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# Cementation in
## *Cleidothaerus albidus* (Lamarck, 1819)
## (Bivalvia: Anomalodesmata: Pandoroidea)

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## Abstract

The pandorid anomalodesmatan *Cleidothaerus albidus* cements to hard substrata by the anterior half of the right valve. Cementation begins after settlement of a lecithotrophic larva during the dissoconch stage (at a mean height of 1.2 mm), presumably after a brief period of byssal attachment. The aragonitic shell comprises a thick inner nacreous layer, with 'chalky deposits', and a thin outer prismatic layer. The persistent periostracum is relatively thick. It is bi-layered with the outer layer being thinner (1-2 µm) on the right cemented valve than the 'upper' left valve ( 10 µm). The inner layer, secreted by the outer component of the periostracal groove, is probably more mucoid. There are no obvious differences in the character of the right valve periostracum between areas of cementation and non-cementation. An extra-pallial cement was discovered under some parts of the attached valve where it had accumulated in 'valleys' in the substratum, providing the necessary smoothing to allow adhesion. The cement was mainly unmineralised but in some patches showed spherulitic growth of (?) aragonite.
   *Cleidothaerus albidus* shows Type B pallial fusion, i.e. fusion of the inner and inner surfaces of the middle mantle folds. Significantly, no arenophilic glands were observed, however, we did identify a large gland within the mantle cavity of the right lobe that was restricted to the anterior portion, i.e. the part of the mantle directly involved with cementation. This structure comprises two types of secretory cells. Since the gland was restricted to only those parts of the mantle that were involved in cementation, we suggest that it may be responsible for the production of the cement that drains, under gravity, to exit the mantle cavity at the pedal gape, coating the attaching periostracum.

## Introduction

The sub-class Anomalodesmata, as its name implies, is an assemblage of disparate species and genera that are contained within 14 extant and 8 extinct families, and constituting approximately 15% of the current familial diversity of the Bivalvia. Most anomalodesmatan families, however, are small, comprising only a few genera most of which also contain a small number of species. Moreover, many anomalodesmatan taxa are highly specialised occupying narrow niches with restricted geographic distributions and most are, therefore, considered "rare". These small disparate families are all that remain of a sub-class which was abundant and widespread throughout the Palaeozoic and Mesozoic (Runnegar, 1974). Morton (1981) believes that the decline in abundance and distribution of this ancient group was due to increasing competition from the more generalist Heterodonta and Pteriomorpha which have become the predominant bivalve space occupiers in today's marine environment, for example the mytilid mussels on rocky shores and venerid and cardiid burrowers in soft sediments.

The relationships of the once successful anomalodesmatan bivalves to the small specialised families which survive are obscure, masked by apparently multiple examples of convergent and parallel evolution (Morton, 1981, 1985; Harper et al., 2000). Morton (1981, p. 53) has likened the extant members of the sub-class to "the outermost twigs of a tree of which most of the main branches, stem and roots have died out". The surviving twigs of the anomalodesmatan tree span a wide range of bivalve morphological diversity. In addition to burrowers and endo- and epibyssate taxa, there are those which build adventitious tubes (Clavagellidae), a range of species contained within the three (Cuspidariidae, Poromyidae, Verticordiidae), probably four (Parilimyidae), predatory families in the deep sea, and nestling (Lyonsiidae) and boring (Clavagellidae) taxa. Additionally, members of three families [species of *Clavagella* (Clavagellidae), *Myochama* (Myochamidae) and *Cleidothaerus* (Cleidothaeridae)] have evolved the ability to cement one of their valves to hard substrata. Cementation appears to have arisen independently in each of these families and, although small and less important than the better known pteriomorph cementers, e.g. oysters, they provide an interesting insight into the polyphyletic evolution of this habit in the Bivalvia (Yonge, 1979; Harper, 1991).

The process of cementation has been most intensively studied for ostreid oysters, where it commences early in ontogeny, e.g. 18 days after egg fertilization in *Ostrea edulis* Linnaeus (Waller, 1981). In the initial stages the pediveliger attaches to its substratum by means of a tanned mucopolysaccharide secreted by the foot and inner mantle fold (Cranfield, 1973a,b,c, 1975). Later, however, a crystalline calcium carbonate cement is developed between the periostracum and the substratum (Harper, 1992, 1997). The spherulitic nature of this cement resembles those secreted under dominantly physico-chemically controlled conditions rather than direct biotic control (Constanz, 1986).

Although there has been considerable research into the evolution of the cemented habit in the oysters, relatively little is known about how and why the cementing clades of Anomalodesmata have arisen. It is also interesting because the habit arose in anomalodesmatans during the late Cenozoic, compared to a late Palaeozoic/early Mesozoic origin for the larger and better known cementing clades (Harper, 1991). Morton (1984) suggested that clavagellids attach their left valve to an adventitious tube by secretions from arenophilic glands around the siphons. Certainly, arenophilic glands are widely used amongst non-cementing anomalodesmatans to attach small sand grains and other detritus to the external surface of their shells, e.g. *Lyonsia* (Prezant, 1979) and *Entodesma* (Morton, 1987). A recent study of attachment in *Myochama anomioides* has demonstrated the presence of a homogenous layer of cement between its shell and the substratum (Harper and Morton, 2000). This cement was composed largely of a non-mineralised material although there was evidence that it did have a calcareous component. Members of the Myochamidae lack arenophilic glands, but it seems probable that other mantle glands are responsible for the secretion of this cement. Despite concerted effort, however, that investigation detected no sign of these.

This study investigates cementation in another exclusively Australasian (both in Australia and New Zealand) anomalodesmatan family, the

Cleidothaeridae Hedley, 1918 (Pandoroidea). The family is monotypic, with *Cleidothaerus* Stutchbury, 1830 appearing first in the Lower Miocene (Beu and Maxwell, 1990). Although there are three recorded extant species, i.e., the type, *C. albidus* (Lamarck, 1819), *C. maorianus* (Finlay, 1827) and *C. plicifera* (Odhner, 1917), it is likely that the first two are synonymous (Morton, 1974) and the taxonomic validity of the latter is unclear.

*Cleidothaerus* cements by its robust, coiled, right valve to hard substrata in the intertidal zone and subtidally to depths of 40 m (Prezant, 1998). There is a pronounced tendency to attach to upward facing surfaces. The combination of the cemented habit and coiled morphology gives a convergent similarity to the heterodont Chamidae. The anatomies of the three putative species have been investigated (Hancock, 1853; Odhner, 1917; Morton, 1974), while Yonge and Morton (1980) described the ligament during their discussion of the pandoroid hinge. This study investigates *Cleidothaerus albidus* and concentrates on its cemented habit, specifically the timing of its attachment and the method by which it adheres.

## Materials and Methods
All available specimens of *Cleidothaerus albidus* in the collections of the Natural History Museum (London), the Australian Museum (Sydney) and the National Museum of Victoria (Melbourne) were examined. Additionally, a number of specimens, collected in 1994 by P.A. Hutchings and R. Bieler, from Fairlight, North Harbour, Sydney, where they were attached to a coarse sandstone (6-9 m depth) were also examined. Particular attention was paid to the 'lower' right valve. Although often obscured by both coiling and adherent substratum, 21 individuals showed details of the earliest part of the shell thereby allowing the size at which cementation occurred to be determined using vernier calipers (to the nearest 0.1 mm). One specimen, which showed a particularly clear nepioconch, free from abrasion and encrusters, was examined with a scanning electron microscope (JEOL 820), in order to study the larval shell.

The nature of the attachment was studied by selecting individuals still attached to their substrata. As noted by Harper (1992, p.39), attachment is best studied in individuals that have grown on an homogeneous substratum which is easy to distinguish and where the surface is not complicated by fouling epibionts. This is, obviously, best achieved by rearing the spat and allowing them to settle on man-made substrata such as glass. Although this has not been possible for this study, it was found that the coarse quartz-rich sandstones which are a frequent substratum, particularly of individuals collected around Sydney, do offer a reasonable alternative, although precise details are often complicated by the presence of bryozoans and coralline algae. Selected attached valves were set in epoxy resin and sectioned along the valve height, whilst others were made into petrological thin sections. The cut surfaces of both blocks and thin sections were polished with carborundum powder, etched with 1% hydrochloric acid for 25 seconds and then examined using SEM. Additionally, the undersides of the right valves of several individuals that had adhering substrata were also investigated by SEM. Elemental compositions were ascertained using elemental dispersive X-ray microanalysis (EDAX) with the LINK AN 10 000 system.

In order to examine anatomical detail, we studied three individuals of *Cleidothaerus albidus*. One specimen (approximately 40 mm in shell height) from the Abrolhos Islands, Western Australia (collected by J.D. Taylor and E.A. Glover), attached to the outside of a pectinid shell, was sectioned in its entirety at 6μm and alternate slides stained in either Ehrlich's haematoxylin and eosin or Masson's trichrome. The right and left mantle lobes only of two other specimens from the collections of the Australian Museum, C387327 from Exmouth Gulf, Western Australia and C387325 from Fraser Island, Queensland, with shell heights of 28 and 69 mm respectively, were also stained and sectioned in the same manner. The precise fixation history of these three specimens are unknown but it seems probable that they were initially fixed in formalin prior to preservation in ethanol. Comparisons were made between these sections and those of *C. maorianus* earlier reported upon by Morton (1974).
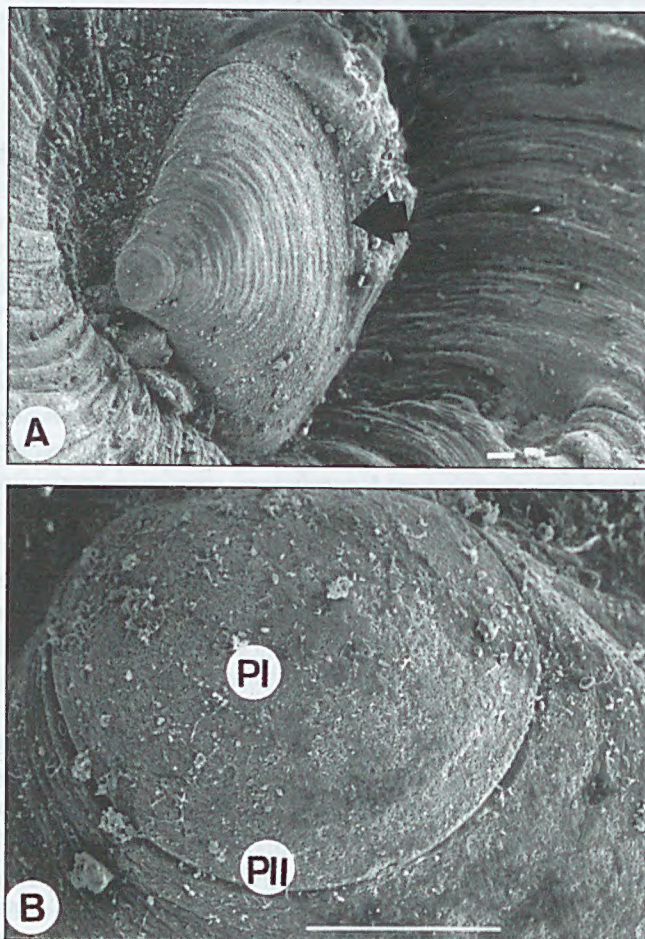


**Figure 1**
Scanning electron micrographs of the earliest part of the right valve of *Cleidothaerus albidus*. **A.** Pre-attachment valve, change to a cemented life habit at the arrow. Scale bar = 100 μm. **B.** Detail of the prodissoconch. Scale bar = 10 μm.
(For abbreviations see p.13).

## Results

Scanning electron micrographs of the earliest formed parts of the right valve of an individual of *Cleidothaerus albidus* revealed details of the prodissoconch and the pre-attachment part of the shell (Fig. 1A and B). The clearly defined, unornamented prodissoconch I (height = 175 μm, length = 210 μm) is fringed by a narrow (25 μm) band of the prodissonch II which has commarginal growth lines (Fig. 1B). The transition between the prodissoconch and dissoconch is also clearly defined. The early portion of the dissoconch is also ornamented with commarginal ridges and furrows, and has a hexagonal surface pattern. It seems likely, from similarity of scale, that this hexagonal pattern reflects the ends of the underlying prismatic shell layer.

The onset of cementation occurs within the dissoconch stage, i.e. much later than oysters (Yonge, 1979) and is marked clearly by a disruption of the idiomorphic shell growth to take up substratal irregularities (Fig. 1A), the most prominent of which are taken up as xenomorphic ornament on the unattached left valve. The mean shell height at which cementation occurs in *Cleidothaerus albidus* was measured to be 1.2 mm (n = 21; sn-1 = 0.2). There is no sign of a byssal notch.

Individuals of *Cleidothaerus albidus* attach to the substratum by the anterior face of the right valve. In most cases the attachment scar is extensive although in some individuals areas of the valve are elevated from the substratum. These non-cemented areas retain idiomorphic shell ornament and show no signs of cement adhering to the outside of the periostracum.

