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Classification of Australian Buliniform Planorbids (Mollusca: Pulmonata)

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ABSTRACT. The genera of Australian buliniform planorbids have been examined anatomically and their classification reviewed. The major conclusions reached are: 1. *Isidorella* is not congeneric with *Bulinus* and is an endemic Australian genus; 2. Iredale's genera *Lenameria, Tasmadora* and *Mutalena* are synonyms of *Physastra* Tapparone-Canefri which, in turn, is a synonym of *Glyptophysa* Crosse. *Glyptamoda* Iredale is also a synonym of *Glyptophysa;* 3. *Oppletora* Iredale, synonymised with *Bulinus* by Hubendick, is actually related to *Glyptophysa* and is placed in a separate subgenus; 4. *Ancylastrum* Bourguignat has been examined and the results confirm Hubendick's opinion that this limpet-like genus is related to *Glyptophysa.* Two species can be separated by simple anatomical characters; 5. The genus *Bayardella* Burch includes two species, *B. johni* and *B. cosmeta,* the latter once considered to be a species of *Glyptophysa;* 6. *Amerianna* Strand includes species with either a terminal or lateral pore on a simple pendant penis; 7. A new genus *Leichhardtia* is erected for the northern species *Bullinus sisurnius* Hedley 1918.

All these genera are placed in the planorbid subfamily Bulininae.

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The African planorbid *Bulinus* Müller, 1781 has become one of the best known and most intensely studied of all molluscs because of its role in the transmission of the human trematode parasite *Schistosoma haematobium* (Bilharz, 1852). Several Australian freshwater molluscs are morphologically similar to Bulinus and, as a consequence, this generic name has frequently been applied to lymnaceans from this country. This has not only caused confusion for taxonomists but has also supported the belief that snails capable of transmitting human schistosomes are present in Australia (Anon, 1972). The name *Bulinus* was first used by Adanson in 1757 in a description of a small freshwater mollusc from Senegal. Since the original description was pre-Linnean, Adanson cannot be quoted as author and Müller, who used the name in 1781, is now given authorship. In 1815, in a compilation of Müller's work, Oken emended the spelling to *Bullinus* and this form was subsequently widely adopted by authors until Pilsbry & Bequaert (1927) pointed out that *Bullinus* Oken is an unnecessary emendation for *Bulinus* Müller, and has no status in nomenclature.

The classification of Australian buliniform planorbids has been confounded since its beginnings by a surfeit of species names and an ignorance of generic relationships. These problems have their origins in the traditional reliance of taxonomists on the molluscan shell as a major taxonomic character, an unfortunate choice in the light of the extreme variability of the freshwater Basommatophora. From 1826, with the description of *Physa novaehollandiae* by Blainville, until 1881 (Tate & Brazier, 1881), 54 species of *Physa* Draparnaud were named from Australia. Tate (1882) was convinced, however, that the sinistrally coiled Australian freshwater snails were not physids and stated ". . . in no instance have I found those distinctions which characterise *Physa* as separable from *Bulinus.* The mantle margin is neither expanded nor digitate".

Cooke (1889) also considered that the "So Called Physae of Australia" were related to *Bulinus.* He also

noted a similarity between some Australian species and the New Guinean *Physastra vestita* Tapparone-Canefri, 1883. This particular group differed from snails similar to *Physa newcombi* Adams & Angas 1863, and for these latter species Tate (1896) erected the genus *Isidorella.*

Iredale (1943) reviewed the classification of all known Australian freshwater gastropods. In dealing with the sinistrally coiled planorbids he examined 106 previously applied names and produced a checklist which included 59 species in six genera, all of which he placed in the family Bullinidae. In the following year Iredale (1944) described another genus, *Mutalena,* bringing the number of genera of Australian buliniform planorbids to seven. These seven genera, including 61 species, were: *Isidorella* Tate, 1896 (11 species), *Amerianna* Strand, 1928 (6 species), *Oppletora* Iredale, 1943 (1 species), *Glyptamoda* Iredale, 1943 (3 species), *Lenameria* Iredale, 1943 (37 species), *Tasmadora* Iredale, 1943 (1 species), and *Mutalena* Iredale, 1944 (2 species).

Hedley & Musson (1891) had commented "Upon few genera has synonymy, that curse of Babel upon Science, fallen heavier than upon the Australian *Bulinus*". In an attempt to solve this problem Hubendick (1948a) collated the scattered descriptions of the numerous molluscs included in *Bulinus* by various authors over about fifty years. Where possible, his investigation included detailed anatomical studies of representatives of the different groups of *Bulinus* s.l. He concluded that the most important character for distinguishing taxa, at least at the generic level, was the structure of the copulatory organ. Two very different forms were described, the normal pendant penis found in most Basommatophora, with the vas deferens opening either terminally or laterally, and the quite different pseudopenis or ultrapenis, which was restricted to two genera, *Bulinus* and *Indoplanorbis* Annandale & Prashad, 1920. Because of the unique nature of their copulatory organs, Hubendick segregated these genera into a subfamily, the Bulininae. He claimed, however, that studies on species previously included in Tate's genus *Isidorella* showed that these also had an ultrapenis and so must be synonymised with *Bulinus. Oppletora jukesii* was also synonymised with *Bulinus.* The other genera from Iredale's Bullinidae were included in the Planorbinae: *Lenameria* and *Tasmadora* were synonymised with *Physastra* and it was tentatively suggested that *Glyptophysa* Crosse and *Glyptamoda* Iredale could be synonyms of *Amerianna.* Hubendick's studies on *Bulinus* were extended to include all planorbids in his monograph 'Phylogeny in the Planorbidae' (Hubendick, 1955a) in which *Isidorella* and *Oppletora* were still included in the Bulininae as synonyms of *Bulinus.* These studies reduced Iredale's six genera to three - two synonymised with *Bulinus,* two with *Physastra* and one with *Amerianna.*

In a later article relevant to this discussion Hubendick (1964) demonstrated that the limpet-like *Ancylastrum* Bourguignat from Tasmania, formerly placed in the Ancylidae or Ferrissiidae, is actually a planorbid closely related to *Physastra.*

Hubendick's studies on planorbids were summarised by Zilch (1959) in his 'Handbuch der Palaozoologie', and this work formed the basis of the most recent discussion and summary of the taxonomic status of Australian freshwater molluscs by McMichael (1967). This author, however, includes *Isidorella* (with *Oppletora* as a synonym) as a valid genus in the subfamily Bulininae.

An important addition to the names applied to Australian planorbids is *Plesiophysa (Bayardella) johni* Burch, 1977. This small, neritiform species from Western Australia was placed in the neotropical genus *Plesiophysa* Fischer because both were thought to have a five-cusped rachidian tooth on the radula, a feature unique among planorbids.

In any discussion of the freshwater molluscs of Australia it is important to recognise that *Physa* now has a wide distribution on this continent, having been introduced from the northern hemisphere by human activity. It is found in all states, sometimes in isolated situations, but usually in and around large population centres. The species of *Physa* found in Australia is, at present, unknown despite the claim by Hubendick (1955b) that specimens of *Physa* in a collection of freshwater snails from Perth were *P. concinna* A. Adams & Angas, 1864, and that this was a truly indigenous representative of the genus. *P. concinna* was described from Arnhem Land and was, from the original description, clearly a species of *Physastra.*

With respect to the Australian buliniform planorbids Iredale's (1943) checklist was the culmination of classifications based primarily on shell characters. By studying internal anatomy Hubendick (1948a, 1955a) provided a broader foundation for a classification but the applicability of his work to the classification of Australian freshwater molluscs is limited because of doubts concerning the origins of the material on which his findings were based. The specimens of *Isidorella subinflata* (Sowerby) which he examined were collected in the Botanic Gardens in Lorenzo Marques, Mozambique by F. Linder in 1936 (Hubendick, 1948a). It was claimed that the species had been introduced from Australia and had been locally identified. The specimens of *"Bulinus dispar"* (Sowerby), which Hubendick examined and concluded should be refered to *Physastra,* were also collected in South Africa (in a private aquarium in Durban), and those he refered to *Physa gibbosa* (Gould), an Australian species with the type locality in Parramatta, Sydney, actually came from Mowewe, Southeast Celebes. Thus the only material definitely from Australia examined by Hubendick in his 'Studies on Bulinus' was a single unnamed species, from Tailem Bend in South Australia, which he placed in *Physastra.* Hubendick (1955a) presented details of the anatomy of one other species,

Amerianna obesa (H. Adams), from Queensland.

The positions taken by both Zilch (1959) and McMichael (1967) were based on acceptance of the anatomical work of Hubendick, without additional supporting evidence.

The proposition that *Glyptamoda* should be considered a synonym of *Glyptophysa* (Hubendick, 1948a; McMichael, 1967; Smith & Burn, 1976), while possibly correct, is also based entirely on similarity of shell structure, not on any knowledge of internal anatomy.

Materials and Methods

Sites of Collection of Mollusc Colonies. Sites of mollusc collections are listed in the appendix at the end of the paper.

Collection and Maintenance of Snail Colonies. Snails were collected from all suitable water bodies and air-freighted to Sydney. They were maintained in either glass aquaria or plastic food containers, in each case with a substratum of marble chips and in artificial pondwater made from distilled water with salts added (Ulmer, 1970). Snails were fed on autoclaved leaves and with a supplement made from dried lettuce, wheat germ and lucerne, ground in a blender. All aquaria were aerated. The colonies were kept in a room maintained at 25°C +/- 3°C. Lights were automatically switched on at 0600 hr and off at 1800 hr.

Examination Techniques. Apart from those sent to Sydney to start laboratory colonies, snails were preserved in the field for later studies. They were first relaxed with menthol crystals, usually overnight, then fixed in one of two ways. Specimens to be sectioned were fixed in aqueous Bouin's fluid, in which they remained for the duration of the field trip, and were then transferred to 70% ethanol with 5% glycerol added. Snails intended for museum collections were fixed in 10% formalin and stored in this solution. Comparison of a number of fixatives for the laboratory reared snails showed the superiority of Heidenhain's Susa and this was used for all laboratory reared specimens prior to sectioning. After fixation the schedule followed included alcohol dehydration, clearing in methyl benzoate and benzene and embedding in low melting point wax. Serial sections were cut at 5 micrometres and stained with Heidenhain's Azan. If possible, fresh specimens from laboratory colonies, as well as fixed material, were examined. In these cases the whole reproductive tract was removed, fixed in Baker's Formaldehyde Calcium and mounted in a lactophenol-PVA mixture to which Chlorazol Black had been added. This medium produced a permanent whole mount in which the tissues were cleared by the lactophenol and the nuclei stained by the Chlorazol Black.

Radulae were obtained by digesting the buccal mass of snails in a saturated solution of sodium hydroxide, washing in water and mounting in the same lactophenol-PVA mountant used for whole mounts.

Drawings of radulae, whole mounts of copulatory organs and of serial sections were made with the aid of a drawing tube.

In the following discussion *Isidorella* is presented first because its anatomy is used to provide a basis for comparison with other taxa. The remaining genera are presented in chronological order of their original description.

The material examined in this study, dried shells, spirit preserved snails, serial sections and whole mounts of radulae and reproductive systems, is deposited in the Australian Museum, Sydney.

Specific Designations. No attempt has been made here to delineate species of *Isidorella, Glyptophysa* or *Amerianna* because the phenotypic plasticity of these snails makes such a task almost impossible if morphological criteria alone are used. It will be necessary for techniques such as isoenzyme electrophoresis to be applied if the validity of the 59 species listed by Iredale (1943) is to be assessed.

TAXONOMY

Class GASTROPODA

Order BASOMMATOPHORA

Family Planorbidae Rafinesque, 1815

Diagnosis. Small to medium sized snails; anatomically sinistral; with long slender tentacles; accessory respiratory structure, the pseudobranch, developed as an outgrowth of the left body wall; blood containing haemoglobin. Shell and internal anatomy, especially the copulatory organ, extremely variable; simultaneous hermaphrodites; egg capsule three layered.

Subfamily Bulininae

Diagnosis. Subfamily as defined by Hubendick (1978). Shell morphology variable; pseudobranch usually secondarily folded. Prostate diverticula arise from one small area of the sperm duct. Gonad acini arranged in a fan-like pattern.

Genus *Isidorella* Tate, 1896
Figs 1–4

Isidorella Tate, 1896: 212. Type species *Physa newcombi* A. Adams & Angas, 1863. Recent, Australia.

Diagnosis. Bulinine snails with a subglobose to oval shell having unshouldered whorls; copulatory organ lacking accessory bursa or flagellum, pendant penis is biramous, prostatic duct absent.

