settepassi (1967) bears an operculum with a terminal, abapical, abaxial nucleus. It appears likely that the specimen examined by Cooke (1916) and quoted by Oyama (1964) had an aberrant operculum, as frequently occurs in both Cymatiidae and Bursidae, and as shells referred to *Bufonariella* and *Dulcerana* are extremely similar in all other features the two "subgenera" are here regarded as synonyms.

Oyama (1964, p.332) proposed the genus *Tritonoranella* for *Bursa ranelloides* Reeve, 1844, because its variceal position is like those of *Tutufa* and Cymatiidae, and unlike that of other Bursidae. *Bursa ranelloides* resembles species of *Bursa* (s. str.) rather than species of *Tutufa* in having an abapically terminal opercular nucleus, in having a shallowly embayed base and relatively small interlocking basal processes on the central radular tooth, and in having both digestive-gland ducts situated close together, one on each side of the bend between the cardiac and pyloric arms of the stomach. Also *B. ranelloides* has a light build, tall spire, sculpture of several rows of small to large nodules on spiral cords, a deeply excavated columella, and short, shallow siphonal canals and closely resembles species of *Bursa* (*Bufonariella*), especially *B. (Bufonariella) granularis* (Röding). The red-brown parietal colour patch of both species of *Tritonoranella* is seen also in many, although not all, species of *Bursa* (*Lampadopsis*), but does not occur in species of *Tutufa*. In short, the only criterion separating *Tritonoranella ranelloides* from *Bursa* (*Bufonariella*) is the variceal position, and certainly *Tritonoranella* is related to *Bursa* rather than to *Tutufa*. The two closely related species *B. ranelloides* (Reeve) and *B. latitudo* Garrard, revised below, are the only species sharing widely spaced varices, and as variceal position is variable in a few species of *Bursa* (*Bufonariella*), the differences between *Tritonoranella* and *Bufonariella* do not seem sufficient bases for a subgenus, and the name *Tritonoranella* Oyama, 1964 is here regarded as a synonym of *Bufonariella* Thiele, 1929.

Iredale (1936, p.310) proposed *Annaperenna* for the single species *Bursa verrucosa* G. B. Sowerby I, 1825. *Bursa verrucosa* resembles coarsely sculptured Japanese specimens of *B. (Bufonariella) ranelloides ranelloides* (Reeve) closely in shape, sculpture, smoothness of surface between nodules, aperture shape and sculpture, and presence of a red parietal area, and differs from *B. ranelloides* only in its rows of larger nodules below the peripheral one, the external surface colouration, and in having all its varices aligned up the sides of the spire. Powell (1967, p.190, fig. 3) described the operculum as

“irregularly ovate with a subterminal nucleus”, and figured a radula with a deeply embayed central tooth, bearing a relatively short main cusp and small interlocking basal processes similar to those of *Bursa bufonia*. There can be little doubt that *Bursa verrucosa* belongs in *B (Bufonariella)* near *B. ranelloides*, and the name *Annaperenna* Iredale, 1936 is therefore regarded as synonym of *Bufonariella* Thiele, 1929.

Species placed in the subgenus *Bufonariella* differ from *Bursa* (s.str.) in their markedly more cymatiid-like appearance, brought about by a thinner and more finely sculptured shell and a markedly taller spire than in species of *Bursa (Bursa)* or *Lampadopsis*.

Some included species are: *Bursa (Bufonariella) granularis* (Röding, 1798) (= *rubicola* Perry, 1811, = *granifera* Lamarck, 1816, = *semigranosa* Lamarck, 1816, = *kowiensis* Turton, 1932, = *cumingiana* Dunker, 1864 [Dunker 1863-4, p.59, pl.19, fig. 7,8]= *affinis* Broderip, 1833, = *cubaniana* d’Orbigny, 1842, = *livida* Reeve, 1844), Indo-Pacific and Caribbean; *B. (Bufonariella) coriacea* (Reeve, 1844), locality?; *B. (Bufonariella) fijiensis* (Watson, 1880), Fiji; *B. (Bufonariella) corrugata* (Perry, 1811) (= *caelata* Broderip, 1833, = *ponderosa* Reeve, 1844, = *louisa* M. Smith, 1948), Caribbean and central Western America; *B. (Bufonariella) calcipicta* (Dall, 1908) (see Keen 1971, fig.965), Panamic; *B. (Bufonariella) pustulosa* (Reeve, 1844), West Africa and Ascension I.; *B. (Bufonariella) dunkeri* Kira, 1961 (Kira 1961, p.54, pl.21, fig. 18; *nomen nudum* in earlier editions), Japan; *B. (Bufonariella) verrucosa* (G. B. Sowerby I, 1825) (= *papilla* Wood, 1828), southwest Pacific; *B. (Bufonariella) scrobilator* (Linnaeus, 1758), Mediterranean; *B. (Bufonariella) latitudo* Garrard, 1961, with subspecies (revised below) *B. latitudo latitudo*, Queensland, *B. latitudo natalensis* Coelho & Matthews, 1970, western Atlantic, and *B. latitudo wolfei* n. subsp., Hawaii; *B. (Bufonariella) ranelloides* (Reeve, 1844), with subspecies (revised below) *B. ranelloides ranelloides*, southern Japan, *B. ranelloides tenuisculpta* Dautzenburg & Fischer, 1906, Atlantic and South Africa, and *B. ranelloides humilis* n. subsp., Western Australia; and *B. (Bufonariella) rehderi* Beu, 1978, Philippine Islands (Beu, 1978).

European Miocene species include *B. (Bufonariella) grateloupi* (d’Orbigny, 1842) (see Cossmann and Peyrot 1923, pl. 15, fig. 42, 43); *B. (Bufonariella) nodosa* (Borson, 1821) (Bellardi 1873, pl 15, fig. 5) and var. *subgranifer* (d’Orbigny, 1842) (Cossmann and Peyrot 1923, p.307, pl. 16, fig. 28, 29); *B. (Bufonariella) pelouatensis* (Cossmann and Peyrot, 1923) (Cossmann and Peyrot 1923, pl. 15, fig. 38, 39); *B. (Bufonariella) inaequicrenata* (Cossmann and Peyrot, 1923) (Cossmann and Peyrot 1923, pl. 15, fig. 44, 45); *B. (Bufonariella) lessonae* (Bellardi, 1873) (Bellardi 1873, pl.15, fig. 10) and var. *occidentalis* (Cossmann and Peyrot, 1923) (Cossmann and Peyrot 1923, pl.16, fig. 16, 17); *B. (Bufonariella) tuberosa* (Borson, 1821) (Bellardi 1873, pl.15, fig. 7); and *B. (Bufonariella) austriaca* (Hörnes and Auinger, 1884) (Bosch *et al.* 1975, pl.13, fig. 2), a species closely related to but shorter than the living *B. scrobilator*.

Subgenus **Colubrellina** Fischer, 1884

Colubrellina Fischer, 1884:656. Type species (by original designation): *Ranella candidata* Lamarck, 1816 (= *Murex conditus* Gmelin, 1791), Recent, Indo-West Pacific.

Posterior canal very short, shallow; spire extremely tall, so that shell resembles *Colubraria*; varices aligned up spire sides; sculpture of many rows of similar fine, sharp granules.

Several recent workers have regarded *Colubrellina* as a full genus, and some have ranked *Bufonariella* (= *Dulcerana*) as a subgenus of it. Oyama (1964, pl.332) included

Colubrellina in his key in genera with "almost terminal (anteriormost) nucleus" in the operculum, so that *Colubrellina* evidently also is closely related to *Bursa* (s.s.) and *Bufonariella*, and here is regarded as a subgenus of *Bursa*.

The subgenus includes only the uncommon Indo-West Pacific *Bursa* (*Colubrellina*) *condita* (Gmelin), recently discussed and figured by Cernohorsky (1972, p.200, fig.12). Specimens of *B. condita* in the Australian Museum are from Tryon I., Capricorn Group, southern Great Barrier Reef, Queensland (C.81612).

Genus **Crossata** Jousseaume, 1881

Crossata Jousseaume, 1881:175. Type species (by original designation): *Ranella ventricosa* Broderip, 1833, Recent, central Western America.

Varices low and weak, almost aligned up spire sides; posterior canals very short and broadly open; shell large, relatively thin, sculptured with large nodules; operculum as in *Bursa*. Radula (Cooke, 1916, p.10, figs.3, 6) with unusually low and broad central tooth bearing only a single large cusp.

Included species are *Crossata ventricosa* (Broderip, 1833), (= *tenuis* Potiez & Michaud, 1838), Recent, Panamic province; *C. californica* (Hinds, 1843), Recent, California; and *C. sonorana* (Berry, 1960) (see Keen, 1971, p.509, fig. 967).

?Subgenus **Olequahia** Stewart, 1926

Olequahia Stewart, 1926:382. Type species (by original designation): *Cassidaria washingtoniana* Weaver, 1912, Eocene, western North America.

Some figures of *Olequahia washingtoniana* resemble *Bufonaria* (e.g., Wenz 1940, fig. 3063; Weaver, 1942, pl.84, fig. 6) but others (e.g., Weaver 1942, pl. 84, fig. 10, 11) closely resemble *Crossata* in their low form, sculpture of weak, widely spaced cords, and broadly open posterior canal. Certainly the broad form, unusual fine, low, widely spaced spiral sculpture, and broadly open posterior canal give *Crossata* a highly distinctive appearance and suggest that it has had a long Tertiary history in Western America. Probably *Olequahia* was ancestral to *Crossata*, and in view of their similarity it seems best at present to treat *Olequahia* as a subgenus of *Crossata*.

Genus **Tutufa** Jousseaume, 1881

Tutufa Jousseaume, 1881:175. Type species: *Murex rana bubo* Linnaeus, 1758 (ICZN Opinion 1074); Recent, Indo-West Pacific.

Shell moderate-sized to extremely large, including the largest Bursidae; posterior and anterior canals very short, spire moderately tall; varices situated at every $\frac{2}{3}$ whorl, i.e. every 240° around spire; operculum with nucleus at or slightly below half height and slightly towards the centre from the abaxial margin; head-foot maculated with red or dark brown.

Subgenus **Tutufa** sensu stricto

Shell very large; columella weakly plicate or smooth; seminal groove open; cephalic tentacles not bearing colour rings; stomach (of *T. bufo*) has typhlosoles both in front of and behind digestive gland ducts.

Included species (revised below): *Tutufa* (*Tutufa*) *bardeyi* (Jousseaume, 1894),

northern Indian Ocean; *T. (Tutufa) bubo* (Linnaeus, 1758), Indo-West Pacific; *T. (Tutufa) bufo* (Röding, 1798), Indo-West Pacific.

Subgenus **Tutufella**, new name

Lampas Schumacher, 1817:252. Type species (by monotypy): *Lampas hians* Schumacher, 1817 (refers to Martini, 1780, vol.4, pl.128, figs. 1236-7) = *Murex rana* var. *rubeta* Linnaeus, 1758; Recent, Indo-West Pacific (not *Lampas* Montfort, 1808, Foraminiferida).

The new name *Tutufella* is here proposed as a replacement name for the preoccupied *Lampas* Schumacher, 1817, not of Montfort, 1808, and takes the same type species.

Shell medium-sized to moderately large; columella closely plicate; seminal groove closed; cephalic tentacles with two dark colour rings; stomach with typhlosole behind digestive gland ducts only.

Included species (revised below) are: *Tutufa (Tutufella) oyamai* Habe, 1973, West Pacific; *T. (Tutufella) rubeta* (Linnaeus, 1758), Indo-West Pacific; *Tutufa (Tutufella?) tenuigranosa* (E. A. Smith, 1914), South China Sea; and *T. n.sp.? aff. rubeta* (Röding), Moçambique.

Genus **Bufonaria** Schumacher, 1817

Buffo Montfort, 1810:575. Type species (by monotypy): *Buffo spadiceus* Montfort, 1810 (= *Murex bufo* Bruguière, 1792), Recent, Caribbean (not *Buffo* Lacépède, 1788, Vertebrata).

Bufonaria Schumacher, 1817:251. Type species (by subsequent designation, Herrmannsen, 1846, p.135): "*Ranella spinosa* Lamck" = *Bufonaria spinosa* Schumacher, 1817 (refers to Martini, 1780, vol. 4, pl. 133, fig. 1274-1276) = *Gyrineum echinatum* Link, 1807; Recent, Indo-West Pacific.

Marsupina Dall, 1904:118 (new name for *Buffo* Montfort, 1810, not of Lacépède, 1788).

Chasmotheca Dall, 1904:118. Type species (by original designation): *Ranella foliata* Broderip, 1833, Indo-West Pacific.

Bursina Oyama, 1964:333. Type species (by original designation): *Ranella nobilis* Reeve, 1844, West Pacific.

This is "*Gyrineum* Link, 1807" of many authors, but not of Link, 1807. The type designation for *Gyrineum* given by Rovereto (1899) is invalid as the designated species, *Ranella spinosa* Lamarck, was not expressly included by Link. The next type designation for *Gyrineum* is that by Dall (1904, p.131), who cited *Murex gyrinus* Linnaeus, 1758 as the type species, and in the same work (p.115) clearly stated that *Gyrineum verrucosum* Link, 1807 is a synonym of *Murex gyrinus* Linnaeus, thereby making *Gyrineum verrucosum* Link the type species of *Gyrineum* Link, 1807, under the Code (Article 69 (a) (vi)). Therefore *Gyrineum* Link, 1807, must be used as a senior synonym of *Apollon* Montfort, 1810 (Cymatiidae), as it has by many recent writers, and the next available name, *Bufonaria* Schumacher, used in its place in Bursidae.

Vokes (1973, p.100) has pointed out that the name *Murex bufo* Bruguière, 1792 (Reference: Actes Soc. H.N. Paris, 1 (1): 126; Sherborn 1902, p.147) is an earlier name for

Bufonaria spadicea (Montfort, 1810). To workers who place all Bursidae in *Bursa*, whether subgenera are used or not, *Tutufa bufo* (Röding, 1798) will be a secondary homonym of *Bufonaria bufo* (Bruguère, 1792), and the species of *Tutufa* must be called *Bursa (Tutufa) lissostoma* (E. A. Smith, 1914), the only synonym proposed for the species. However, when the names are placed in the separate genera *Bufonaria* and *Tutufa*, as is strongly urged here, the secondary homonyms *B. bufo* (Bruguère) and *T. bufo* (Röding) should be retained (International Commission on Zoological Nomenclature, 1964, Article 59 (c)).

Subgenus **Bufonaria** sensu stricto

Varices aligned up spire sides, at least on early part of spire; posterior canals short to very long, when long aligned up previous varices on spire; shell dorsoventrally compressed, light in weight, sculptured with numerous rows of small granules and, in some species, with nodules or spines at the shoulders of the varices. Seminal groove open. Operculum fan-shaped with nucleus in centre of adaxial margin, as in Cassidae subfamily Phaliinae, to subcentral near adaxial margin, to almost central (in *B. nobilis*).

A wide range of shape, degree of spination of the varices, and amount of sculpture of the inner-lip shield is here included in *Bufonaria* s.s., but all types intergrade and there are no anatomical or opercular differences between the synonymised taxa, except as noted below for *Bursina* Oyama. The variceal and siphonal features used by Dall (1904, p.118) and Oyama (1964) to distinguish such "genera" as *Marsupina* and *Chasmotheca* from *Bufonaria* are considered to be specific characters only.

Oyama (1964, p.333) separated "*Bursina*" *nobilis* from *Bufonaria* because its operculum has a central rather than an adaxial nucleus. A live-collected specimen of *Bufonaria nobilis* (Reeve) in the Western Australian Museum (Mariel King Memorial "Pele" expedition, Sta. AHI/5, near Tg. Bt. Kapal, Haruku Islands, east of Ambon, Moluccas, 3°36'S, 128°24'E, 31 May 1970, 45-48 fms; WAM 616-74) has a damaged, elongated operculum, similar in shape to those of *B. rana* and other typical species of *Bufonaria*, but with the nucleus slightly off-centre near the adaxial margin, rather than hard against the adaxial margin. The close similarity of the shell of *B. nobilis* to those of other species here included in *Bufonaria* (s.s.) and the similarity of opercular shape to those of *Bufonaria* suggest that "*Bursina*" *nobilis* belongs in *Bufonaria* (s. str.) A large suite of *Bufonaria margaritula* (Deshayes in Boulenger, 1832) from Tayabus Bay, W. Quezon Province, Luzon, Philippines (J. E. Norton Colln., Western Australian Museum, WAM678-70) shows that this species is similar to *B. nobilis* in its angular shape, with sharp nodes on the varices at the peripheral and basal angulations differing from *B. nobilis* in its much shorter form, especially the shorter spire. The opercula of shells in the suite are all unusually broadly oval for species of *Bufonaria*, and consistently have their nuclei a short distance in from the centre of the adaxial margin, half-way between the position in *B. nobilis* and that in more common species of *Bufonaria* such as *B. rana*. It appears that the position of the opercular nucleus in *Bufonaria* depends on the angle of the parietal area to the columella, as tall-spined species with almost straight inner lips, such as *B. nobilis*, have the opercular nucleus furthest from the columella, short-spined cassid-shaped species with the columella at a marked angle to the parietal area have the opercular nucleus against the columella, and the position is intermediate in species of intermediate shape. Therefore a varied opercular nucleus position is accepted in *Bufonaria*, and *B. nobilis* is regarded as a species of *Bufonaria* (sensu stricto). The name *Bursina* Oyama, 1964 is synonymised with *Bufonaria* Schumacher, 1817.

Some included species: *Bufonaria (Bufonaria) nobilis* (Reeve, 1844); *B. (Bufonaria) echinata* (Link, 1807) (= *spinosa* Lamarck, 1816, = *suensonii* Mörch, 1852); *B.*

crumenoides (Valenciennes, 1832) (Valenciennes 1832, p.297) (= *crumena* of authors, not of Lamarck); *B. elegans* (G. B. Sowerby 2nd ex Beck MS, 1835); *B. foliata* (Broderip, 1833); *B. koperbergae* (Altena, 1942), Pliocene of Java & Timor, Recent in "Siboga" stns. 12 & 306 (Altena 1942, p.109, fig.4, a, b, 5); *B. margaritula* (Deshayes, 1832) (= *neglecta* G. B. Sowerby 2nd 1835); *B. rana* (Linnaeus, 1758) (= *albivaricosa* Reeve, 1844, = *crumena* Lamarck, 1816, not *crumena* of authors); *B. subgranosa* (G. B. Sowerby 2nd, ex Beck MS, 1835); *B. pacator* (Iredale, 1931) (? = *margaritula* Deshayes), all Indo-West Pacific; *B. gnorima* (Melville, 1918), northern Indian Ocean (Melville 1918, p.138, pl. 4, fig. 1); *B. fernandesi* Beu, 1977, Moçambique (Beu 1977); and *B. bufo* (Bruguière, 1792) (= *spadicea* Montfort, 1810, = *crassa* Dillwyn, 1816, = *granulata* Lamarck, 1816), Caribbean. Several of the Indo-West Pacific species were recorded from the Miocene of Java by Martin (1899).

Subgenus **Aspa** H. and A. Adams, 1853

Aspa H. and A Adams, 1853: 106. Type species (by monotypy): *Ranella laevigata* Lamarck, 1816 (= *Murex marginatus* Gmelin, 1791), Miocene to Pleistocene, Europe; Recent, Mediterranean.

Spire very low; varices low and rounded, resembling those of *Argobuccinum* (sensu stricto); shell squat, rounded, finely sculptured; operculum and other features as in *Bufonaria* sensu stricto.

The included species comprise only the Recent Mediterranean *Bufonaria* (*Aspa*) *marginata* (Gmelin) and a lineage of ancestral species in the Tertiary and Quaternary rocks of Europe, perhaps all part of the variation of *B. (Aspa) marginata*: *B. (Aspa) subgranulata* (d'Orbigny, 1842) (Cossmann and Peyrot 1923, p. 313, pl. 15, fig. 54; pl. 17, fig. 7); *B. (Aspa) depressa* (Grateloup, 1840) (Cossmann and Peyrot, 1923, p. 316, fig. 1, 2; pl. 17, fig. 8, 9).

Genus **Bechtelia** Emerson and Hertlein, 1964

Bechtelia Emerson and Hertlein, 1964: 360. Type species (by original designation): *Gyrineum strongi* Jordon, 1936, Pleistocene, Baja, California.

Figures of the type species of *Bechtelia* by Emerson and Hertlein (1964, fig. 59) and Durham (1950, pl. 29, fig. 19, 22) and a plaster cast of the holotype of *Gyrineum strongi* kindly presented by the late Dr Leo Hertlein show that *Bechtelia strongi* has a short, narrow, constricted posterior siphonal canal, a prominently dentate aperture unlike that of any Cymatiidae, and the varices aligned up the spire sides, and thus belongs in the Bursidae. It is perhaps related to "*Marsupina*" *nana* (Broderip and Sowerby, 1829) of the Recent Panamic Fauna. *Bufonaria nana* is far from a typical species of *Bufonaria* with its almost smooth shell surface, but the posterior canals of *B. nana* are deep and extend well up the spire, so it may not be related to *Bechtelia strongi*. At present *Bechtelia* appears to be an endemic monotypic, Panamic Pleistocene genus.

SPECIES REFERRED TO *TUTUFA*

Genus **Tutufa** Jousseau, 1881

The status of type-species designations where the designated name refers to more than one valid taxon is not covered by the Code. Jousseau (1881) designated *Murex lampas* Linnaeus, 1758 as type species of *Tutufa* but strictly speaking this is a species of *Charonia*, by designation by Beu (1970, p. 211). Jousseau presumably intended to designate as type the large bursid generally known as *Bursa* (or *Ranella*) *lampas* until

about 1920, and now usually called either *Bursa* (or *Tutufa*) *gigantea* E. A. Smith or *B. bubo* (Linnaeus). Beu (1973) applied to the International Commission on Zoological Nomenclature to designate *Murex rana* var. *rubeta* Linnaeus, 1758 as type species of *Tutufa*, on the grounds that it was the most commonly used name in the complex, but subsequently Rehder (1974) modified this to an application to designate *Murex rana* var. *bubo* Linnaeus, 1758 as type species. The International Commission on Zoological Nomenclature (1977) designated *Murex rana bubo* Linnaeus, 1758 as type species of *Tutufa* Jousseume in Opinion 1074.

Tutufa is a distinctive genus of Bursidae characterised, as is noted above, by its moderate to extremely large size; by its varices being situated every 240° (i.e., $\frac{2}{3}$ whorl) around the shell as in most Cymatiidae, rather than aligned up the spiræ sides as in most other Bursidae; by the operculum having its nucleus two thirds of the way down the abaxial margin, rather than central, adaxial or abapically terminal as in other Bursidae; by its extremely coarsely nodular external sculpture; and by its relatively tall spire, short anterior canal, and very short posterior canal.

Almost all writers of the nineteenth century molluscan iconographies (Kiener, 1842; Reeve, 1844a, fig. 30; Kobelt, 1871; 1878, pl. 9) regarded the forms here treated as species of *Tutufa* as a single variable species (usually placed in *Triton* or *Ranella*), and used for it the name *Ranella* (or *Triton*) *lampas* (Linnaeus, 1758). Not until E. A. Smith (1914) named some of the supposed varieties were more than a few names applied to the group, and thus the nomenclature is relatively simple compared with that of many Linnaean molluscs, especially Cymatiidae.

Collections and literature I have examined for this study, and especially the anatomy of the species, make it clear that the forms referred to the species *Triton lampas* (or *Bursa rubeta*, etc.) belong in six (or perhaps seven) species of *Tutufa*, three of which are placed in a new subgenus.

In the "subgenus" *Tritonoranella* Oyama, 1964 (here placed as a synonym of *Bufonariella* Thiele, a subgenus of *Bursa* Röding, 1798) two species have been placed in *Tutufa* by some workers, and both consist of three geographic subspecies. In *Tutufa* the six species are the four forms whose nomenclature was debated during the early twentieth century by E. A. Smith (1914), Vanatta (1914) and Hedley (1916a), together with the almost forgotten northern Indian Ocean *Lampas bardeyi* Jousseume (1894, p. 100) and the recently recognised *T. oyamai* Habe (1973, p. 140, text-fig. 2). As was pointed out by Powell (1967, p. 189), the fundamental point in the nomenclature of *Tutufa* is the identification of the figures cited in synonymy by early authors, for example under *Murex rana* var. *bubo* and var. *rubeta* of Linnaeus (1758, p. 748) and *Tritonium tuberosum* and *T. bufo* of Röding (1798, p. 127, 128). Comparison of shells in various growth stages with figures in several editions of the critical works and designations of several lectotypes and a neotype to stabilise the nomenclature in this study showed that most current nomenclature, based on that suggested by Hedley (1916a) is correct (e.g., Oyama and Takemura 1963; Wilson and Gillett 1971). Identity of individual figures is discussed under the relevant taxa.

ABBREVIATIONS

In systematic sections, locality lists, and figure captions, commonly cited Museums and Australian states have been abbreviated as follows:—

Museums

AIM — Auckland Institute and Musuem, Auckland.

AM — Australian Museum, Sydney.
 ANSP — Academy of Natural Sciences, Philadelphia.
 BMNH — British Museum (Natural History), London.
 NM — Natal Museum, Pietermaritzburg.
 NMNZ — National Museum of New Zealand, Wellington.
 NMV — National Museum of Victoria, Melbourne.
 NZGS — New Zealand Geological Survey, Lower Hutt.
 USNM — United States National Museum, Washington, D.C.
 WAM — Western Australian Museum, Perth.

States

NSW — New South Wales.
 Qld — Queensland.
 WA — Western Australia.

MATERIALS AND METHODS

Anatomy

In search of taxonomic criteria that might confirm or deny the species recognised from shell characters, gross anatomical investigation of the mantle cavity, cephalic cavity, vas deferens, penis and alimentary system was undertaken of the species of *Tutufa* for which preserved animals were obtainable (*T. bubo*, *T. bufo*, *T. oyamai*, *T. rubeta*, and *Bursa (Bufonariella) ranelloides humilis*). Radulae also were extracted from these species, and examined by both standard optical techniques and scanning electron microscopy. For comparison a brief survey of the anatomical and radular features of other Bursidae was also undertaken, establishing that Bursidae are completely uniform in gross anatomical features.

Tutufa material dissected in this study is as follows: *T. bufo*: one small incomplete animal from North-West Cape, Western Australia, presented to N.Z. Geological Survey by F. Turnbull; two large, well-preserved, complete animals from 30 m, off Osbourne Shoals, Bate Bay, Cronulla, New South Wales, coll. N. Coleman (Australian Museum, C 73465); 2 of 3 specimens trawled alive at BS. 307, between Bell's Flat and Hutchinson Bluff, Raoul I., Kermadec Islands in 110-120 m, by Mr A. J. Black and Dr F. M. Climo on R. V. "Acheron", 4 April 1973 (N.Z. National Museum, MF 22102). *T. bubo*: one large incomplete animal (mantle missing, gut broken off at anterior end of stomach) from Mauritius, 1871 (Museum of Comparative Zoology, Harvard, No. 3694; shell No. 142885); one small specimen in same condition as above, 0-1 m, Port Ternay, N.W. Mahé, Seychelles, stn. Sy. 21, 10 Feb. 1966 (Academy of Natural Sciences, Philadelphia, 311233); one small specimen in same condition as above two, 0.2 m, between Ambatoloaka and Madirokely, S.W. Nossi Bé, N.W. Madagascar, stn. H56a, 18 and 24 Oct. 1960 (Academy of Natural Sciences, Philadelphia, 253384). *Tutufa oyamai*: one moderately large, complete specimen and one young complete specimen, m.v. "Pele" Mariel King Memorial Expedition stn. ANI/1, S.W. of Tg. Ngabordamlu, Trangan, Aru I., Moluccas, lat. 6°58'S, long. 134°5'E, 27-29 m, 20 June 1970 (Western Australian Museum); one small complete specimen from m.v. "Pele" Mariel King Memorial Expedition stn. KR VI/3-10, N. of Du Rowa, N. of Nuku Rowa, Kai I., Moluccas, lat. 5°32'S, long. 132°41'E, 27-37 m, 11 June 1970 (Western Australian Museum). *Tutufa rubeta*: two excellently preserved, complete, large animals, m.v. "Pele" Mariel King Memorial Expedition stn. C.P.II, 1 mile S. of Tg. Tutuhuhus, Piru Bay, Ceram, lat. 3°15'S, long. 128°10'E, in 0.6 m, 1 June 1970 (Western Australian Museum); a jar of many animals in various states of completeness from Batangas Province, Luzon, Philippine Islands, lat. 13°47'N, long. 120°55'E, 2-9 m, J. E.