## Shell microstructure

As recorded by Taylor et al. (1973), the calcareous part of the valves of *Cleidothaerus albidus* is wholly aragonitic, the bulk of which comprises nacre but with a thin (up to 20 μm) outer prismatic layer which is often not easily discernible (Fig. 2A). This study has also revealed the presence of patches of opaque, white material within the nacre. Investigation by SEM showed that these patches display an open, bladed, crystal texture, with individual blades aligned perpendicular to the growth surface (Fig. 2B). This microstructure is strikingly similar to the 'chalky deposits' recognised in a variety of oyster taxa (Korringa, 1951; Chinzei and Seilacher, 1993; Malchus, 1998).

The external surface of the shell is covered by a red-brown periostracum, which is persistent over all but the most abraded regions. The surface of the periostracum is wrinkled and there was no evidence of either the calcareous spicules or spinules which have been observed in a wide range of other anomalodesmatan taxa (Carter and Aller, 1975). Investigation of the inner surface of the periostracum did not yield any sign of the well-formed hexagonal craters, which correspond to pyramidal bosses on the outside of the shell, reported upon for *Myochama anomioides* by Harper and Morton (2000). SEM of sections through the periostracum covering non-cemented parts of the valve revealed that it has an average thickness of 15 μm, but displays some variability. There was no evidence either of layering or other internal structure using SEM, however, as described later, stained histological sections showed it to be bi-layered.
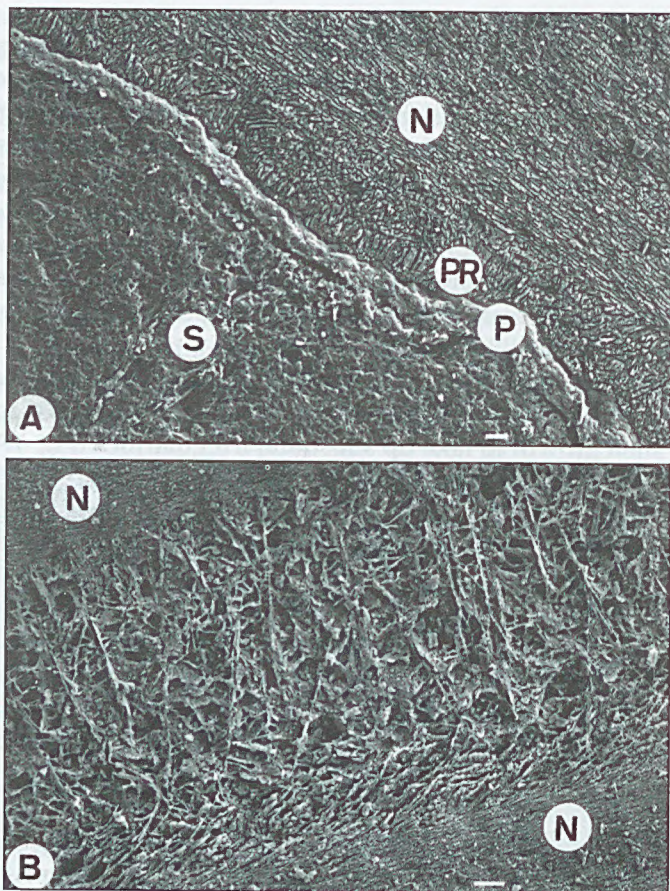
**Figure 2**
Scanning electron micrographs of the microstructure of the right valve of *Cleidothaerus albidus*. **A.** Shell microstructure of the right valve adhering to a sandstone substratum. **B.** Chalky microstructure within the nacreous layer. Both scale bars = 10 µm. (For abbreviations see p.13)

## Cement

During the cementing phase, the anterior face of the right valve follows closely topographic irregularities in the substratum. Figure 3A shows the extent to which the morphology of individual sand grains is reflected in the outer prismatic shell layer. The implication of this is that the periostracal sheet is capable of intricate folding and is applied closely to the substratum. There is no sign that either the thickness or structure of the periostracum is different during cementation as it is in *Etheria elliptica* (Grégoire, 1974) and *Myochama anomioides* (Harper and Morton, 2000). Detailed investigation of the association between the periostracum and substratum shows that it hugs the surface of the sand grains with no obvious material between (Fig. 3B). There are, however, 'valleys' in the substratum, for example, between adjacent sand grains, that are too acute for the periostracum to follow. In these instances, the periostracum bridges the 'valley' and there is an accumulation of cement below it.
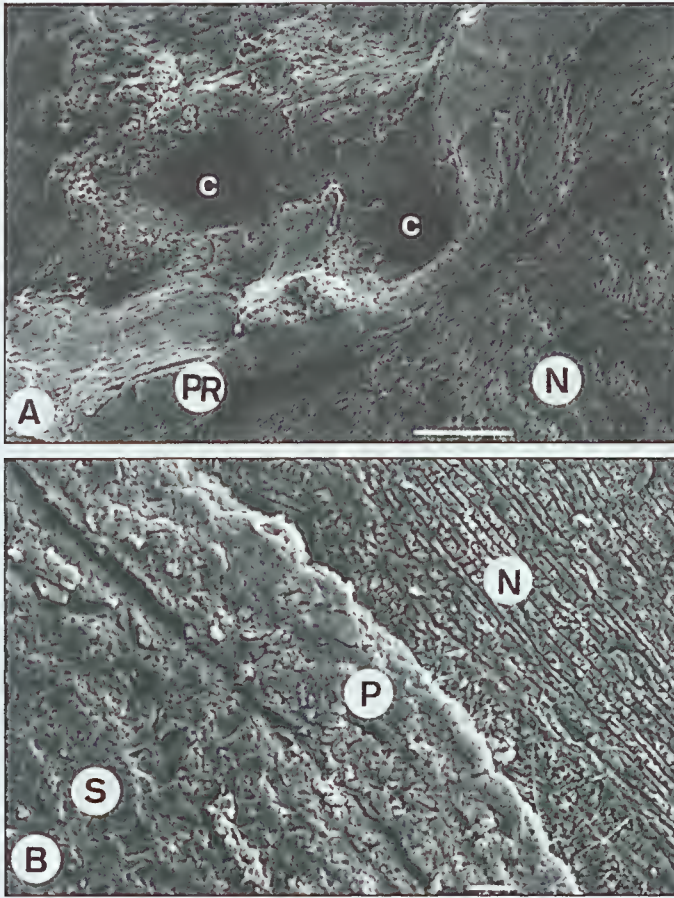
**Figure 3**
Scanning electron micrographs of attachment of *Cleidothaerus albidus*. **A.** Attachment scar viewed from the underneath of a specimen that had been prised away from its substratum, revealing craters embossed into the prismatic shell layer where the valve has moulded over individual sand grains. Scale bar = 100 μm. **B.** Close up of the relationship between the periostracum and a sand grain with obvious intervening cement layer between them. Scale bar = 10 μm. (For abbreviations see p.13).

The extra-periostracal nature of the cement is confirmed by the presence of foreign material trapped within it, some of it recognizable as fragments of molluscan shell (Fig. 4A). Most of the cement has an open, spongey, texture (Fig. 4B), although some of it is composed of fine sheets (Fig. 4D) not dissimilar to the mucous ones illustrated by Taylor et al. (1999, figs 6A, C and D). It is not clear whether the spongey areas contained scattered crystals that have been lost during acid preparation of the specimens. EDAX analysis of areas free of obvious foreign inclusions, and distant from adjacent shell material, revealed that calcium (nor magnesium or strontium) was not present in the spongey areas of cement. This suggests that these areas are not mineralised, although it may be true that small, scattered crystals could have been removed during acid etching. There are, however, occasional areas of spherulitic crystal growth

(Fig. 4C) which are not obviously either trapped inclusions or parts of epibionts overgrown by the cleidothaerid. The crystals associated with the spherulites are accicular, up to 15 μm long and < 1 μm wide. Their morphology suggests that they are probably aragonitic, but the minute volumes involved prohibit the extraction of material for X-ray diffraction analysis. The growth of spherulites which nucleate on the bounding surfaces of the void between the shell and the substratum are reminiscent both of diagenetic growth of minerals in sedimentary rocks (e.g. Bathurst, 1975) and oyster cements (Harper, 1992, 1997).
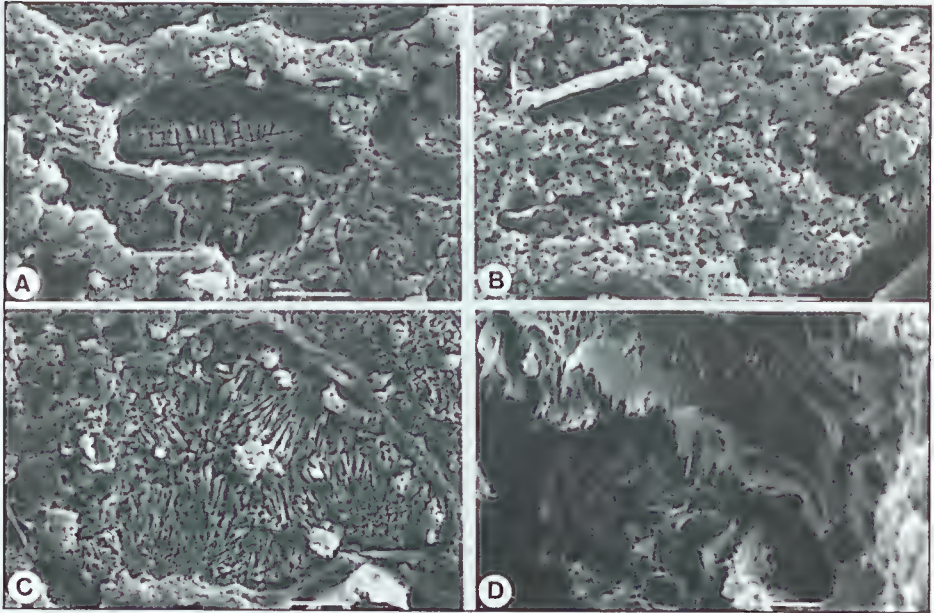


**Figure 4**
Scanning electron micrographs of the cement of *Cleidothaerus albidus*. **A.** Fragment of prismato-nacreous mollusc shell trapped within the cement. **B.** Homogeneous areas of cement displaying a spongey texture. **C.** Spherulitic growth of cement crystals. **D.** ?mucous sheets. All scale bars = 10 μm.

## Mantle margin

The mantle margin of *Cleidothaerus maorianus* has been described by Morton (1974) and shown to comprise the usual three folds. The situation is the same in *C. albidus* and is illustrated in transverse section in Figure 5A. Ventral mantle fusion is of the inner fold and the inner surfaces of the middle folds (FIMF), i.e. type B (Yonge, 1957). [Previously, Morton (1974) had said that such fusion in *Cleidothaerus maorianus* was of type A (inner folds only), but this is incorrect and *Cleidothaerus* thus more closely matches other anomalodesmatans in terms of the degree of mantle fusion (Harper et al. 2000).

The rather swollen ventral mantle margins mainly comprise outer folds which are divided into, larger outer (OMF(1)) and, smaller inner components (OMF(2)). Each mantle lobe contains a pallial nerve (PN) and a small haemocoel (HA). The pallial retractor muscle is divided into two components (PRM1 and PRM 2) which penetrate the inner and outer components of the outer mantle