Description. SHELL. (Fig. 2a) Sinistrally coiled, umbilicate, subglobose to oval; whorls rounded with indented sutures. Aperture large, ovate; parietal lip evenly curved without columella fold or plait. Transverse growth lines common forming prominent ridges on surface of some shells. Spiral

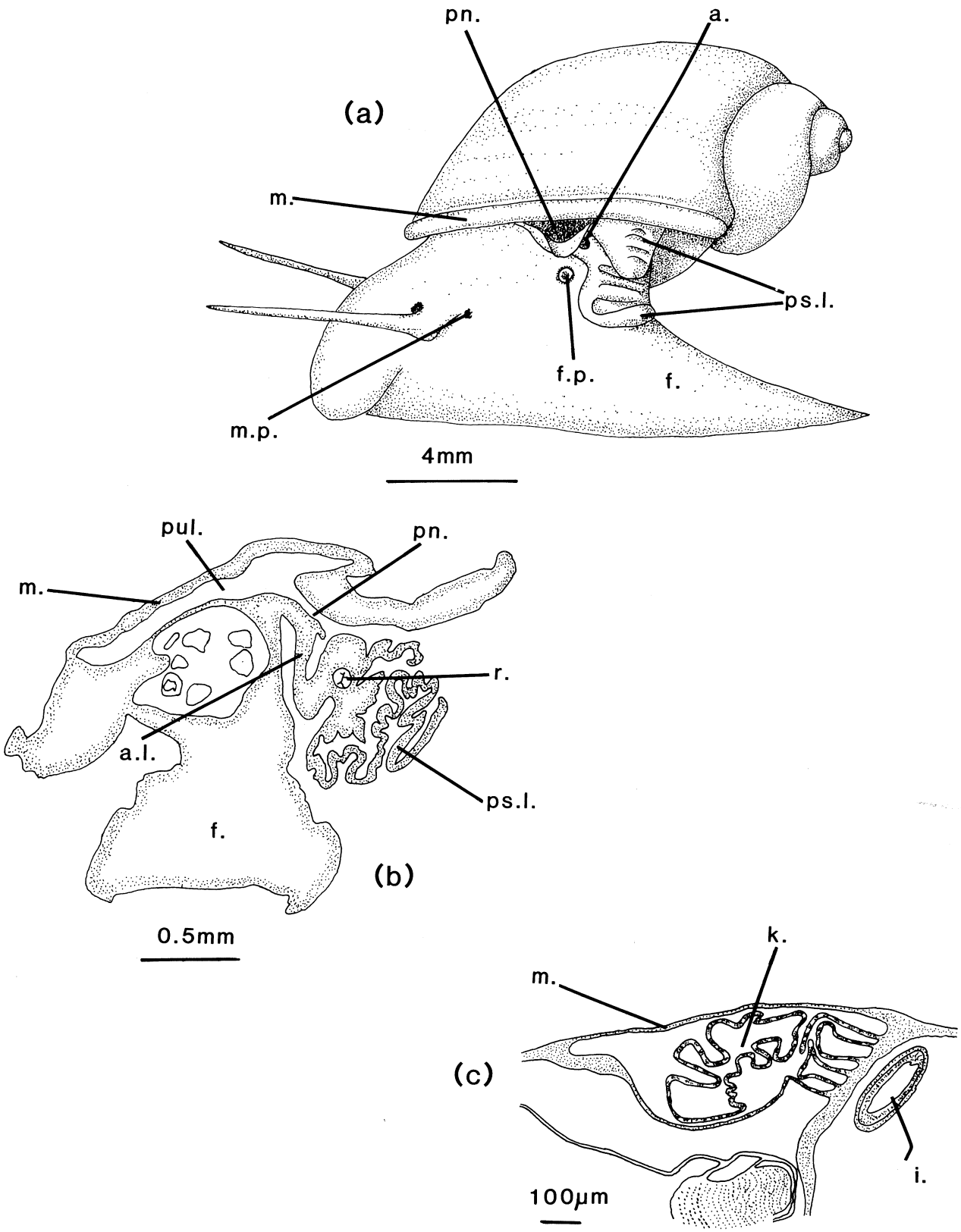

Fig.1. **(a)** *Isidorella newcombi* - left side; **(b)** *I. newcombi,* t.s. showing pseudobranch; **(c)** l.s. of mantle showing kidney. a. anus; a.l. anal lobe; f. foot; f.p. female genital pore; i. intestine; k. kidney; m. mantle; m.p. male genital pore; pn. pneumostome; ps.l. pseudobranch lobes; pul. pulmonary cavity; r. rectum.

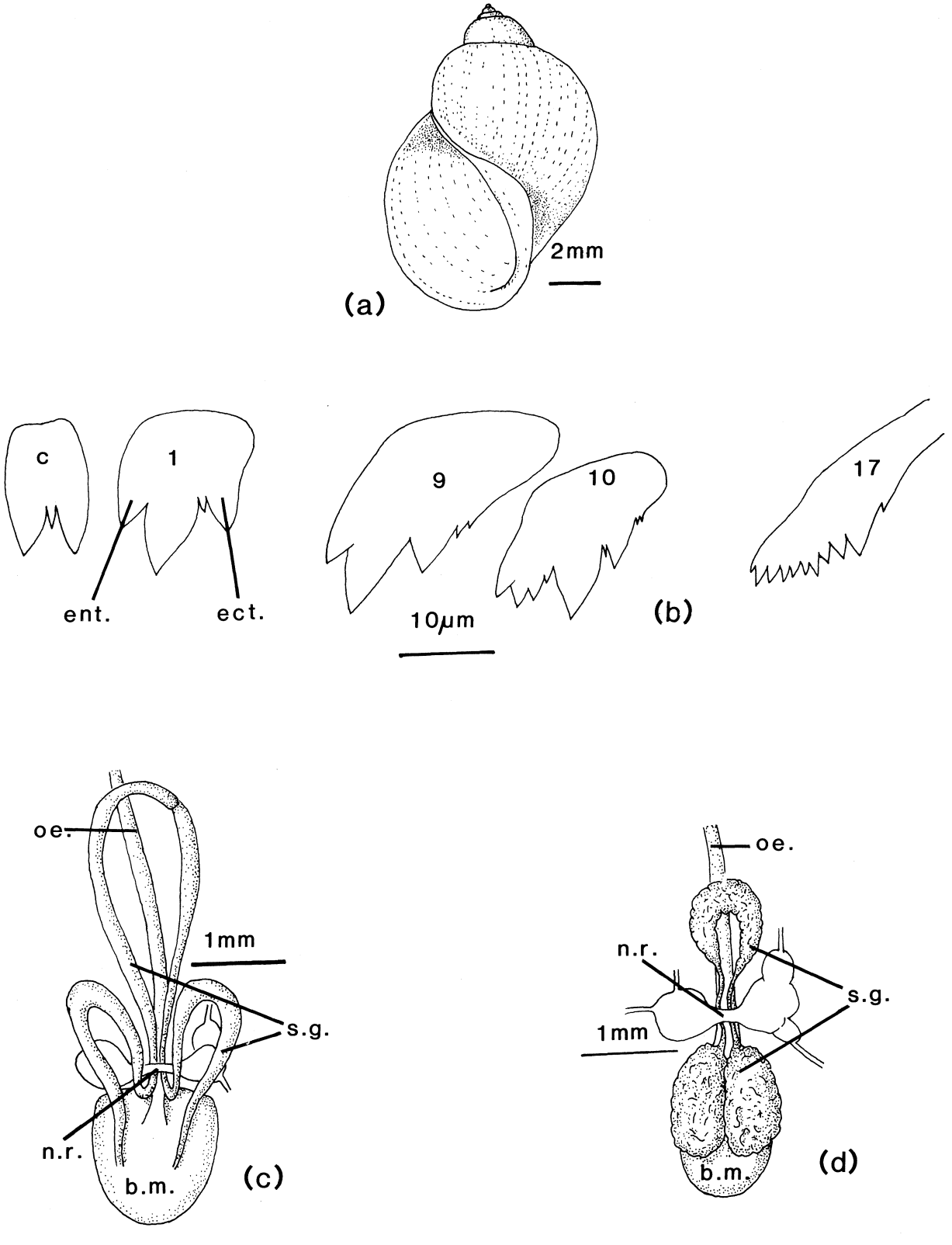

Fig.2. (a) shell of *Isidorella newcombi;* **(b)** radula of *I. newcombi:* c = central tooth, -the number on each tooth designates its consecutive position distally from the central tooth; **(c)** salivary glands of *Bulinus africanus;* **(d)** salivary glands of *I. newcombi.* b.m. buccal mass; ect. ectocone; ent. entocone; oe. oesophagus; n.r. nerve ring; s.g. salivary glands.

rows of periostracal hairs frequently present, especially on shells of young snails.

EXTERNAL MORPHOLOGY. Body pigmentation red; foot elongate, pointed posteriorly; tentacles long, circular in cross section, arising from broad, flat base on sides of head. Eyes situated medially, at base of tentacles. Male genital pore immediately posterior to left tentacle; female genital pore opening through small, slightly elevated papilla, above and posterior to male opening. Pneumostome, pseudobranch and anal lobe situated on left side in vicinity of posterior of shell aperture (Fig. 1a). Rectum opening at tip of anal lobe which bears pseudobranch folds, shorter outer lobe overlapping top of inner lobe; pseudobranch lobes secondarily folded. Anal lobe, an outgrowth of body wall, suspended in mantle cavity (Fig. 1b).

RADULA (Fig. 2b). Central tooth has 2 equal sized cusps, separated by small denticle in radulae from most populations. Lateral teeth tricusped, usually with denticles between mesocone and ectocone. Some lateral teeth bear small denticle on lateral edge of ectocone. Cones of lateral teeth triangular, sides usually slightly convexly curved. Transition from lateral to marginal teeth begining in vicinity of lateral teeth 6–10, marked by a splitting of ectocone into numerous smaller cusps. Marginal teeth exhibit great reduction in size of ectocone and splitting of entocone into many smaller cusps. Mesocone gradually reduced in size and by tooth 20 only slightly larger than entocone cusps.

SALIVARY GLANDS. (Fig 2d). Salivary glands form 2 broad sheets of tissue lying on top of buccal mass; narrow to thin tubes where they pass through nerve ring; join posteriorly, over oesophagus; ducts enter anterior of buccal mass.

MANTLE AND ASSOCIATED STRUCTURES. Kidney traverses inside of mantle, from right to left; distal end reflexed. Renal ridges or folds absent (Fig. 1c); rectal ridge absent.

REPRODUCTIVE SYSTEM. Copulatory organ. Copulatory organ without accessory glands or flagella. Penis sheath ¼ length of praeputium, (Fig. 3b). Biramous, pendant penis (Fig. 3c). Lumen of vas deferens at proximal end of penis wide and strongly ciliated; opening of vas deferens between 2 rami of penis.

Prostate gland. Acini radiate from one point; no collecting prostatic duct present (Fig. 4a).

Insertion of bursa copulatrix. Duct of bursa inserts at distal end of vagina, just inside the body wall (Fig. 4c).

Distribution. Australian mainland with the exception of the Kimberley region, Arnhem Land and northern Queensland. The genus may be absent from Tasmania. I have examined many specimens in museum collections labelled *Isidorella* with reliable information fixing the collection site in Tasmania. All have proved to be specimens of *Glyptophysa.*

Comments. From the information presented above it can be concluded that *Isidorella* is not closely related to *Bulinus.* Several substantial differences are noted.

In discussing the supposed similarity between *Bulinus* and *Isidorella,* Hubendick (1948b) described the salivary glands as being tubular and joining behind the circumoesophageal nerve ring in both taxa. Studies of laboratory colonies of *B. truncatus, B. tropicus* and *B. liratus* held at the School of Public Health and Tropical Medicine, University of Sydney, and of preserved material of *B. africanus,* have all confirmed Hubendick's description for *Bulinus* (Fig. 2c). In no instance, however, has a specimen of *Isidorella* from any locality in Australia shown similar morphology of the salivary glands. They are invariably in the form of flat sheets, as described above.

In *Bulinus* the duct of the bursa copulatrix inserts at the proximal end of the vagina (Fig. 4b) but that of *Isidorella* inserts at the distal end, just inside the body wall (Fig. 4c).

The major difference between *Bulinus* and *Isidorella* is in the nature of the copulatory organ, the feature Hubendick (1948a) described as their major similarity, and the basis for his synonymising of the two genera. When the copulatory organs are examined superficially some similarity is apparent; in both cases they are relatively simple structures without accessory glands or flagella, with a clear demarcation between the praeputium and the penis sheath. Closer examination reveals that the relative dimensions of these two parts of the organ differ. The penis sheath of *Isidorella* is relatively short; only one quarter of the length of the praeputium. The two sections are approximately equal in length in most *Bulinus* (Fig. 3a,b). The internal anatomy of the two organs differs significantly. *Isidorella* has a pendant penis, while *Bulinus* has the characteristic pseudopenis or ultrapenis (Hubendick, 1948, 1955a). The ultrapenis (Fig. 3d) consists of a long, coiled, eversible tube which is attached at both the upper and lower end of the penis sheath. This tube is separated from the wall of the penis sheath by an extensive sinus which appears to have arisen as a result of splitting of the musculature. This is indicated by the lack of any epithelium on the inside of the sheath or on the periphery of the coiled tube (Fig. 3e).

The penis of *Isidorella* shows considerable variation, apparently related to individual reproductive status. In some specimens collected at random and in animals killed at the time of copulation, transverse sections show extensive development of the ciliated epithelium on the outside of the penis and an increase in the size of the two projections below the opening of the vas deferens (Fig. 3f). In other specimens from the same populations the ciliated epithelium is less prominent and the digitations smaller.

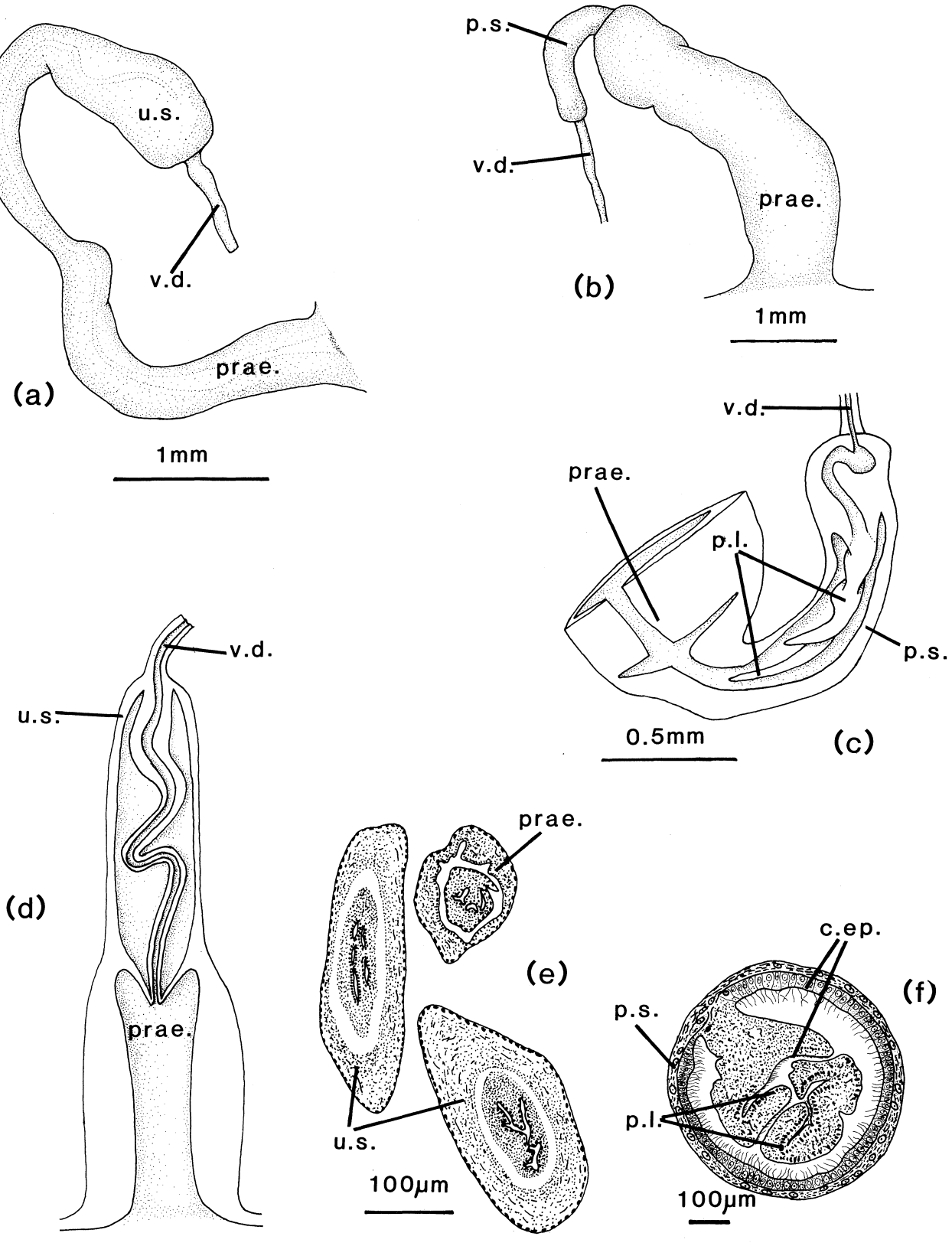

Fig.3. **(a)** copulatory organ of *Bulinus africanus,* external view; **(b)** copulatory organ of *Isidorella newcombi,* external view; **(c)** diagramatic section of penis of *Isidorella;* **(d)** diagramatic section of ultrapenis of *Bulinus;* **(e)** t.s. of ultrapenis of *B. africanus;* **(f)** t.s. penis sheath of *Isidorella.* c.ep. ciliated epithelium; p.l. lobes of penis; prae. praeputium; p.s. penis sheath; u.s ultrapenis sheath; v.d. vas deferens.