Norton colln. (Western Australian Museum, WAM1910-69). *Bursa* (*Bufonariella*) *ranelloides humilis* n. subsp: two topo-paratypes from H.M.A.S. "Diamantina" Stn. 6, lat. 33°S, long. 114°37'E, N.W. of Bunbury, Western Australia, 212-226 m, 15 March 1972 (Western Australian Museum, WAM305-72).

Radula

Radulae of the large species of *Tutufa* were initially prepared for examination by scanning electron microscope. After freeing from all visible tissue they were soaked for at least 24 hours in concentrated potassium hydroxide, and then were cleaned for 1-2 hours in an ultrasonic bath. Specimens appeared completely clean and gleaming after this treatment. About half the ribbon was mounted on an individual SEM stub with double-sided adhesive tape, and lightly coated with carbon and gold-palladium. The other half was mounted on microscope slides in "Euparal" or "Caedax" for standard examination by light microscopy. SEM examination proved extremely unsatisfactory, at least after this amount of cleaning, because of partly dissolved animal tissue coating teeth of most specimens. Therefore most observations and illustrations here are based on light microscopy and the standard type of sketch of microscope mounts, supplemented by some of the scanning electron micrographs.

Taxonomic criteria: summary

The taxonomic significance of various features of some tonnaceans has long been debated. The point debated longest is whether the position of varices or the possession or lack of a posterior siphonal canal in the outer apertural lip is the more significant guide to position in the Cymatiidae (= genus *Triton*, in 19th Century iconographies) or the Bursidae (= genus *Ranella*, in 19th Century iconographies). The present study demonstrates the correctness of the conclusion of most authors during this century; species with a posterior canal all have three accessory salivary glands, and all have interlocking basal projections on their central radular teeth and, regardless of their variceal position, are related to *Bursa*, in the Family Bursidae; whereas species lacking a posterior canal lack also the third accessory salivary gland and the basal projections of the central radular teeth, and are related to *Cymatium*, *Charonia*, and *Ranella* in the Family Cymatiidae. The position of varices (thickened outer apertural lips, strengthening the shell edge) reflects only how much shell is added during each of the animal's brief periods of shell increment (Laxton 1970) and it is not surprising that variceal position is a less useful criterion than animal features such as the operculum, radula, and stomach. In this study, similarities were found between many species in their gross anatomy, in their stomach shape and the position of its digestive gland ducts, of the operculum (as shown by the position of its nucleus) that have dissimilar variceal positions. It is concluded that variceal position is not an important taxonomic criterion. In the classification of Bursidae proposed here, both shells with cymatiid-like varices (at each two-thirds of a whorl) and shells with typically bursid varices (at or near each half whorl) are included in the one subgenus, *Bursa* (*Bufonariella*). In other words, it is concluded that the features of the operculum, radula, and stomach reflect monophyletic histories, whereas variceal position is a plastic feature which, in some taxa, reflects convergence.

It appears from this study that the operculum is one of the most useful features for higher classification in the Tonnacea, demonstrating subfamily relationships in the Tonnidae and Cassidae, and generic relationships in the Ficidae, Bursidae, and some Cymatiidae. At the generic and specific levels, the features of the radula and stomach are the most useful criteria, in conjunction with the traditional assessment of shell characters. In some groups, the shape of the penis (presumably reflecting species recognition characters or the evolution of physical cross-fertilisation barriers) and

whether the seminal duct is open or closed are useful specific and subgeneric criteria. Presumably other criteria will be found in the female reproductive system (beyond the writer's ability).

ANATOMY

Bursidae have been neglected in anatomical studies until recently. D'Asaro (1969) described the eggs, embryogenesis and early organogenesis of *Bursa (Bufonariella) corrugata* (Perry), figuring larval and early post-metamorphosis anatomy. Houbrick and Fretter (1969) greatly increased our knowledge of the anatomy and ecology of several species of cymatiids and bursids including *Bursa (Lampadopsis) cruentata* (Sowerby), *B. (Lampadopsis) rhodostoma* (Sowerby) and *B. (Bufonariella) granularis* (Röding). They figured the external features of the head-foot of *B. cruentata*, the external features of a complete female *B. cruentata*, and a detailed dissection of the proboscis of *B. granularis*, as well as comparable features and a stomach dissection of *Septa (Cymatriton) nicobaricum* (Röding).

Anatomy of *Tutufa*

The foot is relatively small and highly contracted in all specimens seen (all removed from shells after preservation) and has a large anterior pedal gland opening as a shallow slit (for example, markedly shallower than in *Tonna variegata cerevesina* Hedley) across the whole front edge of the foot. The cephalic protrusion is relatively small and simple and bears two relatively long, moderately narrow tentacles with a small black eye on a papilla on the outer edge of each tentacle. The tentacles are highly contractile. The proboscis sheath opens as a large, contractile slit on a low snout between the two tentacles. The entire dorsal and lateral surfaces of the cream to fawn head-foot of *T. rubeta*, *T. bufo* and *T. oyamai* are finely and closely maculated with medium to very dark reddish brown. Those of *Bursa ranelloides humilis* are uniform cream to fawn in well-preserved specimens and, whereas those of *T. bufo* were uniform cream to pale reddish brown in most available specimens, this is apparently because of poor preservation of the epithelium.

The two specimens of *T. bufo* listed above, trawled off Raoul I., Kermadec Is., during 1973 (N.Z. National Museum MF 22102), were dissected to see the external colour of fresh specimens. The head-foot is cream to greyish fawn closely dotted with bright to pale orange-red, and with scattered ill-defined rings of white and pale yellow that are largest and best defined on the dorsal surface of the head. The tentacles are uniform bright orange-red up the eyes, then pale orange shading off to cream over the outer narrow part of each tentacle. Each specimen (one ♂, one ♀) had one tentacle (the right in one specimen, the left in the other) almost lacking darker colour, and the outer tentacle bore fine, closely-spaced, black to brown maculations in a weakly defined ring immediately outside the eye of one specimen, and irregularly placed small patches of similar, fine dark maculations outside the eye of the other specimen. Tentacle colour is evidently highly variable, and not regularly bi-ringed as in the smaller species of *Tutufa*. The hypobranchial gland is very prominent because of its bright vermilion colour. The penis is closely maculated with bright orange red, and has thick rounded edges and a deeply open seminal groove. The proboscis is black, and is expanded to marked lateral lips at its tip, the mouth a wide horizontal slit about a quarter of the width of the flattened proboscis tip.

The cephalic tentacles of *T. oyamai*, *T. rubeta* and *Bursa ranelloides humilis* each bear two dark brown rings of closely spaced maculations on a cream ground on the outer part

of the tentacle beyond the eye, but clearly defined rings are absent in *T. bubo* and *T. bufo*. The rings are similar in *Charonia* but absent in other Cymatiidae I have examined, whereas Cassidae of the subfamily Phaliinae bear two longitudinal dark stripes on the portion of the tentacle beyond the eye, and no transverse rings. The disposition of colour bands on the cephalic tentacles may prove to be a useful guide to relationships in tonnaceans.

The mantle cavity was opened by cutting between the left dorsal ctenidium and the right dorsal hypobranchial gland. The cavity is long and narrow. The pale, grey-brown, mono-pectinate ctenidium is large, long and narrow in all species, with leaflets triangular and longest on the mid-dorsal edge (left edge in dissections). The pale brown, bipectinate osphradium is relatively small, about a fifth to a quarter the length of the ctenidium situated on the left side between the ctenidium and the foot, and placed just behind the incurrent siphon. The hypobranchial gland is large, thick and prominent, but less so in *Tutufa* than in *Bursa* (*Bufonariella*), and markedly less so in both than in *Ficus*. In *Tutufa* the external surface of the hypobranchial gland exposed in the mantle cavity is composed of a large, irregularly and closely folded area on the dorsal side of the rectum, with a less well differentiated, only slightly thickened, red-brown, closely folded area in front, between the anus and the excurrent siphon. The gland is the same length as the rectum in all species, and thus differs markedly in length between species. In *Bursa* (*Bufonariella*) the gland is composed of a flat, markedly thickened, sharply edged, pale red-brown area between the rectum and the ctenidium, with its surface only weakly folded, and with the area in front of the anus only weakly differentiated from the rest of the mantle. The rectum and, in the male, the vas deferens lie between the hypobranchial gland and the foot. The rectum is smooth-walled and ends in a simple anal pore on a short, free, tubular section of rectum, and is slightly broader in *Tutufa* than in *Bursa* (*Bufonariella*). The anus is situated well anteriorly, half way down the level of the osphradium, in *T. rubeta*; well posteriorly, half way between the osphradium and the back of the mantle cavity, in *T. bufo*; at the same level as the anterior end of the osphradium (which is placed more posteriorly than in the other species) in *T. oyamai*; and half way down the relatively very large, posteriorly placed osphradium, and thus two thirds of the distance from the back of the mantle cavity towards the anterior, in *Bursa* (*Bufonariella*) *ranelloides humilis* (mantle missing from all three specimens of *T. bubo*).

In all species the black-surfaced, pleurembolic proboscis is short, broad and pleated into an anterior point when fully retracted, but may be up to three times its contracted length when expanded, and when fully expanded has a transversely flattened, disc-shaped tip with a marginal rim (Fig. 1b, c) as in *Tonna*. In a few observed specimens of *T. rubeta* and *T. bubo* the lateral edges of the proboscis tip were flattened and extended into small lateral lips similar to the relatively larger ones of *Bursa* (*Bufonariella*) *granularis* (Lamarck) figured by Houbriek and Fretter (1969, p.424, fig. 4), and probably such lips can be formed at will by all species of *Tutufa*. The base of the proboscis is attached to the body wall by a ring of closely packed, overlapping, approximately parallel, narrow longitudinal muscles in all species, and in the large *T. (Tutufa) bufo* and *T. (Tutufa) bubo* (but not in *Tutufella*) these are aided by a pair of larger longitudinal muscles that extend further into the cephalic cavity than the other proboscis muscles, one on each side of the proboscis. The base of the proboscis is regularly rounded and not folded in all species of *Tutufa*, but bears a single regular, deep, narrow, and apparently permanent dorsal groove in the two dissected specimens of *Bursa* (*Bufonariella*) *ranelloides humilis*.

The large, weakly bilobate, fused cephalic ganglia lie across the oesophagus immediately behind the proboscis, and the nerve ring and lateral nerve plexi are prominent in all species. The mid-oesophagus turns slightly to the right and is then

straight and simple, running along the right edge of the floor of the cephalic cavity. Its anteriormost third, from shortly behind the nerve ring, is expanded into the large, saccular, smooth, thin walled, internally deeply pleated oesophageal gland. There is some evidence that the shape of the gland and the presence or absence of small folds in the oesophagus at its posterior end might be useful taxonomic criteria, but dissection of a large amount of similarly-expanded and similarly-preserved material would be needed to confirm this.

Behind the nerve ring most of the cephalic cavity is filled by the large, thin-walled, wrinkled, cream-coloured accessory salivary glands. The true salivary glands are relatively small, equidimensional, medium brown bodies; the right one is centro-dorsal immediately behind the cephalic ganglia and of similar size to them, partly enveloped by its two attached accessory glands; the left one lies on the left side alongside the right one to well behind it (the position depends on the degree of extension of the proboscis; in all Bursidae dissected with the proboscis well everted the left salivary gland and its attached accessory gland were markedly posterior). The left accessory gland is much the longest and is narrowly triangular, filling the cephalic cavity behind the other salivary glands, and terminating with its pointed tip in the posterior end of the cavity. The right salivary gland has attached one large and one small accessory gland in all Bursidae examined, the left one much the larger, although only half the size of the left accessory gland; the right one is a small triangular body only about twice the size of the true salivary gland and filling the anteriormost right corner of the cephalic cavity behind the proboscis. In all species the salivary ducts lie alongside the anterior oesophagus and open into the buccal cavity shortly behind the mouth, alongside the odontophore.

The posterior oesophagus passes through the body wall at the back of the cephalic cavity, past the renal gland and pericardium, and joins the stomach through a well-marked sphincter at its anterior end. The cardiac arm of the stomach is a long, narrow, cigar-shaped body with finely and longitudinally pleated, muscular walls, about four to five times as long as its greatest width, passing gradually into the pyloric arm in most species examined but in *T. (Tutufa) bufo* constricted markedly immediately in front of its posterior bend by strongly thickened muscles in the wall. The stomach bends sharply around into the pyloric arm, only half to two-thirds the width of the cardiac arm, only slightly shorter than the cardiac arm, tapered gradually throughout its length to merge imperceptibly into the intestine with no recognisable style sac or terminal sphincter, and with muscular walls whose fine, close, longitudinal pleats continue into the intestine. The anterior digestive gland duct lies in the bend at the posterior end of the cardiac arm. The posterior digestive gland duct lies on the left edge of the venter of the pyloric arm a third of its length from its posterior end, and in all species a small, very narrow typhlosole runs along the left edge of the pyloric arm from the anterior digestive gland duct into the posterior digestive gland duct (major typhlosole, t1?) and from the posterior digestive gland duct forward into the intestine (minor typhlosole, t2?). In almost all bursids examined there is no typhlosole in the cardiac arm, but in *T. (Tutufa) bufo* a prominent fold in the floor of the posterior third of the cardiac arm passes obliquely into the anterior digestive gland duct and is assumed to be an anterior typhlosole. Stomachs of *T. bubo* were not available for dissection, but it seems likely that the constricted base of the cardiac arm and the typhlosole in *T. bufo* are features confined to the subgenus *Tutufa* s. str. and differentiating it from *Tutufa (Tutufella)*. In *T. bufo*, also, the cardiac arm has entirely pleated surfaces, whereas in *T. (Tutufella) rubeta*, the cardiac arm has pleats on its lateral and dorsal walls only, and the anterior end, and in *T. (Tutufella) oyamai* the cardiac arm is entirely smoothly lined (possibly partly because dissected stomachs were distended with unidentified comminuted animal tissue). In all species of *Tutufa* and in *Bursa (Bufonariella) ranelloides humilis* the intestine is straight

from stomach to rectum.

In *Bursa (Bufonariella) ranelloides humilis* the stomach (Fig. 10) is smooth and unpleated throughout, apparently lacking typhlosoles also, and has the two digestive gland ducts situated close together near the bend of the stomach, the anterior in the posterior end of the cardiac arm and the posterior in the posterior end of the pyloric arm, separated by a low rounded ridge. A weak differentiation between oesophagus and stomach is probably not a sphincter. Similarly, the stomach of *Bursa (Bufonariella) granulis* (Fig. 1 m) and *Bursa (Bursa) bufonia* (Fig. 1a) lack anterior sphincters and both digestive gland ducts lie near the bend of the stomach, but both species have a small, narrow typhlosole running back down the pyloric arm from the anterior digestive gland duct. *Bursa (Bufonariella) granularis* is unique among the bursids examined in having a well-marked S-shape bend in the intestine, similar to the larger bend of *Tonna*.

In the large *Tutufa bufo* and *T. bubo* the vas deferens is open as a seminal groove for its entire length, and deeply and obviously open along the penis, whereas in the smaller *T. rubeta*, *T. oyamai* and *Bursa ranelloides humilis* the vas deferens is closed for its entire length, and its course along the penis is visible only as a smooth, faintly raised zone. In *T. bufo* the penis is long and narrow, tapers slightly from base to tip, and has thick, rounded, anterior and posterior edges. In *T. rubeta* the penis has a narrow base and broadens sharply just above the base, then tapers slightly to the tip, and whereas the anterior edge is thick and rounded the posterior edge is thin. In *T. oyamai* the penis has a thin posterior edge as in *T. rubeta* but broadens slightly over the inner two thirds of its length, tapering again slightly over the outermost third. In *T. bubo* the penis is parallel-sided, with a rounded tip and a weakly narrowed base, and with a thin posterior edge as in *T. rubeta* and *T. oyamai*. The penis of *Bursa (Bufonariella) ranelloides humilis* contrasts strongly with those of species of *Tutufa* in having a narrow base and broadening gradually along its length to a broadly rounded, paddle-shaped tip with both anterior and posterior edges thin. In all Bursidae the vas deferens ends at a small, narrowly pointed papilla.

The existence of an open seminal groove in the large species *T. bubo* and *T. bufo*, and presumably also in the closely related *T. bardeyi*, seems to be a fundamental difference from the closed vas deferens of *T. rubeta* and *T. oyamai*, and as it is associated with a minor difference in size and consistent differences in colouration of the cephalic tentacles and in the extent of plication of the columella, it seems best to segregate the species with the two types of vas deferens in two subgenera of *Tutufa*.

The penis of mature *Bursa (Bursa) bufonia* (Gmelin) is flattened and parallel-sided, relatively long and very narrow, only about four times as wide as the closed vas deferens (WAM.835-71, Flying Fish Cove, Christmas Island). A juvenile specimen from Luzon, Philippines with a small, tapered penis and open seminal groove was discussed under the generic diagnosis. Of 14 badly dehydrated specimens of *Bursa* species with black aperture from Batangas Province, Luzon, Philippines (J. E. Norton Colln., Western Australian Museum, WAM.497-69) the one male has a closed vas deferens. Two specimens of *Bursa (Lampadopsis) rhodostoma* (Sowerby) (Batangas Province, Luzon, Philippines, WAM.495-69; Bataan Prov., Luzon, WAM.1909-69) were both female. *Bursa (Bufonariella) granularis* (Lamarck) has an extremely long, narrow, parallel-sided penis with rounded edges, little more than twice the width of the closed vas deferens (W. of Pt. Cloates, N. Western Australia, on reef, Sept. 1968, W.A.M. Nigaloo Expedition, WAM. 841-71; 11 specimens, 2 small ♂, 9 small to large ♀). The three male specimens seen of *Bufonaria margaritula* (Deshayes) have a long, narrow, cylindrical penis only about twice the width of the open seminal groove (9 miles at 125° from Bongao Light, Tawi Tawi Bay,

Sulu Archipelago, 1 small ♂, WAM. 839-71; Tayabus Bay, W. Quezon Province, Luzon, Philippines, J. E. Norton colln., WAM. 678-70, large suite; of 8 removed from shell, 6 ♀ and 2 ♂). A single male of *Bufo naria nobilis* (Reeve) from m.v. "Pele" Mariel King Memorial Expedition stn. AH1/5, near Tg. Bt. Kapal, Haruku Is., E. of Ambon I., Indonesia, 82-88 m (WAM. 616-74) has a long, narrow flattened, parallel-sided penis about three times the width of the central, swollen, closed vas deferens. The existence of both an open seminal groove and a closed vas deferens in different species of *Bufo naria* requires further investigation.

The numbers of male and female specimens seen during this study suggest that populations of Bursidae have a sex ratio markedly dominated by females (more than 3 ♀ : 1 ♂ in large suites).

Radula

The radula of *Bursa (Bursa) bufo nia* (Gmelin) (Fig. 2a) has a relatively small, low central tooth with a shallowly embayed base, wide basal limbs, small, sharply triangular, basal interlocking processes, and a large, long, narrow, sharply pointed main cusp with one to four small, hooked denticles on each side of its base, the number of denticles varying greatly from one tooth to the next and between the two sides of each tooth. The lateral teeth are large and heavily built, with a long, narrowly pointed cusp bent relatively gently down from the base, with a large, square, high base, and with one to three minute denticles on the outer edge of the cusp and none on the inner edge. The marginal teeth are smooth and gently curved, and the inner has a relatively massive, square base whereas the outer has a small base.

The radula of *Bursa (Bufo nariella) ranelloides humilis* (Figs. 2b, 4j, 5a) is similar to that of *B. (Bursa) bufo nia* in that the base of the central tooth is shallowly embayed and the interlocking processes are relatively small and triangular. It differs from that of *B. (Bursa) bufo nia* in having a smaller and narrower cusp, narrower dorsal portion of the base, and larger denticles on the central tooth, a markedly more strongly hooked lateral tooth with a smaller, narrower base, more numerous denticles on the outer edge and a single small denticle on the inner edge, and (as in all other bursids examined) a lighter base of the inner marginal tooth.

Radulae of all species of *Tutufa* differ from those of *B. (Bursa) bufo nia* and *B. (Bufo nariella) ranelloides humilis* in having the base of the central tooth markedly more deeply embayed, so that the basal limbs are relatively long, widely spaced, and narrow, and in having longer and narrower interlocking basal processes. The lateral teeth are still more strongly hooked than in *B. (Bufo nariella)* and have similarly small bases, and differ from those of all other bursids examined, or figured by other workers, in having highly varied, but usually numerous denticles on both inner and outer edges, those on the inner edge being visible only through the tooth in normal orientation, and not merely a small inner denticle protruding towards the mid-line of the radula as in *B. (Bufo nariella)* and most other bursids. Lateral teeth are similar to those of *B. (Bufo nariella)*. Individual specific features are discussed below.

Subgenus **Tutufa** sensu stricto

Tutufa (Tutufa) bardeyi (Jousseume, 1894).

Figs 9a, b, d; 10a, d

Lampas bardeyi Jousseume, 1894:100 (reprint p.3), "Golfe d'Aden".

Bursa (Tutufa) rubeta var. *gigantea*. — E. A. Smith, 1914:230, pl. 4, Fig. 5 (shells from Muscat only).

Bursa (Bufonaria) rubeta var. *bardeyi*. — Bayer, 1932:231.

Shell extremely large, up to 360 mm long, i.e. reaching a larger size than any other species of *Tutufa*. Spire relatively tall, of straight outline, tapering regularly to a narrow apex (tip eroded in all specimens seen). External sculpture of low, broad, extremely ill-defined spiral cords, about eight between periphery and neck on last whorl; interstices filled by one or two low, relatively narrow spiral cords; strongly concave shoulder bears three or four low, ill-defined, relatively narrow spiral cords. Spiral cord at periphery raised into sparse, large, anterioposteriorly compressed, well-rounded nodules, with interspaces wider than the nodules; nodules increase in size over each intervariceal space, so that they are largest immediately before each varix. Major spiral cord below periphery raised into lower, sparser, more gently-rounded nodules than those on peripheral row. Shell surface otherwise smooth and lightly polished to weakly malleated in unencrusted individuals. Outer lip varix weak, the slightly flared thin lip edges forming main part of varix of most specimens seen; outer lip extremely flared and varices on spire flared in one old individual. Interior of outer lip uncallused and wrinkled in conformity with exterior spiral cords in most specimens; bearing a narrow noduled ridge in juveniles; thickened but only weakly noduled in the one old individual seen. Inner lip moderately broadly flared, with a thin columellar shield projecting to the left, well-callused in parietal region to form a projecting pad at posterior end of aperture, constricting the prominent, relatively long, widely open anal canal. Parietal region bearing a thin, raised, callous ridge in most specimens, thickened to a nodule in one old individual; below parietal ridge bearing relatively few, sparse, weakly anastomosing, narrow plicae in juveniles, plicae gradually becoming weaker as shells grow so that large specimens bear a few weak denticles low on inner lip, and the one old individual has a thickened inner-lip shield and only a small irregularly wrinkled area on the lower part of the lip. Aperture white. External colour of unencrusted specimens light to medium reddish-brown, maculated with dark reddish-brown between nodules and in corresponding positions on uppermost three or four major spiral cords, the whole crossed by ill-defined wavy, fawn axial streaks. Animal not seen; operculum dark brown, thick, elongate-oval, with nucleus at between half and one-third the height and situated near the abaxial margin.

DIMENSIONS: Height 348 mm, diameter 221 mm, height aperture + canals 227 mm (BMNH 1899.12.27.8, the specimen figured as "*Bursa (Tutufa) rubeta* var. *gigantea*" by E. A. Smith, 1914, pl. 4, Fig. 5); height 270 mm, diameter 168 mm, height aperture + canals 153 mm (WAM, from East Aden Protectorate); up to 360 mm in height (E. A. Smith, 1914, p.230), up to 380 mm (type) or even 400 mm (Jousseume, 1894, pp.98, 100).

TYPES: Jousseume (1894, p.98) stated that the 400 mm x 250 mm specimen of *Tutufa bardeyi* "figure déjà dans les galeries du Muséum", and it is assumed that this and the holotype (p.100) are in the Muséum National d'Histoire Naturelle, Paris.

REMARKS: *Tutufa bardeyi* is the form included under *Bursa (Tutufa) rubeta* var. *gigantea* by E. A. Smith (1914, p.230; pl. 4, Fig. 5 only) about which he commented "they appear to have less of the tubercular sculpture shown in Reeve's figure (Reeve 1844a, pl. 9, Fig. 30a, of the lectotype of *gigantea* E. A. Smith = neotype of *bubo* Linnaeus). The two huge specimens available to Smith, from Muscat, Gulf of Oman (BMNH 1899.12.27.8, Fig. 9a, d (Smith's figured specimen, examined by the writer) and 1899.12.27.9, Fig. 9b) are eroded and heavily encrusted with foraminifera, bryozoa, polychaete tubes, calcareous algae, and bivalves (*Plicatula*, *Chama*, byssal plugs of *Anomia*) and bored by lithophagine

bivalves, and the very smooth, brightly coloured surface is visible only on smaller specimens and unusually clean individuals (e.g. Fig. 10a, d).

Tutufa bardeyi differs from other species of *Tutufa* in its larger size, more straight-sided spire, more weakly sculptured inner lip, less thickened and more weakly noduled interior of the outer lip, and very much weaker external sculpture. The white aperture is found also in *T. oyamai* and *T. tenuigranosa* which, however, have strongly plicate inner lips. The nearly smooth inner lip is perhaps nearest to that of *T. bubo* which, however, is pink and bears sparse plicae over most of its height, and that of *T. bufo*, which has a red ring around the narrowest part of the aperture. The light to dark reddish-brown colour pattern is markedly brighter than those of almost all other species, and resembles that of *Charonia lampas*. Only occasional specimens of *T. rubeta* have a brighter colour.

Jousseume's (1894, p.100) original description is meagre: "*Lampas Bardeyi*. Testa gigantea (R. Lampas Lam. simillima), costae spirales laevigatae; labrum intus laevigatum, extus expansum, nec varicosum. Alt. 380; diam. maj. 250; min. 180 millim. Hab. Golfe d'Aden", and also (p.98) "*Lampas Bardeyi*, coquille gigantesque qui peut atteindre 40 centimetres de long sur 25 de large; un tres bel exemplaire donné par moi figure déjà dans les galeries du Muséum". The description of the very large size, smooth spiral ribs, and smooth interior of the aperture, together with the comparison with "*Ranella lampas*" (the name Jousseume consistently used for *Tutufa bubo* of this paper) leave no doubt of the identity of the present species with Jousseume's name.

DISTRIBUTION: This apparently rare and almost forgotten species occurs in the north-western Indian Ocean, and probably the Red Sea, from Kenya to at least the Gulf of Oman. Throughout its range it is sympatric with *T. bubo*. Most specimens in collections have been supplied by Dr Don Bosch, American Mission in Muscat, and his generosity to malacologists of the world is acknowledged.