folds, respectively. In the two smaller specimens (from the Abrolhos Islands and Exmouth Gulf) examined, a large pallial gland (PG) occupies about one half of the dorso-ventral surface of the inner surface of the anterior mantle of the right mantle lobe, above the pedal retractor muscles (and thus the pallial line). There is no similar gland in either the right mantle lobe of the larger specimen examined nor the left mantle lobe of any of the specimens. Morton (1974) did not describe any such gland in *C. maorianus* nor were any apparent when we re-investigated those sections. The gland is shown in greater detail in Figure 5B. The outer surface of the mantle (OE) comprises a cuboidal epithelium ~ 4µm tall. It connects by transverse fibres (TF) with the inner epithelium across a haemocoel between 20-30 µm wide. The inner surface of the mantle comprises cells ~ 100µm tall that can be divided into two types, both secretory. The first comprises cells with basal nuclei (4µm in diameter) which contain a loosely vacuolated epithelium that is eosinophilic and stains light blue in Masson's trichrome (SC1). It is probably producing mucus. Interspersed with these cells, however, are equally long secretory cells (SC2) which have apical nuclei (3µm in diameter). This cell type is full of small, basiphilic, spherical granules that stain dark blue in Masson's trichrome. There are no arenophilic glands in the mantle margin of either lobe.
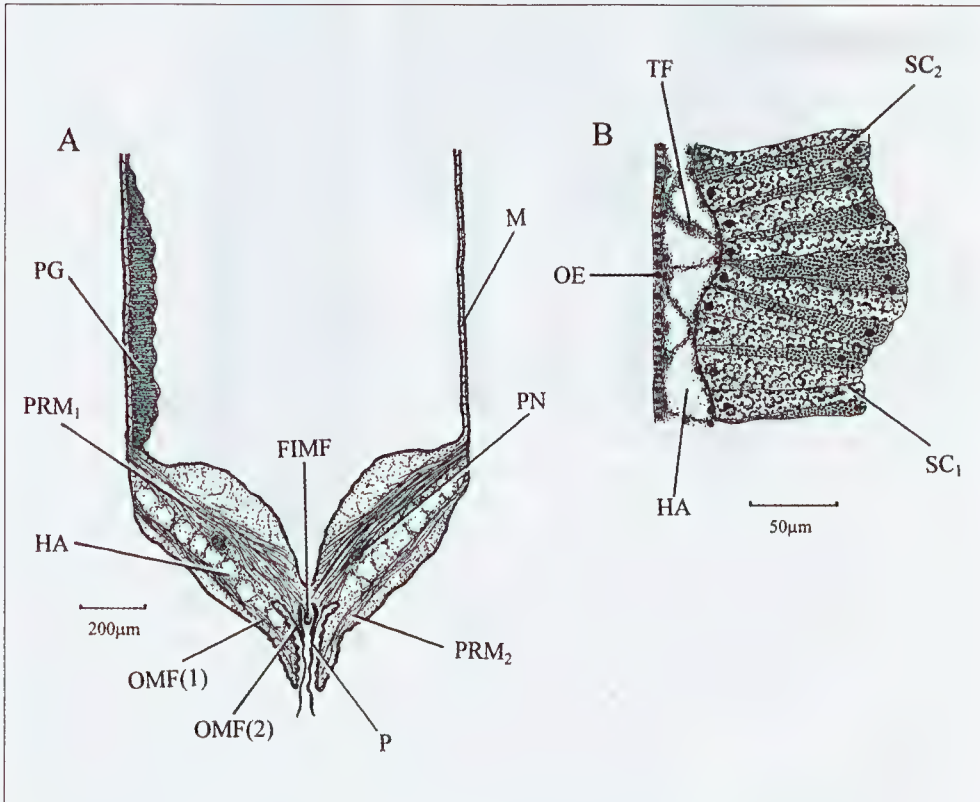


**Figure 5**
*Cleidothaerus albidus.* **A.** A transverse section through the mantle margin, showing the pallial gland on the right mantle lobe only above the pallial line. **B.** detail of the pallial gland. (For abbreviations see p.13).

**The periostracum**
As noted earlier, the periostracum of *Cleidothaerus albidus* when seen in transverse section (Fig. 6) comprises two layers, i.e. a yellow, red-staining, outer layer (OP(R), OP(L)) and a blue staining and, therefore, mucoid, thicker, inner layer (IP(R),IP(L)). Since the outer mantle fold is divided into two components, the outer layer of periostracum is secreted in the inner periostracal groove (PEG2) and is thin (1-2 μm) over the right lobe, that is over the cemented valve (OP(R)), but is up to five times thicker (~10 μm) over the unattached left valve (OP(L)).
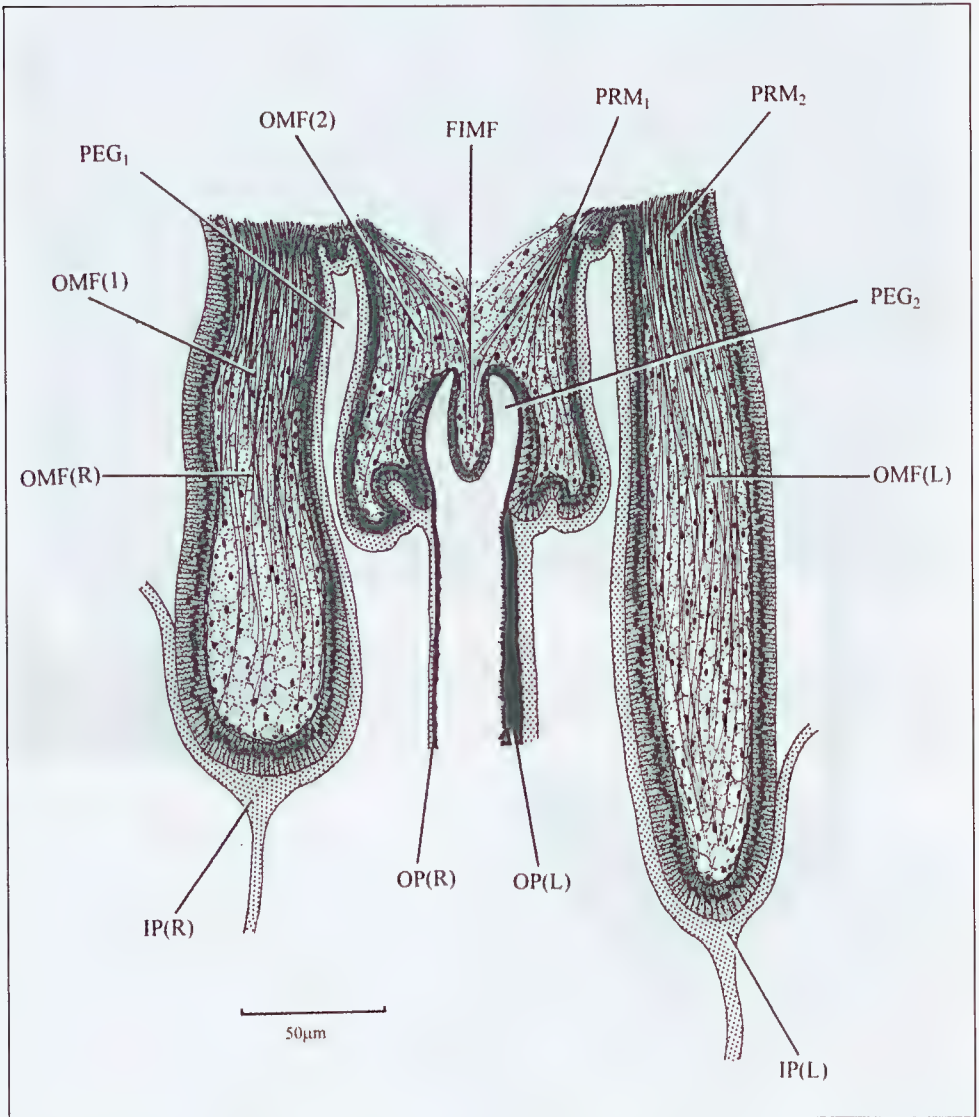


**Figure 6**
*Cleidothaerus albidus*. A transverse section through the ventral mantle margin showing the degree of left and right fusion and the organization of the periostracum.
(For abbreviations see p.13).

The inner layer of the periostracum is of equal thickness on both the left (IP(L)) and right valves (IP(R)) and is secreted against the template of the outer periostracum largely in the outer component of the periostracal groove (PEG1) and is laid down, therefore, by the majority of the inner surface of the outer mantle fold. It can be formed into a light fringe that presumably helps in sealing the shell margin when adducted. If, however, the inner periostracum is of similar structure to that of *Myochama anomioides* (Harper and Morton, 2000) it is likely that it has a much more liquid structure than the outer layer and over which the pallial cement will be secreted to bond the right valve to the substratum. It is possibly significant that the outer periostracum of the 'free' left valve is at least five times thicker than that of the 'attached' right valve.

## Discussion

Like most Anomalodesmata, members of the Cleidothaeridae are simultaneous hermaphrodites (Morton, 1974). Comparison with the data provided by Ockelman (1965) and Berkman et al. (1991) suggests that the large size of prodissoconch I and the high prodissoconch I/II ratio of *Cleidothaerus albidus* recorded here, indicates a lecithotrophic larval phase. The presence of prodissoconch II suggests that brooding does not take place. Morton (1974) observed *Cleidothaerus maorianus* in aquaria spawning during the austral winter, producing larvae that settled at lengths of 0.25 mm, i.e. at a size comparable with the commencement of the dissoconch stage measured in this study. However, cementation does not proceed until the shell has at least quadrupled in size suggesting that, despite the lack of any morphological evidence, e.g. the presence of a byssal notch, the pre-cementation phase is stabilised by a few byssal threads, as are most larval bivalves (Yonge, 1962).

Adhesion between two bodies can only be achieved when they are brought close enough to be held together by electromagnetic interaction (De Bruyne, 1962). This is only possible when the two surfaces are perfectly smooth and such a condition is usually attained when an adhesive fluid is introduced between them. In his study of *Cleidothaerus maorianus* from New Zealand, Morton (1974) was unable to detect glands, pallial or otherwise, that could secrete the attaching cement and suggested, therefore, that attachment must occur by way of a sticky layer of outer periostracum. In this study we have shown that for areas of the substratum which have no pronounced microtopography the periostracum is laid down directly on to it with no obvious modification or need for adhesive. However, where there are distinct notches and valleys within the surface of the substratum, in this case between two grains in the coarse sandstone we have identified the accumulation of cement between the attached valve, i.e. the periostracum, and its substratum. Most of this cement appears unmineralised and is similar to that identified in *Myochama anomioides* (Harper and Morton, 2000). There are, however, scattered pockets within the cement where mineralisation has occurred.

The source of the cement is of obvious interest. The outer layer of periostracum is a solid structure and there is no means for a secretion to pass through it. Instead, it seems likely that the cement is produced by the mantle and applied to the outside of the periostracum. More specifically, we suspect

that the large pallial gland identified in this study may be responsible, since it is restricted to the anterior portion of the right mantle lobe only. It seems logical that the secretion from the right pallial gland exits the mantle cavity via the pedal gape. Since both valves are here in close apposition to the substratum, not only would any internal secretion naturally drain down in this direction but would quickly encounter the anterior margin of the valve, or at least the periostracum covering it, and thereby help to cement any new shell surface being secreted. Cement is only likely to accumulate in topographic hollows within the surface of the substratum.

Failure to locate these cement-secreting glands in *Cleidothaerus maorianus* (Morton, 1974) and in one, the larger, specimen of *C. albidus* examined in this study appears problematic. Harper and Morton (2000) also failed to locate the glands responsible for the similar cement in *Myochama anomioides*. It is possible that, because none of these individuals was cementing actively at the time of death, the glands may not be developed. This is certainly true of the individuals of *M. anomioides* where the ventral valve margins had lifted away from the substratum. The ventral valve margins of the larger specimens of *C. albidus* are not available for study and so it is not possible to state emphatically that it either was or was not cementing at the time of death. Further investigation is obviously required to test this hypothesis.

The form of the cement is interesting and there are similarities with observations on the remarkable arenaceous coatings on the outside of two veneroid bivalves of the genera *Granicorium* and *Samarangia* (Taylor et al., 1999). These authors showed that sand grains were attached to one another and to the shell by a crystalline aragonitic cement, with a texture strikingly similar to early diagenetic marine cements. The crystals had grown in mucus secreted at the ventral valve edge, probably mediated by the action of bacteria, which were also visible in their published micrographs. It seems likely that mucus secreted between the periostracum of *Cleidothaerus albidus* and the substratum forms a similar environment for the growth of a cement. Where this process is advanced, spherulitic areas of cement are developed. Fixation of our specimens is probably not good enough to determine the presence of bacteria associated with the cement.

It is of interest to consider the evolution of cementation within the Pandoroidea. It seems that both *Cleidothaerus* and *Myochama* use similar methods of cementation. There is no doubt, however, that they are not sister-taxa; *Myochama* clearly evolved from the geologically older, free-living, co-familial *Myadora* and it is clear, therefore, that the cemented habit has evolved twice within the Pandoroidea. Since both clades have similar first appearance dates in the fossil record (*Cleidothaerus* in the Lower Miocene and *Myochama* in the Upper Oligocene [Beu and Maxwell, 1990]) and overlapping geographic distributions, it is tempting to speculate that the cemented habit arose in response to the same selection pressures. This seems unlikely, however, since *Myochama*, although capable of cementing to open rock surfaces, will only do so after considerable delay, presumably when the preferred substratum, i.e. the posterior end of living infaunal bivalves, are not available (Harper and Morton, 2000).