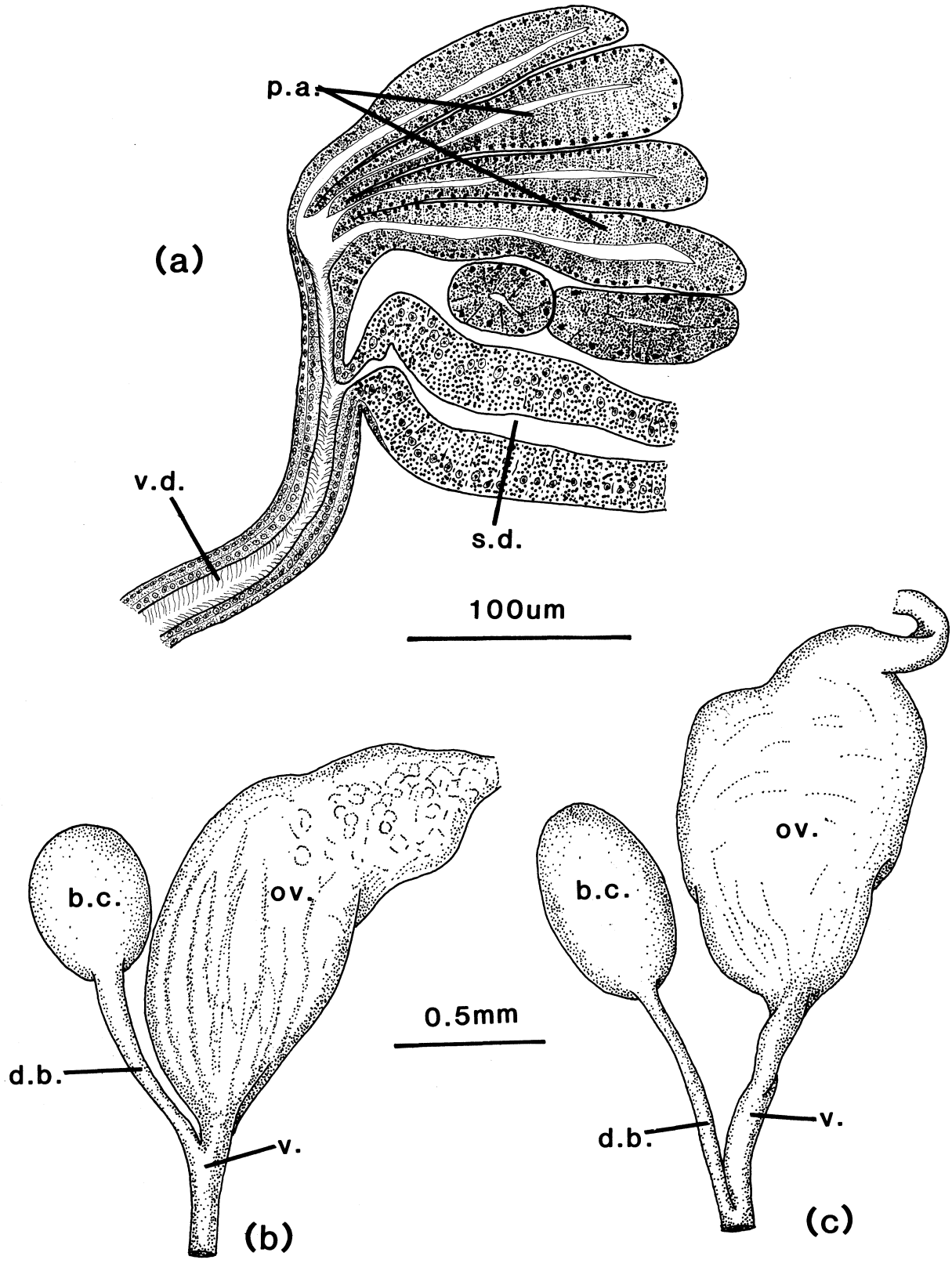

Fig.4. **(a)** section through part of prostate gland of *Isidorella newcombi;* **(b)** distal end of female reproductive tract of *Bulinus;* **(c)** distal end of reproductive tract of *Isidorella.* b.c. bursa copulatrix; d.b. duct of bursa copulatrix; ov. oviduct; p.a. prostate acini; s.d. sperm duct; v. vagina; v.d. vas deferens.

These are the major obvious differences between *Bulinus* and *Isidorella;* in many other respects the two taxa are similar. There are obvious similarities in the general shell morphology, though there is a greater range of shape in *Bulinus.* The broad details of the radulae of these two genera are similar. The anatomy of the alimentary tract of *Isidorella* has not been studied in sufficient detail yet for strict comparison with that of *Bulinus.* Despite Wright's (1961) claim to the contrary, there is no significant difference between the prostate glands of these two genera.

The experience gained in this study indicates that there are no clearcut characters distinguishing between various geographically distinct isolates of *Isidorella.* This was also the conclusion reached by Tate (1896). As a consequence all specimens examined here have been referred to the type species, *I. newcombi.* The localities from which *Isidorella* was collected are listed in the appendix.

Details of the anatomy of the other Australian buliniform planorbids presented subsequently indicate that *Isidorella* is generically distinct.

Hubendick (1958) described the anatomy of *Protancylus adhaerens* P. & F. Sarasin from Sulawesi. This species has a penis with two elongate processes below the lateral opening of the vas deferens. The rest of the anatomy differs markedly from that of *Isidorella* so, unless further study indicates otherwise, the similarity of penis structure should be regarded as a result of convergence.

Ancylastrum Bourguignat, 1883
Figs 5, 6

Ancylastrum Bourguignat, 1853: 63. Type species *Ancylus (Ancylastrum) cumingianus* Bourguignat, 1853; subsequent designation Bourguignat 1853: 170. Recent, Tasmania.*

Legrandia Legrand, 1879: 95. Type species *Ancylus cumingianus* Bourguignat, 1853. *Cumingia* Clessin, 1880: 14. Type species *Ancylus cumingianus* Bourguignat, 1853. Not *Cumingia* Sowerby, 1833.

Tasmancylus Iredale, 1926: 115. Type species *Ancylus cumingianus* Bourguignat, 1853.

Diagnosis. Patelliform bulinine snails; mesocone of lateral teeth rounded with small denticles; copulatory organ having a flagellum, lacking an accessory bursa, penis biramous with a terminal stylet on one ramus or uniramous with a subterminal augur-like fold; bursa copulatrix spatulate; rectal ridge absent.

Description. SHELL. Shell limpet-like, asymmetrical (Fig. 5a). Heterostrophic; apical portion a vestigal spire, projects to right, consists of almost a complete whorl. Apical region with poorly developed spiral striations. Abrupt change between apex and main body of shell which is patelliform; most specimens of *A. cumingianus* have a smooth surface broken by concentric growth lines; some specimens of this species have faint radiating ribs; ribs strongly developed on shell of *A. irvinae.*

EXTERNAL MORPHOLOGY. Body limpet-like; edge of mantle surrounding foot (Fig. 5b); tentacles very short, (this may be a result of the state of fixation of the available material); eyes situated on anteroventral side of tentacle base; pseudobranch unilobed without strong folding (Fig. 5c); rectum opens on anterior margin of pseudobranch, directed posteriorly. Opening of pulmonary cavity a small slit, high on side of body, anterior to pseudobranch.

RADULA (Fig. 5d,e). Central tooth bicusped, cusps with straight inner and curved outer margins (*A. cumingianus*), or equally curved on each side (*A. irvinae*). Lateral teeth with broad, serrated mesocones and small entocones and ectocones. Gradual transition to marginal teeth (*A. irvinae*); by tooth 10 mesocone has narrowed and ectocone is much longer. Marginal teeth with 3 prominent cusps separated by small denticles; denticles also present on lateral edges of entocone and ectocone. No marked development of marginal teeth in *A. cumingianus.*

SALIVARY GLANDS. Salivary glands flat sheets with ribbon-like posterior portions passing through circumoesophageal nerve ring.

REPRODUCTIVE SYSTEM. Copulatory organ. Muscular flagellum, joining penis sheath at same point as insertion of vas deferens. Penis of *A. irvinae* bilobed (Fig. 6a,b). One lobe bears a terminal stylet; second bears, terminally, opening of vas deferens. Penis of *A. cumingianus* unilobed with terminal stylet. Proximal to stylet is an augur-like fold of penis epithelium. Opening of vas deferens occurs in this region (Fig 6d). Nature of prostate gland not determined.

Bursa copulatrix. Bursa copulatrix spatulate (Fig. 6c), duct inserts into distal end of vagina.

Gonad. Gonad proportionally larger than that of other Australian planorbids; completely separated from folds of digestive gland.

Distribution. Highland lakes in Tasmania.

Comments. *Ancylastrum* is related to *Glyptophysa* but is sufficiently different to warrant separate generic placement. This study confirms Hubendick's (1964) findings on the genus and also confirms the validity of the two species described. This conclusion is contrary to that of Johnston (1888), who rejected *A. irvinae* Petterd because he considered the differences in the shells represented the extremes of a continuum.

Glyptophysa Crosse, 1872
Figs 7, 8

Glyptophysa Crosse, 1872: 151. Type species *Physa petiti* Crosse 1872; monotypy. Recent, New Caledonia.

*The validity of the name *Ancylastrum* was discussed by Hubendick (1952), and was confirmed by the International Commission of Zoological Nomenclature in its Opinion 364. Bourguignat did not designate the type species in the original description in February 1853, but did so in May of that year.

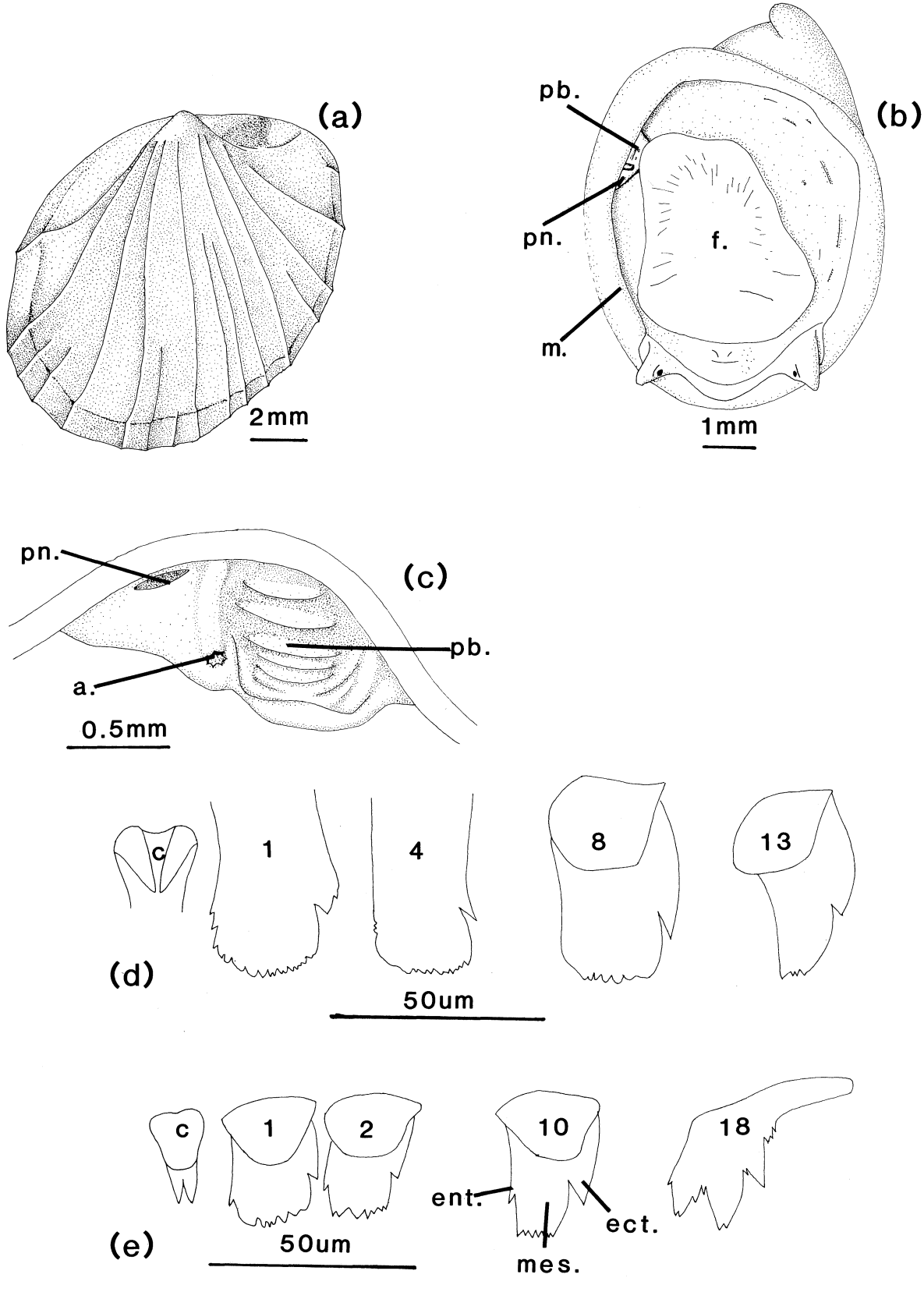

Fig.5. Anatomy of *Ancylastrum.* **(a)** shell of *A. irvinae;* **(b)** *A. irvinae,* ventral view; **(c)** *A. irvinae,* pseudobranch; **(d)** radula, *A. cumingianus:* c = central tooth, -the number on each tooth designates its consecutive position distally from the central tooth; **(e)** radula *A. irvinae.* a. anus; ect. ectocone; ent. entocone; f. foot; m. mantle; mes. mesocone; pb. pseudobranch; pn. pneumostome.