LOCALITIES: "Golfe d'Aden", type (Jousseume, 1894, p.100); Bir Ali and Mukalla, East Aden Protectorate, coll. R. W. George, April 1963 (WAM); Muscat, Gulf of Oman, old individual with thickened, flared aperture, BMNH 1899.12.27.9; Muscat, Gulf of Oman, specimen figured by E. A. Smith (1914, pl.4, Fig. 5), BMNH 1899.12.27.8; Melindi, Kenya, collected alive 1970 (juvenile), BMNH; "Jeffrey's Bay, eastern Cape Province, South Africa", coll. Mrs A. C. Davies, 1964 (almost certainly collected near Mogadiscio, Somalia, where Mrs Davies lived for two years), juvenile, NZGS, WM.10548; Muscat, Oman, NZGS, WM.11582, coll. & pres. D. T. Bosch; Muscat, Oman, USNM 657394, coll. & pres. D. T. Bosch; Muscat Oman, coll. & pres. D. T. Bosch, growth series in American Museum of Natural History.

***Tutufa (Tutufa) bufo* (Röding, 1798)**

Figs 1d, g, p; 2c; 5b, c, f; 6; 11a, c-f; 12a, g

Tritonium bufo Röding, 1798:128 (refers to Martini, 1780, 4, pl.129, Fig. 1238).

Triton lampas.— Lamarck, 1822:180; Kiener, 1842, *Triton*: pl.5, Fig. 1; Reeve 1844a, *Triton*: pl.10, Fig. 30b (only); Lischke, 1869:47; Lischke, 1871:34; Lischke 1874:29; Kobelt 1871:175, pl.37, Figs 3, 4; Kobelt 1878: pl.9, Fig. 2 (not of Linnaeus, 1758).

Bursa (Lampas) hians.—Angas, 1877:179 (Macleay R., N.S.W.) (not of Schumacher, 1817).

Ranella lampas.— Tryon, 1881: pl.19, Fig. 12.

Tritonium lampas var.— Dunker, 1882:31.

Tutufa (Crossata) californica.— Suter, 1906:328 (not *Ranella californica* Hinds, 1843).

Argobuccinum siphonatum.— Iredale, 1910:73 (not *Ranella siphonata* Reeve, 1844).

Bursa (Tutufa) rubeta var. *lissostoma* E. A. Smith, 1914:230, pl.4, Fig. 3.

Bursa bubo.— Vanatta, 1914:80 (in part).

Bursa siphonata.— Oliver, 1914:528 (not *Ranella siphonata* Reeve, 1844).

Bursa bufo.— Hedley, 1916a:42; 1918:67.

Bursa (Tutufa) bufo.— Kira, 1955:43, pl.21, Fig. 20; Kira 1961:55, pl.21, Fig. 20; Kira 1962:57, pl.22, Fig. 20.

Tutufa lissostoma.— Iredale, 1931:214, pl.23, Fig. 5; Okutani, 1970:124, pl.8, Fig. 1; Kuroda, Habe & Oyama 1971:134, pl.34.

Tutufa bufo.— Iredale & McMichael, 1962:55; Oyama & Takemura 1963: *Tutufa* pl.2, Figs 2-4; Powell, 1967:189, pl.36, Fig. 8 (New Zealand); Wilson & Gillett, 1971:80, pl. 50, Fig. 1.

Bursa bubo forma *lissostoma*.— Cernohorsky, 1972:118, pl.32, Fig. 7a.

Bursa bubo lissostoma.— Powell, 1974:205.

Shell to ca. 180 mm high, i.e., the smallest species in the subgenus, with short spire, large oval aperture, almost completely smooth inner lip, and pale flesh pink to white aperture bearing a dark brownish to bright red ring around the most narrowly constricted area, immediately inside the flared inner and outer lips. External sculpture of three major rows of anteroposteriorly compressed nodules, those of the uppermost row the largest, narrowly rounded, and protruding as particularly large nodules on varices; remainder of surface sculptured with closely spaced rows of variable, low and obscure to coarse and prominent rugae. Outer lip strongly flared, its outer edge digitated by exterior ribs, bearing eleven or twelve low, narrowly rounded nodules at innermost edge of flare. Inner lip widely flared, with parietal callous pad constricting large, protruding anal siphon and with about three to six low plicae at base of columella, otherwise smooth. Anterior siphonal canal short, curved strongly to the right, so fasciole is large, prominent, and coarsely rugose. Exterior pale reddish fawn to brown, mottled in varied patterns of small, irregular, medium red-brown splashes.

DIMENSIONS: Height 106.5 mm, diameter 65.5 mm (lectotype of *Bursa (Tutufa) rubeta* var. *lissostoma* E. A. Smith); height 135.0 mm, diameter 78.4 mm (WM 10744, Wedge I., WA, NZGS); height 129.8 mm, diameter 84.7 mm (WM 10743, crayfish pot off Rottneest I., WA, NZGS).

TYPES: The holotype of *Tritonium bufo* Röding, 1798, is the specimen figured by Martini (1780, vol. 4, pl.129, Fig. 1238). Its whereabouts are not known to me.

The specimen of *Tutufa (Tutufa) bufo* (Röding) figured by Smith (1914, pl.4, Fig. 3) as *Bursa rubeta* var. *lissostoma* Smith, lodged in the British Museum (Natural History), reg. no. 197384, and figured in colour by Reeve (1844a, pl.10, Fig. 30b) is here designated the lectotype of *Bursa rubeta* var. *lissostoma* E. A. Smith, 1914. The locality was designated by Kuroda, Habe & Oyama (1971, p.134) as Madagascar.

VARIATION: *Tutufa bufo* is quite variable in external sculpture, and some particularly short specimens have coarsely rugose and nodular external sculpture, with a mottled medium and light brown colour pattern. In collections examined almost all such shells came from New Caledonia or Mocambique, but a single short, very coarsely sculptured specimen from Townsville, Queensland, in the Australian Museum (C. 66562)

is not distinguishable from New Caledonian shells. Many intermediates exist in the collections examined, and the coarsely sculptured shells are assumed to be part of the normal genetic variation of *T. bufo*.

REMARKS: *Tutufa bufo* differs from *T. bardeyi* in its markedly smaller size, its heavier build, its larger and more elongate aperture associated with a relatively broader last whorl and relatively shorter and broader spire, its prominent row of large, sharp nodules around the shoulder, its markedly coarser external spiral and axial sculpture, its pale fawn to pale marbled reddish-brown colour pattern, and, most notably, by its pale flesh pink to white aperture with a deep red to bright red ring around the most narrowly constricted area of the aperture and with broadly flared lips, the inner completely smooth and the outer bearing one row of low modules. The red ring in the aperture is the most distinctive feature and is found only in this species. It differs from *T. bubo* in its smaller size, its larger aperture, its shorter spire, its smoother inner lip, and in bearing the red ring in the aperture; many specimens of *T. bubo* and *T. bufo* are similar in external colour and sculpture, and juvenile specimens of the two species are difficult to distinguish. It differs from *T. rubeta* in its larger size, its markedly smoother exterior, its shorter spire, its paler colour, in the inner lip being smooth rather than coarsely plicate, and in the interior of the outer lip bearing one row of nodules of the same colour as the lip rather than two prominent rows of pale nodules on a deep red background.

NOMENCLATURE: This is the form named *Bursa (Tutufa) rubeta* var. *lissostoma* by E. A. Smith (1914). Vanatta (1914) first suggested that it is a distinct species from *T. rubeta*, and used the name *bubo* Linnaeus for it. Hedley (1916) questioned Vanatta's identifications of the figures cited by Linnaeus, and introduced the name *bufo* Röding for this species.

Röding (1798, pl.128) cited for *Tritonium bufo* the figure by Martini (1780, vol. 4, pl.129, Fig. 1238). The large figure clearly shows the flaring lip, smoother inner lip, large fasciole, and relatively broad last whorl of the species called *B. rubeta* var. *lissostoma* by E. A. Smith (1914), and the newly coloured copy of this figure given by Kuester & Kobelt (1871, pl.37, Fig. 3) clearly shows the relatively smooth outer surface, the large shoulder nodules, and the red ring around the most constricted portion of the aperture that characterise this species.

The similar names *bubo* and *bufo* have long troubled taxonomists. Linnaeus (1758, p.748; 1767, p.1216) spelled the name *bubo* in both binominal editions of "Systema Naturae", and the spelling is evidently not in error. Dr H. A. Rehder (in litt.) pointed out the words' different etymologies, *bubo* signifying the European horned owl and *bufo* a toad, so that the names are different words. Smith (1914, p.227) and Dodge (1957, p.104) noted that Röding "wrote *bufo* instead of *bubo*, a change suggested by Chemnitz as being a typographical error in the Systema". They evidently considered that Röding (1798) intended *T. bufo* to be the same species as *T. bubo* (Linnaeus), and Smith (1914) regarded them as so. Recently Kuroda, Habe & Oyama (1971, p.135) returned to this point of view, although they applied the name *bubo* to the large, coarsely noded, pink-mouthed shell here called *T. bubo*, and used *T. lissostoma* (E. A. Smith, 1914) for the species here called *T. bufo*. Their action cannot be upheld as there can be no doubt that the figure cited by Röding (1798) is of the species with the red-ringed aperture. In at least two recent works (Oyama & Takemura 1963; Wilson & Gillett 1971, p.80) the names *bufo* and *bubo* have been used for different species, and so it is proposed to follow the suggestion by Rehder (1974) and stabilise the name *Tutufa bufo* (Linnaeus) for the species named *Bursa rubeta* var. *gigantea* by E. A. Smith (1914), leaving *T. bufo* (Röding) as the name for the species named *Bursa rubeta* var. *lissostoma* by E. A. Smith (1914).

ECOLOGY: Around Australia, New Guinea and New Zealand, specimens of *Tutufa bufo* have not been collected in shallow water, or at all on the offshore islands of the Great Barrier Reef. Specimens have been taken quite commonly alive at times in depths of about 20 to 80 m by scuba divers collecting on rock reefs, such as the suite collected at Osbourne Shoals, Cronulla, Sydney by Mr N. Coleman, and specimens collected at the Poor Knights Islands in New Zealand. Live specimens have also been taken in small numbers consistently over many years by fish and prawn trawlers in depths of about 80 to 150 m from the continental shelf of eastern and western Australia, from about Sydney to Moreton Bay and Fremantle to Houtman's Abrolhos Islands, and lately in northern New Zealand as far south as the Bay of Islands, i.e., wherever extensive fish and prawn trawling has been carried out around northern Australia and northern New Zealand, and thus probably occur throughout the Indo-West Pacific in this habitat.

EGG MASS: Along with several live animals of *T. bufo* from rocks in about 30 m off Osbourne Shoals, Cronulla, Mr N. Coleman collected an egg-mass, now in the Australian Museum (C. 73465). The mass consists of 48 large, simple, elongate capsules, closely packed together but without regular arrangement, on a simple basal membrane. Each capsule is parallel-sided, approximately 23 mm long and 4 mm wide, flattened laterally, with a few low, irregular, ill-defined folds in the walls, and its outer end is hemispherical. All are about 60-70% filled with relatively large, oval eggs, clearly visible to the naked eye, and consisting almost entirely of bright yellow yolk cells. Eggs measured with a micrometer eyepiece were 0.3-0.4 mm in greatest diameter.

In arrangement and simplicity of the capsules, the egg mass of *T. bufo* resembles those of *Argobuccinum pustulosum tumidum* (Dunker) and *Fusitriton magellanicus laudandus* Finlay. However, capsules of *Argobuccinum* and *Fusitriton* are shorter than those of *Tutufa bufo*, and have flat tops with right-angled edges (see also Laxton, 1969, p.250, pl.2). Egg capsules of two other species of Bursidae have been described. That of *Bursa (Bufonariella) corrugata* (Perry) figured by D'Asaro (1969, p.352, Fig. 1A) and those of two specimens of *Bursa (Bufonariella) granularis* (Perry) observed by me in the Western Australian Museum are quite unlike that of *Tutufa bufo* and closely resemble the highly organised, hemispherical masses formed by such Cymatiidae as *Cabestana spengleri* (Perry) and *Septa parthenopea* (von Salis) (see Laxton, 1969, p.250, pl.1). They contain stalked capsules of triangular section arranged in concentric rows inside a hemispherical basal membrane resembling the skin of half an orange. Cernohorsky (1967, p.313, Fig. 2) figured the egg-mass of *Bursa (Bufonariella) granularis* as a very different structure. Relatively short, simple capsules are sparsely set on end in a translucent, oval, gelatinous mass with vertical edges and a concave top; this was probably the egg-mass of a less highly evolved mesogastropod on which the specimen of *C. granularis* was feeding. As *Charonia* has the same poorly organised type of egg-mass as *Tutufa* (Laxton, 1969, p.250) and as that of *Distorsio* is still more simplified than any described here (D'Asaro, 1969, p.369, Fig. 11), tonnacian egg-masses will probably prove to be useful taxonomic criteria when more are described.

RADULA: The radula of *Tutufa (Tutufa) bufo* (Figs. 2c, 5b, c, f) has a relatively low, broad central tooth with relatively broad basal limbs, and has from three to six hooked denticles on each side of the base of the main cusp, the number varying greatly from tooth to tooth and from side to side of one tooth. The lateral tooth has a strongly hooked cusp with numerous but highly varied, hooked denticles on both inner and outer edges.

DISTRIBUTION: *Tutufa bufo* is relatively common on the continental shelf of Western Australia as far south as Cape Naturaliste (Wilson and Gillett, 1971, p.80) and on the continental shelf of eastern Australia to a little south of Sydney, on both coasts as far

north as trawling is carried out. Presumably the lack of specimens from northern Australia merely reflects a lack of sampling. It occurs at Lord Howe I., and has been recorded on several occasions as a beach shell at Raoul I. in the Kermadec Islands (Suter, 1906, p.328; Iredale, 1910, p. 73; Oliver, 1914 p.528). Three living specimens were trawled recently off Raoul I. in 110-120 m by Dr F. M. Climo, N.Z. National Museum, from A. Black's R.V. "Acheron". Recently the species has been collected sparsely in northern New Zealand (first recorded by Powell, 1967, p.189). Elsewhere it is recorded from "south of central Honshu, at 10-20 fathoms (18-36 m) depth" (Kira, 1962, p.68) and "Honshu (Boso Peninsula as northern limit), Shikoku and Kyushu . . . On rocks and gravels from 10 m to 50 m deep" and from Sagami Bay (Kuroda, Habe & Oyama, 1971, p.134) in Japan; "Indian Ocean, Madagascar, Red Sea" (E. A. Smith, 1914, p.230); Bouganville, Solomon Islands (Powell, 1967, p.189); Nagasaki, Japan, and Manila (Lischke, 1869, p.47, referring to Reeve, 1844a, fig. 30b); Seychelles Bank, Indian Ocean (Okutani, 1970, p.124, pl. 8, fig. 1); and Dar es Salaam (Spry, 1968, p.18). Lischke (1869, p.47; 1871, p.34; 1874, p.29) and many other early workers recorded "*Triton lampas*" from a large range of localities, but it has usually not been possible to determine which species of *Tutufa* was referred to in each record. No specimens of *T. bufo* were taken by the M.V. "Pele" Mariel King Memorial Expedition to the Moluccas, or by the earlier M.V. "Pele" expedition to the Sulu Archipelago, or in J. E. Norton's extensive collecting in the Philippines (all material from these three examined in the Western Australian Museum) but this probably merely reflects lack of trawling on the continental shelf. A single specimen has recently been recorded from Hawaii (Fair 1973).

The southernmost specimens seen from the western Indian Ocean are both the short-spined, coarsely sculptured form: low spring tide mark, among rocks in reef, west shore Quissirua Jamal, North-East Islands, Conducia Bay, Moçambique, leg. K. Grosch (NM, H117), the sole specimen seen with weak plicae over whole height of columella; 1 m below low spring tide mark, north of Chacos, southwest Conducia Bay, Mocambique, leg. K. Grosch (NM, H118).

LOCALITIES: Australia: 4 alive, 27 m off Osbourne Shoals, Bate Bay, Cronulla, NSW, 22 March 1970, N. Coleman (C 73465, AM); "Triton" dredgings, Sydney Harbour, NSW, Capt. Comtesse, 3 shells recorded by Iredale (1931, pl.23, fig. 5) (C 57794, AM); 24 m, off Shark Pt., Clovelly, NSW, 1966, N. Coleman (C 72751, AM); off Ballina, NSW, AM Swain Reefs Exped., 1962 (C 106123, AM); fish trap off Port Macquarie, NSW, pres. T. A. Garrard (C 106119, AM); fish trap off Trial Bay, NSW, April 1960, pres. J. Kerslake (C 106121, AM); same data., WAM; 9 m, on rocky reef top, off Palm Beach, Gold Coast, southern Qld, coll. J. Laxton (C 106523, AM); trawled in 55 m, off Wide Bay, Qld, T.A. Garrard Colln. (C 66570, AM); trawled off Tin Can Bay, Qld, pres. J. Kerslake (WAM); 130-180 m, north of Cape Moreton, Qld, T. A. Garrard Colln. (C. 64631, AM); off Moreton Bay, Qld, 79 m 27°27'22"S, 153°39'E, H.M.A.S. "Kimbla", 29 March 1969 (C 77065, AM); trawled off Southport, Qld, T. A. Garrard Colln. (C 106118, AM); 130-180 m, off Cape Moreton, Qld, A.W.B. Powell Colln. (AWBP 51224, AIM); Townsville, Qld, T.A. Garrard Colln. (short, coarsely sculptured shell — Fig. 11e, f) (C 66562, AM); 60 m, off Beagle I., WA, cray pots, Poole Bros., Dec. 1964 (WAM) Beagle I., WA, cray pots, Poole Bros., April 1962 (WAM); Beagle I., WA, cray pots, Poole Bros., 1964 (N 3958, WAM); 11-18 m, W of Flat I., near Long I., off Onslow, WA, B. R. Wilson on "Davena", 1960, Hawaiian W.A. Exped. (WAM); Onslow, WA, pres. I. Blair (C 90848, AM); 3 km S of Vlaming Head Lighthouse, NW Cape, WA, pres. L. Figgis (C 86156, AM); SE end of Dirk Hartog I., Shark Bay, WA, "Davena", 14 May 1960 (WAM. 949-69); 38 m, Middle channel, Houtman's Abrolhos Islands, WA, J. Seabrook, 1965 (WAM); Houtman's Abrolhos Islands, WA, F.R.V. "Lancelin", March 1963 (WAM); 65 m, off Green Head, WA, pres. Mr Baudain (N 751, WAM); cray pots in 130-160 m, Wedge I., WA, pres. J. Yates (WM 10744, NZGS);

CSIRO stn. 3, 28 Jan. 1964, 128-137 m, beam trawl, 30°06'S, 114°32'E, NW of Jurien Bay, WA (WAM); Jurien Bay, WA, pres. Mrs Parkin (WAM); Cray pots, Jurien Bay, WA pres. Mrs Dobbyn (N 3986, WAM); Cray pot, 4-5 m, Blackledge, WA, FRV "Lancelin", July 1963 (N 4099, WAM); Cray pots, Rottnest I., WA, pres. Mr & Mrs W. Back (WM 10743, NZGS); SW of Rottnest I., WA, 145-150 m, M. V. "Bluefin", 17 Sept. 1963 (WAM); HMAS "Daimantina" Stn. 4, W of Mandurah, 33°33'S, 115°4'E, 110 m, 23 Nov. 1970 (WAM); cray pots, 55 m, off Cape Naturaliste Reef, Poole Bros. on M.V. "Bluefin", March 1962 (WAM).

Lord Howe I.: Middle Beach, Lord Howe I., recorded by Hedley (1916, p.41) (C 29189, AM).

Kermadec Islands: Empty shells on beach, Denham Bay, Raoul I., T. F. Cheeseman, 1887 (AM 19183, AIM); Denham Bay, Raoul I., W. R. B. Oliver Colln. (MF 11381, NZNM); Raoul I., 75-85 m, "Galathea" Exped., 3 March 1952 (Powell 1967, p.189); BS 307, 3 live in 110-120 m, between Bell's Flat and Hutchinson Bluff, Raoul I., 4/4/1973, F. M. Climo & A. J. Black, R. V. "Acheron" (MF 22102, NZNM); BS 313, 1 empty, 150-200 m, NW of Raoul I., R.V. "Acheron", 4/5/1973 (MF 22122, NZNM).

New Zealand: Scuba dived in 30-45 m, Poor Knights Islands, off eastern Northland Peninsula, recorded by Powell (1967, p.189) and specimens in several private collections; in crayfish pots off coast north of Bay of Islands, in colln. Mr G. Clifford, Russell; Doubtless Bay, Northland, live specimens trawled in 90-110 m, in colln. Mrs E. Atkinson, Mangonui; several trawled in shallow water off Rangaungu Bay, Northland, in colln. Mr H. Seelye, Houhora; alive on *Zostera* flat opposite Paua, Parengarenga Harbour, Northland, with *Conus kermadecensis* (Powell 1974, p.205).

***Tutufa (Tutufa) bubo* (Linnaeus, 1758)**

Figs. 2d, 4a, 11b, 12f, 13, 14a, c-d.

Murex lampas Linnaeus, 1758:748 (in part, figure by Gualtieri, 1742, pl. 50, fig.D, only; Rondelet, 1555, p.81 (= *Charonia lampas*) was designated lectotype by Beu 1970, p.211); Hanley 1855:286 (in part).

Murex rana var. *bubo* Linnaeus, 1758:748.

Murex lampas var. *bubo*. — Linnaeus, 1767: 1216; Gmelin 1791:3532.

Triton lampas. — Lamarck, 1822:180 (in part); Reeve 1844a, *Triton*: pl.9, fig.30a (only); Lischke 1869:47 (in part); Lischke 1871:34; Lischke 1874:29.

Bursa lampas. — Schepman 1909:118.

Bursa (Tutufa) rubeta var. *gigantea* E. A. Smith, 1914:230, pl.4, fig. 4 (only).

Bursa bubo. — Vanatta, 1914:80 (in part); Hedley 1916a:42; Hedley 1922:165 (use as a trumpet); Cernohorsky 1967a:311, pl.42, fig.1; Cernohorsky 1967b:42, pl.1, fig.1; Cernohorsky 1972:118, pl.32, fig. 7 (only); Salvat & Rives 1975:307, fig. 178.

Bursa rubeta gigantea. — McMichael, 1960:78, fig. 159; Rippingale and McMichael 1961:69, pl.7, fig. 20.

Tutufa bubo. Oyama & Takemura, 1963: *Tutufa* pl.2, fig. 5; Habe & Kosuge 1966:46, pl.16, fig. 10.

Bursa lampas or *rubeta* var. *gigantea*. — Spry, 1968:18, fig. 121.

Shell reaching approximately 300 mm in height, i.e. the second-largest species in the genus, with moderately tall spire, strongly flared apertural lips, uniformly flesh pink to

white subcircular aperture, and moderately long anterior siphonal canal with large fasciole. External sculpture of three or more major rows of large, anteroposteriorly compressed nodules, on most specimens largest at periphery and particularly prominent on varices, last whorl of many specimens rendered biangulate by lower row of nodules being almost as large as peripheral ones; remainder of surface sculptured with many closely spaced rows of irregular, narrowly rounded rugae, rendering entire surface coarsely and irregularly nodulose. Outer lip widely flared, its outer edge digitated by external ribs, interior smooth on large adults but bearing a row of 12-14 small, sharp nodules on immature specimens. Inner lip widely flared, with a narrow parietal rib constricting the relatively short anal canal, plicated well inside aperture by low, widely spaced, simple plaits over entire height below parietal rib (Fig. 4a). Fasciole very prominent in a few specimens (Fig. 14a, d) but usually smaller than that of *T. bubo*. Exterior cream to pale brown, finely and irregularly maculated with medium to dark red-brown splashes.

DIMENSIONS: Height 254 mm, diameter 160 mm (neotype of *Murex rana* var. *bubo*); height 222 mm, diameter 125 mm (paralectotype of *Bursa rubeta* var. *gigantea*); height 195 mm, diameter 120 mm (off Southport, Qld, AM, C 69752); height 218 mm, diameter 141 mm (Fiji, NZNM, MF 18474).

TYPES: The neotype (designated below) of *Murex rana* var. *bubo* Linnaeus, also designated the lectotype of *Bursa rubeta* var. *gigantea* E. A. Smith, is in the British Museum (Natural History), No. 1974147; paralectotype of *B. rubeta* var. *gigantea* E. A. Smith also in BMNH, No. 1914.6.29.1.

Neotype and lectotype designations: Hedley (1916) was the first to suggest that the figure cited for *Murex rana* var. *bubo* by Linnaeus (Rumphius 1705, pl.28, fig.C) refers to the species named *gigantea* by E. A. Smith. Rumphius' pl.28, fig. C (available to me in later editions only) is a poorly drawn dorsal view, reproduced in reverse so that the shell appears sinistral, and could refer to almost any species of *Tutufa* (Fig. 12f). Rumphius (1742, p.60) gave the following description of this shell (free translation): "*Buccina tuberosa*, or knobby kinkhorn. This species is smaller than the preceding (*Buccina Tritonis*), usually only a hand long, wrinkled over the entire body and completely set with knobs, without lustre or elegance, of a dirty white colour, but rare to find, and therefore valuable. The interior is a beautiful white like porcelain, and here it is called Hector". This suggests that Rumphius was describing either the species here called *T. bubo*, or *T. oyamai* Habe. The two figures available to me (Rumphius 1711, pl.28, Fig. C; 1742, pl.28, Fig. C) differ markedly, the surface sculpture being shown more carefully as a markedly finer nodulation in the earlier edition. It is concluded that this figure cannot be certainly identified with a particular species, but probably refers to the species here called *T. bubo* as it is relatively common in shallow water in the Indo-West Pacific and has a pale, flesh-pink aperture that fades to white in many beach shells.

According to Dance (1966, p.53), "no authentic Rumphius shells are now known", and it can safely be assumed that the holotype of *Murex rana* var. *bubo* Linnaeus is lost. Dance (1967) listed species of Mollusca not represented in Linnaeus' collection, and although *Murex rana* is not listed, varieties were not considered for the list, and Mr S. P. Dance reports (*in litt.*, August 23, 1972) that there are no specimens of either varieties *bubo* or *rubeta* of *Murex rana* in Linnaeus' collection. Hanley (1855, p.284-5) also makes no mention of Linnaeus having specimens of the varieties of *M. rana*, and Rehder (1974) noted that the specimen identified as *Murex lampas* in the collection of Queen Ulrica of Sweden, worked on by Linnaeus (1764), is a specimen of *Ranularia lotoria* (Linnaeus, 1758). It is concluded that there are no shells in existence that could be considered

original type material of *Murex rana* vars. *bubo* and *rubeta* of Linnaeus, 1758, and as the cited figure is not identifiable, a neotype is here designated of *Murex rana* var. *bubo* Linnaeus.