## Acknowledgements

## Key to abbreviations used in the figures

| | |
|---|---|
| C | Craters where individual sand grains are reflected on the cemented scar. |
| FIMF | Fused inner and middle (inner surfaces) mantle folds |
| HA | Haemocoel |
| IP(L) | Inner layer of periostracum (left mantle lobe) |
| IP(R) | Inner layer of periostracum (right mantle lobe) |
| M | Mantle |
| N | Nacre |
| OE | Outer epithelium |
| OMF(L) | Left outer mantle fold |
| OMF(R) | Right outer mantle fold |
| OMF(1) | Outer component of the outer mantle fold |
| OMF(2) | Inner component of the outer mantle fold |
| OP(L) | Outer layer of periostracum (left valve) |
| OP(R) | Outer layer of periostracum (right valve) |
| P | Periostracum |
| PI | Prodissoconch I |
| PII | Prodissoconch II |
| PR | Prismatic outer shell layer |
| PEG(1) | Outer element of the periostracal groove |
| PEG(2) | Inner element of the periostracal groove |
| PN | Pallial nerve |
| PRM(1) | Inner element of the pallial retractor muscles |
| PRM(2) | Outer element of the pallial retractor muscles |
| S | Sandstone substratum |
| SC1 | Secretory cell Type 1 |
| SC2 | Secretory cell Type 2 |
| TF | Transverse fibres |

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# Freshwater snails of the genus *Gyraulus* (Planorbidae) in Australia: taxa of the mainland

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## Abstract

Species of *Gyraulus* (Basommatophora: Planorbidae) are among the most widely distributed and abundant of freshwater snails in Australia Twenty species-group taxa have been described previously from shells collected on the Australian mainland, of which *G. ordessus* (Iredale) is the type species of *Glyptanisus* Iredale, 1943. In addition 3 species described from Tasmanian materials have been reported from the south-eastern mainland. Taxa found in mainland Australia are here revised according to morphological observations on type materials, other empty shells collected during the 19thC and early 20thC, and about 8300 alcohol-preserved whole snails from 258 localities, mostly collected during the last 30 years. Illustrations are provided here for the first time for 8 species-group taxa named by Iredale (1943): *hesperus, idenus, leonatus, metaurus, ordesus, pelorius, speranus* and *stabilis*.

Observations on the shell and body (pigmentation, kidney, intestinal loop and genital organs) suggest that the previously reported *Gyraulus* fauna of mainland Australia may represent no more than 7 valid species, 6 of *Gyraulus* sensu stricto and 1 of *Gyraulus (Pygmanisus)*. A third subgenus, *G. (Plananisus)* Iredale, 1943, should perhaps be recognised for *G. meridionalis*, currently placed in *Gyraulus* s.s., but which has a distinctive form of copulatory organ. Since *G. ordessus* is treated as a junior synonym of *G. (G.) waterhousei*, Iredale's *Glyptanisus* is a synonym of *Gyraulus* s.s.

Additions made here to the Australian fauna are *G. edgbastonensis* sp. n., known only from a few artesian springs in western Queensland, and *G. chinensis* Dunker, 1848, for which the present record in eastern South Australia probably results from introduction through human agency.

The presence in south-eastern mainland Australia of species that live also in Tasmania was confirmed by examination of soft parts. *G. meridionalis* (syn. *tasmanicus*) is present in southern Victoria and eastern South Australia, but seems to be much less widely distributed than reported previously on the basis of identification from the shell alone. *G. (Pygmanisus) scottianus* (including as synonyms the mainland taxa *leonatus* and *pelorius*) is a little more widespread, extending into southern Queensland.

During development of the penis in Australian species of *Gyraulus* s.s., the cellular lining of the distal end of the penis sheath apparently contributes material for the chitinisation of the penial stylet.

Zoogeographical relationships of the Australian fauna of *Gyraulus* appear to lie entirely with SE Asia, though the distinctiveness of the Australian fauna, especially in the soft parts, suggests a long history of independent evolution. Since all indigenous Australian taxa have non-patchy mantle pigmentation, whereas all SE Asian taxa are patchy, it would seem that the non-patchy character-state appeared early in the ancestry of the Australian fauna, preceding the development of other distinctive anatomical characters. Morphological data should be supplemented by molecular analysis, in order to improve understanding of species-boundaries within *Gyraulus* s. s. in Australia and to clarify relationships with the species of SE Asia.

## Introduction

This is the second part of a revision of the genus-group and species-group taxa of *Gyraulus* (Planorbidae) found in Australia, according to morphology of the shell and anatomy. Type material, all dry shells, of almost every named taxon has been examined. Anatomical data were obtained from a large amount of

more recently collected material, kindly provided by individuals and institutions in Australia, most notably the Australian Museum, Sydney. The first part of this study (Brown, 1998) was devoted to the taxa of Tasmania, whose names pre-date all but one of the many names founded on shells collected on the mainland.

**Table 1.**
Classifications of *Gyraulus* found in Australia, according to Smith (1992) and present paper. Arrangement is in the alphabetical order of those species recognised as distinct.

| Smith, 1992 | Present paper |
|---|---|
| *Gyraulus* Charpentier, 1837 | Subgenus *Gyraulus* sensu stricto |
| *Gyraulus coranus* (Iredale, 1943) | G. *atkinsoni* (Johnston, 1879) |
|   *Planorbis fragilis* Tate, 1896 | G. *chinensis* (Dunker, 1848) |
| G. *essingtonensis* (Smith, 1883) | G. *edgbastonensis* sp. n. |
| G. *gilberti* (Dunker, 1848) | G. *essingtonensis* (Smith, 1883) |
|   *Planorbis fragilis* Smith, 1883 |   *Glyptanisus coranus* Iredale, 1943 syn. n. |
|   *P. brazieri* Clessin, 1885, new | G. *gilberti* (Dunker, 1848) |
|     name for *fragilis* Smith |   *Planorbis brazieri* Clessin, 1885 |
|   *Glyptanisus idemus* Iredale, 1943 |   *P. daemeli* Clessin, 1885 comb. n., syn. n. |
| G. *hesperus* (Iredale, 1943) |   *P. fragilis* Smith, 1883 |
| G. *isingi* (Cotton & Godfrey, 1932) |   *Glyptanisus idenus* Iredale, 1943 |
| G. *macquariensis* (Smith, 1883) |   *Planorbis macquariensis* Smith, 1883, syn. n. |
| G. *meridionalis* (Brazier, 1875) |   *Planorbis planissimus* Clessin, 1885, comb. n., |
| G. *stabilis* (Iredale, 1943) |     syn. n. |
| G. *tasmanicus* (Tenison-Woods, 1876) |   *Glyptanisus speranus* Iredale, 1943, syn. n. |
| G. *waterhousei* (Clessin, 1885) |   *Gl. stabilis* Iredale, 1943, syn. n. |
|   *Glyptanisus caroli* Iredale, 1943 |   *Gyraulus* sp. Shea, 1995 |
|   *Gl. ordessus* Iredale, 1943 | G. *hesperus* (Iredale, 1943) |
|   *Gl. metaurus* Iredale, 1943 | G. *isingi* (Cotton & Godfrey, 1932) |
|   *Gl. speranus* Iredale, 1943 |   *Glyptanisus caroli* Iredale, 1943, syn. n. |
| |   *Pygmanisus parvus* Cotton, 1943, comb. n., |
| *Pygmanisus* Iredale, 1943 |     syn. n. |
| *Pygmanisus leonatus* Iredale, 1943 | G. *meridionalis* (Brazier, 1875) |
|   *P. pelorius* Iredale, 1943 |   *Planorbis tasmanicus* Tenison-Woods, 1876 |
| *P. parvus* Cotton, 1943 | G. *mienanus* Brown, 1998 |
| *P. scottianus* (Johnston, 1879) |   *Planorbis cathcarti* Petterd, nomen nudum |
| | G. *waterhousei* Clessin (1885) |
| Species *incertae cedis* |   *Glyptanisus metaurus* Iredale, 1943 |
| *Planorbis atkinsoni* Johnston, 1879 |   *Gl. ordessus* Iredale, 1943 |
| *P. cathcarti* Petterd, 1889 | |
| *P. daemeli* Clessin, 1885 | |
| *P. planissimus* Clessin, 1885 | Subgenus *Gyraulus (Pygmanisus)* |
| | G. *(P.) scottianus* Johnston, 1879 |
| |   *Pygmanisus leonatus* Iredale, 1943, syn. n. |
| |   *P. pelorius* Iredale, 1943, syn. n. |

*Gyraulus* comprises small freshwater snails, usually planispiral (in some ancient lakes pseudodextral with a spire), distributed worldwide except for South America south of Venezuela. The most comprehensive taxonomic studies of recent decades have been for the species of Africa (Brown & Van Eeden, 1969), Europe and Asia (Meier-Brook, 1983) and Tasmania (Brown, 1998). Penial morphology, particularly a dagger-like stylet, distinguishes *Gyraulus* from certain other planorbid genera which are similar in the shell, but have a very differently constructed penis; such snails (*Ceratophallus* and *Afrogyrus*) are apparently restricted to the Afrotropical region. One impetus to the study of Australian planorbids with this form of shell has been to find out whether any of these Afrotropical planorbids is present also in Australia.

Twenty-five species-group taxa named from Australian materials and which are candidates for inclusion in *Gyraulus* were cited by Iredale (1943) under *Glyptanisus, Plananisus* and *Pygmanisus*. All of these and also *Pygmanisus parvus* Cotton, 1943 were known for many years only from empty shells. The first anatomical observations were not made until the 1970s (Brown, 1981; Meier-Brook, 1983, pp 97-98); all copulatory organs examined had the penial stylet characteristic of *Gyraulus*. Smith & Kershaw (1979, 1981) recognised only 3 distinct species of *Gyraulus* in SE Australia, while Smith (1992) listed a total 13 species for Australia and 4 additional taxa with *Gyraulus*-like shells as incertae cedis (Table 1).

The number of biologically distinct species of *Gyraulus* living on the mainland of Australia seems likely, according to morphological observations, to be far fewer than the total of named species-group taxa. Original descriptions are mostly brief and the shell characters given often appear trivial. Unfortunately, most features of both the shell and anatomy, from which taxonomic characters have been taken for characterising species in this genus, vary continuously, making difficult the separation of morphological taxa. Yet, the possibility remains that sibling species exist, whose detection may have to await the availability of genetic data.

The primary aim of this study was to establish more clearly the characteristics of all the species-group taxa of *Gyraulus* named from shells collected in mainland Australia, by examining type material and, especially for data about soft parts, a large number of specimens collected in recent decades. This was a necessary preliminary to comparing the fauna of mainland Australia with those of Tasmania and of SE Asia. It is desirable that morphological data should be assessed in the light of direct evidence of genetic affinities obtainable by allozyme electrophoresis and molecular sequencing. The application of such techniques may perhaps be encouraged by the present attempt to clarify the classical taxonomy of these snails.

## Materials and Procedure of Study

Dry shells being either type material or early-collected representative specimens of all the species-group taxa referable to *Gyraulus* described from specimens collected in Australia were examined. Extensive other recently collected material was examined, comprising about 8300 alcohol-preserved snails in about 260 collectors' samples, in the collections of the Australian Museum Sydney and the
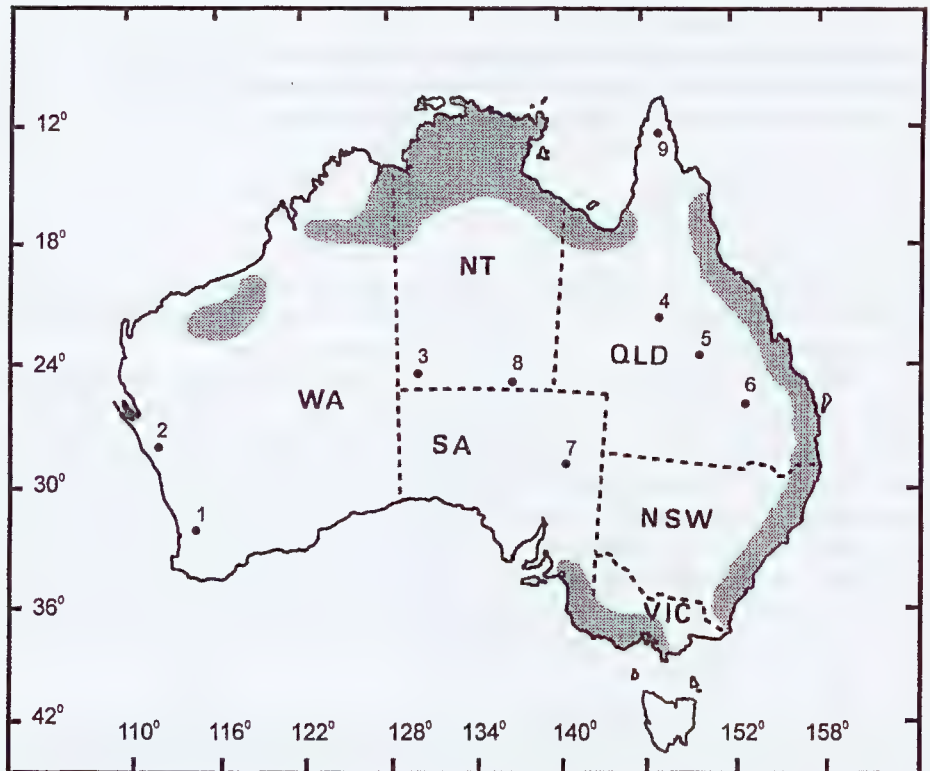
**Figure 1.**
Areas of origin (shaded) and isolated localities (numbered) for material of *Gyraulus* from Australia reported on in this paper. 1, Perth. 2, Murchison River. 3, George Gills Range. 4, Julia Creek. 5, Barcaldine area. 6, Carnarvon Gorge National Park. 7, North Flinders Ranges (Moro Gorge and Weetootla Spring). 8, River Finke area. 9, Cape York (type locality for *Planorbis daemeli* and *P. planissimus*) [all other type localities lie within one or other of the shaded areas].