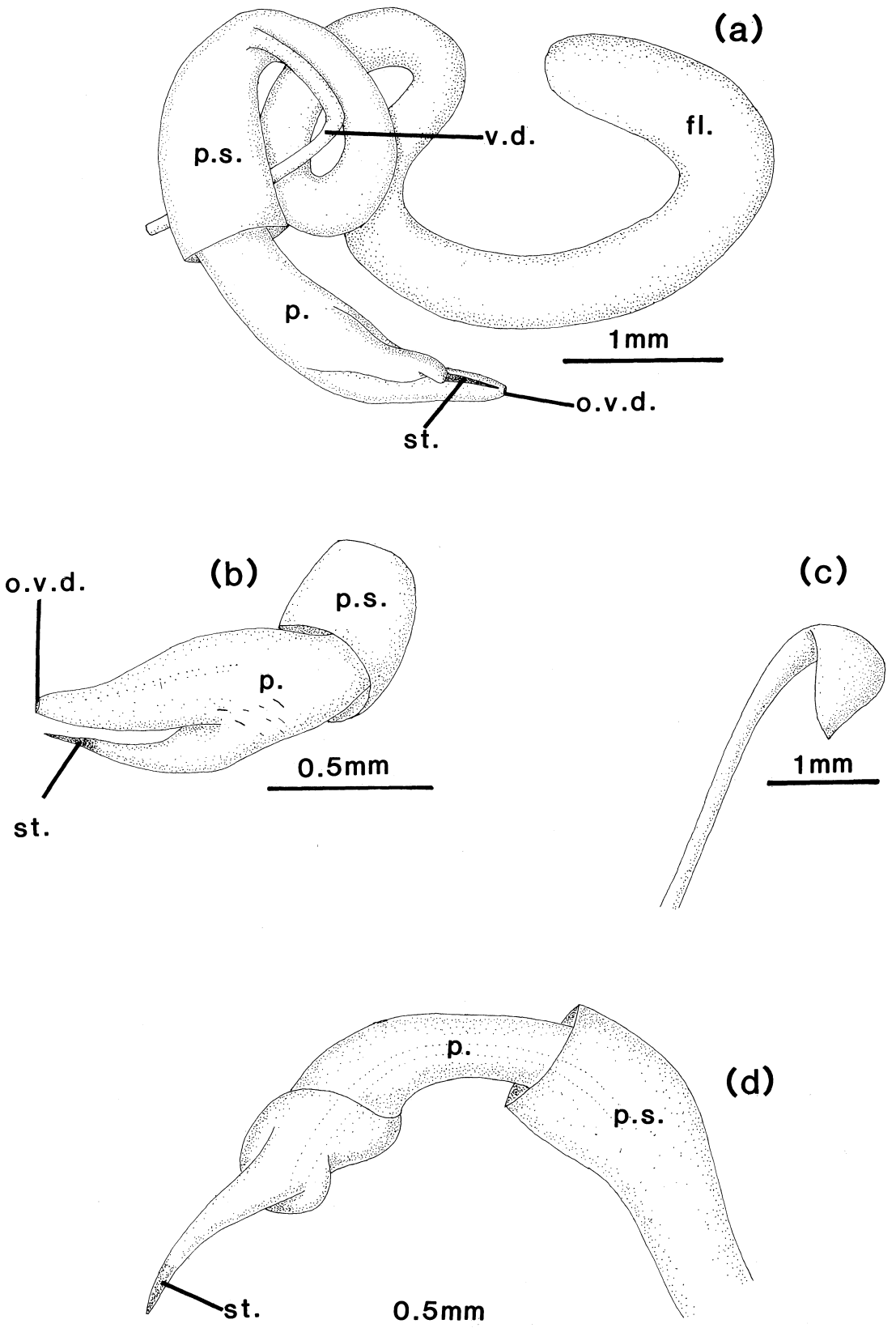

Fig.6. *Ancylastrum,* continued. **(a)** *A. irvinae,* copulatory organ - penis exposed; **(b)** bifid penis of *A. irvinae;* **(c)** *A. cumingianus,* bursa copulatrix. **(d)** *A. cumingianus,* penis; fl. flagellum; o.v.d. opening of vas deferens; p. penis; p.s. penis sheath; st. stylet; v.d. vas deferens.

Diagnosis. Bulinine snails with the shell varying from globose to high spired, with smooth surface or spiral lirae, whorls round or carinate, distinct columellar fold present; copulatory organ with a flagellum, lacking an accessory bursa, penis uniramous with terminal stylet, bursa copulatrix globose; rectal ridge present; single renal ridge on roof of pulmonary cavity.

Remarks. Two subgenera are recognised within *Glyptophysa.* The nominate subgenus is widespread and encompasses species previously included in *Physastra* Tapparone-Canefri, 1883.

Key to the Subgenera of *Glyptophysa*
(based on shell characters)

1. Shell elongately conic to oval; whorls rounded or carinate; spire prominent. *Glyptophysa*

——Shell globose; whorls flattened; spire depressed. ..... *Oppletora*

Subgenus *Glyptophysa* s.s.

In addition to *Glyptophysa* Crosse the following taxa are included in this subgenus.

Physastra Tapparone-Canefri, 1883: 246. Type species *Physa (Physastra) vestita* Tapparone-Canefri, 1883; monotypy. Recent, New Guinea.

Lenameria Iredale, 1943: 215. Type species *Physa gibbosa* Gould, 1847; original designation. Recent, Parramatta, N.S.W.

Glyptamoda Iredale, 1943: 220. Type species *Physa aliciae* Reeve, 1862; original designation. Recent, southeastern Australia.

Tasmadora Iredale, 1943: 221. Type species *Physa aperta* Sowerby, 1874; original designation. Recent, Hamilton, Tasmania.

Mutalena Iredale, 1944: 121. Type species *Mutalena reperta* Iredale, 1944; original designation. Recent, western New South Wales.

Description. SHELL. (Fig. 7 a,b). Sinistral; elongately conic to oval; whorls carinate, rounded with indented sutures or shouldered; body whorl smooth or with prominent lirae having a serrated appearance resulting from small projections of periostracum; aperture pyriform to oval, posterior of outer lip angulated or evenly curved, columella with a distinct fold; spire of from 2–6 whorls may be truncate.

EXTERNAL MORPHOLOGY. Externally similar to *Isidorella,* except that foot has a rounded posterior end in *Glyptophysa.*

RADULA (Fig. 7 d,e). Central tooth with 2 equal cusps separated by a denticle; tricusped lateral teeth have denticles between major cusps; transition to marginal teeth gradual, number of ectocone denticles and entocone cusps progressively increasing; mesocone and ectocone of marginal teeth progressively decrease in size with increasing distance from centre of radula.

SALIVARY GLANDS. Flat sheets of tissue, pass through nerve ring; ducts insert into top of buccal mass.

MANTLE AND ASSOCIATED STRUCTURES. Prominent ridge on inner surface of mantle; ridge on ventral surface of kidney; distal end of rectum bears a ridge which forms outer pseudobranch lobe.

REPRODUCTIVE SYSTEM. Copulatory organ. Muscular flagellum joins penis sheath at insertion of vas deferens (Fig. 8a); penis with lateral pore and terminal stylet (Fig. 8b). The copulatory organ figured (Fig. 8c) was everted when snail was fixed and demonstrates form taken during copulation.

Prostate gland and bursa copulatrix. Both organs similar to those described for *Isidorella.*

Distribution. Australia, New Guinea, New Caledonia, New Zealand, Moluccas, Philippines, Sumatra, islands of South Pacific east to Tahiti, Malaysia (introduced). The number and distribution of species in this subgenus is uncertain.

Comments. Specimens of the type species from New Caledonia have not been examined in this study. However, Starmuhlner (1970) has adequately described *G. petiti* and his description would be equally applicable to *Physa aliciae,* the type species of Iredale's genus *Glyptamoda.* Whether this species should be synonymised with *G. petiti* can only be determined by further study. *G. aliciae* has been compared in detail with species previously included in *Physastra, Lenameria, Tasmadora* and *Mutalena.* The only differences noted relate to shell shape and sculpture. Meier-Brook (1983) and Brown (1980) have both described a range of variation within the planorbid genera *Gyraulus* and *Bulinus* respectively which exceeds that between these four Australasian taxa.

Subgenus *Oppletora* Iredale 1943

Oppletora Iredale & Whitley, 1938: 64. (Nomen nudum).

Oppletora Iredale, 1943: 222. Type species *Physopsis jukesii* H. Adams, 1861; original designation. Recent, northern Australia.

Description. SHELL. Shell sinistral, globose, spire markedly depressed, body whorl constitutes most of shell (Fig. 7c). Aperture oval, well-developed columellar fold.

EXTERNAL MORPHOLOGY. External anatomy similar to that of *Glyptophysa.* Foot rounded posteriorly; rectal lobe folded to form outer pseudobranch lobe (Fig. 8e). Pigmentation of foot and mantle relatively slight.

RADULA (Fig. 7f). Central tooth bicusped, lacks central denticle. First lateral teeth tricusped with a denticle between the mesocone and ectocone. Early transition to marginal teeth; ectocone of tooth 4

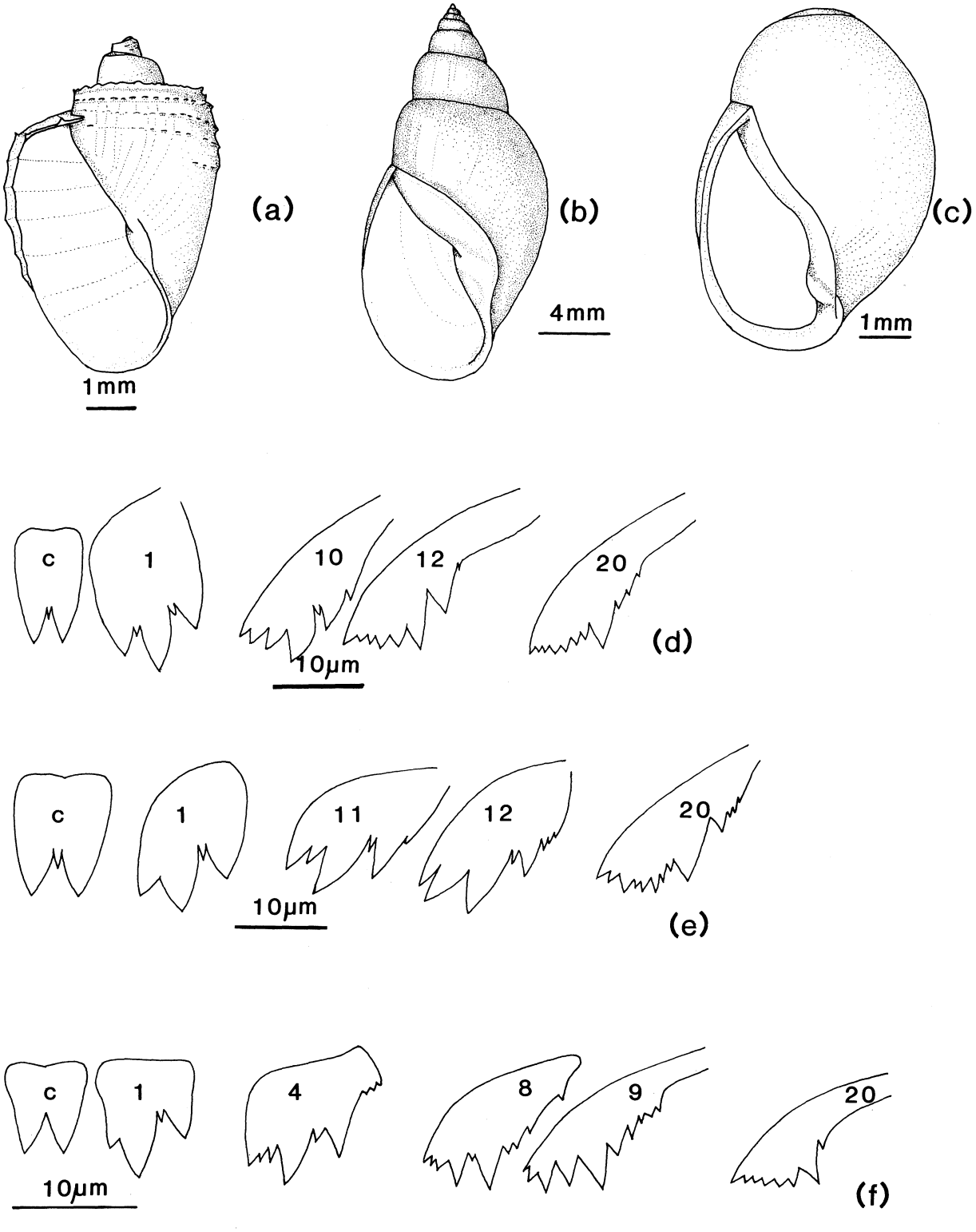

Fig.7. Anatomy of *Glyptophysa.* **(a)** shell of *G. aliciae;* **(b)** shell of *G. concinna;* **(c)** shell of *G. (Oppletora) jukesii;* **(d)** radula of *G. aliciae;* **(e)** radula of *G. concinna;* **(f)** radula of *G. (Oppletora) jukesii.*