The holotype of *Murex rana* var. *bubo* Linnaeus, the specimen figured by Rumphius (1705, pl.28, Fig. c), presumably came from the island of Ambon, in Indonesia. As is noted above, the shells included in *Bursa rubeta* var. *gigantea* by E. A. Smith (1914, p.230) include two large specimens of *Tutufa* (*Tutufa*) *bardeyi* (Jousseume), and the specimen figured as *Triton lampas* by Reeve (1844a, pl.9, Fig. 30a), which is also the large Philippine Islands shell from the Cuming collection, figured by Smith (1914, pl.4, Fig. 4) and refigured here (Fig. 13b, c). Smith discussed atypical features of the specimens of *T. bardeyi*, and therefore considered the specimen with coarsely nodular external sculpture and pale, flesh-pink aperture as typical of his "variety" *gigantea*. The specimen figured by Smith (1914, pl.4, Fig. 4) and in colour by Reeve (1844a, pl.9, Fig. 30a), lodged in the British Museum (Natural History), and bearing the register number 1974147, is here designated the lectotype of *Bursa rubeta* var. *gigantea* E. A. Smith, 1914. The locality is "Philippine Islands (found on the reefs)" (Reeve, 1844a, pl.9). As was suggested by Rehder (1974, p.12) the lectotype of *Bursa rubeta* var. *gigantea* E. A. Smith, 1914, is here designated the neotype of *Murex rana* var. *bubo* Linnaeus, 1758. The specimen was described by Smith (1914, p.230) and is figured here (Fig. 13b, c). Therefore the name *Murex rana* var. *bubo* applies to the large, coarsely nodulose shell with a pale, flesh-pink aperture, usually regarded as typical "*Bursa lampas*" and named *Bursa rubeta* var. *gigantea* by Smith (1914), leaving the name *Tritonium bufo* Röding, 1798, as the earliest name for the smaller species with a bright red ring in the aperture.

REMARKS: *Tutufa bubo* differs from *T. rubeta* and *T. bufo* in reaching a much greater size (up to about 300 mm), in its uniform pale pink aperture, in its taller spire than that of *T. bufo* and shorter spire than that of *T. rubeta*, in its inner lip bearing more sculpture than that of *T. bufo* but less than that of *T. rubeta*, in its extremely coarsely nodulose external sculpture, and in its colour pattern being paler than that of *T. rubeta*, although similar to that of *T. bufo*. From *T. bardeyi* it differs in its slightly smaller maximum size, its much coarser external sculpture lacking the polish of *T. bardeyi*, its markedly paler colour pattern, its slightly shorter spire and, principally, by the apertural features. The aperture of *T. bubo* is entirely uniform pale flesh-pink (fading to white in dead shells) with one row of low nodules inside the outer lip, lower than those of *T. bufo*, higher than those of *T. bardeyi*, and very different from the two prominent rows in *T. rubeta*; the inner lip is sparsely but prominently plicate on the parietal area and on the interiormost portion of the columella, whereas in *T. bardeyi* the white aperture has only a few faint plications on the columella, the red-ringed aperture of *T. bufo* has a smooth inner lip, and the uniform red aperture of *T. rubeta* has a strongly and closely plicate inner lip.

RADULA: The radula of *Tutufa* (*Tutufa*) *bubo* (Fig. 2d) is similar to that of *T. bufo*. The central tooth differs from that of *T. bufo* in its slightly taller form, slightly more deeply embayed base and narrower basal limbs, and in the highly irregular denticles being formed as serrations (often merely weak notches) in a thin flange alongside each edge of the main cusp. The lateral tooth is less sharply hooked than in *T. bufo* and has fewer, smaller denticles on the outer edge, and on the inner edge the denticles are formed as highly irregular serrations on a wide flange, as on the edges of the central tooth. In many teeth the flange on the inner edge is smooth.

ECOLOGY AND DISTRIBUTION: *Tutufa bubo* seems mainly to have been collected on coral reefs, usually below low tide by snorkeling or scuba diving but occasionally intertidally, and a few live specimens have been taken in trawls or dredges from sand substrates on the inner continental shelf of eastern Australia. During the M.V. "Pele"

Mariel King Memorial Expedition to the Moluccas (material examined at Western Australian Museum) only four juvenile specimens of *T. bubo* were obtained, one on an intertidal coral reef and three by dredging in 11-37 m. The only good, large, live-collected specimen from Australia in the Australian Museum was trawled off Southport, Moreton Bay, Queensland (depth not recorded). Occasional live juvenile specimens have been taken close to the northern New South Wales coast as far south as Minnie Water. It is rare in Western Australia. There is one specimen from the Kermadec Islands in the N.Z. National Museum. Elsewhere it is recorded from the Philippine Islands (lectotype; Reeve, 1844a); Dar es Salaam (Spry, 1968, p.18); Zanzibar (BMNH photograph); Rarotonga, Cook Islands (C106115) and Gilbert Islands (C60), both in Australian Museum; Marquesas (Salvat & Rives, 1975, p.307, Fig. 178); Cernohorsky (1967b, p.42) recorded it from "East Africa to Polynesia and the Hawaiian Islands", but I know of no authentic records from as far east as Hawaii; the records by Fair (1973, pl.3) presumably refer to *Bursa latitudo wolfei* n. subsp., not mentioned in her article. The southernmost specimen seen from the western Indian Ocean, apart from the juvenile from off Durban (see under *T. rubeta*), is from 3 m below low spring tide mark, north of Chacos, south-west Conducia Bay, Moçambique, leg. K. Grosch (NM, H119).

LOCALITIES: Australia: Trawled off Minnie Waters, N.S.W., November 1, 1963, juvenile (C 70011, AM); beach, Fairfax I., Bunker Group, Qld, J. Booth, 1968 (C 69053, AM); beach, Caloundra, Qld, J. Kerslake Colln. (AM); rubble crest in centre of island, One Tree I., Capricorn Group, Qld, coll. A. G. & J. I. Beu, Dec. 1971 (WM 11581, NZGS); trawled off Southport, Moreton Bay, Qld (C 69752, AM); beach, Cairns, Qld, T. A. Garrard Colln (C 106114, AM); trawled off Cooktown, Qld, Grigg Colln (NMV); 30 m, off Biggada Creek, Barrow I., WA. Aug. 1973 (215 mm high) (WAM).

Kermadec Islands: Raoul I., Kermadec Islands, Haylock Colln (MF 8787, NZNM).

Subgenus **Tutufella**, new name

Tutufa (Tutufella) rubeta (Linnaeus, 1758)

Figs 1b, c, e, j, k; 3; 4g-i; 5d, e; 7; 9c; 12b-e; 14d

Murex rana var. *rubeta* Linnaeus, 1758:748 (refers to Rumphius, 1705, pl.28, Fig. D).

Murex lampas var. *rubeta*.— Linnaeus, 1767:1216; Gmelin 1791:3532.

Tritonium tuberosum Röding, 1798:127 (refers to Martini 1780, vol. 4, pl.128, Fig. 1236-7).

Triton lampas.— Lamarck, 1816: pl.420, Figs 3a, b, *Liste*, p.5 (not of Linnaeus, 1758); Lamarck 1822:180 (in part).

Triton lampas var.— Kobelt, 1871:175, pl.40, Figs 7, 8.

Lampas hians Schumacher, 1817:252 (same Fig. as for *T. tuberosum* Röding).

Murex lampas.— Wood, 1828: pl.25, *Murex*, Fig. 28d (not of Linnaeus, 1758).

Tritonium lampas.— Anton, 1839:83.

Lampas caledonensis Jousseaume, 1881:177 (syntype Fig. E. A. Smith 1914, pl.4, Fig. 2).

Bursa (Tutufa) rubeta, typical var.— E. A. Smith, 1914:228, pl.4, Figs 1, 2.

Bursa rubeta.— Vanatta, 1914:80; Hedley 1916a:41; Cernohorsky 1972:118, pl.1, Fig. 5.

Bursa (Bufonaria) rubeta.— Cooke, 1916:9 (radula).

?*Bursa (Ranella) bubo*.— Adam & Leloup, 1938:151.

Bursa (Bufonaria) bubo rubeta.—M. Smith, 1948: pl.10, Fig. 11.

Tutufa rubeta.— Oyama & Takemura, 1963: *Tutufa* pl.2, Fig. 1; Habe & Kosuge 1966:46, pl. 16, Fig. 8.

Shell small (to about 110 mm high); with tall spire, short anterior siphonal canal, and small, oval, extremely rugose aperture. Anterior canal bent strongly to the right, but fasciole less prominent than in *T. bufo*, as canal is short. External sculpture of three major spiral cords, the peripheral one (and, in many specimens, lower ones) bearing low, rounded, irregular nodules that protrude little on varices; interspaces completely filled by slightly weaker secondary and tertiary spiral cords, the whole bearing small, rounded, irregularly placed gemmae, so that the overall appearance is more evenly nodulose than in other species. Outer lip flared narrowly, its outer edge digitated by external spiral cords, bearing a row of 12-14 short, rounded nodules on the inner edge of the flare, and a second row of low, elongate ridges further inside the aperture, matching outer nodules in position, separated from outer nodules by a narrow smooth zone; deep red, with nodules pale pink to white. Inner lip bright to deep red, bearing a closely and coarsely anastomosing pattern of paler plicae over its entire height, and a short row of small nodules on parietal callous pad, constricting the short anal sinus. Exterior of clean shells deep to bright red, coarsely and irregularly mottled with paler red.

DIMENSIONS: Height 83 mm, diameter 48 mm (Port Moresby, New Guinea, MF 21548, NZNM); height 91 mm, diameter 53 mm (Madang, New Guinea, C 73398, AM); height 101 mm, diameter 59 mm (One Tree I., Capricorn Group, Qld, WM 11632, NZGS).

TYPES: The holotype of *Murex rana* var. *rubeta* Linnaeus, 1758 is the shell figured by Rumphius (1705, pl.28, Fig. D). Its whereabouts are unknown. Similarly, the shell figured by Martini (1780, vol. 4, pl.128, Fig. 1236-7) is the holotype of both *Tritonium tuberosum* Röding, 1798 and *Lampas hians* Schumacher, 1817. Its whereabouts are unknown also. The syntypes of *Lampas caledonensis* Jousseaume, 1881 are presumably in Muséum d'Histoire Naturelle, Paris; one syntype was figured by E. A. Smith (1914, pl.4, Fig. 2). The figures by both Rumphius (see Fig. 12e) and Martini (see Figs 12b, d) both undoubtedly refer to the species universally known as *Tutufa rubeta*, and there are no nomenclatural complications with this species.

ECOLOGY: *Tutufa rubeta* is collected commonly alive on coral reefs in northern New Guinea (specimens in AM) and specimens were taken quite commonly alive from coral reefs below low tide in the Philippines by divers collecting for J. E. Norton (material in WAM). Two specimens were taken alive in 0.6 m of water on coral in Piru Bay, Ceram, during the M.V. "Pele" Mariel King Memorial Expedition (material in WAM). Common empty shells on beaches and reef flats of outer coral atolls of the Capricorn and Bunker groups, southern Great Barrier Reef, show that the species lives commonly a short distance below low tide in this area. Live specimens have *not* been taken by trawling on the continental shelf, but in both eastern and Western Australia occasional specimens with hermit crabs have been taken from crayfish pots or fish traps, south of the area where live specimens have been collected. Therefore *Tutufa rubeta* seems virtually restricted to coral reefs, although a few specimens apparently occur on other substrates in deeper water at the southern end of its range.

RADULA: In the radula of *Tutufa (Tutufella) rubeta* (Figs 3, 4g-i), the central tooth has narrower basal limbs and slightly longer interlocking basal processes than in *T. (Tutufa) bubo* and *T. bufo* and the relatively few (two or three on most teeth) denticles on each side are situated very close to the base of the cusp. The lateral tooth has a more sharply

hooked main cusp than in any other of the examined species of *Tutufa*, and the highly varied denticles are larger on the outer edge than in other species and, on most teeth, increase in size regularly towards the cusp. The denticles on the inner edge of the lateral tooth are highly varied also, and most teeth have only one denticle. A lateral tooth is figured (Fig. 3, lower tooth) in different orientation from usual, turned approximately halfway between normal resting orientation and turned fully outwards, showing that in this orientation the denticles on the lateral teeth of *Tutufa* resemble those of other bursids more than they do in normal rest position.

DISTRIBUTION: Around Australia specimens of *Tutufa rubeta* have been collected from north of Fremantle in southern Western Australia to northernmost New South Wales. Elsewhere it is recorded from "Timor, Goram I., Tonga Is., . . . Islands of Ticao and Luzon, Philippines (Cuming), New Caledonia (Jousseume)" (E. A. Smith, 1914, p.229); common in collections from Madang and the Port Moresby area, New Guinea (Australian Museum) and from the Philippine Islands, the Moluccas and the Sulu Archipelago (Western Australian Museum), and a few specimens have been seen from Diego Garcia and Mauritius (Australian Museum). I have seen no records from the Pacific as far east as Hawaii.

Australian Localities: Reef ca. 10 km NE of Coffs Harbour, northern N.S.W., 64 m, in fish trap, with hermit crab, June 19, 1976, coll. J. Ogg & I. Loch (C 103414, AM); Lady Elliot I., Qld, coll. A. E. Wright, May 1962 (C 69194, AM); Fairfax I., Bunker Group, Qld, many on beach, coll. J. Booth, 1968 (C 69053, AM); common with hermit crabs on main reef flat to east of hut, One Tree I., Capricorn Group, Qld, coll. A. G. & J. I. Beu, Dec. 1971 (WM 11632, NZGS); Tryon I., Capricorn Group, coll. J. Kerlake, Sept. 1954 (C 105985, AM); Broadhurst Reef, E of Townsville, Qld, alive subtidal, coll. I. Loch, Oct. 11-12, 1975 (C 104778, AM); Broadhurst Reef, E of Townsville, Qld, alive subtidal, coll. I. Loch, Nov. 9-10, 1974 (C 105987, AM); Wheeler Reef, NE of Townsville, Qld, empty shell subtidal, coll. I. Loch July 15, 1973 (C 105988, AM); Capre Cay, 22°09'S, 152°46'E, Swain Reefs, outermost Great Barrier Reef, AM Exped. Oct. 22, 1962 (C 72661, AM); South I., Lizard I., Qld, 0.5-12 m, alive off E face, coll. W. F. Ponder & I. Loch, Dec. 13, 1975 (C 104436, AM); Lizard I., Qld, coll. P. H. Colman, I. Loch & W. F. Ponder, Nov.-Dec. 1974 (C 99329, AM); New Year I., 50 km ENE Coker I., Northern Territory, 10°54'S, 133°02'E, beach, coll. P. H. Colman, Nov. 5, 1969 (C71982, AM); beach, Biggada Ck., Barrow I., WA, Aug. 1973 (WAM); alive, intertidal, North-west Cape, WA, in colln. F. Turnbull, Perth; coast at Warra Station, between Carnarvon and Exmouth, WA, 1973, pres. R. Hancey (C 93317, AM); crayfish pot off Houtman's Abrolhos Islands, WA, in colln. Mr and Mrs W. Back, Perth; crayfish pots set in unrecorded localities off Fremantle, WA (? off Rottneest I.), three specimens, in collns. H. Baker, Fremantle, and Mrs G. Hansen, Perth.

***Tutufa (Tutufella) cf. rubeta* (Linnaeus)**
Figs. 10b, c.

A single specimen from Moçambique differs strikingly from all other specimens examined of *T. rubeta* (Linnaeus). Firstly, its external coloration is markedly paler than that of *T. rubeta*, being cream with pale red-brown maculations, rather than the brick to deep red of Pacific specimens. Secondly, the interior of the outer apertural lip is markedly paler than in *T. rubeta* (again, cream rather than bright to deep red) so that the denticles are not set off prominently by their background, and the inner lip is markedly darker than in Pacific specimens, so that the white plicae show up prominently on their dark brown background, rather than all of the inner lip being of almost the same pale to bright red as in *T. rubeta*. Thirdly, the prominent and clearly double row of nodules inside

the outer lip of *T. rubeta* corresponds to a single row of longer, lower nodules on the Moçambique specimen, as if the two rows of *T. rubeta* were united across the variceal channel but commenced a little deeper into the aperture. In shell shape and sculpture, apertural shape and lip flaring, and variceal shape and position the specimen agrees in all details with normally coloured specimens of *T. rubeta*.

A normally coloured specimen of *T. rubeta* recorded from Natal by Smith (1914, p.229) is of doubtful location (see below), but undoubted Indian Ocean specimens of *T. rubeta* have been examined in the Australian Musuem collection: C 36429, Mauritius; C 52794, Diego Garcia I., Indian Ocean, Hargraves Colln. Both have the typical two rows of nodules inside the outer lip. So the status of the Moçambique specimen must remain in doubt until more material can be examined from a range of Indian Ocean localities, and especially more from Moçambique, but it seems likely that an un-named taxon of *Tutufa* (*Tutufella*) (whether a species, or a subspecies of *T. rubeta*, is not clear) occurs in the south-western Indian Ocean.

DIMENSIONS: height 77.6 mm, diameter 44.5 mm.

LOCALITY: Moçambique I., Moçambique, collected and donated A. Enes (G 3444, Natal Museum).

E. A. Smith's South African specimens:

Smith (1906, p.41) recorded a specimen as "*Bursa lampas*" from "Durban Bluff", South Africa. A photograph (Fig. 11b) of this specimen kindly sent by the British Museum (National History) shows it to be a juvenile specimen of *Tutufa* (*Tutufa*) *bubo* (Linnaeus), and to judge from its very fresh condition it was probably dredged or trawled out to sea off Durban Bluff rather than collected in shallow water. As *T. bubo* is relatively common in the northern western Indian Ocean it seems possible the specimen really came from off Durban. The specimen is registered as No.1906.7.7.6, labelled "Durban Bluff, G. W. Westcott", and is 34.7 mm high and 22.5 mm in diameter.

Smith (1914, p.229) also recorded under "*Bursa* (*Tutufa*) *rubeta*, var.1, typical" a shell from "Port Natal (Brit. Mus.)". A photograph (Fig. 12c) of this specimen kindly sent by the British Museum (Natural History) shows it to be typical *T. rubeta* (Linnaeus). The label reads "Port Natal, J. Sanderson. Reg. No. 1861.7.3.29", so that the specimen was registered in 1861. Mr R. N. Kilburn of the Natal Museum (*in litt.*, April 1972) knows of no modern records of any species of *Tutufa* from South Africa, and strongly doubts that Smith's specimen could have come from Natal. The "Natal" specimen is presumably wrongly localised, and the Durban Bluff specimen may be also.

***Tutufa* (*Tutufella*) *oyamai* Habe, 1973**

Figs. 1f, i, l, q, 2e, 4b-f, 15d-i.

Gyrineum (*Lampas*) *ranelloides*. — Melville & Standen, 1899:163 (not *Triton ranelloides* Reeve, 1844) (Torres Strait).

?*Ranella* (*Lampas*) *lampas*. — Martin, 1899:148, pl.23, fig. 346, 346a (Miocene of Java) (not of Linnaeus, 1758).

?*Bursa tenuigranosa*. — Vanatta, 1914:80; Hedley 1916a:42 (?not of Smith, 1914).

Tutufa tenuigranosa. — Habe, 1961:47, pl.24, fig. 4; Oyama & Takemura 1963: *Tutufa* pl.1, Fig. 6, 7,; Habe 1964: 76, pl.24, fig. 4 (not of E. A. Smith, 1914).

Tutufa bubo. — Wilson & Gillett 1971:80, pl.54, fig.2, 2a (in part not *Murex rana* var. *bubo*

Linnaeus, 1758).

Tutufa oyamai Habe, 1973:140, text-fig. 2.

Shell small (to about 75 mm high), with moderately short to moderately tall spire, moderately long anterior siphonal canal, moderately prominent fasciole, and small, uniform white aperture with entirely plicate inner lip. External sculpture of three narrow major spiral cords on last whorl, the peripheral one bearing large, anteroposteriorly compressed, narrowly rounded nodules that are particularly large on varices, but lower cords weakly nodulose; interspaces filled by numerous low, fine, closely spaced, secondary and tertiary spiral cords; entire surface finely and closely gemmate. Outer lip flared narrowly, its outer edge digitated by external ribs, its inner edge bearing a row of 12 to 14 low, paired nodules. Inner lip moderately widely flared into a narrow, thin, parietal and columellar shield, smooth around its outer edge, the more interior portion bearing a row of low nodules on the parietal callous pad, constricting the relatively long, narrow, anal sinus, and coarsely and closely plicate for its entire height below parietal callus. Exterior uniform pale fawn to medium red-brown.

DIMENSIONS: Height 63.2 mm, diameter 46.4 mm (holotype); height 72.0 mm, diameter 47.8 mm (paratype, Taiwan: Habe 1973, p.141); height 73.3 mm, diameter 44.5 mm (Karachi: Habe 1973, p.141); height 60.0 mm, diameter 39.7 mm (paratype, Fig. 15e,h, Taiwan, WM 11274, NZGS); height 55.8 mm, diameter 37.5 mm (64 m, off Fraser I., Qld, WM 10758, NZGS).

TYPES: Holotype (NSMT-MO. 42372) and paratype (NSMT-MO. 42373) in National Science Museum, Tokyo (Habe 1973, p.141); paratype in NZGS (WM 11274).

REMARKS: *Tutufa oyamai* differs from the four species described above in its relatively small size, in having a shorter spire than that of *T. rubeta*, in its thin, light build, and in having crisp, finely nodulous external sculpture formed by low, narrow, well-defined axial growth ridges crossing the many low, narrow, well-defined spiral threads. The aperture is uniformly white with a flared inner lip densely covered with low, narrow, closely spaced, weakly anastomosing plicae, lower and less coarsely anastomosing than in *T. rubeta*, and with the lightly flared outer lip bearing a complexly digitate outermost edge and a single row of small, paired, white nodules or ridges inside. The flared inner lip leaves a small false umbilical hollow below the fasciole, not as large as that of *T. tenuigranosa*.

RADULA: The radula of *Tutufa (Tutufella) oyamai* (Figs. 2e, 4b-f) has a central tooth very similar to that of *T. rubeta* but with even narrower and slightly straighter basal limbs and smaller and sharper interlocking basal processes. The denticles are similarly strongly hooked in the two species. The lateral tooth is markedly less strongly hooked, has a smaller base with fewer protruberances, and has smaller denticles on the base of the cusp than in *T. rubeta*. The outer edge of most specimens has three denticles that are strongly hooked, as on the central tooth, and the inner edge has from none to three denticles (one on most teeth) that are small and obscure.

ECOLOGY: *Tutufa oyamai* is a moderately common species throughout the eastern Indian Ocean and western Pacific ocean. Most specimens have been taken by trawling or dredging on sand substrates in water to about 100 m deep. It is taken not uncommonly around Taiwan by prawn trawlers, and not uncommonly off northern New South Wales and southern Queensland by both prawn and fish trawlers. The M.V. "Pele" Mariel King Memorial Expedition to the Moluccas in 1970 took 14 specimens at eight stations ranging from intertidal coral reefs (one specimen) to dredgings in up to 84 m; most specimens and all live specimens were taken in about 30-55 m.

DISTRIBUTION: Around Australia *T. oyamai* has been taken from northern-most New South Wales around to Houtman's Abrolhos Islands in central Western Australia. Elsewhere it has not been regarded as a distinct species, and records are scarce; it is quite common in collections from Taiwan, the Philippines, and the Moluccas. There are no records from Hawaii or from the western Indian Ocean west of Karachi, and it is apparently restricted to the eastern Indian and Western Pacific Oceans. Habe (1973, p.142) recorded *T. oyamai* from "off Tung Chiang, Taiwan (Formosa) at the depth of 20-50 m" (type) and from Honshu (Wakayama Prefecture) southwards in Japan, and Formosa, China, Philippines, and Karachi.

Australian Localities: Fish trap, off Woolgoolga, northern NSW, J. Kerslake Colln. (C 106021, AM); off Cape Moreton, Qld, purchased L. Moore, 1976 (C 103871, AM); off Tin Can Bay, Qld, coll. T. Neilsen (C 62479, AM); off Tin Can Bay, Qld, J. Kerslake Colln. (WAM); off Wide Bay, Qld, T. A. Garrard Colln., 5 specimens (C 66561, AM); trawled, 64 m off Fraser I., Qld, J. Kerslake Colln. (WM 10758, NZGS); Great Barrier Reef Exped., 1929, dredge stn. 12, 18-28 m, Penguin Channel, Qld (C 82262, AM); Murray I., Torres Strait, Haddon Colln., the specimens recorded as *Gyrineum (Lampas) ranelloides* by Melvill & Standen (1899, p.163), Fig. 15g (Manchester Museum); CSIRO stn. 208, 27°40'S, 113°20'E, NW of Bluff Pt., WA, 130.8 m, beam trawl, 10 Oct. 1963 (WAM); 65 km W of Cape Jubert, WA, 40 m, coll. R. W. George on "Dorothea", 13 Oct. 1962 (WAM).

***Tutufa (Tutufella) tenuigranosa* (E. A. Smith, 1914)**

Figs. 15a, c

Bursa (Tutufa) rubeta var. *tenuigranosa* E. A. Smith, 1914:231, pl.4, Fig. 6.

?*Bursa tenuigranosa*. — Vanatta, 1914:80; Hedley, 1916a:42 (? not of E. A. Smith, 1914).

Tutufa tenuigranosa. — Habe, 1973:139, text-fig. 1.

Shell large (to 210 mm high), with tall spire, moderately long anterior siphonal canal, moderately prominent fasciole, deep but narrow false umbilical chink, and moderately large, uniform white aperture with entirely plicate inner lip. External sculpture of three narrow major spiral cords on last whorl, the upper two bearing numerous, low, rounded, closely spaced nodules that protrude only weakly on varices, the interspaces filled by numerous low, narrow, closely spaced, secondary and tertiary spiral lirae, the whole surface finely and closely gemmate with even, smooth, rounded nodules. Outer lip narrowly flared, its outer edge coarsely fluted but less obviously digitated than in *T. oyamai*, its inner edge bearing about 12 to 14 small, widely spaced nodules, less clearly paired than those of *T. oyamai*. Inner lip moderately widely flared into a thin parietal and columellar shield resembling that of *T. oyamai*, with a low parietal nodule that constricts the short, relatively wide anal sinus, closely and coarsely plicate over entire height below parietal callus. Fasciole relatively narrow, leaving a deep, narrow, false umbilical chink behind columellar callus shield. Exterior cream-yellow flecked with dark brown, similar to those of *T. bubo* and *T. bufo*.

DIMENSIONS: Height 185 mm, diameter 91 mm (lectotype); height 210 mm, diameter 113 mm; height 192 mm, diameter 103 mm (2 Hong Kong specimens; Habe 1973, p.140).

TYPES: Habe (1973, p.139) treated E. A. Smith's figured specimen of *Tutufa tenuigranosa* as a holotype, but it does not have this status as Smith (1914, p.231) stated that the largest specimen was 210 mm high (i.e., he had more than one specimen) and did not designate type specimens for any of the varieties proposed in his 1914 paper. The specimen of *Bursa (Tutufa) rubeta* var. *tenuigranosa* E. A. Smith figured by Smith (1914,

pl.4, Fig. 6) is here designated the lectotype of *Bursa (Tutufa) rubeta* var. *tenuigranosa* E. A. Smith. It is an unlocalised shell lodged in the British Museum (Natural History), bearing the register number 1914.6.29.4 (Fig. 15a).

REMARKS: Habe (1973, p.139) pointed out that *Tutufa tenuigranosa* is a different species from the more common and more widespread *T. oyamai*. It differs from *T. oyamai* in its much larger size, its taller spire, its lower varices that are only weakly hollowed and buttressed behind, its lower peripheral nodules, its slightly more coarsely and sparsely plicate inner lip, its less clearly paired nodules inside the outer lip, and its deep false umbilical chink present in no other species of *Tutufa*. Its size, shape, and external colouration are most like those of *T. bubo* and *T. bufo*, from which it differs in its weak sculpture and its coarsely plicate inner lip.

Tutufa tenuigranosa resembles *T. oyamai* closely in one of the apparently diagnostic features of *Tutufella*, the closely and entirely plicate inner lip, and so is tentatively referred to *Tutufa (Tutufella)*. Examination of the seminal groove will be necessary to confirm its subgeneric location.