South Australian Museum, Adelaide. Areas of origin are shown in Fig. 1 and details of collecting sites are given in the accounts of species-group taxa. The study proceeded in two phases, because the receipt of the bulk of the material was received in two batches, both from The Australian Museum, Sydney, separated by an interval of 13 years. The first batch, received in 1985, comprised 125 samples of *Gyraulus*, mostly with Registration Numbers in the 144-series, representing all the mainland states and particularly NT, QLD and NSW. For all of these samples, measurements were taken (see Shell below) of the largest intact shell. These data were used to compare the overall variation in this material, which represented a large geographical area, with the variation displayed by type material of the numerous named taxa (Figs 4, 6). For some of these samples, shells from wide size ranges were drawn and measured, in order to assess allometric changes in form. At least one copulatory organ from many of these samples was mounted as a permanent preparation. The second batch of material, received in 1998, comprised 112 samples, mostly with Registration Numbers in the 345-series, from all the states except NSW. These snails from the

northern states were identified by comparison with the material identified previously, and for most of these samples the copulatory organ was examined only externally. The samples from SA and VIC in this batch proved of particular interest as they included snails that could be identified from their copulatory organ as *Gyraulus meridionalis* of Tasmania.

Acronyms and abbreviations are:

|  |  |  |
|---|---|---|
| AMS | - | Australian Museum, Sydney (all Registration Numbers have the prefix 'C') |
| BMNH | - | Natural History Museum, London |
| E | - | east, eastern |
| km | - | kilometre |
| N | - | north, northern |
| NMV | - | Museum of Victoria, Melbourne |
| NSW | - | New South Wales |
| NT | - | Northern Territory |
| p./ pp. | - | page/pages |
| pl./pls. | - | plate/plates |
| QLD | - | Queensland |
| S | - | south, southern |
| SA | - | South Australia |
| Sp./spp | - | species |
| SAMA | - | South Australian Museum, Adelaide |
| VIC | - | Victoria |
| W | - | west, western |
| WA | - | Western Australia |
| ZMB | - | Zoologische Museum der Humboldt Universiteit, Berlin |

## Methods
### Shell
Preparation techniques, descriptive terms and measurements were described by Brown (1998). All measurements were taken from drawings made using the Wild M5 binocular microscope with camera lucida attachment. Number of whorls was measured to the nearest 0.01 of a whorl (Fig. 2A). For reasons explained by Brown (1998), the profile (peripheral) view of the shell is illustrated here as pseudodextral, i.e. with the aperture on the observer's righthand side (Fig. 2B), and the flat sides of the shell are termed left (Fig. 2A) and right. The Depression Angle measured in the earlier study was not employed here, as its discriminatory value appeared no better than that of the Flatness Index (a/b) (Fig. 2B) used by Brown & Van Eeden (1969) and Meier-Brook (1983).

### Anatomy
Anatomical features and their taxonomic characters are reviewed in Meier-Brook (1983) and Brown (1998). For many specimens, data were recorded for pigmentation, kidney, intestine, copulatory organ, prostate gland, bursa copulatrix, seminal vesicle and ovotestis. Radulae were prepared from only a few specimens, since the radula has proved of little taxonomic value in my experience, confirmed by Meier-Brook (1983). All dissections were of preserved animals, some well extended but most retracted to a varying degree, up to one-

third of the last whorl. Copulatory organ and kidney were stained in safranin and mounted in Canada balsam. Radulae were stained in Mallory's stain (Brown, 1980, p. 443), mounted in Canada balsam and examined under the optical microscope.
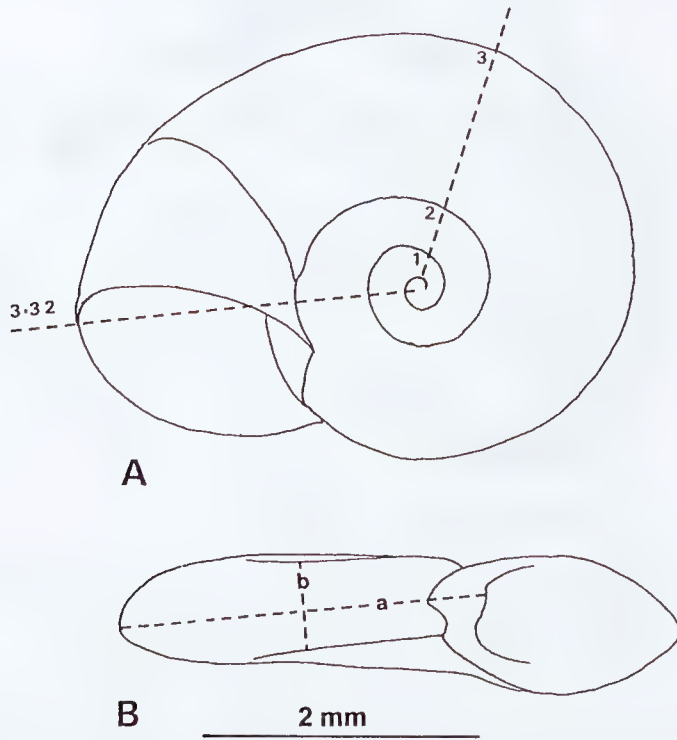


**Figure 2.**
**A**, Left side of *Gyraulus*, showing method of measuring the number of whorls (after Brown, 1998). First the completed whorls were counted along an axis fitted by eye to the proximal curve of the protoconch in a drawing of the shell, made by camera lucida. A protractor placed on the drawing was then used to determine the extent of any uncompleted whorl, measuring to the nearest 0.01 whorl up to the outermost point on the apertural lip. **B**, Profile view of shell, showing the dimensions (a) and (b) , which were used to calculate the flatness index (a/b). (a) was measured along a line constructed to span the greatest diameter of the last whorl less the aperture; (b) is the height of the whorl perpendicular to the mid-point of (a).

## Classification at genus-group level

Apparently all of the small  (shell diameter less than 6 mm) species of Planorbidae found in Australia belong either to *Helicorbis* (shell lentiform and sometimes septate, penis lacking stylet) or to *Gyraulus* (shell discoid, never septate, of less than 5 whorls, penis with chitinous stylet; Brown & Van Eeden, 1969 and Meier-Brook, 1983). Seven subgeneric divisions in the World fauna of *Gyraulus* were recognised by Meier-Brook (1983).
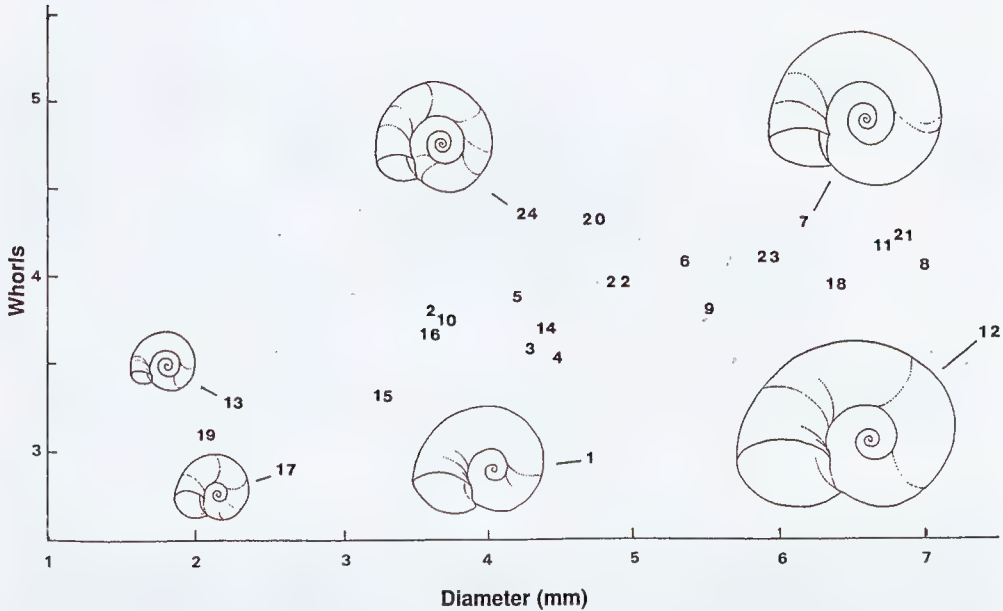
**Figure 3.**
Relationship between number of whorls and shell diameter for types, or representative specimens, of species of *Gyraulus* from mainland Australia. Each taxon is represented by one or two shells. Note the isolated position of *G. edgbastonensis* sp. n., caused by its completing only about 3 rapidly increasing whorls at the large diameter of nearly 5 mm. **1.** *G. (Gyraulus) edgbastonensis* sp. nov. Large paratype (AMS 144985). **2.** *G. (G. ) caroli* (Iredale). Holotype (NMV F549). **3.** *G. (G.) coranus* (Iredale). Probable syntype (AMS 002153). See also no. 8. **4.** *G. (G.) daemeli* (Clessin). Lectotype (ZMB 13223a). **5.** *G. (G.) essingtonensis* (Smith). Syntype (BMNH 41.10.12.157-167). **6.** *G. (G.) essingtonensis* (Smith). BMNH 45.5.14.32-39. Possibly from the same series as the syntypes. **7.** *G. (G.) fragilis* (Smith = *brazieri* Clessin). BMNH 79.5.21.743-8. Apparently from the same series as the types. **8.** *G. (G.) fragilis* (Smith = *coranus* Iredale). Syntype (SAMA D5130). See also no. 3. **9.** *G. (G.) gilberti* (Dunker). Syntype (BMNH 1969143). **10.** *G. (G.) hesperus* (Iredale). Syntype (AMS 100594). **11.** *G. (G.) idenus* (Iredale). Syntype (AMS 033768). **12.** *G. (G.) isingi* (Cotton & Godfrey). Syntype (SAMA D10603, 'holotype'). **13.** *G. (Pygmanisus) leonatus* (Iredale). Syntype (AMS 151711). **14.** *G. (Gyraulus) macquariensis* (Smith). Syntype (BMNH 43.9.20.55-60). **15.** *G. (G.) mccoyi* (Iredale). Syntype (VMM F442-4). **16.** *G. (G.) metaurus* (Iredale). Probable syntype (AMS 051737). **17.** *G. (G.) ordessus* (Iredale). Syntype (AMS 100621, 'probable holotype'). **18.** *G. (G.) parvus* (Cotton). Holotype (SAMA D14131). **19.** *G. (Pygmanisus) pelorius* (Iredale). Probable syntype (AMS 111731). **20.** *G. (Gyraulus) planissimus* (Clessin). Syntype from Rockhampton (ZMB 102385). **21.** *G. (G.) speranus* (Iredale). Largest syntype (AMS 000263). **22.** *G. (G.) stabilis* (Iredale). Probably a syntype (AMS 100610, 'holotype'). **23.** *G. (G.) stabilis* (Iredale). BMNH 87.5.19.85-96. Probably from the same series as the types. **24.** *G. (G.) waterhousei* (Clessin). Probable syntype (ZMB 19069).
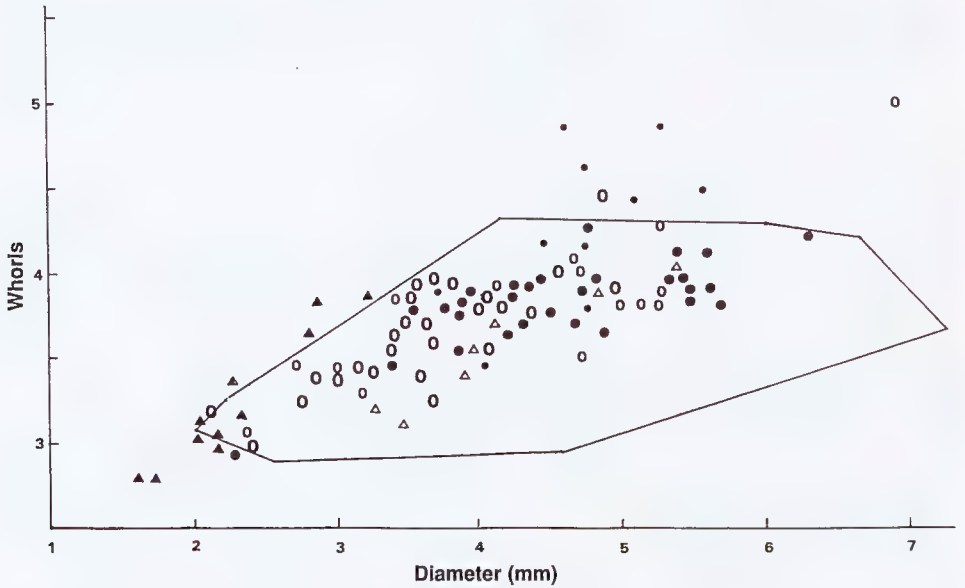
**Figure 4.**
Relationship between number of whorls and shell diameter for *Gyraulus* from mainland
Australia. The polygon outlines the distribution of type material shown in Fig. 3. Each
symbol represents one large shell from each of 98 samples of snails, coded according to
their classification in the present paper: *essingtonensis* (○), *gilberti* (●), *hesperus* (0), *isingi*
(▲), *scottianus* (△), *waterhousei* (●).
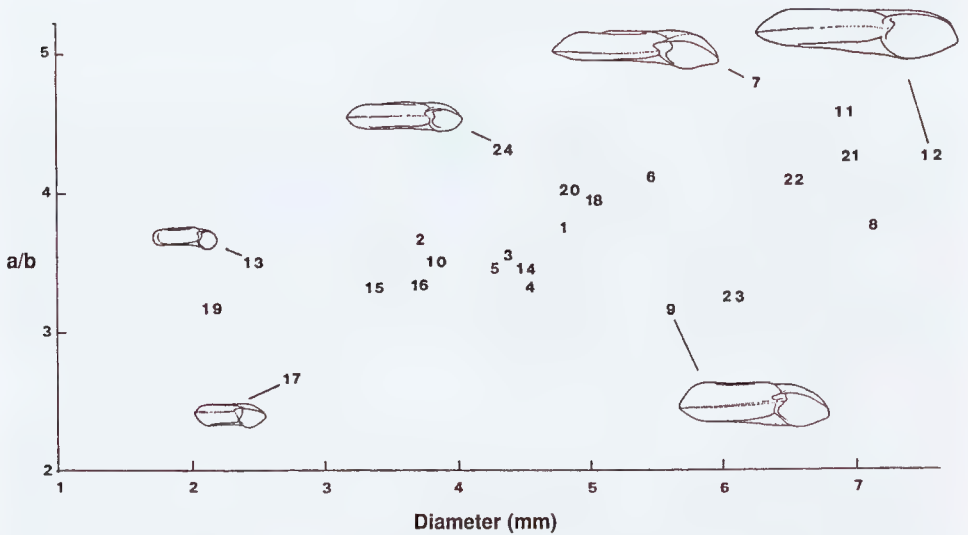