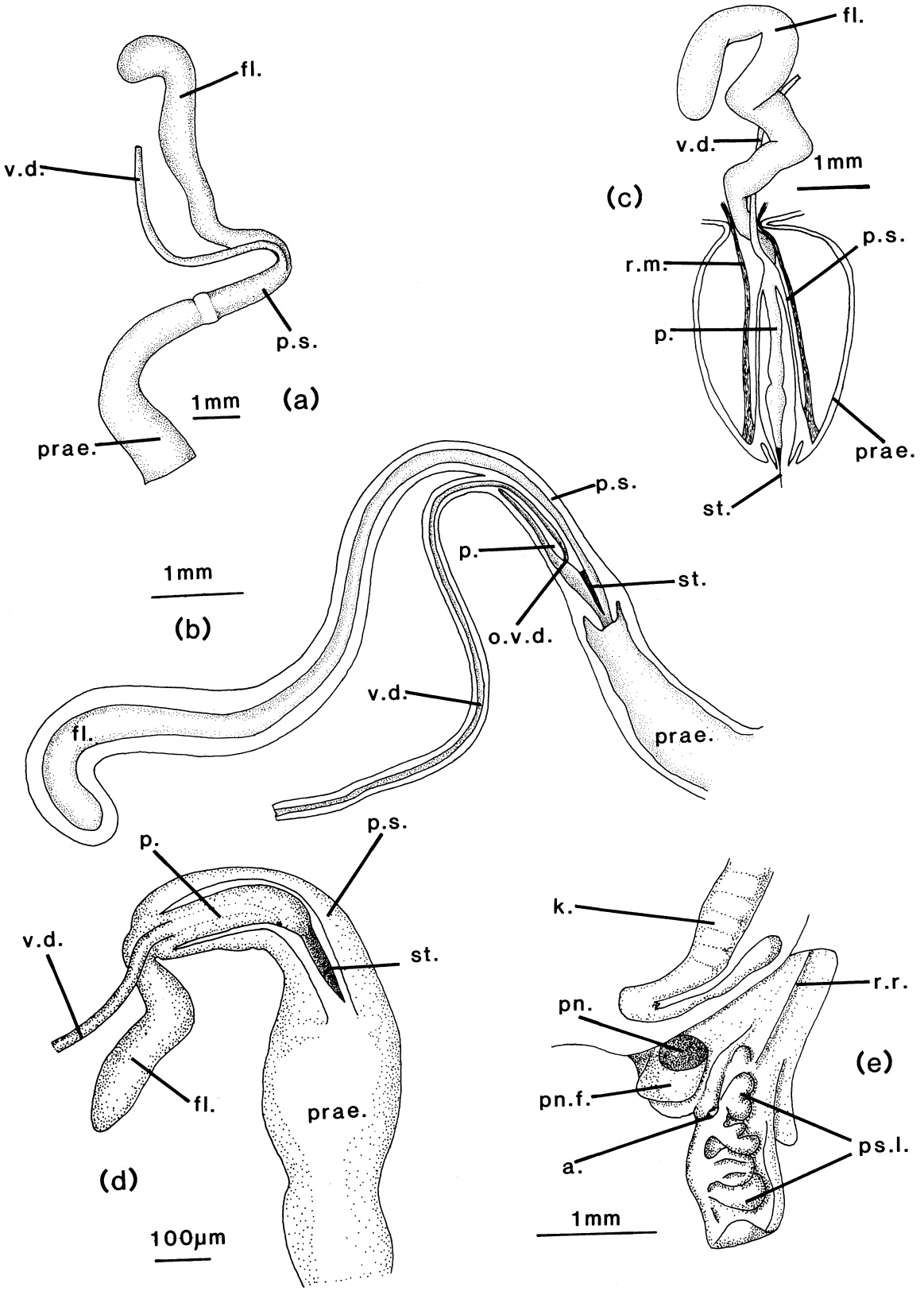

Fig.8. Anatomy of *Glyptophysa* continued. **(a)** copulatory organ of *G. concinna,* external view; **(b)** copulatory organ of *G. concinna,* internal structure; **(c)** copulatory organ of *G. aliciae,* internal structure, penis everted; **(d)** copulatory organ of *G. (Oppletora) jukesii,* external view; **(e)** pseudobranch of *G. (Oppletora) jukesii.* a. anus; fl. flagellum; k. kidney; o.v.d. opening of vas deferens; p. penis; pn. pneumostome; pn.f; pneumostome fold; prae. praeputium; p.s. penis sheath; ps.l. pseudobranch lobes; r.m. retractor muscles; r.r. rectal ridge; st. stylet; v.d. vas deferens.

divided into 3 small cusps, denticles at base of ectocone. Extreme marginal teeth comb-like with a much divided entocone and reduced ectocone.

SALIVARY GLANDS. The salivary glands are similar to those described for *Isidorella.*

REPRODUCTIVE SYSTEM. Copulatory organ. Copulatory organ with flagellum relatively shorter and stylet relatively longer than for *Glyptophysa* s.s. Opening of vas deferens lateral (Fig. 8d).

Prostate gland. No collecting ducts for the prostate acini.

Bursa copulatrix. Bursa copulatrix globose, duct inserts distally on vagina.

Distribution. There is a single species with a patchy distribution from the Kimberley region to Arnhem Land.

Comments. *Oppletora* is most closely related to *Glyptophysa.* Whilst the differences, mainly in shell shape and in the relative proportions of organs, are consistent, they are relatively minor by comparison with those between genera such as *Isidorella* and *Glyptophysa. Oppletora* is placed as a subgenus within *Glyptophysa.*

Genus *Amerianna* Strand, 1928
Figs 9, 10

Ameria H. Adams, 1861: 143. Type species *Physa (Ameria) carinata* H. Adams, 1861. Not *Ameria* Walker, 1854, Lepidoptera.

Amerianna Strand, 1928: 63. Type species *Physa (Ameria) carinata* H. Adams, 1861; original designation. Recent, Boyne River, Queensland. New name for *Ameria* H. Adams, 1861.

Diagnosis. Bulinine snails having a carinate shell with a truncate spire; copulatory organ a uniramous, pendant penis with a terminal or lateral pore; bursa copulatrix elongate; 3 ridges on roof of pulmonary cavity, rectal ridge present.

Description. SHELL. (Fig. 9a,b) Sinistral, cylindrical shell; spire normally truncate, rarely elevated. Body whorl strongly keeled or with rounded shoulders. Aperture almost as long as shell, angular posteriorly, narrowly curved anteriorly. Slight columellar fold. Surface usually smooth; some specimens, especially juveniles, with spiral rows of periostracal hairs.

EXTERNAL MORPHOLOGY. Heavy body pigmentation masks haemoglobin with speckled grey. Pseudobranch more extensively folded than in other genera described (Fig. 9d); fused to mantle edge at anterior, upper margin.

RADULA (Fig. 9c). Central tooth bicusped without denticle between cusps; cusps of equal size. Lateral teeth tricusped with denticle between the mesocone and ectocone. Transition to margial teeth begins at about tooth 12 which has prominent ridges on the base lateral to ectocone. Tooth 13 similar but shows slight splitting of entocone; this change progresses laterally in combination with subdivision of ectocone.

SALIVARY GLANDS. Branched, flat plates; pass through circumoesophageal nerve ring. Ducts insert into top of buccal mass.

MANTLE AND ASSOCIATED STRUCTURES. Three small ridges traverse inside of mantle roof; one anterior, two posterior to kidney (Fig. 9e).

REPRODUCTIVE SYSTEM. Copulatory organ. Demarcation between penis sheath and praeputium not pronounced; accessory structures lacking; simple pendant penis. Opening of vas deferens terminal or lateral (Fig. 10a,b). Praeputium with irregular muscular folds on internal wall.

Prostate gland. Prostate gland with separate prostatic duct leading from base of acini to junction of sperm duct and vas deferens (Fig. 10c).

Bursa copulatrix. Bursa copulatrix elongate oval; duct inserts into distal end of vagina.

Distribution. Northern regions of Australian mainland, New Guinea, Moluccas, Philippines. Introduced into Java (Butot, 1954), Thailand (Brandt, 1974) and Nigeria (Brown, 1983). The number of species and their distribution is uncertain.

Comments. Throughout its range within the Australian/Southwest Pacific region *Amerianna* exhibits considerable variation in shell morphology, though the majority of described species have shortened spires and most are carinate. All have a simple pendant penis, but the opening of the vas deferens may be terminal or lateral. Because the two kinds of penis are found in snails with similar shell morphology, it is not yet possible to conclude with certainty the position of the type species *A. carinata.* Brown (1983) did, however, illustrate a penis with a terminal pore for specimens he concluded were *A. carinata* collected at Ibadan, Nigeria. These were compared with specimens from the type series held in the British Museum (Natural History). There is no clear pattern of geographic separation of the two forms.

Cotton (1943) erected the subgenus *Ameriella* for *A. bonushenricus* because of the distinctive shell morphology. Walker (1985) retained this division for species of *Amerianna* with a lateral penis pore, and included in the subgenus *Bullinus sisurnius* Hedley 1918. This species was included because of the form of its penis and its possession of a prostatic collecting duct. Further examination of material of this species has led to the conclusion that *B. sisurnius* is generically distinct. It is discussed later in this review.

Until further studies are performed on this genus as a whole, no decision on the number of subgeneric taxa can be made and there appears to be insufficient reason to use *Ameriella* as a subgenus. Two forms distinguishable on shell morphology, *A. carinata* and *A. bonushenricus* are present in Australia, but both kinds of penis structure are found in snails with carinata-like shells. The number of species of *Amerianna* from outside Australia is also uncertain,

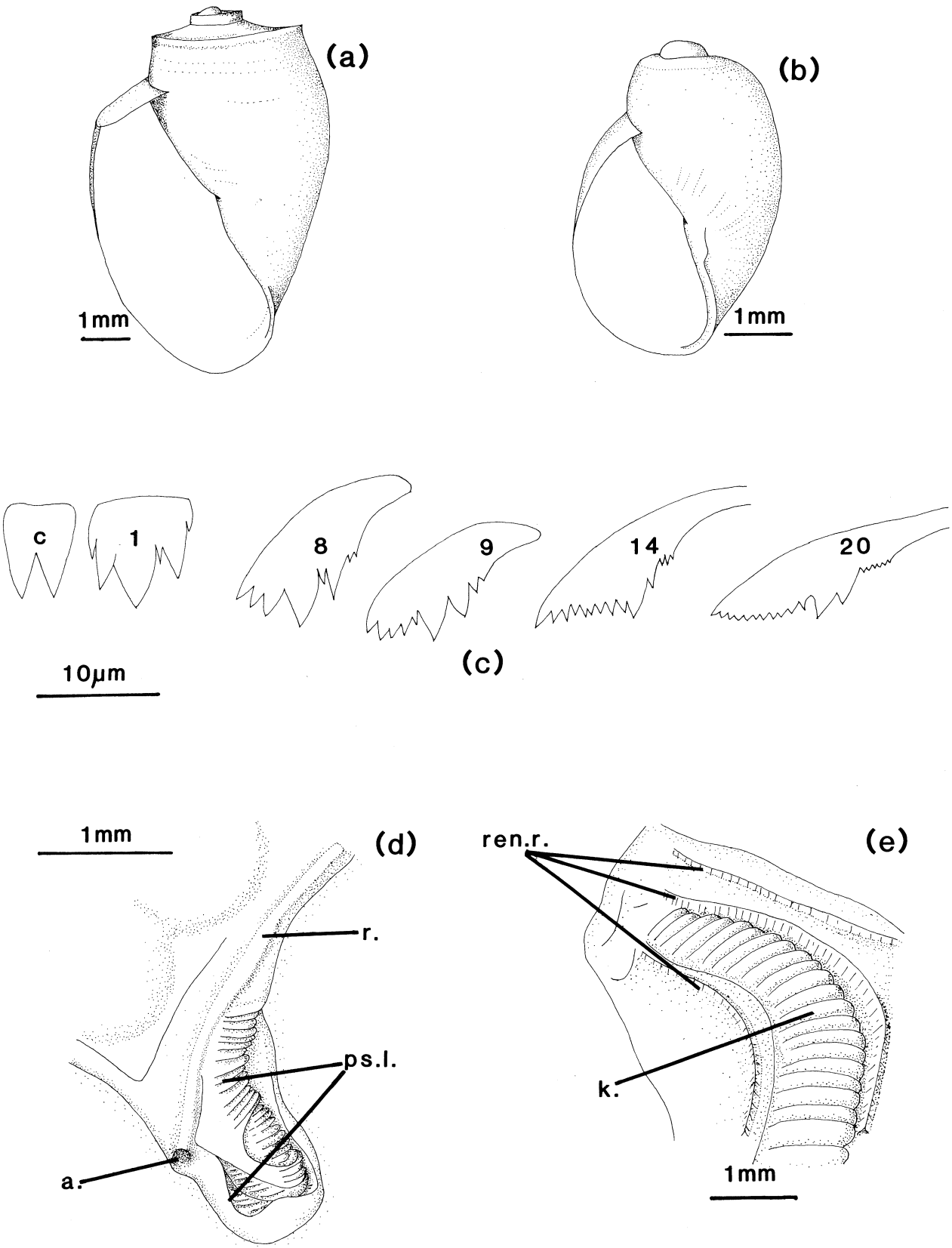

Fig.9. Anatomy of *Amerianna.* **(a)** *A. carinata,* shell; **(b)** *A. bonushenricus,* shell; **(c)** *A. carinata,* radula: c = central tooth, -the number on each tooth designates its consecutive position distally from the central tooth; **(d)** *A. carinata,* pseudobranch; **(e)** *A. carinata,* kidney and renal ridges. a anus; k. kidney; ps.l. pseudobranch lobes; r. rectum; ren. r. renal ridges.

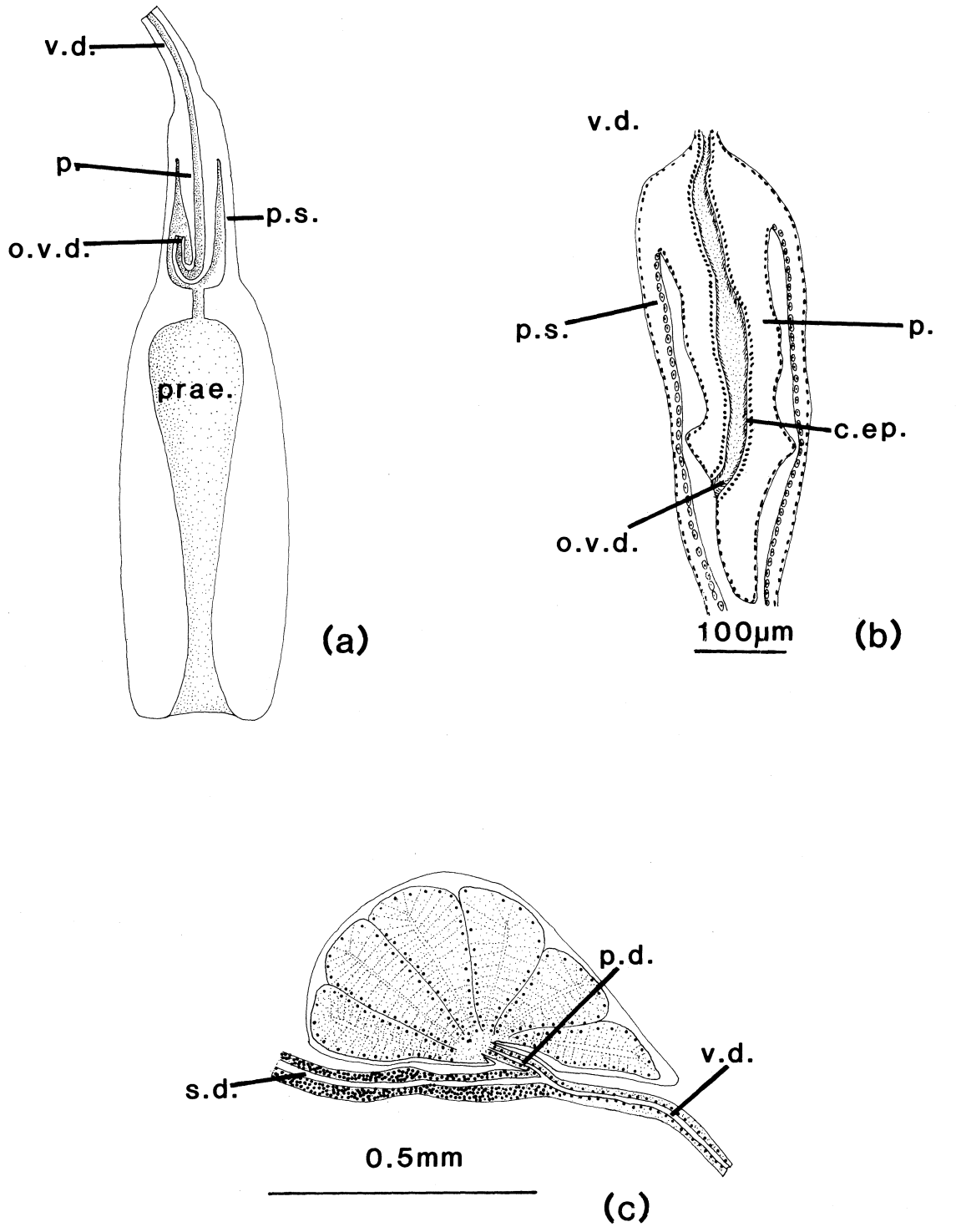

Fig.10. *Amerianna,* continued. **(a)** *A. carinata,* section of copulatory organ; **(b)** *Amerianna* sp., Mt. Isa, Qld., l.s., penis; **(c)** *A. bonushenricus,* prostate gland. c.ep., ciliated epithelium; o.v.d. opening of vas deferens; p. penis; p.d. prostatic duct; prae. praeputium; p.s. penis sheath; s.d. spermduct; v.d. vas deferens.

but at least three, *A. leopoldi, A. buruanus* and *A. pesigani,* appear to be valid.