DISTRIBUTION: the lectotype and paralectotypes are unlocalised. Recorded by Habe (1973) from about 200 m, off Hong Kong, in the South China Sea. Recent records by shell collectors are from prawn trawlers off Taiwan, and there are two immature specimens from Taiwan in the National Science Museum, Tokyo (NSMT 48445), with a specimen of *Bursa ranelloides ranelloides*. *T. tenuigranosa* seems to occur only in deep water in the South China Sea.

Fossil record of *Tutufa*:

The only records of fossils that presumably belong in *Tutufa* are from the Neogene and Quaternary of Indonesia. Most references to these faunas list only *Ranella* or *Bursa lampas*, with no figures to show which species was intended: Schepman (1907, p.181), post-Tertiary of the Celebes; Martin (1919, pp.88, 132), general faunal lists; van der Vlerk (1931, p.241), general faunal list. Altena (1942, p.108) identified his material from the Kendeng beds of East Java (Pleistocene) as "*Bursa (Ranella) rubeta* (Roeding)", referred to Smith's (1914) revision, but did not refer to any of Smith's "varieties" or figure his specimens. The sole identifiable figure is that by Martin (1899, p.148, fig. 346, 346a) whose figure of "*Ranella (Lampas) lampas*" appears to be of *Tutufa (Tutufella) oyamai* Habe. The specimen is recorded as "Ein Exemplar aus der Menengteng — Schlucht, in Cheribon", Java (Miocene).

Genus **Bursa** Roding, 1798

Subgenus **Bufonariella** Thiele, 1929

For synonymy and type species see p. above. The two species considered below have been thought to be related to *Tutufa* by some recent authors, and Kuroda, Habe & Oyama (1971, p. 133) went so far as to provide a subfamily Tutufinae to include *Tutufa* and *Bursa (Bufonariella) ranelloides* (Reeve), presumably because the varices of *B. ranelloides* are arranged in the same cymatiid-like manner as are those of *Tutufa*. However, it is shown above that the stomach, opercular, radular and apertural features of *B. ranelloides* are closely similar to those of *Bursa* and especially of its subgenus *Bufonariella*, so variceal position is considered to be an insignificant criterion and *B. ranelloides* is placed in *Bufonariella*. *Bursa ranelloides* and *B. latitudo* have their varices aligned up the spire sides on the earliest few spire whorls, in any case, and come to resemble *Tutufa* species progressively down the shell. The two species discussed below superficially resemble

Tutufa, however, and have been considered related to it by some authors, and so are revised here.

DISTRIBUTION: The two *Tutufa*-like species of *Bursa* (*Bufonariella*) considered in this paper have remarkably wide distributions for species of Bursidae. Fig. 20 shows the distribution of the three subspecies recognised in each species. Beu (1976b) discussed the distribution of *Bursa* (*Bufonariella*) *ranelloides*, a member of a group of very few species (all Tonnacea) found in the Atlantic, off South Africa, in Australasia (Western Australia only, in this case) and in Japan, apparently dispersed around the Southern Ocean by the circum-polar current during Pleistocene time. Occurring in eastern Australia, Hawaii, and the western Atlantic, *B. latitudo* appears to represent a formerly much wider distribution in the West Pacific, and was presumably dispersed to the Atlantic through Panama before late Pliocene time, when the Panama seaway closed. The two species are sympatric only in the Caribbean Sea at present.

***Bursa* (*Bufonariella*) *latitudo* Garrard, 1961**

Shells from eastern Australia, Hawaii and the western Atlantic Ocean, discussed by Wolfe (1975), are here considered to belong in a complex of subspecies closely related to *B. ranelloides* (Reeve). *Bursa latitudo* differs from *B. ranelloides* in reaching a markedly larger adult size, in having a taller spire, in having the sculptural cords and nodules arranged very similarly but markedly narrower, with wider spaces and more numerous interstitial spiral cords between primary spiral cords, and the nodules more pointed than corresponding ones of *B. ranelloides*, in having a more sharply and widely reflected outer lip, in having prominent sculpture on the inner and outer lips, and in having the red-brown parietal colour patch partly to completely masked by the parietal plicae on large specimens.

The animal and operculum of *B. latitudo* are unknown and thus the generic position will remain slightly in doubt until the position of the opercular nucleus is described, but the external sculpture and the plication and colouring of the inner lip are so strongly similar to those of *B. ranelloides* that a position in *Bursa* (*Bufonariella*) seems highly likely.

***Bursa* (*Bufonariella*) *latitudo latitudo* Garrard, 1961**

Figs. 16 g-i

Bursa latitudo Garrard, 1961:15, pl.2, fig.2.

Specimens of the *B. latitudo* complex from Queensland are of very similar proportions to those of *B. latitudo wolfei* n.subsp. from Hawaii, but differ from Hawaiian specimens in their consistently smaller and more narrowly pointed major nodules, much finer and more closely spaced interstitial spiral cords and rows of fine nodules, and more sparsely and narrowly plicate inner lip callus that becomes more thickened with age so that the parietal colour patch is not visible on large shells.

DIMENSIONS: height 95 mm, diameter 55 mm, height of aperture less posterior sinus 26 mm (holotype; Garrard, 1961, p.15); height 54.4 mm, diameter 33.5 mm, height of aperture plus canals 26.3 mm (C 66528); height 57.0 mm, diameter 34.4 mm (C. S. Wolfe colln.).

Holotype (F.21,111) in National Museum of Victoria.

DISTRIBUTION: The subspecies has been taken only rarely, off southern

Queensland, in water more than 100 m deep. Only three specimens have been seen during this study. The paratype recorded by Garrard (1961, p.15) is a broken and encrusted specimen of *Ranella australasia* (Perry) (Australian Museum, C 63353).

LOCALITIES: trawled off Moreton I., Southern Queensland, in 230 m, holotype (F21,111, NMV); 100-130 m, off Caloundra, southern Queensland, T.A. Garrard Colln., one specimen (C 66528, AM); trawled in 110 m, ENE Cape Moreton, southern Queensland (collection of Charles S. Wolfe, Fort Worth, Texas).

***Bursa (Bufonariella) latitudo natalensis* Coelho & Matthews, 1970.**

Figs. 16a-f.

Bursa finlayi.— McGinty, 1962: 39, pl.3, fig. 1 only (paratype), not conspecific with holotype).

Bursa (Colubrellina) natalensis Coelho & Matthews, 1970:1, Fig.1-3.

Bursa (Colubrellina) tenuisculpta natalensis. — Abbott, 1974:167.

The western Atlantic subspecies of *Bursa latitudo* is distinguished from *B. latitudo latitudo* by its extremely elongate form, more closely and coarsely plicate inner lip especially on the lower part of the columella, markedly more strongly plicate outer lip with plicae extending further on to the flared section of the outer lip than in either of the other subspecies, and moderately to markedly coarser interstitial sculpture. In addition the peripheral and basal rows of nodules of some specimens are markedly larger and more anteroposteriorly compressed than those of *B. latitudo latitudo*, but this is not a consistent difference as nodule size is much more variable in *B. latitudo natalensis* than in the eastern Australian form.

DIMENSIONS: height ca. 50 mm, diameter ca. 20 mm (holotype of *B. natalensis*, dimensions not stated, calculated from scaled illustration); height 82.5 mm, diameter 39.2 mm (paratype of *B. finlayi*); height 73.6 mm, diameter 33.9 mm (USNM 735915, off Nevis, British West Indies).

TYPES: Holotype of *B. natalensis* in Museu Nacional, Rio de Janeiro (no. 3527) (Coelho & Matthews 1970, p.4); paratype of *B. finlayi* in USNM (673601).

REMARKS: Comparison of the holotype and paratype of *Bursa finlayi* McGinty (McGinty 1962, p. 39), loaned by the U.S. National Museum, showed that they belong in two different species. The holotype (Fig. 19a, b) is a small, strongly noduled specimen of *B. ranelloides tenuisculpta* (Dautzenberg & Fischer) resembling the common form of *B. ranelloides ranelloides* from Japan, and similar coarse variants and intergrading more finely sculptured specimens have been seen from several Caribbean *B. ranelloides tenuisculpta* populations (Figs. 19c-g). The paratype (Figs. 16c,d) is an extremely narrow and elongate, coarsely sculptured specimen agreeing closely in all its details, except its larger peripheral nodules, with the holotype of *B. ("Colubrellina") natalensis* Coelho & Matthews, 1970 (Coelho & Matthews 1970; illustration copied as Fig.16a). Another Caribbean shell, from off Nevis, British West Indies, has the same interstitial sculpture, extremely tall spire, and coarse apertural plicae as in the holotype of *B. natalensis*, but has markedly weaker peripheral nodules (Fig. 16f) and it is concluded that the holotype of *B. natalensis* is a moderately coarsely sculptured specimen, the Nevis shell is a weakly sculptured specimen, and the paratype of *B. finlayi* is a very coarsely sculptured specimen of the same taxon, here regarded as a geographic subspecies of *B. latitudo* Garrard, and not closely related to *Bursa (Colubrellina) condita* (Gmelin), type species of

Colubrellina Fischer. Wolfe (1975, fig. 3) illustrated a small, weakly sculptured specimen of the Caribbean form he called *B. finlayi*, and two specimens in his collection have been examined through the courtesy of Col. Wolfe. The shells are similar to the specimen from Nevis and to the holotype, and confirm the distinctive features of the Atlantic subspecies (Figs. 16b,e). These shells all have similar faint, red-brown, axial colour streaks and a large number of fine, closely spaced interstitial spiral threads that distinguish them readily from specimens of *B. ranelloides tenuisculpta*, even when the coarsely sculptured outer-lip flange is broken off (as in the Nevis specimen).

LOCALITIES: crayfish (= spiny lobster) pots in 40-50 m off Pirangi, near Natal, Rio Grande do Norte, Brazil, holotype and four paratypes of *B. natalensis*; fish trap in 220 m, Bay of Matanzas, Matanzas, Cuba, J. Finlay, March 1961 (paratype of *B. finlayi*, USNM 673601); shell trap in 230 m, WSW of Charlestown, Nevis, British West Indies (USNM 735915); fish trap in 180 m, off Bahia de Anasco, west coast of Puerto Rico, two specimens in colln. Charles S. Wolfe, Fort Worth, Texas.

***Bursa (Bufonariella) latitudo wolfei* n.subsp.**

Fig 17

Bursa lampas. — Tinker, 1952:98; 99, centre fig. (not *Murex lampas* linnaeus, 1758).

Bursa finlayi. — Wolfe, 1975:12, fig.1,2 (not *B. finlayi* McGinty, 1962).

Shell large for subgenus, relatively thick and heavy, relatively wide as in *B. latitudo latitudo* but with the coarse sculpture of *B. latitudo natalensis*. Varices aligned up spire sides on initial three to four teleoconch whorls, but becoming progressively more widely spaced down shell so that they are situated at each two-thirds of a whorl on the last one or two whorls. Aperture large and oval, with thickened and strongly reflected inner and outer lips, and short, widely open anterior and posterior siphonal canals. Outer lip white, coarsely plicate along inner edge of reflected flange by about 15 short, narrow ridges. Inner lip white except for a large, deep brownish red parietal colour patch, mostly masked by the large, closely spaced plicae on mature shells; plicae similar to those of *B. latitudo natalensis* on lower columellar area, but markedly wider, straighter, less anastomosing, and more closely spaced on parietal area than in *B. latitudo natalensis*, so that two especially wide, slightly convex plicae border the posterior canal. Sculpture of one row of peripheral nodules, on most specimens prominent and strongly anteroposteriorly compressed; one row of smaller nodules around a slight basal angulation; two rows on the shoulder, one between the peripheral and basal angles, about four on the base, and four or five fasciolar rows of small, closely spaced nodules; and numerous finely beaded tertiary and quaternary cords. Exterior pale reddish brown, with diffuse medium reddish brown zones between pale nodules on most spiral cords, on varices, and in faint axial streaks.

DIMENSIONS: height 95.0 mm, diameter 56.4 mm (holotype); height 104.4 mm, diameter 58.3 mm (paratype, Honolulu Aquarium); height 94.4 mm, diameter 51.0 mm (small-noduled paratype, collection S. Handrahan, Honolulu); height 92.7 mm, diameter 53.2 mm; height 73.0 mm, diameter 45.6 mm (two paratypes in collection Charles S. Wolfe, Fort Worth, Texas).

HOLOTYPE (BPBM 8936) presented to Bernice P. Bishop Museum, Honolulu, by Charles S. Wolfe; two paratypes in collection Charles S. Wolfe, Fort Worth; one paratype (the specimen figured by Tinker 1952) in Honolulu Aquarium; one paratype in collection S. Handrahan, Honolulu.

LOCALITIES: crab trap, 58 m, off Makaha, Oahu, Hawaii (holotype); crab trap,

120 m, off Kahuku, Oahu, Hawaii (one paratype, C. S. Wolfe Colln.; one paratype, S. Handrahan Colln.); crab trap, 120 m, off Haleiwa, Oahu, Hawaii (small paratype, C. S. Wolfe Colln.); Nanakuli, Oahu "deep water" (paratype, Honolulu Aquarium). Apparently endemic to Hawaii.

REMARKS: *Bursa latitudo wolfei* differs from *B. latitudo latitudo* in having markedly coarser nodules, especially between the primary spiral cords, and in having markedly coarser and more closely spaced apertural plicae, especially on the inner lip. It is similar in shape to *B. latitudo latitudo* and similar in sculpture to *B. latitudo natalensis*, but differs from *B. latitudo natalensis* in its considerably wider shape, shorter ridges inside the outer lip, and wider and more closely spaced plicae on the inner lip.

The sharing of shape with the eastern Australian *B. latitudo latitudo* and of sculpture with the western Atlantic *B. latitudo natalensis* makes the Hawaiian form a neat geographical and morphological intermediate between the other two widely separated populations, supporting the contention that all three are geographic subspecies of a single species.

The new subspecies is named in honour of Charles S. Wolfe, now of Fort Worth, Texas, who loaned or arranged loans of the only Hawaiian specimens the writer has seen and who has contributed several interesting articles on Hawaiian Bursidae and Cymatiidae to "Hawaiian Shell News".

***Bursa (Bufonariella) ranelloides* (Reeve, 1844)**

Bursa ranelloides differs from *B. latitudo* in its smaller size (rarely over 65 mm high), its coarser sculpture of rounded rather than sharply pointed nodules, its more strongly excavated inner lip which retains the bright red-brown parietal colour patch at all sizes, and in having markedly fewer interstitial spiral gemmate cords.

The record of "*Gyrineum (Lampas) ranelloides*" from Murray I., Torres Strait, by Melvill and Standen (1899, p.163) was based on juvenile specimens of *Tutufa (Tutufella) oyamai* Habe, as shown by one of their specimens kindly loaned by Mr C. Pettitt, Manchester Museum (Fig. 15g). Hedley (1909, p.31) also recorded "*Gyrineum ranelloides*" from Queensland, but presumably merely on the basis of Melvill and Standen's record as there are no specimens from eastern Australia in any collections I have examined. Therefore *B. ranelloides* and *B. latitudo* apparently are sympatric in the western Atlantic Ocean only, although they occur sympatrically with other species of *Bufonariella*, especially *B. (Bufonariella) granularis* (Röding), in all areas they inhabit.

Bursa (Bufonariella) ranelloides has developed three geographic subspecies, the nominate one in Japan (and, doubtfully, the Philippines), *B. ranelloides tenuisculpta* (Dautzenberg & Fischer) from the eastern and western Atlantic (Azores, type locality) and South Africa, and *B. ranelloides humilis* n. subsp. from central and southern Western Australia.

***Bursa (Bufonariella) ranelloides ranelloides* (Reeve, 1844)**

Figs 18d, f-i

Triton ranelloides Reeve, 1844a: pl.3, Fig. 10a, 10b; Reeve, 1844b:118; Lischke 1871:37.

Simpulum papillosum A. Adams, 1870:419.

Ranella cruentata.— Tryon, 1881:267 (in part not *Bursa cruentata* Sowerby, 1835).

Bursa ranelloides.— Kuroda & Habe, 1952:43.

Buffonariella [sic] *ranelloides*.— Habe, 1961:47, pl.24, Fig. 3.

Buffonariella ranelloides.— Habe, 1964:76, pl.24, Fig. 3; Beu 1971:110, pl.8, Fig. 8 (holotype *Simpulum papillosum* A. Adams); Kuroda, Habe & Oyama 1971:134, pl.33, Figs 5, 6.

Tritonoranella ranelloides.— Oyama, 1964:332.

The nominate subspecies reaches about 80 mm high, although it is rarely more than 65 mm high. The sculpture consists of a very weakly developed subsutural row of nodules, an upper peripheral row of five to nine medium to large, widely spaced, well-rounded nodules in each intervariceal space, a lower peripheral row of rounded nodules that are slightly smaller and slightly more closely spaced than in the upper row, a further row of smaller rounded nodules below the periphery in some specimens, and the basal and intermediate peripheral spiral cords bear low and sparse nodules. The spire is moderately tall, and the varices are broadest at the upper peripheral row of nodules. The colour is cream, closely and finely maculated with pale reddish brown, with prominent darker red-brown patches on the varices and between all large nodules. The parietal colour patch is deep reddish-brown to "purple" (Reeve) and the apertural plicae are relatively weakly developed, and fine and close on the inner lip.

DIMENSIONS: Height 49.6 mm, diameter 32.2 mm (holotype of *B. ranelloides*); height 55.8 mm, diameter 33.2 mm (Tosa Bay, Shikoku, WM 11277, NZGS); height 50.0 mm, diameter 29.4 mm (Sagami Bay, Honshu, WM 11276, NZGS); height 56.8 mm, diameter 35.5 mm (Kuroda, Habe & Oyama 1971, p.134, pl.3, Fig. 5); height 79.3 mm, diameter 43.7 mm (Kuroda, Habe & Oyama 1971, p.134, pl.3, Fig. 6; Sagami Bay, Honshu).

TYPES: Reeve (1844a, pl.3, Figs 10a, b) had only one specimen of *Triton ranelloides*, and it is here regarded as the holotype. Photographs of the specimen kindly sent by the British Museum (Natural History) (Figs 18d, f) show that the shell (BMNH 1967594) is a worn, partly polished beach shell 49.65 mm high, with large nodules, closely resembling large-noduled Japanese shells (e.g., Fig. 18i). The worn nodules show the white inner shell material, but between the nodules the shell surface is sculptured exactly as in Japanese shells and bears a very similar colour pattern to that of Japanese shells (see also Reeve, 1844a, pl.3, Figs 10a, b — the specimen had a markedly brighter colour pattern in 1844 than it has now). Reeve (1844a, caption to p.3, Figs 10a, b) gave the locality "Matnog, Province of Albay, Island of Luzon, Philippines (found on the reefs); Cuming". The species has not subsequently been recorded from the Philippines, and the holotype so very closely resembles southern Japanese specimens that there can be little doubt that Cuming attached the wrong locality to this shell, among the many other wrong localities that have been recorded in his collection, and that the holotype is a beach shell from southern Japan. Dr Tadashige Habe has lent me a specimen trawled off Cebu, Philippine Islands (NSMT 55501, National Science Museum, Tokyo). It is a small, narrow, medium red-brown specimen with extremely narrow, small, sharply pointed nodules, closely resembling the Japanese small-noduled specimens included in their var. *tenuisculpta* by Dautzenberg & Fischer (1906, pl.2, Figs. 19, 20), but not closely resembling the large-noduled, beach-worn holotype of *Bursa ranelloides*. It occurred with a specimen of *Bursa rehderi* Beu, 1978, recorded from depths of 208-640 m off the Philippines, so probably this sample was taken in deep water and represents the southern limit of the north-west Pacific subspecies. Japanese shells are here considered to constitute the nominate subspecies of *B. ranelloides*, and *Simpulum papillosum* A. Adams (holotype (BMNH 1967680) figured by Beu 1971, pl.8, Fig. 8; type locality "Takano-Sima, Japan") is

synonymised with *B. ranelloides*.

DISTRIBUTION: Recorded from five stations in Sagami Bay at 65-87 m depth by Kuroda, Habe & Oyama (1971, p.134); "Boso Peninsula, Honshu, and southwards" (Habe, 1964, p.76); "Honshu (Boso Peninsula as northern limit), Shikoku, Kyushu . . . On sandy bottom of 50-200 m deep" (Kuroda, Habe & Oyama 1971, p.134). Taiwan, dredged with two *Tutufa (Tutufella) tenuigranosa* (E. A. Smith) (NSMT 48445); off Cebu, Philippine Islands (NSMT 55501).

Bursa (Bufonariella) ranelloides tenuisculpta Dautzenberg & Fischer, 1906

Fig. 19

Bursa ranelloides var. *tenuisculpta* Dautzenberg & Fischer, 1906:36, pl.2, Figs 15-18.

Bursa (Tutufa) tenuisculpta.— Morrison, 1949:10; Abbott 1954:198.

Bursa finlayi McGinty, 1962:39, pl.3, Figs 1a, 2, 3 (not Fig. 1); Abbott 1974:167.

Bursa tenuisculpta [sic]. — Scheltema, 1972:864, Figs 1c, 2a.

Bursa (Colubrellina) tenuisculpta.— Abbott, 1974:166, Fig. 1778.

Specimens of *B. ranelloides* from South Africa and the Caribbean and Dautzenberg & Fischer's coloured figures (1906, pl.2, Figs 15-18) of shells from the Azores and Madeira differ from Japanese specimens in their slightly smaller size; their taller and narrower form brought about mainly by a taller spire; in having only a pale reddish-brown or, in large specimens, even completely absent parietal colour patch; in having the varices broadest at the lower peripheral row of nodules or, in specimens where the peripheral nodules are very large, in having the varices about equally broad at both peripheral angles; in having extremely coarse, prominent, widely spaced, strongly anastomosing plicae on the inner lip and equally strong simple ones on the outer lip, the two series both passing well out on to the flared lips; and in having smaller and markedly more sharply pointed external nodules of different arrangement. Atlantic shells have the following sculpture: a subsutural row of fine, low, closely spaced nodules of the same size as those in the lower peripheral row, markedly larger than those in the subsutural row of *B. ranelloides ranelloides*; seven to 13 small, relatively close, sharp nodules in each intervariceal space in the upper peripheral row; smaller and closer nodules than above in the lower peripheral row; and an intermediate peripheral row and several basal rows of small, close nodules very little smaller than those in the lower peripheral row. The colour pattern lacks the large dark patches on the varices and between the nodules of Japanese shells.

Atlantic and South African specimens thus differ consistently from Japanese ones in their colour, shape, apertural plicae, and sculptural details, especially the sharper nodules. The Japanese population is highly variable in sculpture and at least 20% of Japanese shells approach Atlantic ones in the fineness of the nodules (as is to be expected between subspecies), but the nodules remain sharper and the shape remains different in Atlantic specimens. A similar range of variation in nodule size is seen in Atlantic shells; the holotype of *Bursa finlayi* McGinty (discussed under *B. latitudo natalensis*) and similar shells are coarsely noded specimens of *B. ranelloides tenuisculpta* resembling *B. ranelloides ranelloides* in the size of their peripheral nodules, but in Atlantic populations only about 20% of specimens are as coarsely sculptured as Japanese shells. Atlantic and South African specimens are here considered to belong in a distinct geographic subspecies, for which the name *tenuisculpta* is available.

DIMENSIONS: Not stated by Dautzenberg & Fischer (1906); lectotype approx. 68 mm high, 38 mm wide (from their pl.2, Figs 15, 16, at natural size); height approx. 43 mm, diameter approx. 25 mm (paralectotype, Madeira, Dautzenberg & Fischer 1906, pl.2, Figs 17, 18); height 48 mm, diameter 20.5 mm (holotype of *Bursa finlayi* McGinty); height 63 mm, diameter 35 mm (NM 9928, SE of Durban Bluff, South Africa).

TYPES: Dautzenberg & Fischer (1906) included Japanese finely-sculptured specimens (e.g., their pl.2, Figs 19, 20) in their var. *tenuisculpta*. Therefore the specimen from off the Azores figured by Dautzenberg & Fischer (1906, pl.2, Figs 15, 16) is here designated the lectotype of *Bursa (Lampas) ranelloides* var. *tenuisculpta* Dautzenberg & Fischer, 1906. The lectotype is presumably in the Oceanographic Institute, Monaco. The holotype of *Bursa finlayi* McGinty is in USNM (634570).

DISTRIBUTION: Scheltema (1972, Fig. 4) recorded larval shells of *Bursa (Bufonariella) ranelloides tenuisculpta* from many Atlantic localities in plankton tows, from the eastern Caribbean along the north coast of Brazil, from the coast north of Cape Verde to the Gulf of Guinea, and in a single sample off Angola. With this width of distribution of larvae the occurrence of the subspecies in the eastern Atlantic, in the western Atlantic from the Florida Keys to the West Indies, and in South Africa is not surprising, and the dispersal of occasional specimens seems quite feasible between the widely distributed populations (Atlantic-South Africa, Japan, Western Australia) here considered to be geographic subspecies of the single species *Bursa ranelloides*.

LOCALITIES: Eastern Atlantic: "Expedition of 1897: Stn. 899, depth 200 m. Princess Alice Bank, Azores. One living example" (lectotype of *tenuisculpta*; translated from Dautzenberg & Fischer, 1906, p.36); "expedition of 1901: Stn. 1242, depth 240 m. Banc de Seine, Madeira. Six dead examples" (translated from Dautzenberg & Fischer, 1906, p.36). **Western Atlantic:** 215° off Sombrero Key Light, Middle Florida Keys, 210 m, "Triton" Sta. 615, July 8, 1951 (holotype of *Bursa finlayi* McGinty, 1962, USNM 634570); 180-550 m, north of the Virgin Islands (USNM 430336); "Eolis" sta. 146, 180 m, off Key West, Florida (USNM 417778); State Univ. Iowa dredge sta. 29, Bahia Honda, Cuba (USNM 543506); dredged, 230 m, Dry Tortugas, Florida, 1971 (two excellent specimens in collection Charles S. Wolfe, Fort Worth); "The U.S. National Museum collections include specimens dredged in from 50 to 125 or more fathoms [90 to 230 m], from off Sand Key and Key West, Florida; off Bahia Honda, Cuba; from north of the Virgin Islands; and from the Arrowsmith Bank, Yucatan" (Morrison, 1949, p.10), presumably the basis of the record by Abbott (1954, p.198) from "South-east Florida and the West Indies. Dredged on rare occasions". **South Africa:** off Tugela River mouth, Natal, in 37 m, donated G. Scott, November, 1972, two dead specimens (Figs 19h, j) (A12, NM); trawled south-east of Durban Bluff, Natal, in 275 m, donated G. Scott, August, 1972, one dead specimen (Figs 19i, k) (9928, NM).

***Bursa (Bufonariella) ranelloides humilis* n. subsp.**

Figs 1o, r; 2b; 4j; 5a; 18a-c, e.

Gyrineum ranelloides.— Verco, 1912:219, pl.16, Figs 6, 7; Hedley, 1916b:196 (not of Reeve, 1844).