**Figure 5.**
Relationship between flatness index (a/b) and shell diameter, for types or representative
specimens of *Gyraulus* from mainland Australia. Shells numbered as in Fig. 3.
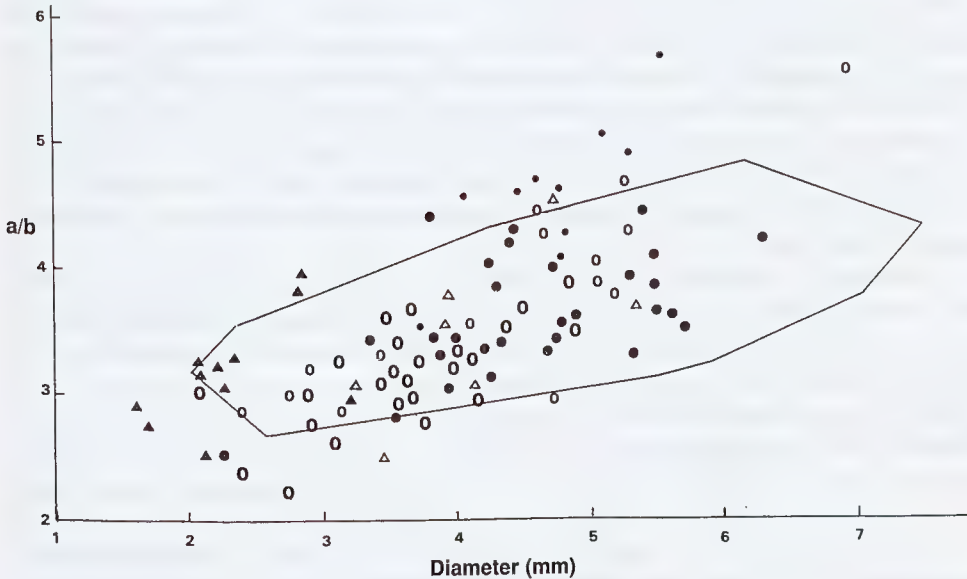
**Figure 6.**
Relationship between flatness index (a/b) and shell diameter for *Gyraulus* from mainland Australia. The polygon outlines the distribution of the type material shown in Fig. 5. Each symbol represents one large shell from each of 98 samples of snails, coded according to their classification in the present paper: symbols as in Fig 4.

As an introduction to the subgeneric classification of Australian *Gyraulus*, we must first consider genus-group names introduced by Iredale (1943). Before Iredale's list (1943) of the freshwater Mollusca of Australia, the local *Gyraulus*-like snails were classified as *Planorbis*. Iredale did not mention *Gyraulus*, but classified 20 species with shells of this form in three newly created genera:

*Glyptanisus* Iredale, 1943, type species *Glyptanisus ordessus* Iredale, 1943 –for shells strongly keeled peripherally;

*Plananisus* Iredale, 1943, type species *Planorbis tasmanicus* Tenison-Woods, 1876 – for shells with rounded whorls;

*Pygmanisus* Iredale, 1943, type species *Planorbis scottiana* Johnston, 1879 – very small shells with rounded whorls.

The first two were regarded as synonyms of *Gyraulus* by Brown (1981) followed by Smith (1992), and they are considered further here under G. (*Gyraulus*). *Pygmanisus* was maintained as a separate genus by Smith (1992), but according to anatomical data for snails from Tasmania, it seems ranked better as a subgenus (Brown, 1998).

Most of the snails examined during this study conform to *Gyraulus* sensu stricto (Meier-Brook, 1983, pp 99-100), in the more or less planispiral shell, commonly angulated whorls, straight kidney margins, and the arrangement of prostate lobes regularly and closely in a single row. *Gyraulus* s. s. occurs probably throughout mainland Australia wherever there is suitable habitat.

The only other subgenus currently recognised to occur in Australia is *G. (Pygmanisus)*, characterised by its small size (shell diameter less than 4 mm), entirely rounded whorls, undulate kidney margins, and few and irregularly arranged prostate lobes. This group is restricted to the south-eastern mainland and Tasmania.

However, a third subgenus, *G. (Plananisus)*, perhaps should be recognised for *G. meridionalis*, currently classified in *Gyraulus* sensu stricto; this species is found only in Tasmania and a small part of Victoria and its penial morphology is highly distinctive.

### Classification at the species level

Smith & Kershaw (1979, 1981) recognised only 3 distinct species of *Gyraulus* in SE Australia, including Tasmania, and placed 6 other species in synonymy (Smith & Kershaw, 1979). Smith (1992) listed a total of 13 species (Table 1), comprising 10 *Gyraulus* and 3 *Pygmanisus*; 8 other species were included in synonymies under *Gyraulus*. At the same time, Smith treated 4 additional taxa with *Gyraulus*-like shells as 'incertae sedis'. The present classification (Table 1) proposes 8 additional synonymies, but one new species is described and an introduced species is added to the Australian list. In all, 11 distinct species are recognised, though with doubt for some, comprising 10 of *Gyraulus* s. s. and 1 of *Gyraulus (Pygmanisus)*.

Paucity of species-differentiating characters is a worldwide difficulty in the taxonomy of *Gyraulus* (Meier-Brook, 1983). Whether this reflects inadequacy in the morphological approach, or indicates that many named taxa are synonyms of a few highly variable and widely distributed species, is a question whose answer must await evidence from molecular genetics. Continuous variation in taxonomic characters is compounded in the case of the shell by its indeterminate and allometric mode of growth, which shows no clear boundary between protoconch and teleoconch, and has no distinct mature stage.

Two shell characters often used to differentiate species of *Gyraulus* from one another are the number of whorls at given shell diameter, and the amount of depression of the whorls (with which is usually correlated angulation at the periphery). These morphospaces are illustrated in Figs 3-6, using measurements of 24 type specimens and the largest shells available from each of 98 samples.

In respect of whorls the distribution of most of the types (Fig. 3) is what may be expected from a general correlation with shell diameter. However, at diameter of 4 to 5 mm there is a difference of nearly a full whorl between *G. waterhousei* (no. 24, 4.34 whorls) and *G. daemeli* (no. 4, 3.53 whorls), while *G. edgbastonensis* sp. n. (no. 1) is distinctly isolated with only 3 whorls. When a polygon enclosing the distribution of the types is superimposed on the distribution of the non-types in respect of whorls (Fig. 4), some of the non-types lie well outside the polygon, because they have up to about half a whorl more,

i.e. one *G. essingtonensis* (upper right), and several *G. waterhousei.*

For the flatness index (a/b), the distribution of the types (Fig. 5) is what would be expected from the generally observed correlation that results from allometric growth of the *Gyraulus* shell, between greater depression (higher values for a/b) and shell diameter. The more depressed shells among the types, having a/b more than 4.2, are *G. waterhousei* (no. 24), *G. idenus* (no. 11) and *G. brazieri* (no. 7); the least depressed are *G. stabilis* (no. 23), *G. gilberti* (no. 9) and *G. ordessus* (no, 17).   A considerable number of the non-types are more depressed than any type of a similar diameter (Fig. 6); most of these are *G. waterhousei*, with a large *G. essingtonensis* (upper right).  Some of the smaller non-type shells are considerably less depressed than any type; the two shells with a/b less than 2.5 are both *G. hesperus.*

Although the types are widely scattered in the plots for both whorls and (a/b), much of the space amongst them is filled more or less evenly by non-types.  Some of the unoccupied morphospace within both polygons (Figs 4, 6) towards the upper end of the size range is due to the unusually large size of some types.

**Systematic account**

<div align="center">

Family **Planorbidae**

Subfamily **Planorbinae**

***Gyraulus*** Charpentier, 1837

</div>

*Type species: Planorbis hispidus* Draparnaud, 1805, designated by Dall, 1870 (= *Planorbis albus* Mueller, 1774).

Shell planispiral or rarely (in some ancient lakes) pseudodextral with elevated spire; 2-10 mm in diameter, with 3 to 5 whorls, which may be rounded or angular, with or without a keel.  Penis with sub-terminal opening, and at the tip a chitinous stylet, sharply demarcated from the soft tissue, commonly furled and dagger-like.   Other planorbid genera with this type of stylet differ in the proportional height of the shell whorls and slower rate of whorl increase (e.g. Meier-Brook, 1983, figs 109, 110).

Synonymous groups founded on Australian taxa are:

> *Glyptanisus* Iredale, 1943 [see under *Gyraulus (Gyraulus)*]
>
> *Plananisus* Iredale, 1943 [see under *Gyraulus (Gyraulus)*]
>
> *Pygmanisus* Iredale, 1943 [see *Gyraulus (Pygmanisus)*].

<div align="center">

Subgenus ***Gyraulus*** sensu stricto

</div>

Shell planispiral, with the last whorl sometimes a little deflected to the left, aperture more or less oval; periphery rounded or angled, with or without keel, commonly with periostracal fringe; surface may be smooth, but most species have spiral striation, often forming a reticulate pattern, usually most visible on the left side.  Kidney margins straight. Prostate lobes 8-40, arranged regularly and closely in a single row.  [Diagnosis after Meier-Brook, 1983, with minor modifications]

*Glyptanisus* Iredale, 1943: 224.
*Type species: Glyptanisus ordessus* Iredale, 1943 - from Hunter River District, NSW, by original designation.

Named for a group of species distinguished as "strongly keeled peripherally, with the mouth oblique and discontinuous, the surface commonly spirally sculptured" (Iredale, 1943). The type species appears to be an incompletely grown specimen of the most angular form of *G. waterhousei* (Clessin, 1885). Since this species conforms in both shell and anatomy to *Gyraulus (Gyraulus)*, there is no reason to maintain *Glyptanisus*.

*Plananisus* Iredale, 1943: 224.
*Type species: Planorbis tasmanicus* Tenison-Woods, 1876 - from Tasmania, by original designation.

Named for a series of species with whorls rounded and "mouth oblique, but in the same plane almost free" (Iredale, 1943). Contrary to Iredale's description, recent observations on material of the type species from Tasmania (Brown, 1998) show that its whorls are not consistently rounded, but vary widely in shape, and this taxon seems indistinguishable from the earlier-named *Planorbis meridionalis* Brazier, 1875. Although these snails conform in both shell and anatomy to *G. (Gyraulus)* as currently defined, they have a distinctive form of copulatory organ, which might justify recognition of a subgenus *Gyraulus (Plananisus)* (see further under *G. meridionalis*).

Species-group taxa of *Gyraulus* sensu stricto follow in alphabetical order.

### *Gyraulus (G.) brazieri* (Clessin, 1885)
(Figs 3 & 5, shell no. 7; Fig. 7)

*Planorbis fragilis* Brazier, Smith, 1883: 294, pl. 7, figs 1-3.
*Planorbis brazieri* Clessin, 1885: 166, pl. 24, fig. 6 [new name for *P. fragilis* Smith, non Dunker, 1850]; -Smith, 1992: 269, as junior synonym of *Gyraulus gilberti*.
*Glyptanisus brazieri* – Iredale, 1943: 226.