Hubendick (1957) erected the monotypic genus *Patelloplanorbis* for a patelliform freshwater snail from West Irian. The internal anatomy of the type species *P. tigiensis* Hubendick, 1957, is similar to that of *Amerianna.* This is especially true of the pendant penis, which has a terminal pore. Further study is needed to determine the degree of relationship between these genera.

Genus *Bayardella* Burch, 1977
Figs 11, 12

Bayardella Burch, 1977: 80. Type species *Plesiophysa (Bayardella) johni* Burch, 1977, original designation. Recent, Northern Australia.

Diagnosis. Bulinine snails with neritiform or cylindrical shell with surface having raised spiral ribs and transverse striae; copulatory organ with accessory bursa, lacking flagella, large muscular bulb transversed by duct of accessory bursa and into which penis protrudes is suspended in proximal end of praeputium; anus on anterior edge of rectal lobe.

Description. SHELL. Small, sinistral shell, neritiform or cylindrical, with low spire (Fig. 11a,b). Aperture large, oval to pyriform, length almost equal to whole shell, with continuous periostracal fringe; columellar margin reflected and slightly curved without columellar fold; deep umbilicus present. Surface of body whorl with prominent raised spiral ribs and less conspicuous transverse striae, giving appearance of small, incised rectangles.

EXTERNAL MORPHOLOGY. Tentacles filiform. Pseudobranch unilobed or bilobed with secondary folding (Fig. 12a). Rectum opens on anterior edge of rectal lobe. Foot rounded posteriorly.

RADULA. Central teeth with 2 equal or unequal cusps, left cusp often considerably larger, each flanked by a smaller cusp or denticle (Fig. 11c,d). Lateral teeth tricusped with denticles or small cusps between mesocone and ectocone and on lateral edge of mesocone; entocone small, mesocone large, smaller ectocone subdivided into 3 unequal cusps. Transition to marginal teeth involves gradual reduction in size of larger cusps and development of pectinate structure by division of cusps.

SALIVARY GLANDS. Salivary glands tubular; do not pass through circumoesophageal nerve ring (Fig. 12b).

REPRODUCTIVE SYSTEM. Copulatory organ. Accessory bursa arising from top of praeputium (Fig. 12c). Penis sheath narrower than praeputium, approximately ⅓ as long. Sheath has thin, muscular wall lined internally by simple epithelium of flattened cells with elongate, ovoidal nuclei with scattered chromatin. Penis muscular, with laterally opening vas deferens and minute stylet at tip. Lumen of penis sheath opens into large muscular bulb suspended from proximal end of praeputium. Duct from accessory bursa enters bulb at level of attachment to praeputium and traverses it vertically, connecting at lower end to duct which is continuous with lumen of penis sheath. Opening of both ducts to lumen of praeputium via branches traversing lower end of muscular bulb (Fig. 12d). Bulb thin walled, containing large sinus formed by splitting of muscle layers. Sinus lacks internal epithelium and is lined by muscle tissue. Epithelium of accessory bursa consists of columnar cells with large, ovoidal, basal nuclei with scattered chromatin (Fig. 12e).

Prostate gland and bursa copulatrix. Prostate gland without prostatic duct. Bursa copulatrix globose.

Distribution. *Bayardella johni* is widely distributed throughout the Kimberley and Victoria River regions of northern Australia. *B. cosmeta* occurs in central, eastern and southeastern Australia.

Comments. Several anatomical features point to the unique taxonomic position of *Bayardella.* Hubendick (1955) described the anus of *Plesiophysa ornata* as being posterior to the pseudobranch; that of *Bayardella* opens on the anterior edge of the rectal lobe.

Initial observations (Burch, 1977) indicated that the central tooth of *B. johni* was five cusped, having a single mesocone flanked by two cusps on each side. *Plesiophysa* has a radula with a five-cusped central tooth (Hubendick, 1955). Subsequent studies on the radula of *P. (B). johni,* using light microscopy (this study) and scanning electron microscopy (Burch & Jeong, 1984), have independently concluded that the original observations were in error. These two studies differ, however, in their interpretation of the nature of the central tooth. Burch & Jeong (op. cit.) describe and figure an asymmetrical central tooth with one major cusp flanked on each side by two unequal cusps or denticles. Apart from the asymmetry, this is similar to the original description by Burch (1977). Some of the material examined in this study was collected at the same time and place as that used by Burch & Jeong (Bow River, Kimberley region, northwestern Australia, 13th May, 1978). Radulae from three separate snails have been examined and teeth have been studied in the intact radula and separated from the radula by long digestion in NaOH. In every case the central teeth have two unequal main cusps, the left cusp being considerably larger, flanked by a smaller denticle (Fig. 12c). Radulae of specimens of *B. cosmeta* from Bridgeport in Victoria have central teeth with equal sized cusps, while those from central Australia are similar to those of *B. johni.*

Superficially the copulatory organs of *Bayardella johni* and *B. cosmeta* are similar to those described by Hubendick (1967) for some species of *Camptoceras* Benson, 1843. Both genera have an accessory bursa arising from the top of the praeputium. It was a combination of this feature and marked similarity of shell morphology which led

Burch (1977) and Burch & Jeong (1984) to place *Glyptamoda cosmeta* into the genus *Camptoceras.* The internal structure of this bursa, revealed in whole mounts and serial sections (Fig. 12 d,e), is markedly different from that of the copulatory organ of *Camptoceras.*

Bayardella and *Camptoceras* differ in several other respects. The pseudobranch of *Bayardella* is a folded structure lying posterior to the anus; the simple, unfolded pseudobranch of *Camptoceras* lies anterior to the anus (Hubendick, 1967). The nature of the lateral and marginal radula teeth of *Camptoceras* differ from those of *Bayardella* and the salivary glands of *Camptoceras* are globose (Hubendick, 1955), rather than tubular.

Two species, *Bayardella johni* and *B. cosmeta,* are recognisable within the genus. They are readily distinguished by shell morphology (Fig. 11a,b).

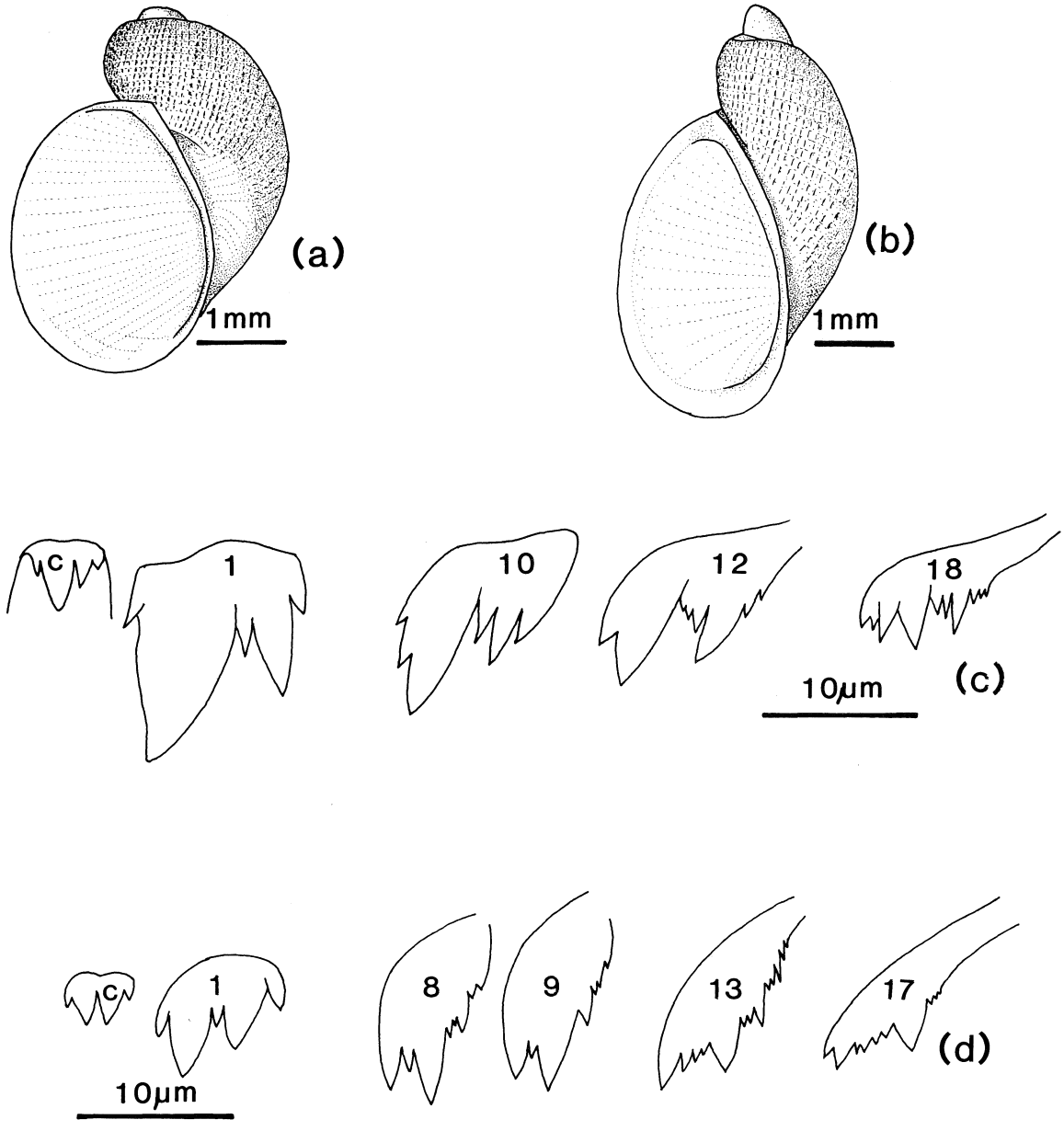

Fig.11. Anatomy of *Bayardella* **(a)** shell of *B. johni;* **(b)** shell of *B. cosmeta;* **(c)** radula of *B. johni:* c = central tooth, -the number on each tooth designates its consecutive position distally from the central tooth; **(d)** radula of *B. cosmeta.*

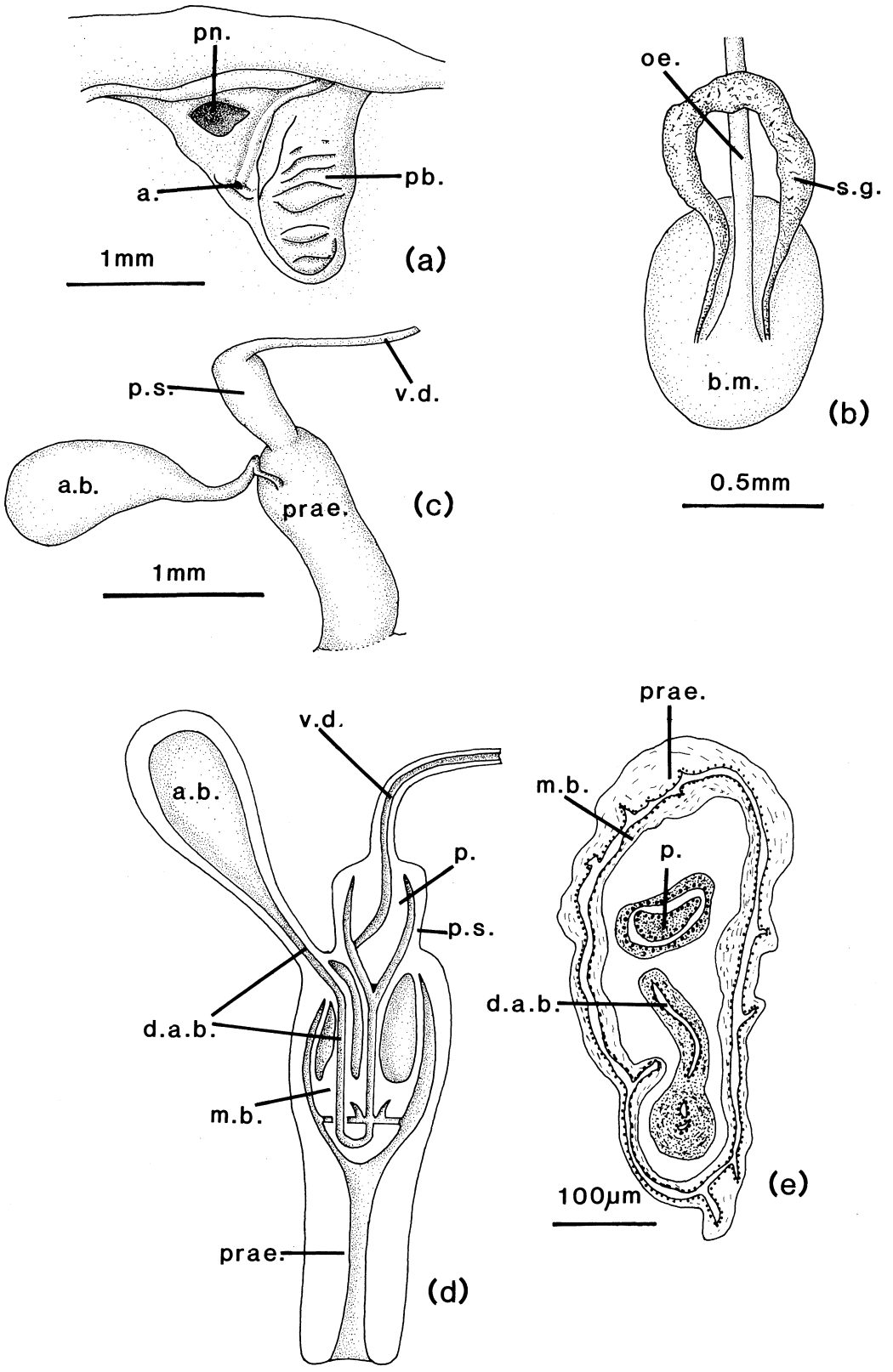

Fig.12. **(a)** pseudobranch of *B. johni;* **(b)** salivary glands of *B. johni;* **(c)** copulatory organ of *B. cosmeta;* **(d)** copulatory organ of *Bayardella,* diagramatic view; **(e)** transverse section through copulatory organ of *B. johni.* a. anus; a.b. accessory bursa; b.m. buccal mass; d.a.b. duct of accessory bursa; m.b. muscular bulb; oe. oesophagus; p. penis; pb. pseudobranch; pn. pneumostome; prae. praeputium; p.s penis sheath; s.g. salivary glands; v.d. vas deferens.