Specimens of *Bursa ranelloides* dredged off southern and south-western Western Australia differ from both *B. ranelloides ranelloides* and *B. ranelloides tenuisculpta* in their small size (up to 45 mm high); their relatively very short spires, very short siphonal canals, and very strongly inflated last whorls, producing much shorter and broader shells; in having sculpture of more nearly uniform-sized rows of nodules, the upper

peripheral row smaller than in *B. ranelloides ranelloides* and of similar size to that of *B. ranelloides tenuisculpta* and the other rows all relatively coarser than in both the other subspecies; in their uniform pale straw-yellow colour, with only faint reddish-brown patches on the last few varices of large specimens; in their small but bright blood-red parietal colour patches; and in their apertural plicae being less prominent and sparser than in *B. ranelloides tenuisculpta* and more prominent than in *B. ranelloides ranelloides* and not extending as far out of the aperture as in either of the other subspecies. The external sculpture consists of one subsutural row of coarse nodules of the same size as those in the lower peripheral row, an upper peripheral row of 4-10 medium-sized, slightly quadrate, slightly pointed, moderately closely spaced nodules in each intervariceal space, a lower peripheral row of nodules that are only slightly smaller and closer than in the upper peripheral row, and an intermediate peripheral row and several basal rows that are relatively very coarsely noded, the uppermost two basal rows having nodules only slightly smaller than in the lower peripheral row. The anterior siphonal canal is consistently very short, and very strongly twisted to form a broadly rounded fasciole extending well to the left of the inner lip. The large number of Western Australian shells seen are remarkably consistent in their distinctive features and form a well-defined geographic subspecies.

DIMENSIONS: Height 40.2 mm, diameter 27.8 mm (holotype); height 45.1 mm, diameter 29.3 (figured large paratype, WAM. 310-72); height 43.8 mm, diameter 28.2 mm (dissected topoparatype); height 24.7 mm, diameter 15.9 mm (small figured paratype, WAM. 309-72).

TYPES: Holotype (WAM 305-72) and nine paratypes (WAM 305-72, WAM 309-72, WAM 310-72, WAM 312-72) in Western Australian Museum.

RADULA: The radula and operculum were described and figured by Verco (1912, p.219) and more have been available in this study to confirm Verco's descriptions. The operculum is lanceolate, with the nucleus at the pointed abapical end, and bright yellow-brown. The radula (Figs 2b, 4j, 5a) resembles that of *Bursa* rather than that of *Tutufa* in its central tooth having a shallowly embayed base with relatively small interlocking basal processes. It differs from that of *Bursa (Bursa) bufonia* in having a narrower base to the cusp and larger denticles on the central tooth, and in having markedly smaller and more numerous cusps on the lateral teeth.

LOCALITIES: WAM 305-72, 33°S, 114°37'E, North-west of Bunbury, W.A., 212-226 m, H.M.A.S. "Diamantina", DM. 1/72 stn. 6, live holotype, two live adult paratypes, 1 live juvenile paratype; WAM 309-72, 34°14'S, 114°27'E, West of Cape Hamelin, W.A., 190-161 m, H.M.A.S. "Diamantina" stn. 19, three live paratypes; WAM 310-72, 33°15'S, 114°36'E, north-west of Bunbury, W.A., 161-165 m, H.M.A.S. "Diamantina" stn. 25, one live paratype; WAM 312-72, 32°43'S, 114°48'E, south-west of Mandurah, W.A., 192-179 m, H.M.A.S. "Diamantina" stn. 29, two live paratypes. The following material identified by the writer is also referred here: South Australian Museum, live specimen trawled in 185 m, Great Australian Bight 130 km west of Eucla, by Sir Joseph Verco (Verco, 1912, p.219); N4348, north-west of Rottneest I., W.A., on sponge, 155 m dredged B. R. Wilson on "Bluefin", 15 Aug. 1962 (WAM); N4339, north-west of Rottneest I., W.A., on sponge and sand, 199-214 m, dredged B. R. Wilson on "Bluefin", 14 Aug. 1962 (WAM); south-west of west end of Rottneest I., W.A., 130 m, dredged B. R. Wilson on "Bluefin", Sep. 1965 (WAM).

The following H.M.A.S. "Diamantina" material obtained by Dr B. R. Wilson during 1972 has not been examined personally, but was identified by Dr Wilson (all in Western Australian Museum): WAM 306-72, 33°S, 114°41'E, north-west of Bunbury, W.A., 183 m,

stn. 7 (one live); WAM 307-72, 34°S, 114°28'E, west of Cape Freycinet, near Margaret River, southern W.A., 195-219 m, stn. 12 (one live); WAM 308-72, 34°25'S, 114°36'E, west south-west of Cape Leeuwin, southern W.A., 146-142 m, stn. 17 (one live); WAM 311072, 32°45'S, 114°47'E, south-west of Mandurah, W.A., 220 m, stn. 28 (one live); WAM 313-72, 32°S, 115°6.7'E, west of Garden I., W.A., 176-182 m, stn. 33 (one live); WAM 314-72, 33°S, 114°37'E, north-west of Bunbury, W.A., 219-221 m, stn. 6/11 (12 dead); WAM 315-72, 34°S, 114°28'E, west of Cape Freycinet, W.A., 195-219 m, stn. 12 (one dead); WAM 316-72, 34°S, 25.5'E, west south-west of Cape Leeuwin, W.A., 190-174 m, stn. 16 (two dead); WAM 317-72, 34°15'S, 114°30'E, west of Cape Hamelin, W.A., 219-274 m, stn. 18 (one dead); WAM 318-72, 34°14'S, 114°27'E, west of Cape Hamelin, W.A., 190-161 m, stn. 19 (two dead); WAM 319-72, 33°44'S, 114°26.1'E, south-west of Cape Naturaliste, W.A., 238-183 m, stn. 21 (four dead); WAM 310-72, 32°45'S, 114°47'E, south-west of Mandurah, W.A., 220 m, stn. 28 (two dead); WAM 321-72, 30°58'S, 114°49'E, west north-west of Lancelin, W.A., 212-215 m, stn. 41 (2 dead); WAM 322-72, 30°10'S, 114°13'E, west north-west of Jurien Bay, W.A., 178-179 m, stn. 48 (one dead); WAM 323-72, 29°43.5'S, 114°20'E, north-west of Beagle I., W.A., 183 m, stn. 52 (one dead); WAM 324-72, 29°58'S, 114°27'E, north-west of Green Head, W.A., 197-219 m, stn. 64 (one dead); WAM 325-72, 31°16'S, 114°54'E, south-west of Ledge Point, W.A., 274 m, stn. 74 (one dead) (a total of 25 localities).

SUMMARY: classification of the Bursidae that have been assigned to *Tutufa*

Genus *Bursa* Röding, 1798

Subgenus *Bufonariella* Thiele, 1929.

Bursa (Bufonariella) latitudo latitudo Garrard, 1961, E. Australia.

latitudo natalensis Coelho & Mathews, 1970, W. Atlantic.

latitudo wolfei n.subsp., Hawaii.

ranelloides ranelloides (Reeve, 1844), Japan.

ranelloides humilis n.subsp., W. Australia.

ranelloides tenuisculpta Dautzenberg & Fischer, 1906, E. & W. Atlantic & South Africa.

Genus *Tutufa* Jousseaume, 1881

Subgenus *Tutufella*, new name for *Lampas* Schumacher, 1817,

Tutufa (Tutufella) oyamai Habe, 1973, West Pacific & E. Indian Ocean.

bubo (Linnaeus, 1758), Indo-West Pacific.

bufo (Röding, 1798), Indo-West Pacific.

Subgenus *Tutufella*, new name for *Lampas* Schumacher, 1817, *Tutufa (Tutufella) oyamai* Habe, 1973, West Pacific & E. Indian Ocean.

rubeta (Linnaeus, 1758), Indo-West Pacific.

tenuigranosa (E. A. Smith, 1914), South China Sea.

?n. sp. aff. *rubeta* (L.), Moçambique.

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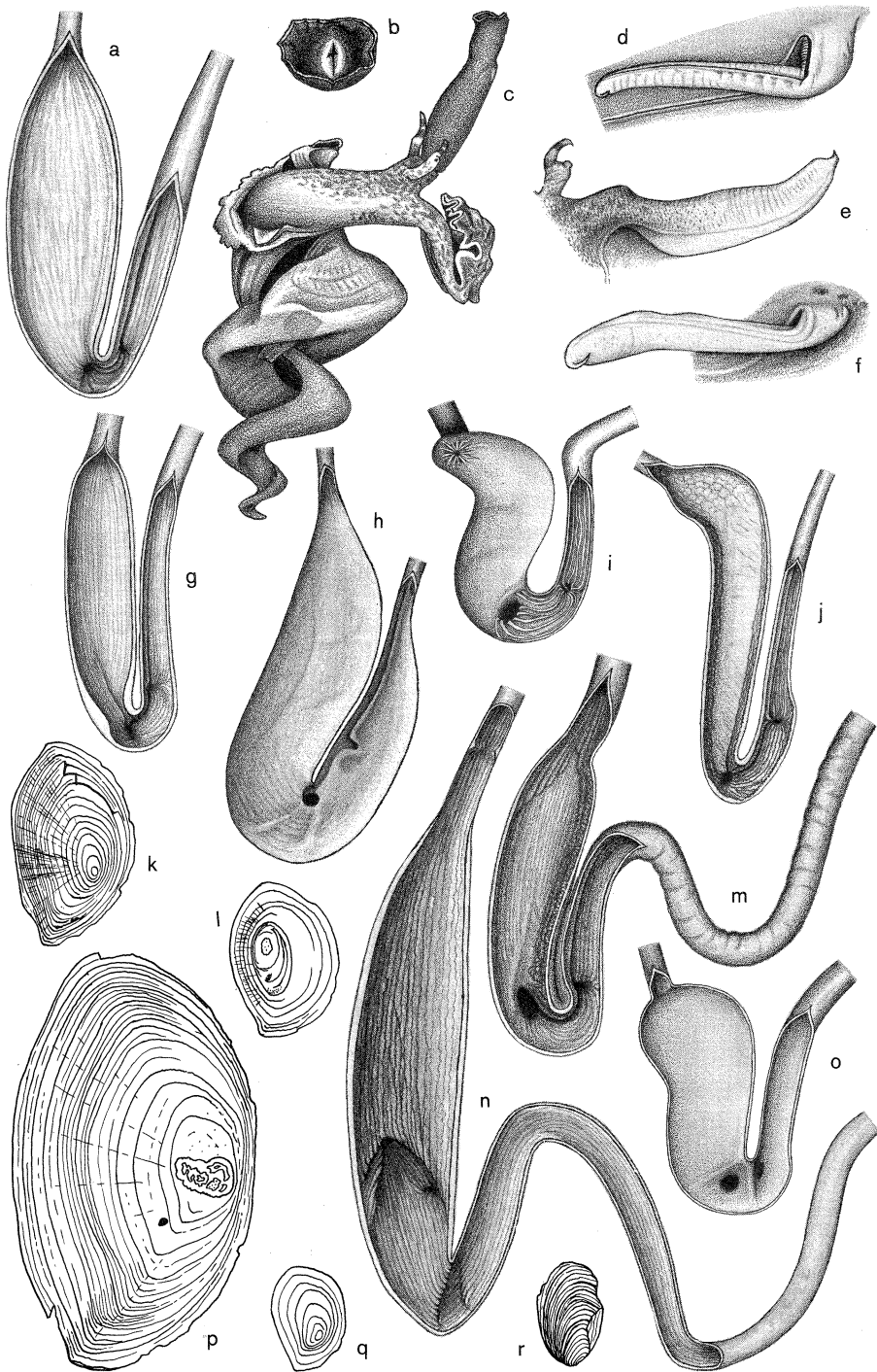
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Fig. 1 a, g-j, n-o stomachs of tonnageans, opened by mid-dorsal section (not to scale). **a.** *Bursa (Bursa) bufonia* (Gmelin), Flying Fish Cove, Christmas Island; WAM 835-71. **g.** *Tutufa (Tutufa) bufo* (Röding), off Osbourne Shoals, Bate Bay, Cronulla, N.S.W.; AM, C 73465. **h.** *Charonia lampas rubicunda* (Perry), F. R. V. "Kapala" stn. 71-37-04, east of Broken Bay, N.S.W., 230 m; AM, C 79170. **i.** *Tutufa (Tutufella) oyamai* Habe, m.v. "Pele" Mariel King Memorial Exped. Stn. ANI/1, S.W. of Tg. Ngabordamlu, Trangan, Aru I., Moluccas, 27-29 m; WAM. **j.** *Tutufa (Tutufella) rubeta* (Linnaeus), m.v. "Pele" Mariel King Memorial Exped. stn. CPII, 1 mile S.W. of Tg. Tutuhuhus, Piru Bay, Ceram. 0.6 m; WAM. **m.** *Bursa (Bufonariella) granularis* (Röding), W of Pt. Cloates, N Western Australia, on reef, WAM 841-71. **n.** *Tonna variegata cervesina* Hedley, Bay of Islands, New Zealand; NZGS. **o.** *Bursa (Bufonariella) ranelloides humilis* n. subsp., paratype, H.M.A.S. "Diamantina" stn. 6, N.W. of Bunbury, Western Australia, 212-226 m; WAM 305-72. **b, c.** Complete animal of female *Tutufa (Tutufella) rubeta* (Linnaeus) removed from shell; mantle retracted, proboscis partly expanded (X1). **b.** — anterior view of proboscis tip (X2), showing lips around central mouth. Same specimen as in Fig. 1j. **d-f.** Penes of *Tutufa* (not to scale). **d.** — *Tutufa (Tutufa) bufo* (Röding), lateral view, same specimen as Fig. 1g and Fig. 6. **e.** *Tutufa (Tutufella) rubeta* (Linnaeus), dorsal view of penis lying forward; same specimen as Fig. 1b, c, j and Fig. 7. **f.** — *Tutufa (Tutufella) oyamai* Habe, lateral view, same specimen as Fig. 1i. **k, l, p-r.** Opercula of Bursidae, all enlarged X1.5. **k.** — *Tutufa (Tutufella) rubeta* (Linnaeus), same specimen as Fig. 1b, c, j and Fig. 7. **l, q.** — *Tutufa (Tutufella) oyamai* Habe, two specimens showing abnormal and normal nuclear position, same locality as Fig 1f, i. **p** — *Tutufa (Tutufa) bufo* (Röding), off Osbourne Shoals, Bate Bay, Cronulla, N.S.W.; AM, C 73465. **r** — *Bursa (Bufonariella) ranelloides humilis* n. subsp., paratype, same specimen as Fig. 1o and Fig. 8.



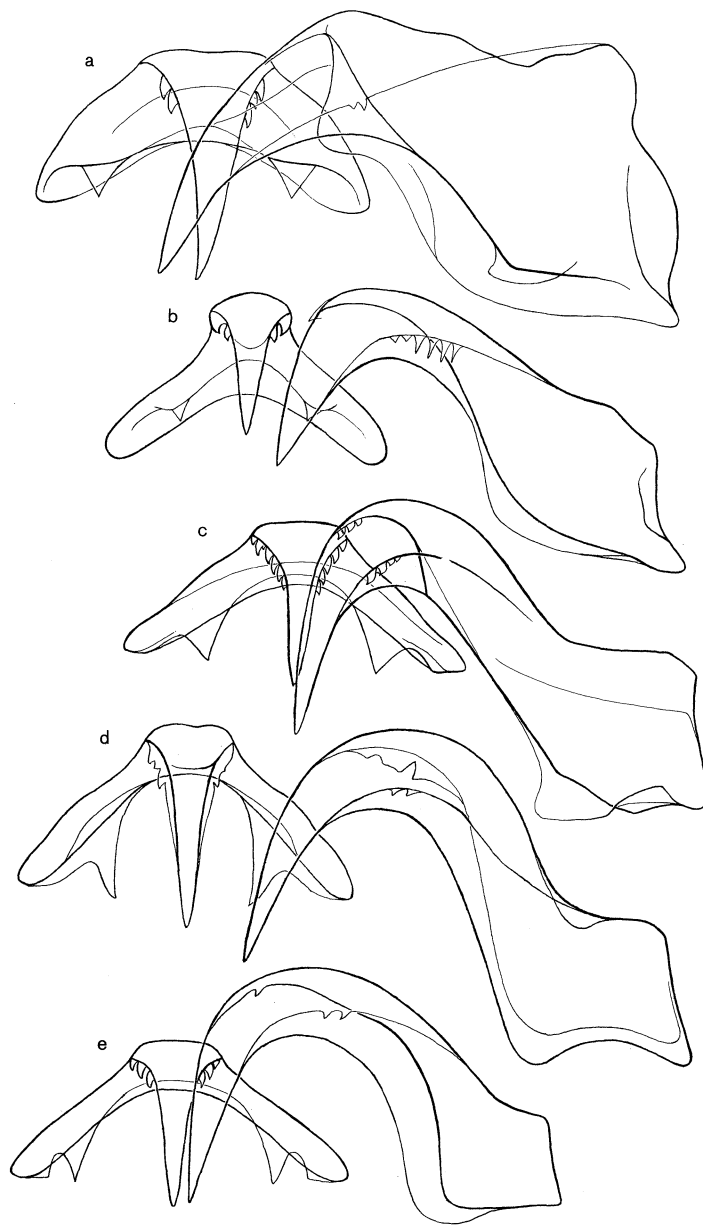


Fig. 2. Central and lateral teeth from half of one row of radula of Bursidae (not to scale). **a** *Bursa* (*Bursa bufonia*) (Gmelin), Flying Fish Cove, Christmas Island; WAM 835-71. **b** *Bursa* (*Bufonariella ranelloides humilis*) n. subsp., paratype, H.M.A.S. "Diamantina" stn.6, N.W. of Bunbury, Western Australia, 212-216 m; WAM 305-72. **c** *Tutufa* (*Tutufa*) *bufo* (Röding), off Osbourne Shoals, Bate Bay, Cronulla, N.S.W.; AM, C 73465. **d** *Tutufa* (*Tutufa*) *bubo* (Linnaeus), Port Ternay, N.W. Mahé, Seychelles; ANSP 311233. **e** *Tutufa* (*Tutufella*) *oyamai* Habe, m.v. "Pele" Mariel King Memorial Exped. stn. ANI/1, Aru I., Moluccas; WAM.

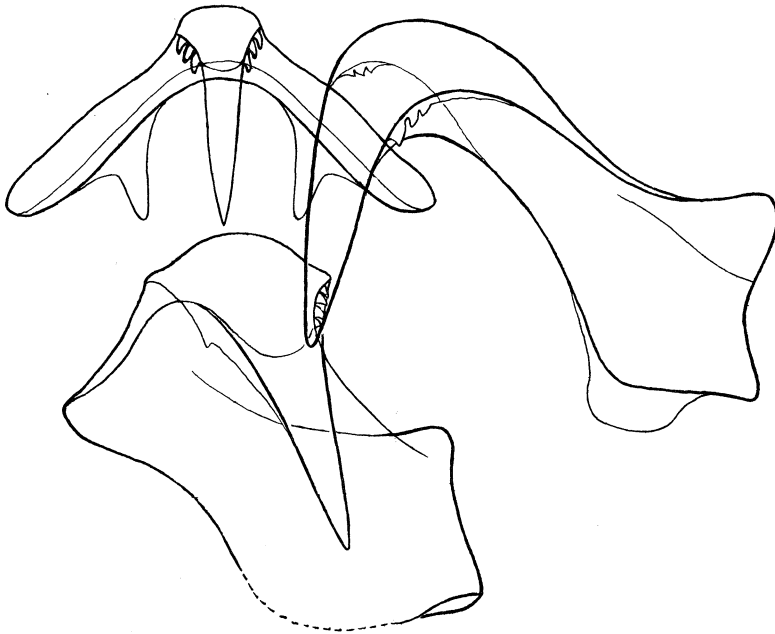


Fig. 3. *Tutufa (Tutufella) rubeta* (Linnaeus), central and lateral teeth from one half row of radula in normal resting position, plus (lower sketch) lateral tooth turned half outwards; m.v. "Pele" Mariel King Memorial Exped. stn. CP.II, Piru Bay, Ceram, Moluccas; WAM.

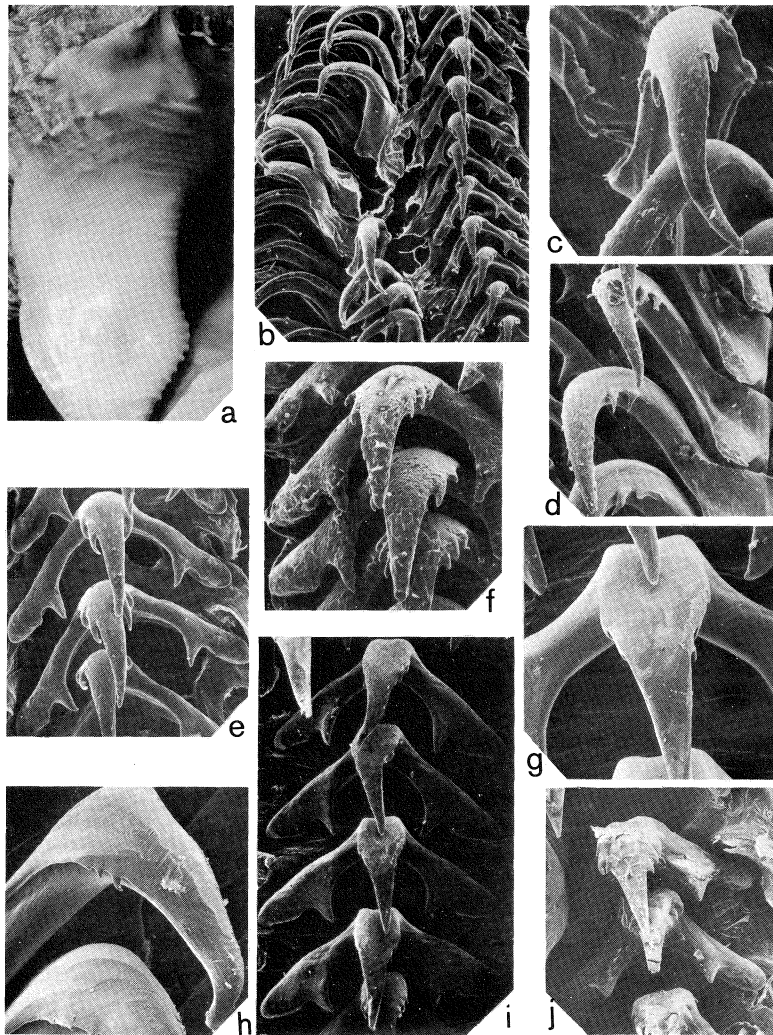


Fig. 4 **a.** *Tutufa (Tutufa) bubo* (Linnaeus), neotype, and lectotype of *Bursa rubeta* var. *gigantea* E. A. Smith, columellar sculpture (turned 30° to left); the similar *T. bardeyi* has a smooth columella. BMNH 1899.12.27.8 (X 0.6). **b-j.** Scanning electron micrographs of radulae of *Tutufa* and *Bursa (Bufonariella)*. **b.** *Tutufa (Tutufella) oyamai* Habe, general view of undisturbed central teeth and displaced left lateral and marginal teeth, X 90; m.v. "Pele" Mariel King Memorial Exped. sta. KR VI/3-10, Kai I., Moluccas (WAM). **c.** Left lateral tooth of same radula as in Fig. 4b, turned half outwards, X 285. **d.** Right lateral teeth of same radula as in Fig. 4b, in normal rest position, X 215. **e.** Central teeth of same radula as in Fig. 4b, X 215. **f.** *Tutufa (Tutufella) oyamai* Habe, central teeth of larger specimen than in Fig. 4b (poorly cleaned), X 220; m.v. "Pele" Mariel King Memorial Exped. Sta. ANI/1, Aru I., Moluccas; WAM (drawn in Fig. 2e). **g.** *Tutufa (Tutufella) rubeta* (Linnaeus), main cusp of central tooth, X 220; m.v. "Pele" Mariel King Memorial Exped. Sta. CP II, Piru Bay, Ceram; WAM (drawn in Fig. 3) **h.** Cusp of left lateral tooth of same radula as in Fig. 4g, X 180 (scratches are artificial). **i.** Portion of row of central teeth of same radula as in Fig. 4g, X 95. **j.** *Bursa (Bufonariella) ranelloides humilis* n. subsp., paratype, central teeth of radula (poorly cleaned), X 140; H.M.A.S. "Diamantina" Sta.6, N.W. of Bunbury, Western Australia; WAM 305-72 (drawn in Fig. 2b).

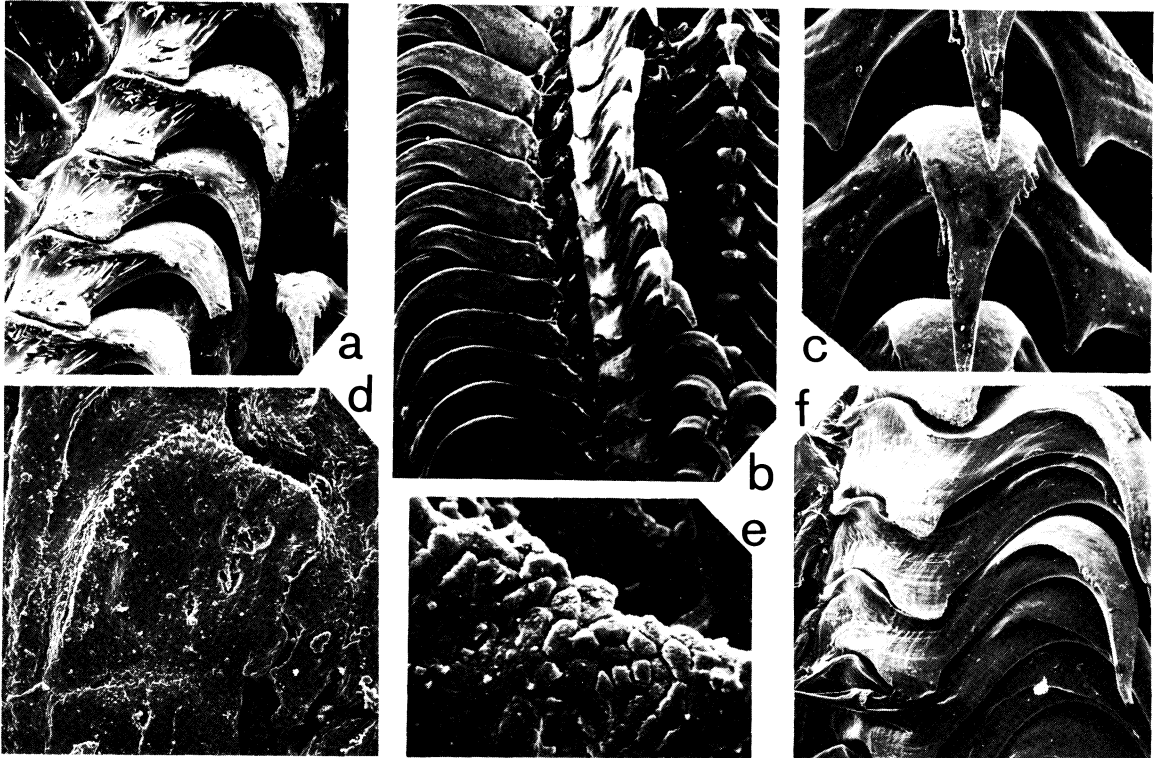


Fig. 5 Scanning electron micrographs of *Tutufa* radulae and jaw plates. **a.** Left lateral teeth of same radula as in Fig. 4j, X 75. **b.** *Tutufa (Tutufa) bufo* (Röding), general view of little-disturbed radula showing interlocked teeth, X 20; off Osbourne Shoals, Bate Bay, Cronulla, New South Wales; AM, C 73465 (drawn in Fig. 2c). **c.** Main cusps of central teeth of same radula as in Fig. 5b, X 90. **f.** Left lateral teeth of same radula as in Fig. 5b, showing interlocked bases, X 70. **d., e.** *Tutufa (Tutufella) rubeta* (Linnaeus), jaw plate, attached to section of "lip" epidermis; m.v. "Pele" Mariel King Memorial Exped. sta. CP II, Piru Bay, Ceram; WAM. **d.** anterior half of damaged plate, X 140; **e.** platelets of central anterior edge, X 690.