*Type locality:* Ipswich [near Brisbane], Queensland.

*Type material examined:* None (see Remarks).

*Representative material examined:* BMNH 79.5.21.743-8, 6 dry shells, from Ipswich, QLD, presented by J. Brazier, labelled *Planorbis* sp. [probably from the same series as the types]; ZMB18900, 5 dry shells from Tasmania, leg. Krafft, reported by Clessin, 1885 [probably belonging to the different species *G. meridionalis* (Brazier, 1875), see below].

*Description of shell* (Figs 3 and 5, shell no. 7; Fig. 7):
Original description: "This species is more compressed than *P. gilberti* and more acutely keeled. Being flatter, the lower surface is less sunken in the middle. Hab. Ipswich, Queensland (Brazier)." (Smith, 1883). Smith's figured shell

corresponds closely in size and shape to the largest shell (Fig. 7) in a series of 6 (BMNH) that probably came from the same series (see Remarks). These shells are large (the smallest 4.7 mm diameter), strongly depressed (a/b 3.7-4.8), acutely angled, keeled to a varying degree at or below mid-whorl, and fringed; left side of whorls strongly curved to subangled; microsculpture of numerous wavy transverse ridges intersected by spiral striae and ridges, strongest on left side. Of the additional material reported by Clessin, I have seen two shells from Tasmania (ZMB 18900); these are only weakly angled and are so similar to type material of *G. meridionalis* (Brazier) from Circular Head, Tasmania (AMS 100598) as to be possibly from the same sample.

*Dimensions of shells selected from BMNH 79.5.21:*

|          | whorls | diameter (mm) | a/b  |
|----------|--------|---------------|------|
| largest  | 4.29   | 6.18          | 4.78 |
|          | 4.22   | 6.04          | 4.54 |
|          | 4.24   | 5.82          | 4.44 |
| smallest | 3.82   | 4.66          | 3.73 |



2 mm

**Figure 7.**
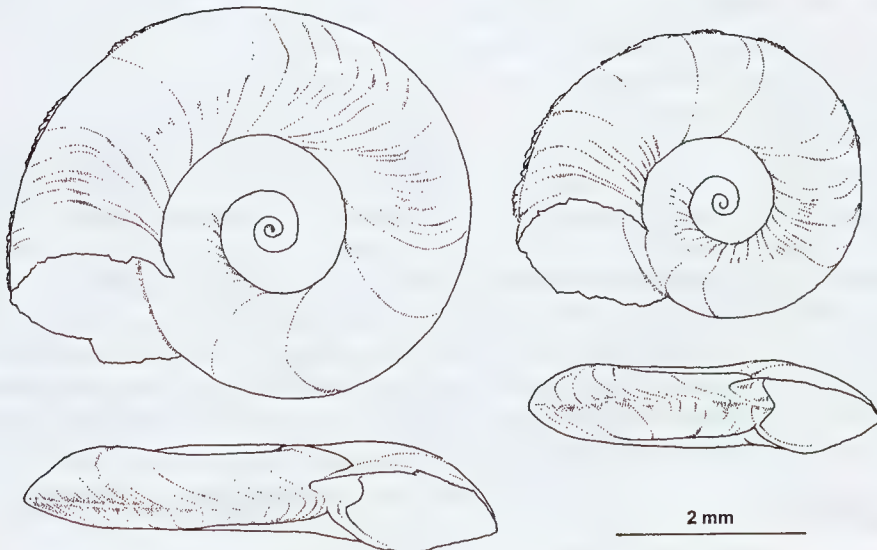*Gyraulus brazieri* (Clessin, 1885; new name for *Planorbis fragilis* Smith, 1883). The largest and smallest of 6 shells apparently from the same series as the types, from Ipswich, QLD (BMNH 79.5.21.743-8). The lip of each shell is somewhat broken. Only the more prominent sculpture is indicated; the shell surfaces have numerous, fine, irregular transverse ridges, and only a few spiral striae.

*Remarks:* E. Smith (1883) explained that he published the name *Planorbis fragilis* Brazier because he had seen it attached to specimens sent by C. E. Beddome, of Hobart, to J. Taylor, of Leeds. The present whereabouts of these shells is unknown. They could not be found in the collections of the NMH London, the Leeds City Museum (Dr A. Norris, in litt. to the author, March 1996) or the National Museum of Wales, Cardiff (A. Turner, in litt. to the author). Smith (1992) referred to "syntypes (probable), SAMA D5130" for *P. fragilis* Smith, in synonymy of *G. gilberti*, but these actually are specimens of *fragilis* Smith identified by Tate (1896) that Iredale (1943) re-named *Glyptanisus coranus*. The examples from Tasmania (ZMB 18900) are very likely *G. meridionalis* (Brazier); this and other species of *Gyraulus* sensu stricto known from Tasmania are distinguished by their penial structure from any taxa found in Queensland. Since the shell figured by Smith (1883) does not seem to depart significantly from the range of variation observed in material from southern Queensland identified here as *G. gilberti*, I follow B. Smith (1992) in treating *G. brazieri* as a junior synonym.

### *Gyraulus (G.) caroli* (Iredale, 1943)
(Figs 3 and 5, shell no. 2; 21 A-C)

*Glyptanisus caroli* Iredale, 1943: 225 [under *G. waterhousei*], for *Planorbis waterhousei* Clessin of Gabriel, 1939: pl. 3, figs 29, 29a, 29b; - Smith, 1992:270, as synonym of *Gyraulus waterhousei* Clessin.

*Type locality:* Portland, Victoria.

*Type material examined:* Holotype, a dry shell, NMV registered earlier as 71224 and later as F549 (this number cited by Gabriel, 1939 in explanation of his pl. 3).

*Description:* The original description is very brief : "differing [from *Planorbis waterhousei* Clessin] in the more rounded whorls, etc [sic]." (Iredale, 1943). The type examined corresponds well to Gabriel's figure. In its general form and particularly the median angle, slowly increasing whorls and weak spiral sculpture it resembles syntypes of *G. waterhousei*. The brown colour is darker than usual in *Gyraulus* shells from Australia.

*Dimensions of syntype examined:*

| whorls | diameter (mm) | a/b |
|---|---|---|
| 3.78 | 3.6 mm | 3.65. |

*Remarks:* Iredale may have been encouraged to differentiate *caroli* by Clessin's figure of *waterhousei*, which exaggerates its depression and angulation. There is considerable similarity between the holotypes of *G. caroli* and that of *G. parvus* (Cotton) from the Torrens River, Adelaide, and both species appear to be junior synonyms *G. isingi*, the most widely distributed species of *G. (Gyraulus)* in SA and VIC.

### *Gyraulus (G.) chinensis* (Dunker, 1848)
### (Fig. 28 D)

*Planorbis chinensis* Dunker, 1848: 41.
*Gyraulus chinensis* – Meier-Brook, 1983: 56-57; - Brown, Gracio & Meier-Brook, 1998: 203-323. [Selected references from an extensive literature]
The following two taxa are listed with doubt – see Remarks:
*Gyraulus essingtonensis* Meier-Brook [probably non Smith, 1883], 1983: 82, footnote 4.
*Gyraulus* sp.2 of Meier-Brook, 1983: 97.

*Type locality:* Hong Kong.

*Material examined:* SAMA D19044 (7 wet). SA, "Crescent Pond", totally surrounded by thick scrub, about 3 miles W of Picaninnie Ponds, 20 miles SSE of Mt Gambier; Oct 1980, P. Horne.

*Shell:* The present specimens are probably not fully grown (maximum diameter 3.6 mm), and they are considerably decalcified. In accordance with previous descriptions (Meier-Brook, 1983; Brown et al., 1998) the whorls are little if at all depressed (a/b 3.2), rounded or only obtusely angled, and lack a fringe. Spiral sculpture is weak or lacking.

*Anatomy* (Fig. 28 D): Description for a large specimen of 3.6 mm in diameter. Pigmentation forming a distinct pattern (Fig. 28 D), visible through the shell wall. Head with patch of small grey spots in the mid-dorsal area, tentacles with conspicuous black masses internally. Mantle roof on either side of kidney with numerous small patches of grey to black; anterior margin with scattered black spots. The same pigmentation pattern was observed in all the 5 bodies available. Kidney margins straight, no internal septa seen. Intestine with long posterior lobe extending back beyond stomach. Copulatory organ 1.5 mm long in snail of diameter 3.6 mm; penis sheath broadly swollen proximally, vas deferens much narrower than the penis sheath and attached to it terminally. Penis slender and attached at the end of the sheath, penis pore opening a short distance from the tip. Prosobranch lobes 15. Bursa copulatrix tapered. Seminal vesicle large, with about 8 bluntly spinous convolutions. Ovotestis lobes about 25.

In most respects the soft parts resemble those of *G. chinensis* from West Africa described by Brown et al. (1998). The Australian specimens differ in having less distinct dark spots in the proboscis and the anterior foot.

*Comparison with other species:* *G. chinensis* is readily distinguishable from any other taxon of *Gyraulus* known from Australia by the patchy distribution of pigmentation in the mantle roof and tentacles. Such a pattern is found also in other species known from south and east Asia (Meier-Brook, 1983, p. 66, Key), of which, *G. eugyne* Meier-Brook differs in its more inflated bursa copulatrix, *G. malayensis* Meier-Brook in its wider vas deferens (not much narrower than the penis sheath) and the position of the penis pore (in the middle or within the

proximal half of the penis), and *G. tokyoensis* Mori, 1938 in its larger shell (to 7 mm) with acute angle, keel and broad fringe. Also having a patchy pigmentation is *G. convexiusculuus* (Hutton, 1849), a species reported from a large area of south and east Asia, including north-east New Guinea (Starmuehlner, 1976; Brown, 1981). This highly variable species was regarded as a species complex or 'Rassenkreis' by Brown (1981, p. 70) and it was placed in the Rassenkreis of *G. chinensis* by Meier-Brook (1983, pp. 60, 65). Whether such snails from New Guinea should be referred to *G. convexiusculus* or to *G. chinensis* remains an open question.

*Remarks:* A patchy pigmentation of the mantle was reported by Meier-Brook (1983, p. 82, footnote 4) for snails identified as *G. essingtonensis*, from the Kimberley region of WA. However, no such pigmentation was observed during the present study in any of the many specimens of this species examined, including extensive topotypical material. Therefore it appears possible that the snails seen by Meier-Brook may have belonged to an isolated population of *G. chinensis*.

*Gyraulus* sp. 2 of Meier-Brook (1983), from 10 km south of Bombala, NSW, was thought likely by Meier-Brook to be a sister species to *G. brongersmai* van Benthem Jutting (1963) of western New Guinea, according to resemblances in the shell. Meier-Brook noted similarities in anatomical features among these two species and *G. chinensis*. *G. brongersmai* and other endemic species of New Guinea were included in a group of taxa with a patchy mantle pigmentation (Meier-Brook, 1983, fig. 115). However, Meier-Brook stated (p.82) that neither of the two species from eastern Australia that he examined had any pigmentation at all, and so one cannot be confident in identifying his "sp. 2" with *G. chinensis*.

Meier-Brook also reported the presence in western New Guinea of *G. chinensis*, according to his examination of snails from Merauke that had been identified as *G. convexiusculus* by van Benthem Jutting (1963); Meier-Brook, 1983, fig. 114, p. 111 (material).

*G. chinensis* is an invasive snail, at least in western Europe, where it has been found during recent decades from Iberia northwards to Germany, though it is not known to overwinter out of doors in the latter country (Gloer & Meier-Brook, 1994). In Italy, southern France, the Iberian Peninsula and West Africa, this snail has appeared in rice-growing areas. It is surprising that *G. chinensis* has not become widely established in Australia. Remarkably, the specimens from SA reported here were collected from an apparently isolated pool "totally surounded by thick scrub".

*Distribution:* Australia (a single locality in SA near Mt Gambier, present paper; possibly other isolated localities, see Remarks above), south Asia (Meier-Brook, 1983), Western Europe and Guinea Bissau in West Africa (Brown et al., 1998).

**_Gyraulus (G.) coranus_** (Iredale, 1943)
(Fig. 3 and 5, shells nos 3 and 8; 15 J-O)

*Planorbis fragilis* (Brazier), Smith – Tate, 1896: 216, pl. 19, fig. 23.

*Glyptanisus coranus* Iredale, 1943: 226 [new name for *Planorbis fragilis* Tate, 1896, non Smith, 1883].
*Gyraulus coranus* – Smith, 1992: 269.