Genus *Leichhardtia* n.gen.

Fig. 13

Type species. *Bullinus sisurnius* Hedley, 1918. Recent, Paterson Range, Western Australia.

Diagnosis. Bulinine snail having subglobose shell with unshouldered whorls; copulatory organ lacking accessory bursa or flagellum, pendant penis uniramous with lateral pore; prostatic duct present; rectal ridge absent.

Description. SHELL (Fig. 13a). Small (up to about 7mm in length), sinistral subglobose shell; spire depressed, whorls rounded; mature specimens have 3 or 4 whorls; aperture eliptical, parietal lip gently curved, parietal callus adheres to body whorl; umbilicus present; body whorl traversed by spiral rows of striae which bear periostracal hairs in living specimens.

EXTERNAL MORPHOLOGY. Tentacles filiform. Pseudobranch trilobed and secondarily folded, small dorsal lobe projects above level of pneumostome (Fig. 13b). Rectum opens on anterior edge of middle pseudobranch lobe. Posterior end of foot rounded.

RADULA (Fig. 13c). Central tooth with 2 unequal major cusps with minor cusps at base of each. Right cusp usually, but not invariably, longer. Denticle present between major cusps; small denticles on lower lateral edge of right major cusp and occasionally on left. Lateral teeth tricusped with prominent denticles between cusps; first lateral has a single denticle between mesocone and ectocone and small denticles on lateral edge of entocone and on outer edge of base of ectocone. Transition to marginal teeth at about tooth 6; characterised by splitting of entocone into smaller cusps and reduction in size of ectocone. Teeth at extreme margins pectinate.

SALIVARY GLANDS. Salivary glands flat sheets which pass through nerve ring; ducts insert into rear of buccal mass.

MANTLE STRUCTURES. No rectal fold present. Large renal fold on ventral side of kidney (Fig. 13b).

REPRODUCTIVE SYSTEM. Copulatory Organ. Penis is muscular and pendant (Fig. 13d). There are two muscular folds at the distal end (Fig. 13e). Opening of vas deferens is lateral. Praeputium has ciliated epithelium and prominent muscular folds.

Prostate gland. Prostate acini empty into small ciliated ducts which join main prostatic duct.

Bursa Copulatrix. Bursa copulatrix elongate oval. Duct inserts at distal end of vagina.

Distribution. Throughout Kimberley region, into western Northern Territory.

Comments. The differences in copulatory organ structure indicate that Iredale's (1943) placing of *L. sisurnia* in *Lenameria* was incorrect. So too was its inclusion in *Isidorella* by Walker (1984), a decision based on the general similarity of shell morphology and the fact that the complex penis structure of *I. newcombi* could have been derived from that of *Leichhardtia*. The nature of the reproductive system, a simple pendant penis and a system of prostatic collecting ducts, suggests some degree of relationship with *Amerianna*. The unequal cusps of the central radula tooth may indicate association with *Bayardella*. The genus is named for Ludwig Leichhardt who made a significant contribution to the exploration of Australia's north.

Discussion

The characters used in assessing the relationships between Australian and African buliniform planorbids are summarised in Table 1. The variability exhibited by these molluscs in shell shape is illustrated by the range of character states which can be applied to a single taxon, reinforcing the conclusion that the shell must be considered of limited value in separating the genera of Australian buliniform planorbids. Of genera described up to the time of Iredale's (1943) checklist and based on shell characters alone, only *Isidorella* remains unchanged. Even with this genus, geographic distribution has unquestionably been important in the retention of a separate identity because of the similarity of these shells to those of African *Bulinus*. In this instance, evidence available from the shell alone would suggest the combining of actually distinct genera. In other instances the reverse is true; anatomical studies have shown that taxa separated on shell characters are congeneric. In the case of *Ancylastrum* the original familial placement has been shown, by anatomical evidence, to be incorrect.

Although many aspects of the anatomy provide useful taxonomic characters, the most consistent differences between groups of species were apparent from studies of the reproductive tract, especially the copulatory organ and prostate gland. This finding is in concordance with that of Hubendick (1955a) in relation to planorbids in general. Apart from the rearrangement of genera based on these criteria, a number of particular points arise.

Most importantly, the use of *Bulinus* as a generic name for freshwater snails from Australia is not justified. From the work of Hubendick (1948a, 1948b, 1955a), and from that of numerous authors since, it is evident that all species of *Bulinus* (and *Indoplanorbis*) have an ultrapenis. No Australian mollusc studied possesses this structure. As mentioned previously, the material on which Hubendick (1948a) based his claim of synonymy between *Bulinus* and *Isidorella* actually came from Lorenzo Marques in Mozambique. It is almost certain that the specimens were of *Bulinus,* either *B. globosus* or *B. africanus.* Hubendick stated that the shell was similar to that of the former and the anatomy to that of the latter. It is stressed that specimens of *Isidorella* from all parts of Australia have been examined in detail and in no instance has a pseudopenis or ultrapenis been found.

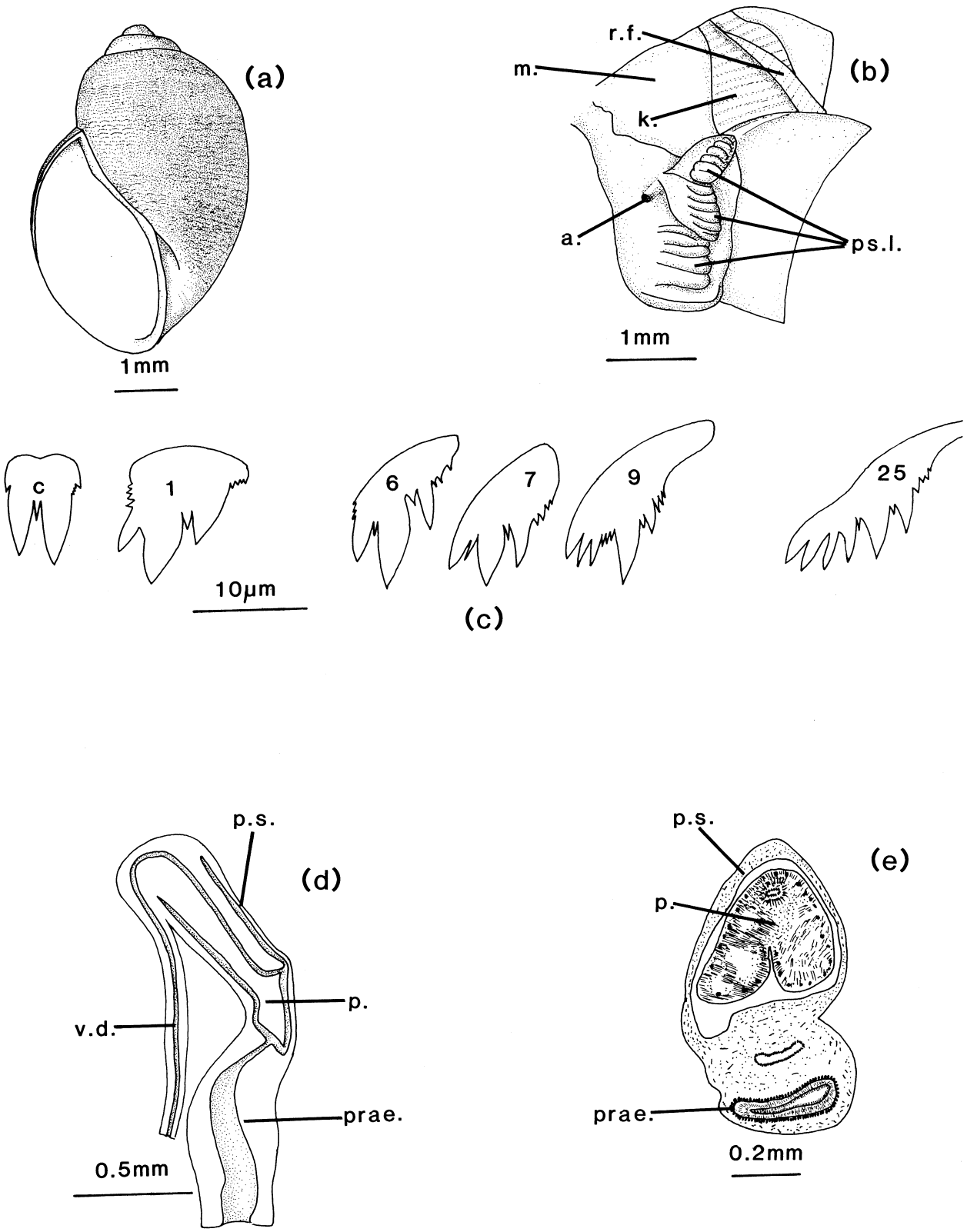

Fig.13. Anatomy of *Leichhardtia sisurnia.* **(a)** shell; **(b)** pseudobranch and renal fold; **(c)** radula: c = central tooth, -the number on each tooth designates its consecutive position distally from the central tooth; **(d)** copulatory organ, l.s.; **(e)** copulatory organ, t.s. a. anus; k. kidney; m. inner surface of mantle - folded back; p. penis; ps.l. pseudobranch lobes; prae. praeputium; p.s. penis sheath; r.f. renal fold; v.d. vas deferens.

Wright's (1961) claim that the prostate glands of Australian bulinine planorbids differ from that of *Bulinus* is incorrect, at least for the genera other than *Amerianna* and *Leichhardtia*. The essential details of the glands are similar in both geographic groups. All the Australian bulinine planorbids have prostate glands with the acini branching from a small area of the sperm duct or from a separate prostatic duct. The gonad acini are arranged in a fan-like pattern in all cases. They, therefore, are included in the subfamily Bulininae as defined by Hubendick (1978). This subfamily is wider in definition than the same author's (1955a) grouping which included only those genera which have an ultrapenis (*Bulinus* and *Indoplanorbis*).

Walker (1984) discussed the geographical relationships of the buliniform planorbids of Australia. Although the classification presented then differs from that presented here in detail (*Leichhardtia sisurnia* is now separated from *Isidorella* and *Physastra* is synonymised with *Glyptophysa*), the general concept of a Gondwanan origin for these snails is still strongly supported.

Table 1. Summary of differences and similarities between genera and subgenera of African and Australian buliniform planorbids.

Key to abbreviations: + = character present; — = character absent; +/— = taxon variable with respect to character; —/+ = character present but slightly developed. *(A.c) Ancylastrum cumingianus; (A.i) Ancylastrum irvinae; (B.c) Bayardella cosmeta; (B.j) Bayardella johni; (G) Glyptophysa s.s.; (O) G. (Oppletora).*

	Bulinus	Isidorella	Ancylastrum	Glyptophysa	Amerianna	Bayardella	Leichhardtia
Shell							
globose	+	+		+(O)			
sub-globose	+	+		+(G)			+
medium spired	+	+		+(G)		+(B.c)	
high spired	+			+(G)			
spire truncate	+				+		
carinate	+			+(G)	+		
patelliform			+				
transverse ribs	+		+/—(A.i)			+	
spiral lirae	+			+(G)		+	+
peirostracal hairs		+		+/—	+/—		+/—
columellar fold	+			+	—/+		
External Anatomy							
pseudobranch:							
unilobed			+			+(B.j)	
bilobed	+	+		+	+	+(B.c)	
trilobed							+
foot:							
pointed	+	+					
rounded	+		+	+	+	+	+
tentacles:							
long-filiform	+	+		+	+	+	+
short			+				
Internal Anatomy							
radula:							
central tooth symmetrical	+	+	+	+	+	—	—
ectocone of 1st lateral divided						+	
large rounded mesocones			+				
salivary glands:							
tubular and do not pass through nerve ring						+	
tubular, pass through nerve ring	+						

flat, branched sheets, pass through n.r.		+	+	+	+		+
rectal ridge	+	—	—	+	+	—	—
renal folds	+/—	—					—
1 ridge on roof of pulmonary cavity			?	+		—	—
3 ridges on roof of pulmonary cavity	—	—	?	—	+	—	
single fold on ventral side of kidney	+/—	—	?	—	—	—	+
Reproductive Tract							
copulatory organ:							
accessory bursa	—	—	—	—	—	+	—
flagellum	—	—	+	+	—	—	—
penis							
uniramous		—	+(A.c)	+	+	+	+
biramous		+	+(A.i)	—	—	—	—
stylet	—	—	+	+	—	—/+	—
lateral pore		—	+(A.i)	+	+	+	+
terminal pore		—	+(A.c)	—	+	—	—
pseudopenis	+	—	—	—	—	—	—
bursa copulatrix:							
rounded	+	+		+		+	
elongate					+		+
spatulate			+				
prostatic duct	—	—	?	—	+	—	+

Key to the Genera and Subgenera of Australian Buliniform Planorbids

This key is based on the structure of the copulatory organ and on shell morphology.