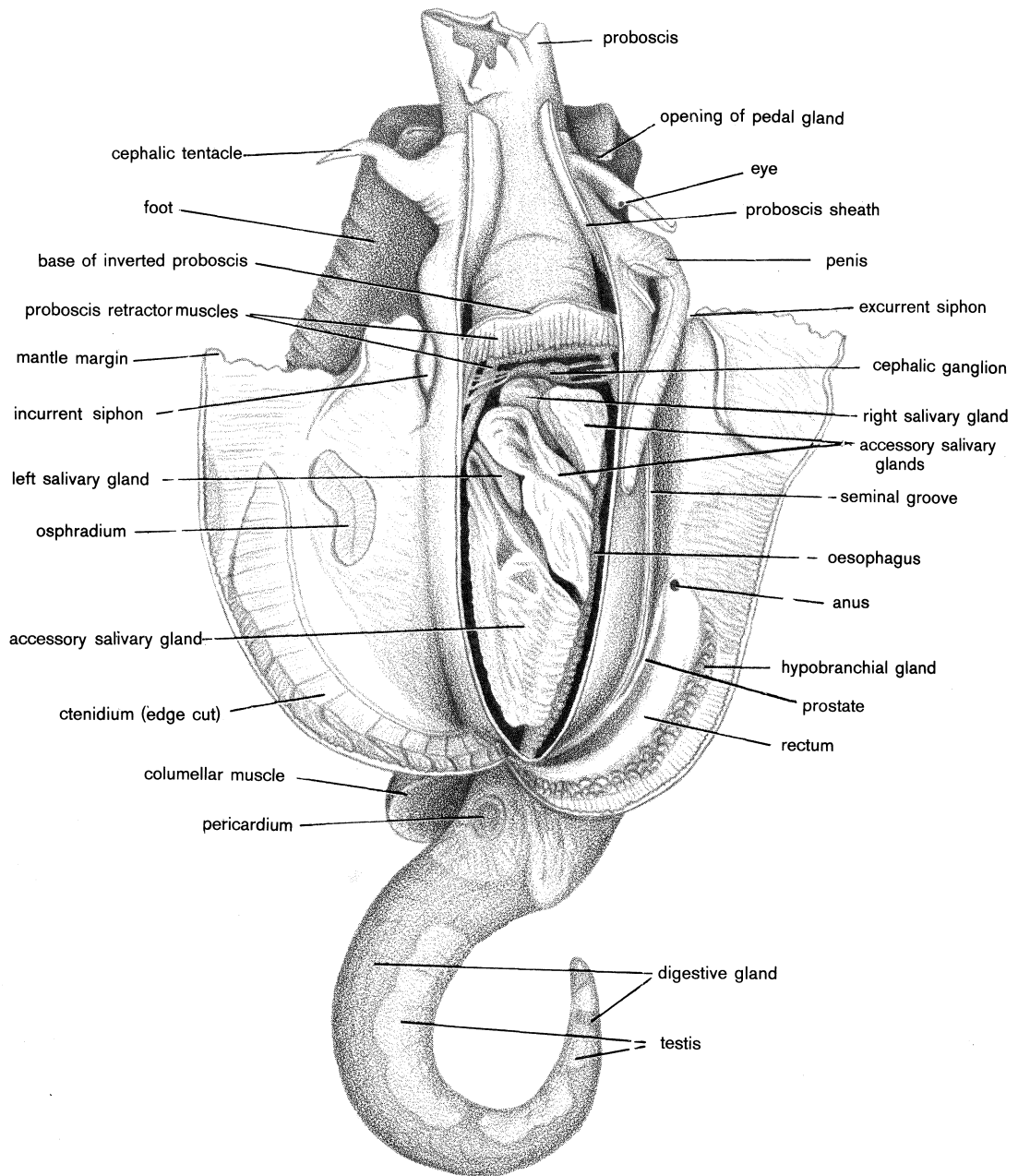


Fig. 6. *Tutufa (Tutufa) bubo* (Röding), sketch of gross anatomy of mantle and cephalic cavities. Length of whole animal in position shown is approx. 13 cm. Off Osbourne Shoals, Bate Bay, Cronulla, N.S.W., 30 m; AM, C 73465.

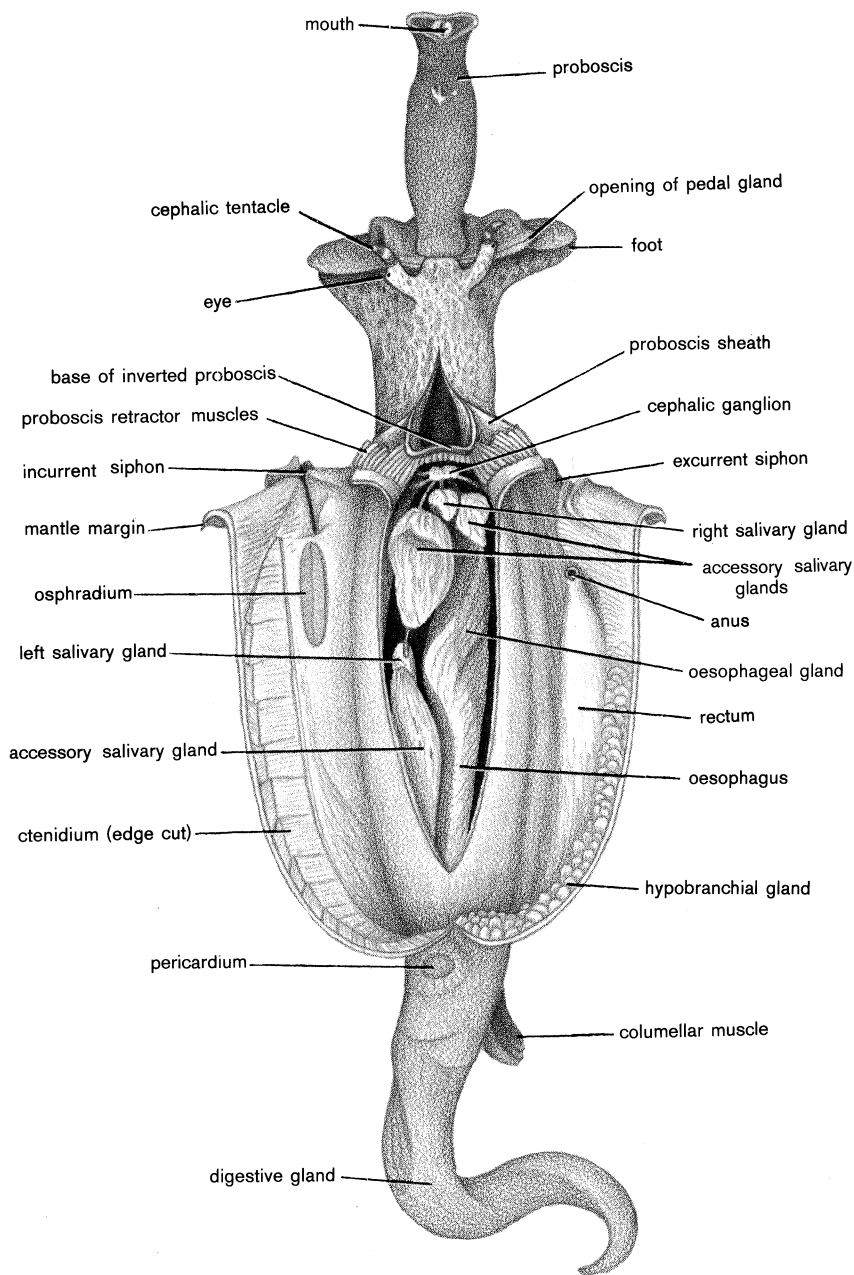


Fig. 7. *Tutufa (Tutufella) rubeta* (Linnaeus), sketch of gross anatomy of mantle and cephalic cavities (approx. X 1.5); m.v. "Pele" Mariel King Memorial Exped. stn. CP II, Piru Bay, Ceram, Moluccas; WAM.

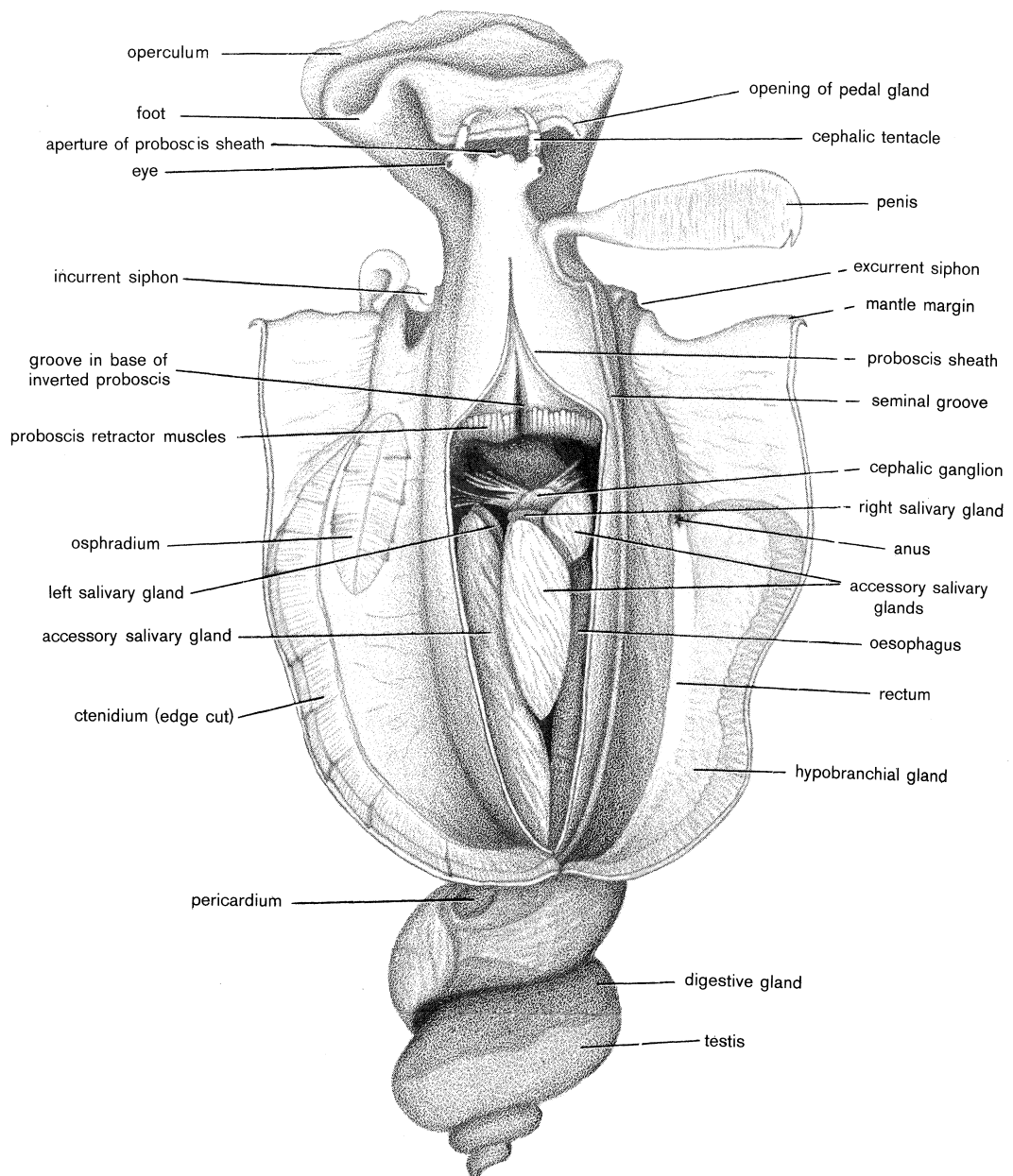


Fig. 8. *Bursa (Bufonariella) ranelloides humilis* n.subsp., paratype, sketch of gross anatomy of mantle and cephalic cavities (approx. X 4). H.M.A.S. "Diamantina" stn. 6, N.W. of Bunbury, Western Australia, 212-226 m; WAM 305-72.



Fig. 9. a,b,d, *Tutufa (Tutufa) bardeyi* (Jousseume). a,d. Paralectotype of *Bursa (Tutufa) rubeta* var. *gigantea* E. A. Smith, 1914, figured by Smith (1914, pl. 4, fig. 5), Muscat, Oman; BMNH 1899.12.27.8 (X 0.33). **b.** Previously unfigured paralectotype of *Bursa (Tutufa) rubeta* var. *gigantea* E. A. Smith, 1914, Muscat, Oman; BMNH 1899.12.27.9 (X 0.25). **c.** *Tutufa (Tutufella) rubeta* (Linnaeus, 1758), Port Moresby, New Guinea; NZNM, MF 21548, X1.



Fig. 10. **a,d** *Tutufa (Tutufa) bardeyi* (Jousseau, 1894), Bir Ali and Mukalla, East Aden Protectorate; WAM, X 0.5. **b,c.** *Tutufa (Tutufella) cf. rubeta* (Linnaeus), pale specimen with dark inner lip, Moçambique Island, Moçambique; NM, G 3444 (X1.)

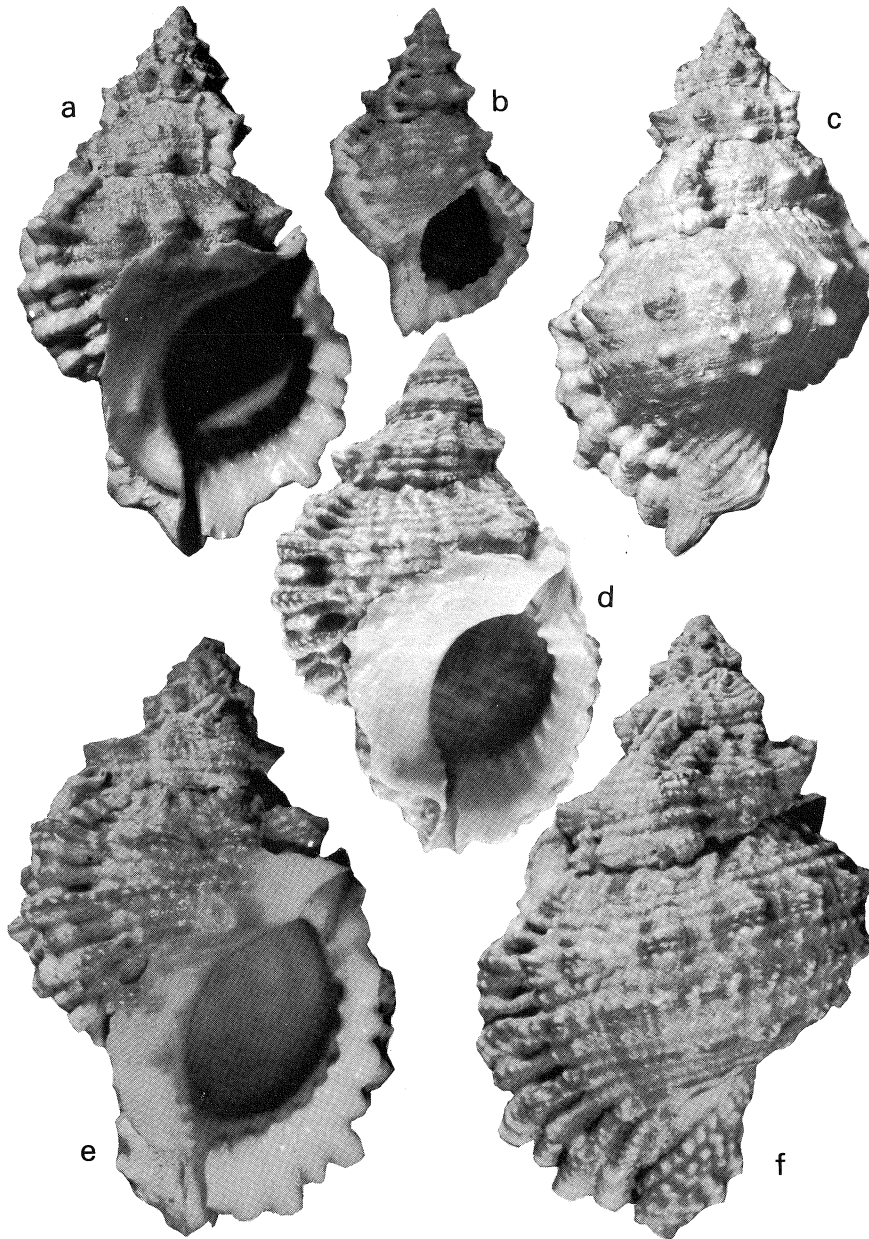


Fig. 11. a, c-f *Tutufa (Tutufa) bufo* (Röding, 1798). **a, c.** 130-160 m, off Wedge I., central Western Australia; NZGS, WM 10744 (X 0.66). **d.** lectotype of *Bursa (Tutufa) rubeta* var. *lissostoma* E. A. Smith, 1914, unlocalised; BMNH 197384 (X 0.8). **e,f.** Townsville, Queensland; AM, C 66562 (X1). **b.** *Tutufa (Tutufa) bufo* (Linnaeus, 1758) juvenile, specimen recorded as "*Bursa lampas*" by E. A. Smith (1906), Durban Bluff, South Africa; BMNH 1906.7.7.6 (enlarged X 1.6).

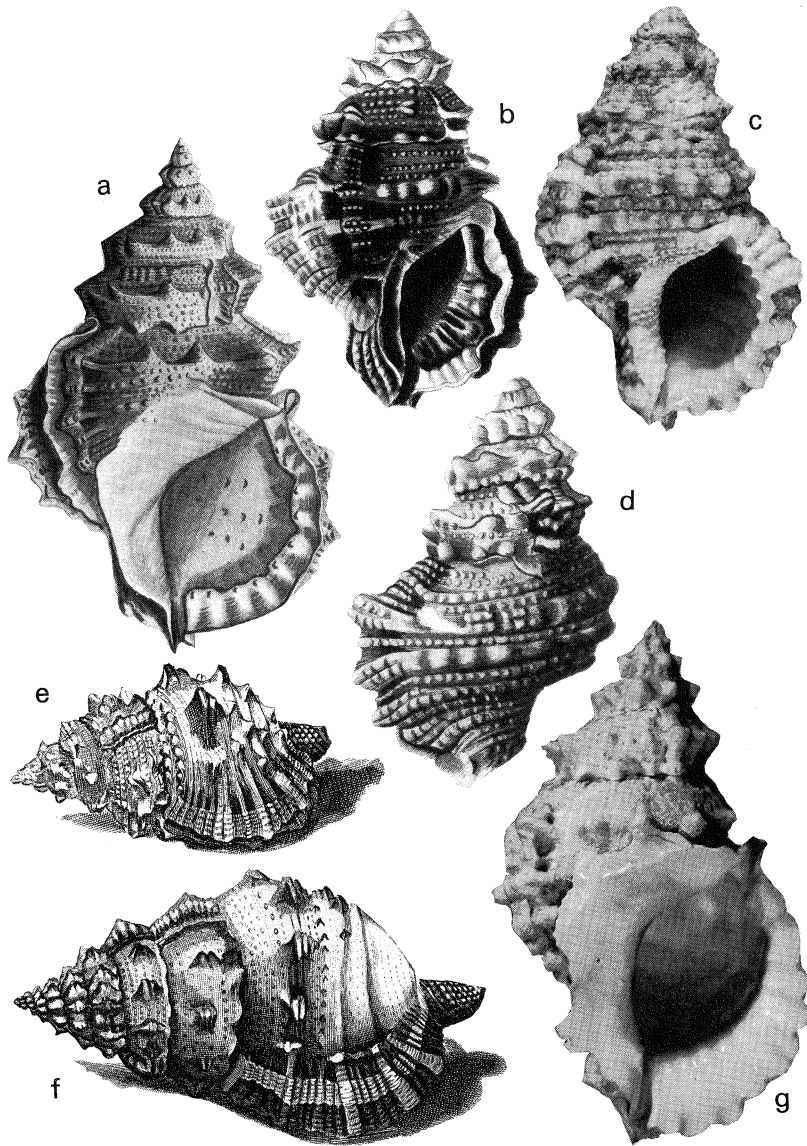


Fig. 12. **a** *Tutufa (Tutufa) bufo* (Röding, 1798), copy of Martini's (1780, pl. 129, fig. 1238) figure cited for *Tritonium bufo* by Röding (1798, p. 128), reduced to X 0.5. **b-e.** *Tutufa (Tutufella) rubeta* (Linnaeus, 1758). **b,d.** — copy of Martini's (1780, pl. 128, fig. 1236, 1237) figure cited for *Tritonium tuberosum* by Röding (1798, p. 127), X1. **c.** — locality?; specimen recorded from "Port Natal" by E. A. Smith (1914); BMNH 1861.7.3.29 (X 0.94). **e.** — copy of Rumphius' (1711, pl. 28, fig. D) figure cited for both *Murex rana* var. *rubeta* Linnaeus, 1758, and *Tritonium rubeta* Röding, 1798 (X1). **f.** *Tutufa (Tutuba) bufo* (Linnaeus, 1758), copy of Rumphius' (1711, pl. 28, fig. C) figure cited for *Murex rana* var. *bubo* Linnaeus, 1758 (X 0.66). **g.** *Tutufa (Tutufa) bufo* (Röding, 1798), off Port Macquarie, New South Wales; AM (X 0.66).

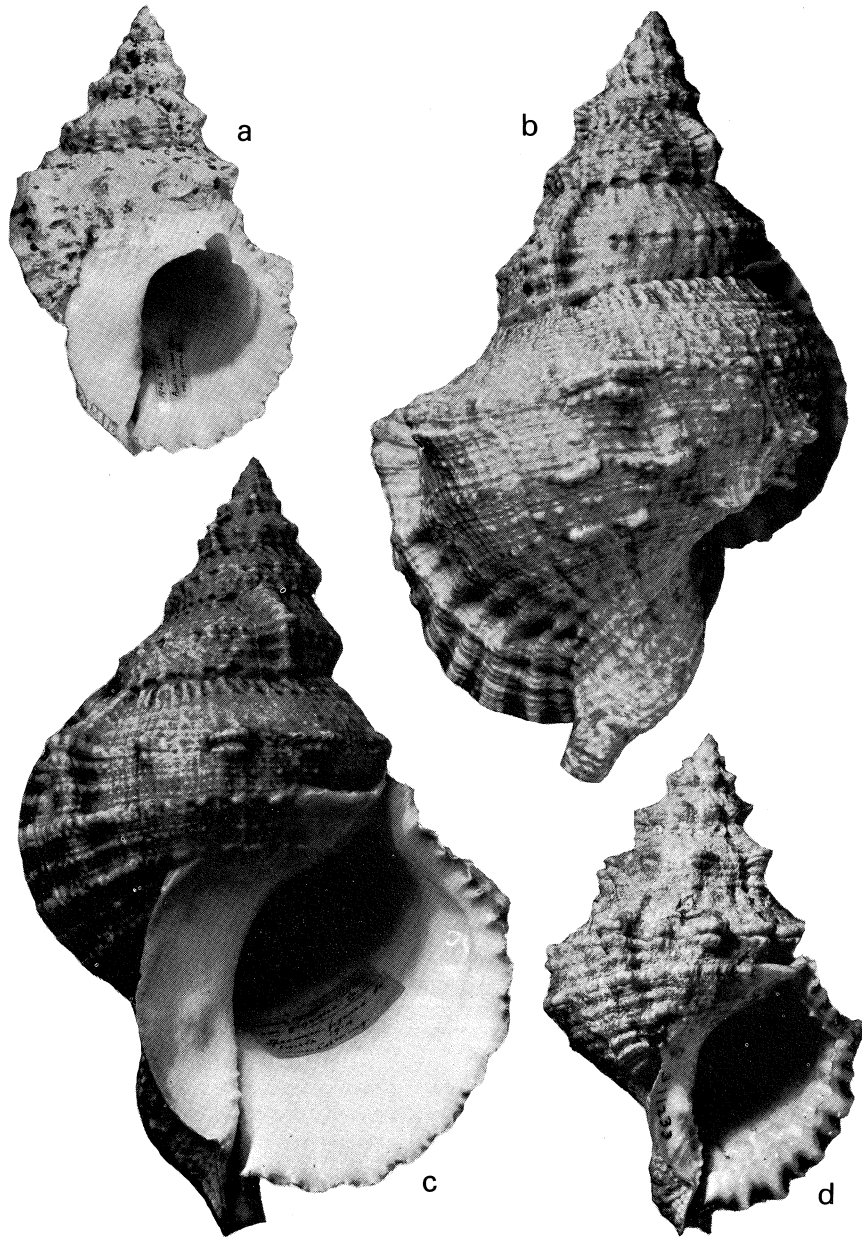


Fig. 13. *Tutufa (Tutufa) bubo* (Linnaeus, 1758). **a.** Previously unfigured paralectotype of *Bursa rubeta* var. *gigantea* E. A. Smith, 1914, unlocalised; BMNH 1914.6.29.1 (X 0.44). **b,c** Neotype of *Murex rana* var. *bubo* Linnaeus, 1758, and lectotype of *Bursa (Tutufa) rubeta* var. *gigantea* E. A. Smith, 1914; "Philippine Islands (on the reefs)", BMNH 1974147 (X 0.5). **d.** Young specimen dessected in this study, Port Ternay, N.W. Mahé, Seychelles; ANSP, 311233 (X 0.66).

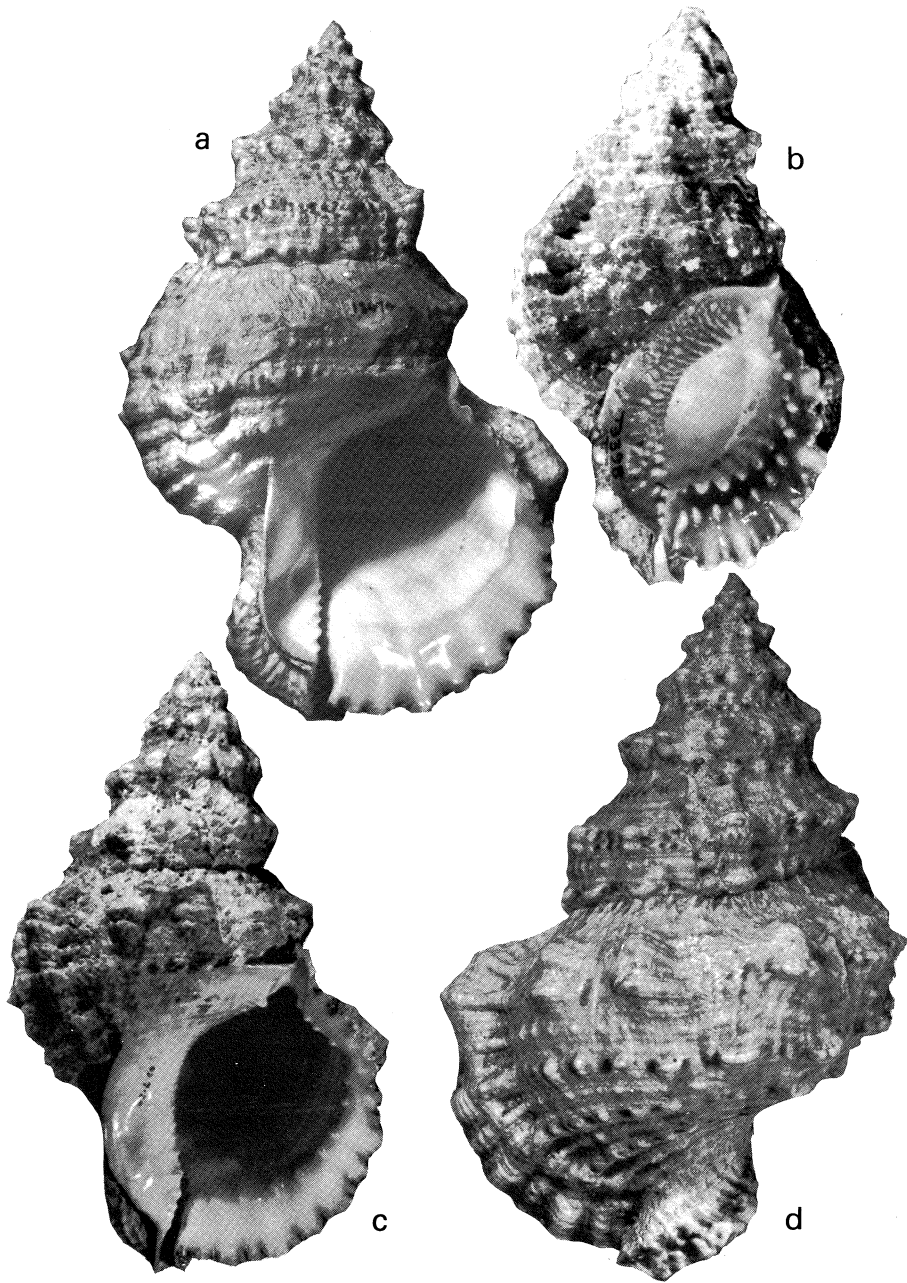


Fig. 14. **a, c-d.** *Tutufa (Tutufa) bubo* (Linnaeus, 1758), **a, d.** Fiji, NZNM, MF 18474 (X 0.5) **c.** — off Southport, Queensland; AM c 69752 (X0.5) **b.** — *Tutufa (Tutufella) rubeta* (Linnaeus, 1758) Madang, New Guinea; AM, C 73398 (X1).

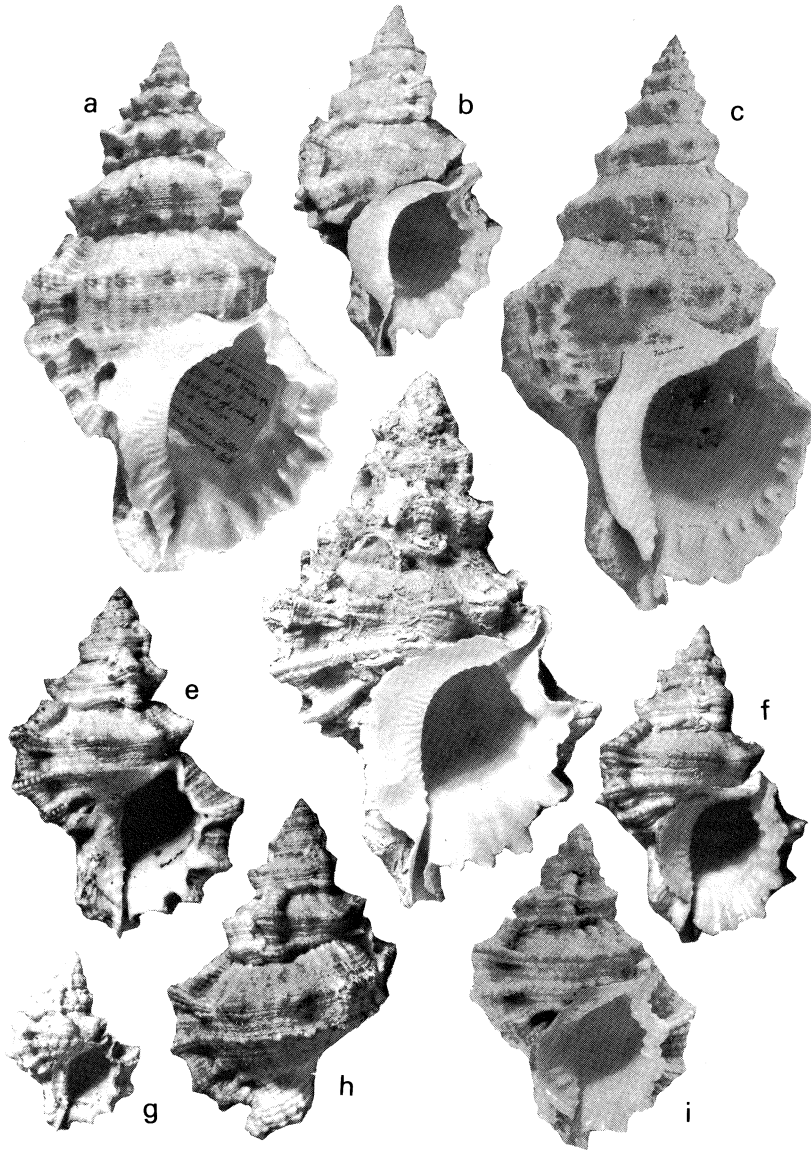


Fig. 15. a, c. *Tutufa (Tutufella) tenuigranosa* (E. A. Smith, 1914). **a** — lectotype of *Bursa (Tutufa) rubeta* var. *tenuigranosa* E. A. Smith 1914, unlocalised, BMNH 1914.6.29.4 (X 0.5). **c**. — off Hong Kong South China Sea, figured by Habe (1973, text-fig. 1); NSMT (X 0.5). **d-i.** *Tufuta (Tutufella) oyamai* Habe, 1973. **d**. — specimen dissected in this study, m.v. "Pele" Mariel King Memorial Expedition stn. ANI/1, dredged 4.5-5.0 m, Aru I., Moluccas; WAM (X 1.5). **e, h**. — paratype, Taiwan, pres. Dr T. Habe; NZGS, WM 11274 (X1). **f**. — off Fraser I., Queensland; NZGS, WM 10758 (X1). **g**. — Murray I., Torres Strait, one of three specimens recorded as *Gyrineum (Lampas) ranelloides* by Melvill and Standen (1899, p.163); Haddon Colln., Manchester Museum (X1). **i**. — holotype, Taiwan, photo courtesy Dr T. Habe; NSMT (X1).

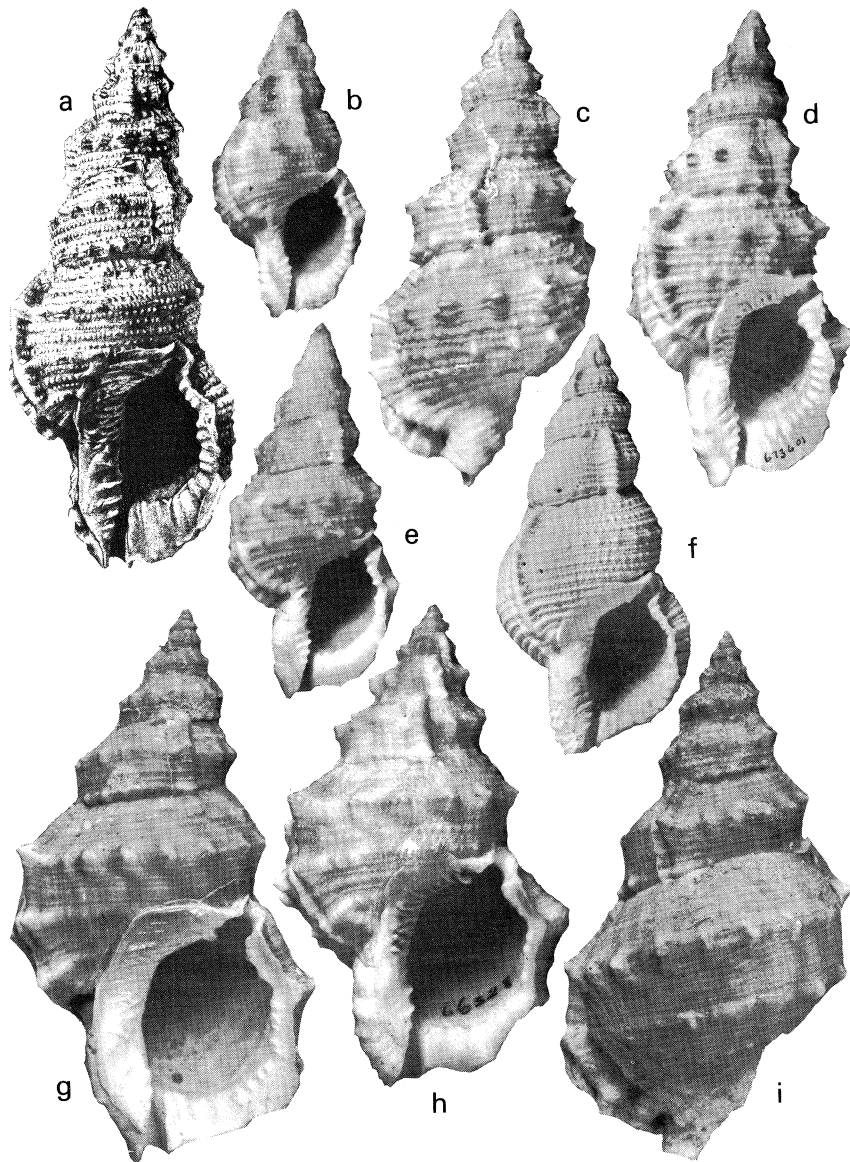


Fig. 16. a-f. *Bursa (Bufonariella) latitudo natalensis* Coelho & Matthews, 1970. **a.** — holotype, copy (at published size) of fig. 1 (Coelho & Matthews 1970, p.3), crayfish pots in 40-50 m, off Pirangi, Natal, Rio Grande do Norte, northeast Brazil (enlarged X 1.9). **b, e.** — fish trap in 180 m, off Bahia de Anasco, W. coast of Puerto Rico; C.S. Wolfe Colln (X1). **c, d.** — paratype of *Bursa finlayi* McGinty, 1962, fish trap in 220 m, Bay of Matanzas, Cuba; USNM 673601 (X1). **f.** — shell trap in 230 m, WSW of Charlestown, Nevis, British West Indies; USNM 735915 (X1). **g-i.** *Bursa (Bufonariella) latitudo latitudo* Garrad, 1961. **g, i.** — holotype, off Moreton I., Queensland, 230 m; National Museum of Victoria, F. 21111 (X1). **h.** — 100-130 m, off Caloundra, Queensland; AM, C 66528 (X 1.5).

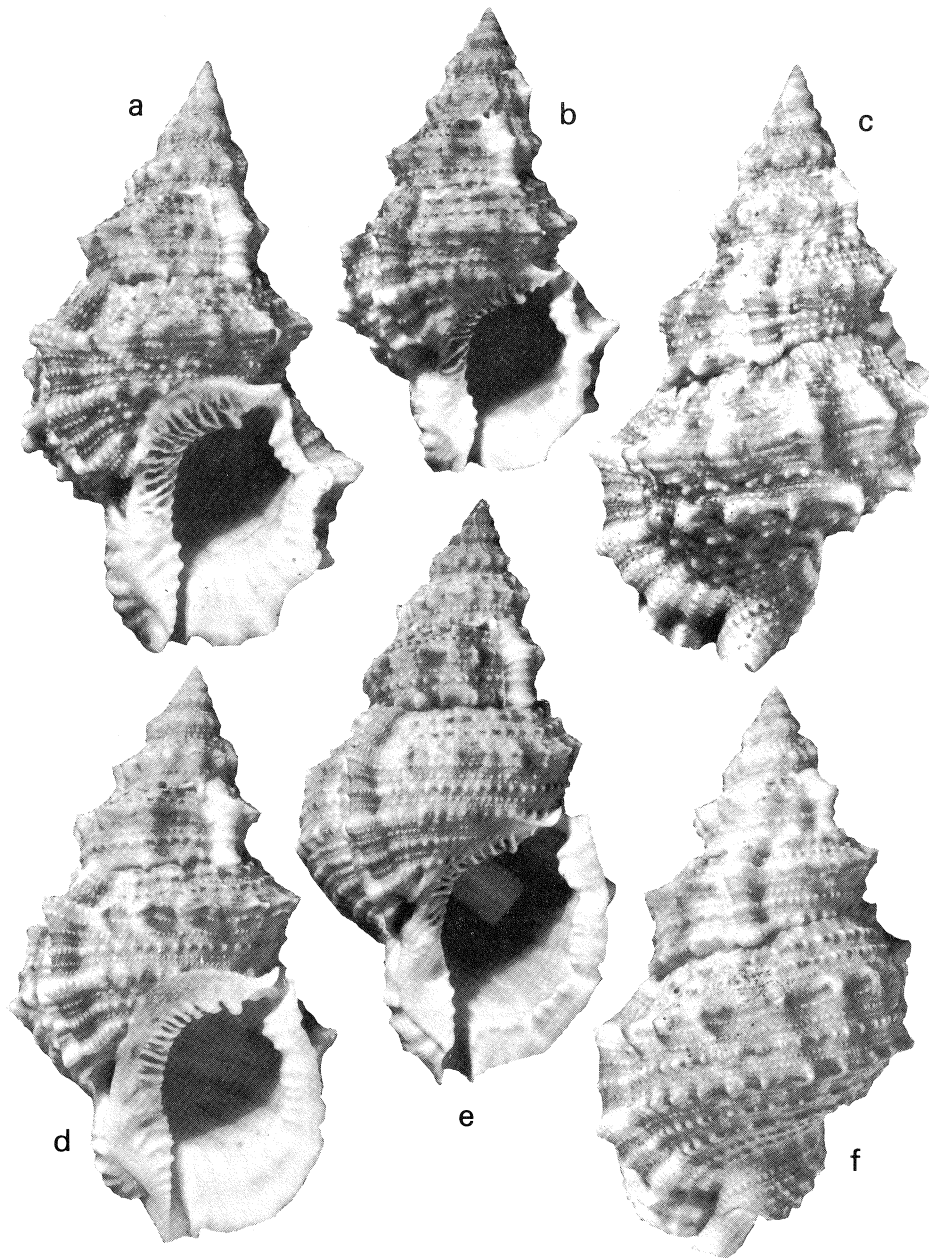


Fig. 17. *Bursa (Bufonariella) latitudo wolfei* n. subsp., Hawaii, all X1. **a,c.** — Holotype, crab trap in 58 m, off Makaha, Oahu; Bernice P. Bishop Museum, BPBM 8936. **b.** — paratype, crab trap in 120 m, off Haleiwa, Oahu; C. S. Wolfe Colln. **d, f.** — paratype, 120 m, of Kahuku, Oahu; C. S. Wolfe Colln. **e.** — paratype, locality as Fig. 15 d, f; S. Handrahan Colln.

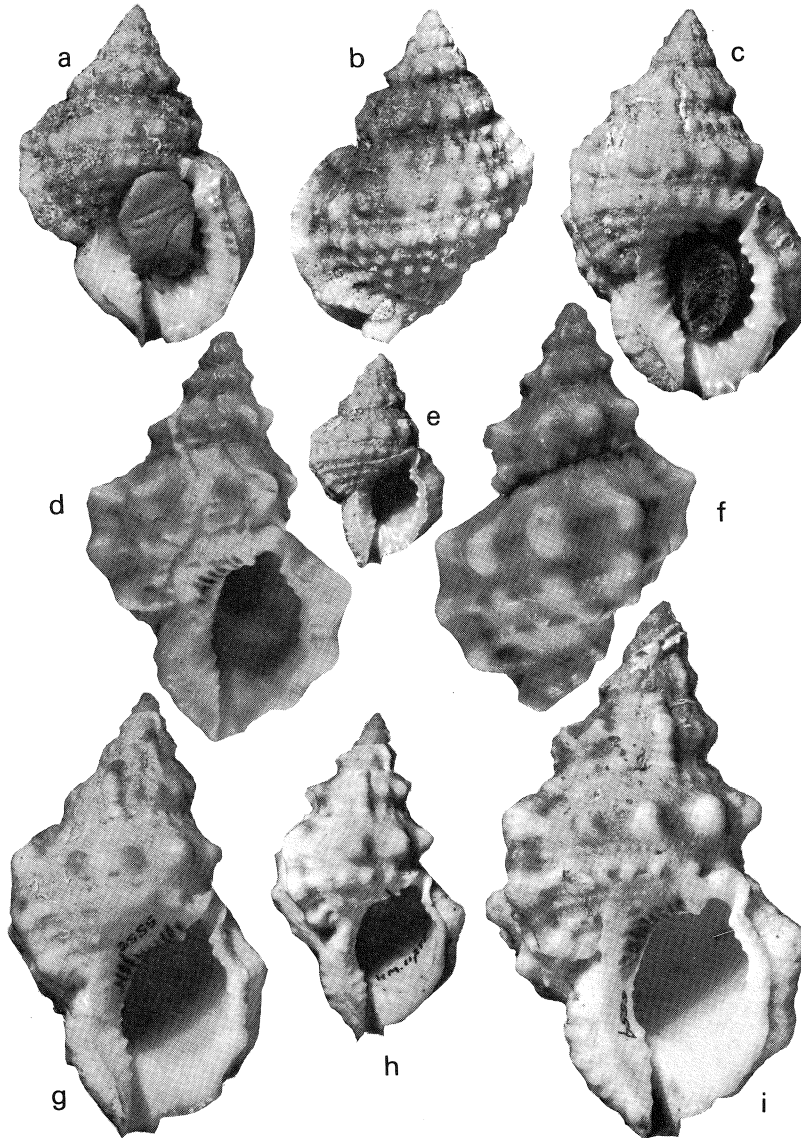


Fig. 18. **a-c, e.** *Bursa (Bufonariella) ranelloides humilis* n. subsp., Western Australia, all X 1.5. **a,b.** — holotype, H.M.A.S. "Diamantina" stn. 6, NW of Bunbury, 212-226 m; WAM 505-72. **c.** — paratype, H.M.A.S. "Diamantina" stn. 25, NW of Bunbury, 161-165 m WAM 310-72. **e.** — juvenile paratype, H.M.A.S. "Diamantina" stn. 19, W of Cape Hamelin, 190-161 m; WAM 309-72. **d, f-i.** *Bursa (Bufonariella) ranelloides ranelloides* (Reeve, 1844), Japan. **d., f.** — holotype, "Matnog, Province of Albay, Luzon, Philippine Islands" (really from southern Japan); BMNH 1967594 (X 1.44; height = 49.65 mm). **g.** — 90 m, Tosa Bay, Shikoku, weakly noded specimen; NZNM, MF 5558 (X 1.5). **h** — Tosa Bay, Shikoku; NZGS, WM 11277 (X1), **i.** — 35 m, Tosa Bay, Shikoku, the common large-noduled form; NZNM, MF 5559 (X 1.5).

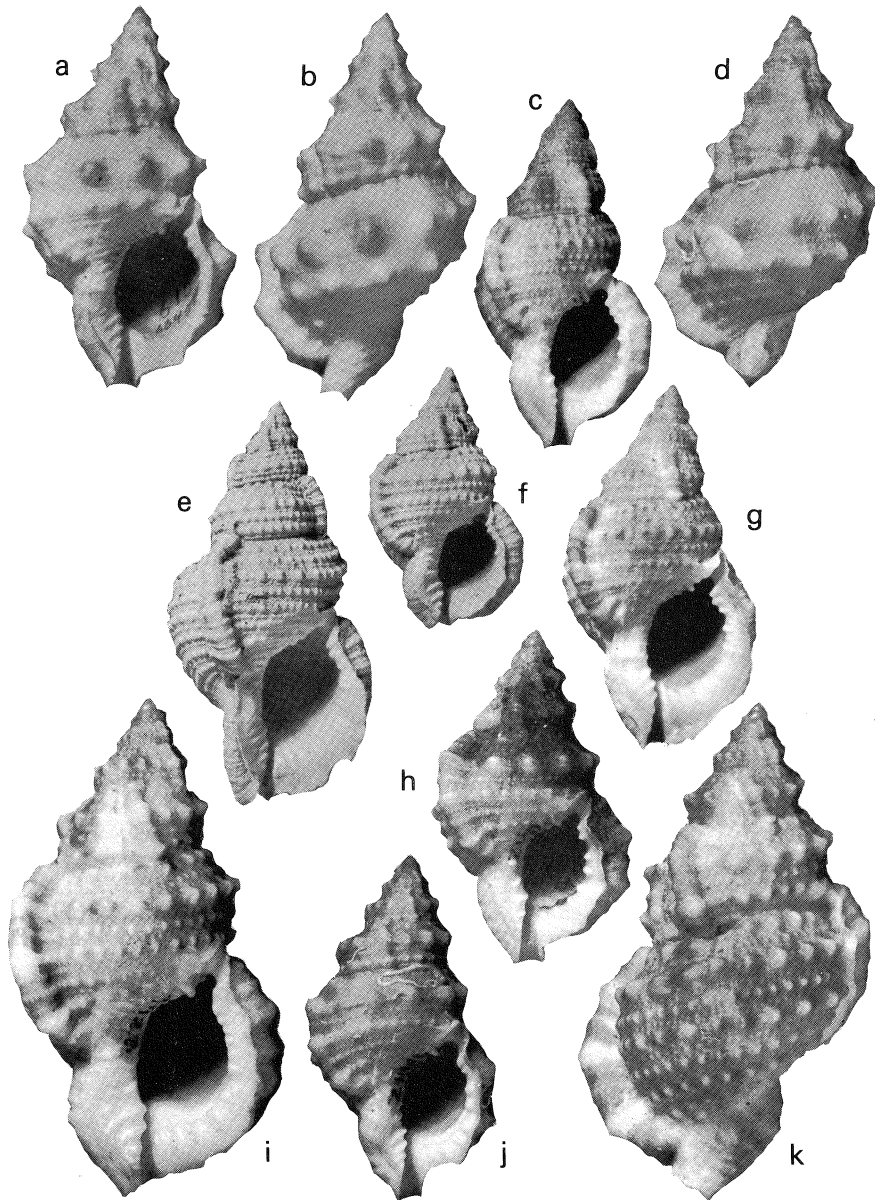


Fig. 19. *Bursa (Bufonariella) ranelloides tenuisculpta* Dautzenberg & Fischer, 1906. **a,b.** Holotype of *Bursa finlayi* McGinty, 1962, 210 m, off Sombrero Key Light, middle Florida Keys, "Triton" stn. 615; USNM 634570 (X 1.5). **c,g.** 230 m, Dry Tortugas, Florida; C. S. Wolfe Colln. (X1). **d.** — N of Virgin Islands, 180-550 m; USNM 430336 (X 1.5). **e.** — "Eolis" stn. 146, 180 m, off Key West, Florida; USNM 41778 (X1). **f.** — State Univ. Iowa dredging stn. 29, Bahia Honda, Cuba; USNM 543506 (X1). **h,j.** — off mouth of Tugela River, Natal, South Africa, 32 m, Nov. 1972; Natal Museum, A12 (X 1.5). **i,k.** — 275 m, SE of Durban Bluff, South Africa, Aug. 1972; Natal Museum, 9928 (X 1.5).

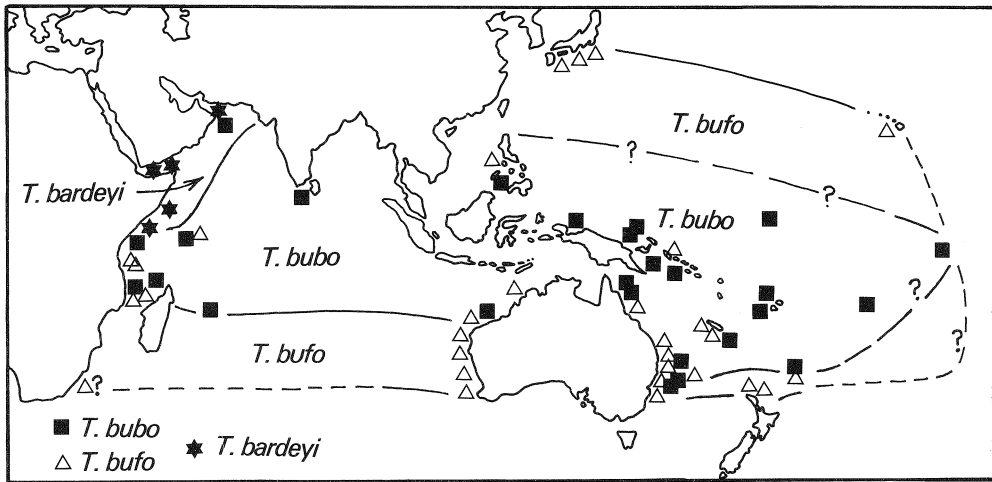


Fig. 20. Distribution of species of *Tutufa* (*Tutufa*), based on published records and on the collection of the Australian Museum.

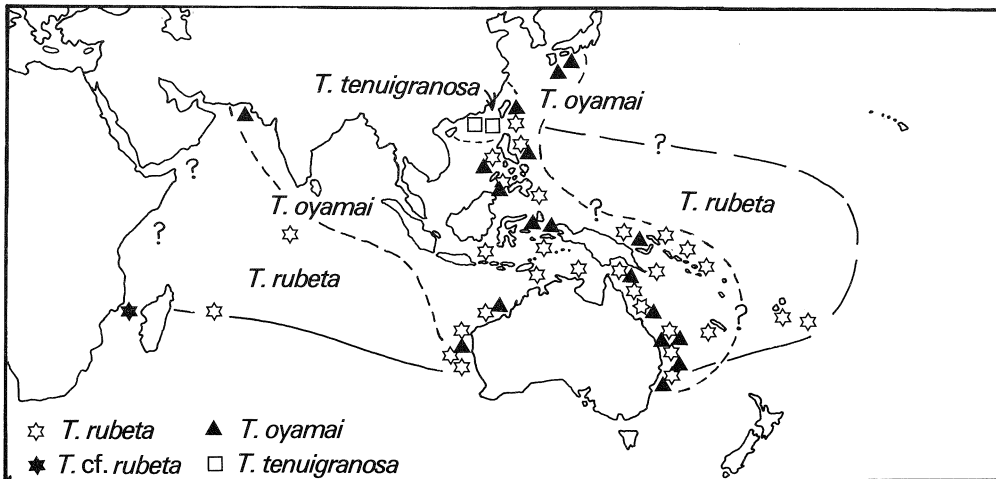


Fig. 21. Distribution of *Tutufella* (*Tutufella*), based on published records and on the collection of the Australian Museum.

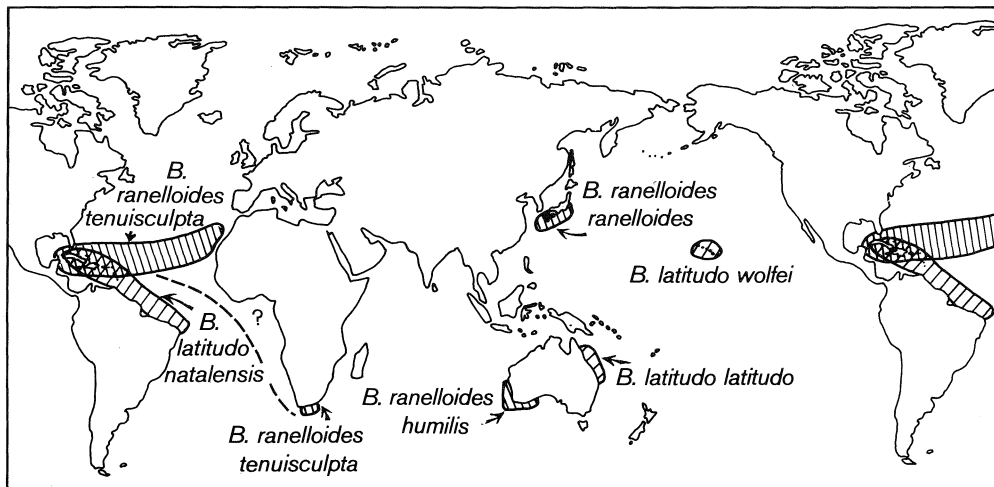


Fig. 22. Distribution of subspecies of *Bursa* (*Bufonariella*) *latitudo* and *B.* (*Bufonariella*) *ranelloides*.