1. Copulatory organ without an accessory bursa or flagellum. 2

——Copulatory organ with an accessory bursa or flagellum. 4

2. Pendant penis with 2 folded processes. ..... *Isidorella*

——Pendant penis uniramous. 3

3. Shell cylindrical, whorls carinate. ..... *Amerianna* s.s.

——Shell subglobose, whorls with rounded shoulders. ..... *Leichhardtia*

4. Copulatory organ with a muscular flagellum on the proximal end of the penis sheath. 5

——Copulatory organ with an accessory bursa connected to the praeputium. ..... *Bayardella*

5. Penis bilobed or with augur-like folds proximal to the stylet. ..... *Ancylastrum*

——Penis unilobed. 6

6. Shell with a pronounced spire, whorls carinate or with rounded shoulders ..... *Glyptophysa* s.s.

——Shell globose with depressed spire. ..... *Glyptophysa (Oppletora)*

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APPENDIX

Snails used in this study have been collected or supplied by various individuals who are listed alphabetically.

A short description of the habitat of each collection site and a list of associated molluscs is given.

List of Collectors and Suppliers of Snails

Name	Affiliation
J.C. Boray (JCB)	Parasitology laboratory, Agricultural Research Station, Glenfield, NSW.
J.B.Burch (JB)	University of Michigan, Ann Arbor, Michigan.
P.Colman (PC)	Australian Museum, Sydney.
P. Davis (PD)	Western Australian Department of Agriculture.
D. Feughelman (DF)	formerly School of Public Health and Tropical Medicine, University of Sydney.
D. McMichael (DM)	formerly Australian Museum, Sydney.
W.F. Ponder (WP)	Australian Museum, Sydney.
C. Roper (CR)	Associate of Australian Museum, Sydney.
R.C. Russell (RR)	School of Public Health and Tropical Medicine, University of Sydney.
B.J. Smith (BS)	National Museum of Victoria, Melbourne.
J. Stoddart (JS)	formerly Western Australian Museum, Perth.
J.C. Walker (JW)	School of Public Health and Tropical Medicine, University of Sydney.
P. Whelan (PW)	Department of Health, Darwin, N.T.

TAXON

***Isidorella newcombi* s.l.**

Colony		Locality collected or origin of sample	Collector	Date
I	1	Suggan Buggan, Vic. 148°20′E;37°00′S, in farm dam	BS	2.4.1972
I	2	Birthday Tank, Sunset, Victoria. 141°30′E;34°56′S.	BS	13.4.1973
I	3	Glenfield, N.S.W. 150°53′E;34°00′S. In stream.	WP	1973
I	4	Coleambally, N.S.W. 145°52′E;34°43′S. In grass filled road-side borrow pit.	JW	Sept,1973
I	5	Cooma Creek, N.S.W. 149°10′E;36°13′S. Amongst aquatic vegetation at edge of creek.	WP	1973
I	6	Hay, N.S.W. 144°55′E;34°33′S. In low lying land beside road. With *Glyptophysa (Physastra), Austropeplea lessoni* and *Physa* sp.	JB/DF	23.9.1975
I	7	Fish River, Oberon, N.S.W. 149°45′E;36°22′S. In water supply tunnel. With *Glyptophysa aliciae* and *G. (Physastra).*	PC	1974
I	8	Great Sandy Desert, W.A. 122°33′E;22°53′S. In rock hole.	JS	26.4.1979
I	9	New Norcia, W.A. 116°13′E;30°59′S.	JS	May,1979
I	10	Simpson's Gap, Central Australia. 133°43′E;23°42′S. In pools at base of rocks — floating algae	JW/JB	30.5.1979
I	11	Jay Creek, C.A. 133°31′E;23°46′S. In pools in creek bed.	JW/JB	30.5.1979
I	12	Alice Springs, C.A. 133°52′E;23°33′S. In quarry, 20.6 kms north of town.	JW/JB	31.5.1975
I	13	Tephrina Gorge, C.A.134°19′E;23°31′S. John Hayes Rock Hole, permanent pools in quartzite gorge. With *Gyraulus, Petancylus.*	JW/JB	2.6.1979

I	14	N'Dhala Gorge, C.A. 134°28′E;23°45′S. In rock pools. With *Petanclyus.*	JB/JW	2.6.1979
I	15	Serpentine Gorge, C.A. 132°59′E;23°45′S. In rock pools.	JB/JW	3.6.1979
I	16	Glenn Helen, C.A. 132°50′E;23°43′S. In small pool at base of ochre cliff.	JB/JW	3.6.1979
I	17	Hugh River, C.A. 133°20′E;23°46′S. Flowing water, algal covered stones. With *Gyraulus.*	JW/PC	10.6.1979
I	18	Spencer Gorge, C.A. 133°17′E;23°44′S. Rocky water hole.	JW/PC	10.6.1979
I	19	Hale River, Ruby Gorge, C.A. 134°59′E; 23°29′S. Running water with reeds at edge. With *Gyraulus.*	JW/PC	13.6.1979
I	20	Paddy's Hole, near Arltunga, C.A. 134°43′E; 23°29′S. Permanent rock pool.	JW/PC	13.6.1979
I	21	Binya, 145°41′E;29°00′S; 112 kms south of Cunnamulla, s.w. Qld. In overflow puddle of trough in bore drain.	CR	7.12.1980
I	22	Rushes Creek, N.S.W. 148°45′E;36°22′S. In vegetation at edge of creek. With *Austropeplea tomentosa* and *Gyraulus.*	JW	Dec.1981
I	23	Echuca, Vic. 144°44′E;36°13′S. In irrigation drain.	RR	1982
I	24	Burragate, N.S.W. 149°40′E;36°34′S. In water-cress beds. With *A. tomentosa.*	JW	13.4.1983
I	25	Bathurst, N.S.W. 149°20′E;33°23′S. With *A. tomentosa, G. (Physastra).*	JCB	May 1984

Ancylastrum

Two samples, one of each species of this genus, were available for study. Neither sample had information on habitat or associations with other molluscs.

Ancylastrum cumingianus. 2 specimens, collected by D. McMichael at the southern end of Great Lake, Tasmania, in 1960. From the collection of the Australian Museum, Sydney.

Ancylastrum irvinae. 5 specimens collected by C.E. Beddome, Great Lake, Tasmania, 24.3.1894. From the collection of the Australian Museum, Sydney.

Glyptophysa s.s.

Glyptophysa aliciae

G	1	Fish River, Oberon, N.S.W. 149°45′E;36°22′S. In water supply.	WP	Feb.1975
G	2	Lake Eucumbene, N.S.W. 148°35′E;36°05′S. In streams running into western end of lake.	JW	1976
G	3	Greenbushes, W.A. 116°03′E;33°51′S. In small streams, with *Austropeplea lessoni.*	PD	15.1.1986

Glyptophysa (*Physastra* types)

P	1	Inverell, N.S.W. 150°53′E;29°55′S. In water overlying pasture.	JW	Dec.1970
P	2	North Stradbroke Island, Qld. 153°25′E;27°30′S. In swamp at Dunwich.	JW	June 1973
P	3	North Stradbroke Island, Qld. 153°27′E;27°22′S. In roadside ditch at Amity Point.	JW	June 1973
P	4	Torrens River, Adelaide, S.A. 138°35′E;34°55′S.	JW	Sept.1979
P	5	Avondale, Sydney. 151°05′E;33°45′S. In small dam.	JW	Dec.1973
P	6	Casino, N.S.W. 153°02′E;28°40′S.	JB/WP/PC	May 1975
P	7	Proserpine, Qld. 148°35′E;20°21′S.	JB/WP/PC	May 1975
P	8	Fish River, Oberon, N.S.W. 149°45′E;36°22′S.	JW	1975
P	9	Lake Cargellico, N.S.W. 146°24′E;33°18′S. Roadside ditch	JB/DF	22.9.1975
P	10	Junee, N.S.W. 147°35′E;34°42′S. Roadside ditch. With *Physa.*	JB/DF	25.9.1975
P	11	Alstonville, N.S.W. 153°30′E;28°50′S.	PC	1975
P	12	Daly River, N.T. 130°35′E;13°45′S. In billabong With *Amerianna, Austropeplea.*	JB/WP	11.6.1976
P	13	Humpty Doo, N.T. 131°15′E;12°40′S. Fogg Dam at irrigation project. With *Gyraulus, Austropeplea* and *Amerianna.*	JB/WP/PC	14.6.1976
P	14	Harrison Dam, Humpty Doo, N.T. 131°15′E; 12°40′S. With *Gyraulus, Austropeplea.*	JB/WP/DF	16.6.1976
P	15	St. Albans Common, N.S.W. 150°58′E;33°15′S. In swamp.	JW/JS	Jan.1978
P	16	Wyndham, W.A. Parry's Lagoon. 128°15′E;15°32′S. With *Austropeplea vinosa, Amerianna carinata, Gyraulus.*	JW/JS	7.5.1978
P	17	Palm Valley, Central Australia. 132°40′E;24°03′S. Non flowing water in creek bed. With *A. vinosa.*	JW/JB	31.5.1979

P	18	Ellery Gorge, C.A. 133°05′E;23°47′S.	JW/JB	3.6.1979
P	19	Ormiston Gorge, C.A. 132°44′E;23°37′S. In water holes at the edge of Ormiston Creek. With *Plotiopsis, Petancylus.*	JW/JB	3.6.1979
P	20	Hugh River, C.A. 133°20′E;23°46′S. With *Gyraulus, Petancylus.*	JW/PC	10.6.1979
P	21	Mildura, Vic. 142°10′E;34°15′S.	RR	June 1980
P	22	Burdekin Falls, Qld. 147°09′E;20°39′S.	PC	1981
P	23	Ayr, Qld. 147°15′E;19°33′S. In ponds of sewage treatment works.	PC	1984

Specimens from other sites in Australia and from regions outside Australia. I have examined specimens of *G. (Physastra)* sp. in the collections of the Australian Museum, Sydney, and the National Museum of Victoria, Melbourne. In the latter are many collections from Tasmania, while the former includes specimens from New Zealand, New Guinea, New Caledonia, Tahiti and West Irian. I have also examined specimens from Sorsogon, Philippines.

Glyptophysa (Oppletora) jukesii

GJ	1	Smith Point, Cobourg Peninsula, N.T. 132°10′E; 11°08′S. In lagoon behind Ranger's station. With *Gyraulus* and *Austropeplea vinosa.*	JB/WP/DF	1.6.1976
GJ	2	Lagoon, south of Katherine, N.T. Near the King River.	JB/WP/DF	10.6.1976
GJ	3	King Billabong. 130°01′E;15°47′S. Large lagoon with water lillies, beside Victoria Highway, N.T. With *Gyraulus* and *Notopala.*	JW/JB	19.5.1978

Amerianna

Amerianna carinata

A	1	Nebo Creek, Qld. 148°41′E;21°41′S.	JB/WP/PC	5.5.1975
A	2	Humpty Doo, N.T. 131°51′E;12°40′S. Fogg Dam, at irrigation project. With *A. vinosa, G.(P) concinna* and *Gyraulus.*	JB/WP/DF	16.6.1976
A	3	Cheese Tin Creek, Kununurra, W.A.128°16′E;15°42′S. In isolated pools in the bed of drying stream. With *Bayardella johni, Gyraulus, Petancylus.*	JW/JS	7.5.1978
A	4	Lake Argyle, W.A. 128°50′E;16°20′S. In lagoon near Spillway Creek. With *A. vinosa.*	JB/JW/JS	9.5.1978
A	5	Hidden Valley, Kununurra, W.A. 128°45′E;15°43′S. With *A. (Ameriella) sisurnia.*	JW/JB	14.5.1978
A	6	Mount Isa, Qld. 139°30′E;20°43′S. In dam.	JW	1980
A	7	Darwin, N.T. 130°52′E;12°28′S. In small creek. With *A. vinosa.*	PW	29.6.1984

Amerianna bonushenricus

A	8	Bow River. 128°07′E;17°15′S. On stones in isolated pools in river bed. With *B. johni, Gyraulus, A. vinosa, Petancylus* and *Notopala.*	JW/JB/JS	13.5.1978

Bayardella

Bayardella johni

Bj	1	Bell Creek Crossing, King Leopold Ranges, W.A. Collected by B.J. Wilson and S. Slack-Smith.	JS	27.8.1975
Bj	2	Kununurra W.A. 128°10′E;15°42′S. In pools in bed of Cheese Tin Creek. With *Gyraulus* and *Petancylus.*	JW/JS	7.5.1978
Bj	3	Bow River, W.A. 128°07′E;17°15′S. On stones in isolated pools in river bed. With *A. (Ameriella) bonushenricus, Gyraulus, Austropeplea vinosa, Petancylus* and *Notopala.*	JW/JB/JS	13.5.1978

In addition to these samples, I have also examined the type specimens in the collections of the Australian Museum, Sydney. This also applies to the second species of this genus, *B. cosmeta.*

Bayardella cosmeta

Bc	1	Bridgewater, Vic. 143°58′E;36°36′S. Aestivating on sticks and bark beside the Loddon River. This material is in the collection of the National Museum of Victoria, Melbourne.	BS	16.5.1973
Bc	2	Palm Valley, C.A. 132°44′E;24°02′S. In a small pool in the bed of a south flowing tributary of Palm Creek. On algal covered leaves and rocks.	JW	9.6.1979

Leichhardtia
Leichhardtia sisurnia

L	1	Hidden Valley, Kununurra, W.A. 128°45′E;15°43′S. Small pool with stones, gravel bottom, filled by runoff. With *A. carinata.*	JW/JB	14.5.1978
L	2	Kununurra, 129°02′E;16°00′S. In small creek beside Duncan Highway. 43km sth of Kununurra.	JB/JW	16.5.1978
L	3	Jasper Creek, 130°41′E;16°03′S. Pond filled with aquatic vegetation beside Top Springs-Timber Creek road, N.T.	JB/JW	19.5.1978

I have examined the type specimens of *Leichhardtia sisurnia* in the collection of the Australian Museum, Sydney.

Other planorbids used in this study

In addition to the Australian species listed above, I have had material of two genera, *Bulinus* and *Indoplanorbis* for comparative studies. This material was: *Bulinus truncatus* from Egypt, *Bulinus tropicus* from Rhodesia, *Bulinus sericinus* from Ethiopia, and *Bulinus octoploidus* from Ethiopia, all supplied by Professor J.B. Burch. In addition I had available a colony of *Indoplanorbis exustus* collected by Professor Burch in Madras, India, in 1979. *Bulinus (Physopsis) globosus* collected in NW Liberia by W. Hofler and H.J. Knuttgen on 4.5.1975. These fixed specimens, from a laboratory colony, were supplied by Dr. C.M. Meier-Brook, Tropenmedizinisches Institut, University of Tubingen.