*Type locality:* South Australia, Lake Eyre basin, "Dead shells in the rejectamenta of the River Finke at Crown Point and Running Water; living in Palm Creek, off Glen Palms, and in the Hugh River at Stuart's Pass." The following information was kindly supplied by Dr John Walker: Crown Point is at approximately 134°21'E, 25°31'S, Palm Creek is a small tributary of the Finke River, in Palm Valley, at 132°44'E, 24°02'S, the Hugh River crosses the Alice Springs to Hermansburg road at 133°20'E, 23°46'S, and Stuart's Pass is probably a little south of there, where the river emerges from the ranges.

*Type material examined:* SAMA D5130, syntypes; 2 dry shells (one labelled `holotype') from Palm Creek, ex Tate collection. AMS 002153, labelled `probable syntype', 1 shell from central Australia, presented by Mr W. Horn.

*Description:*
Original description: "The shells of this species are more compressed and more acutely keeled than those of *P. gilberti*, as stated in the original diagnosis. A more valuable diagnostic character is afforded by the position of the keel, and in consequence the form of the aperture. In *P. gilberti* the keel is central, and in *P. fragilis* it is far below the middle." (Tate, 1896).
　　　The larger of the syntypes from Palm Creek (Figs 3 and 5, shell no. 8; 15 J-L) is 7 mm in diameter and exceptionally big for a *Gyraulus* from Australia, and it is unlikely that the shell figured by Tate could have been over 10 mm wide as indicated by his scale of magnification. The smaller one has the angle near the left side, as described and figured by Tate, but the larger shell is angled near mid-whorl. These syntypes are only a little more depressed than the syntypes of gilberti, and only the larger one is more acutely keeled. Both shells have the left side rather deeply concave and the whorls are strongly curved to subangled. Spiral striae and ridges are conspicuous on the smaller shell. The probable syntype (AMS; Figs 3 and 5, shell no. 3, 15 M-O) resembles the smaller of the shells from Palm Creek in size and shape and has even stronger sculpture.

*Dimensions:*

|                    | whorls | diameter (mm) | a/b  |
|--------------------|--------|---------------|------|
| Syntypes (SAMA)    | 4.04   | 7.0           | 3.76 |
|                    | 3.69   | 4.4           | 3.33 |

Remarks: Iredale did not give any character whereby he distinguished *coranus* from *fragilis* of Smith. Perhaps he was impressed by the fact that the example figured by Tate is obviously less depressed than the one figured by Smith. The examples of *coranus* seen appeared likely to belong to the same species as the snails tentatively identified here as *G. essingtonensis*, found in the George Gills Range, which lies about 350 km north-west of the Finke River area.

*Gyraulus (G.) daemeli* (Clessin)
(Figs 3 and 5, shell no. 4; 16 A-C)

*Planorbis daemeli* Clessin, 1885: 189, pl. 28, fig. 6; - Kilias, 1967: 152; - Smith, 1992: 277 (under 'species incertae cedis').
*Glyptanisus daemeli* (Clessin) – Iredale, 1943: 226.

*Type locality:* Australia, Cape York.

*Type material examined:* ZMB No. 13223a, Lectotype (dry shell) [designated by Kilias, 1967, who referred also to two paralectotypes, both damaged].

*Description:*
Original description: (translated from the German) 'Shell depressed, almost evenly flat above with only the middle sunken sunken; underside convex, weakly sunken in the middle; very thin-walled, finely striate, corneous: 4 whorls, increasing moderately rapidly, sharply keeled, weakly curved above and strongly curved below, according to how close is the keel to the upper side, so is the suture deeper below; last whorl twice as wide as the penultimate one; aperture lanceolate; peristome sharp, interrupted . . . Diam. 5 mm, alt. 0.8 mm" (Clessin, 1885).
    The lectotype (Figs 3, 5, 16) corresponds satisfactorily to the Clessin's description. It may be added that the angle is in parts keeled and fringed, and there is microsculpture of irregular transverse ridges cut here and there by weak spiral striae.

*Dimensions of lectotype:*

| whorls | diameter (mm) | a/b |
|--------|---------------|-----|
| 3.53   | 4.50          | 3.32 |

*Comparison with other taxa:* Clessin commented that though *daemeli* stood close to *gilberti*, it was almost as depressed as *Planorbis waterhousei*, but distinguished from it by the position of the keel, which his figures show to be at mid-whorl in the latter taxon, but a little towards the right side in *daemeli*. The lectotype resembles the syntypes of *gilberti* in degree of depression, shape of peripheral angle and the weak microsculpture. Differences were evident in the shallower concavity of the left side of the lectotype, the weaker curvature of the whorl on that side and the position of the keel, nearer to the right side, which is flatter, with the inner whorls more deeply sunken. Further, the angle continues acutely to the lip of *daemeli*, whereas it becomes obtuse in *gilberti*. Another shell from Cape York (ZMB18239) is part of the type material of *Planorbis planissimus* Clessin, 1885. Clessin did not compare these taxa; his figures show *planissimus* to be more depressed. Although this difference was evident when the two shells from Cape York were compared, they still appeared to be conspecific.

*Remarks:* No material recently collected from Cape York was available. Shells resembling the lectotype of *daemeli*, having an acute angle situated nearest to the right side, were present in some of the samples from southern Queensland and

identified as *G. gilberti*, e.g. from near Gympie (AMS 144859), Proserpine (AMS 144867) and Rockhampton (AMS 144872). Shells obtained nearer Cape York, south of Cooktown, are different (see AMS 144870-71 under *G. gilberti*), being more like *G. hesperus*. Despite differences in the type materials noted above, *G. daemeli* appears to be a junior synonym of *G. gilberti*.

### *Gyraulus (G.) edgbastonensis* sp. n.
(Figs 3 and 5, shell no. 1; 8-10, 20 M-O, 26 A)

*Type locality:* Australia, Queensland, "Big Spring", about 31 km north-east of Aramac and about 3 km south-east of "Edgbaston" homestead, 22° 45′S 145° 25′ 30″E, snails collected from the upper outflow, 26 Sept 1984, W.F. Ponder and P.H. Colman [Station no. 73A in Ponder & Clark, 1990: 1, fig. 1 (map), fig. 3 (habitat) and Appendix 1]

*Type material:* AMS 144985, Holotype (dry shell and wet body) and about 50 paratypes (wet and dry); BMNH 2000 0382, 3 paratypes (dry) from the same sample. Also about 200 paratypes (wet, AMS 345432) with the same collection data, 2 paratypes (wet AMS 144986)) with same locality data apart from collected at head of "Big Spring", about 60 paratypes (wet, AMS 144987) with same locality data apart from being labelled simply "Big Spring", and 1 paratype (wet, AMS 144988) with same locality data apart from being collected from a small seep. Another 250 paratypes (wet, SAMA D19033), "Big Spring, from the flood plain", 4 May 1988, stn 9B, W. Zeidler [Station Z9B in Ponder & Clark, 1990: Fig. 1 and Appendix 1].

*Additional material:*
AMS 347253 (33 wet); "Pool 3", near Edgbaston homestead, 22°45′S 145°25.5′E, middle of spring, Sept 1991, P. Unmack. AMS 347256 (5 wet); same data as for AMS 347253, except "near head of spring". AMS 347259 (2 wet); "Blue Eye Spring" near Edgbaston homestead, 22°45′S 145°25.5′E, middle, 30 Sept 1991, P. Unmack. AMS 347260 (1 wet); same data as for AMS 347256 except "lower outflow". AMS 347261 (100 wet); "Spring 3" near Edgbaston homestead, same coordinates, middle outflow, Sept 1991, P. Unmack. AMS 347263 (150 wet); "Spring 6" near Edgbaston homestead, same coordinates; from head of spring, Sept 1991, P. Unmack. SAMA D19029 (18 wet); artesian spring about 3.3 km SE of Edgbaston homestead, 22°45.30′S 145°25.40′E, small spring with water bubbling through sand, stn 10, 4 May 1988, W. Zeidler [Station Z10 in Ponder & Clark, 1990: fig. 1, fig. 3C and Appendix 1]. SAMA D19031 (6 wet); artesian spring 2.4 km NE of Edgbaston homestead, 22°42.45′S 145°25.25′E, 3 May 1988, stn 7, W. Zeidler [Station Z7 in Ponder & Clark, 1990: fig. 1 and Appendix 1]. SAMA D19032 (100 wet); artesian spring about 11 km due SSE of Edgbaston homestead, 28 km directly NE of Aramac, 22°47.20′S 147°25.40′E, small mound supporting large natural pond, sampled near source, 4 May 1988, W. Zeidler [Station Z12 in Ponder & Clark, 1990: Fig. 1, Fig. 3D and Appendix 1].
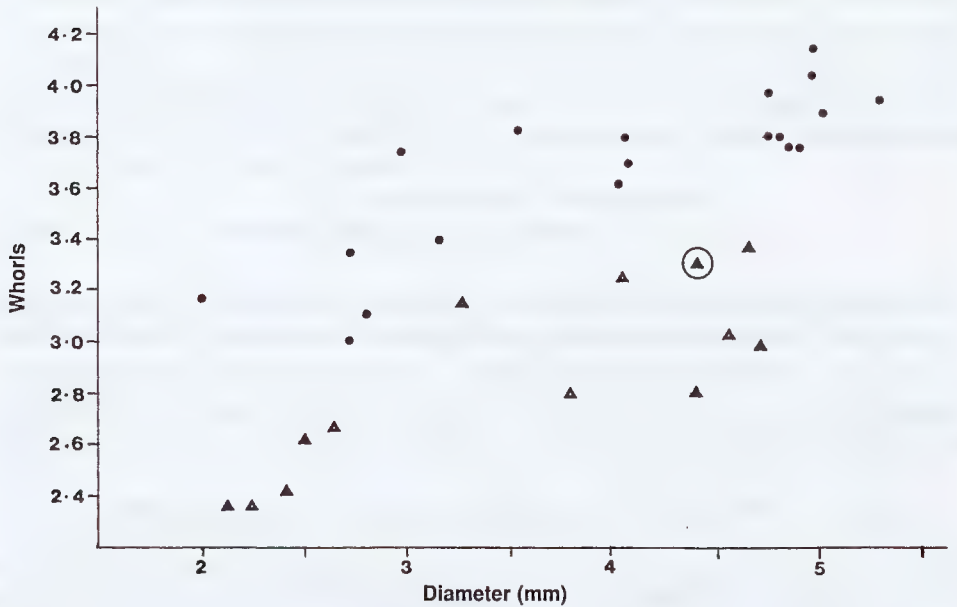
**Figure 8.**
*Gyraulus edgbastonensis* sp. n. and *G. gilberti.* Relationship between number of whorls and shell diameter. Triangles = *G. edgbastonensis*; holotype (encircled) and 12 paratypes (AMS 144985). Spots = *G. gilberti*; representative specimens from near Gympie, QLD (n = 19, AMS 144859).
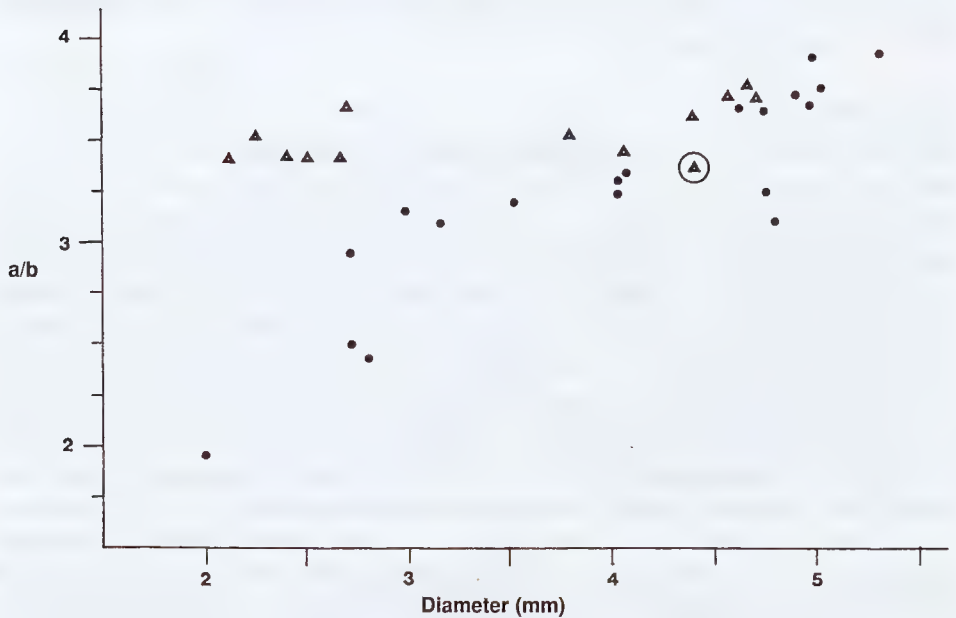


**Figure 9.** *Gyraulus edgbastonensis* sp. n. and *G. gilberti.* Relationship between shell flatness index (a/b) and shell diameter. Symbols as in Fig. 8. Note that while some large shells of each species are similarly depressed, the smaller shells of *G. edgbastonensis* are much more depressed (having higher a/b values) than small *G. gilberti*.
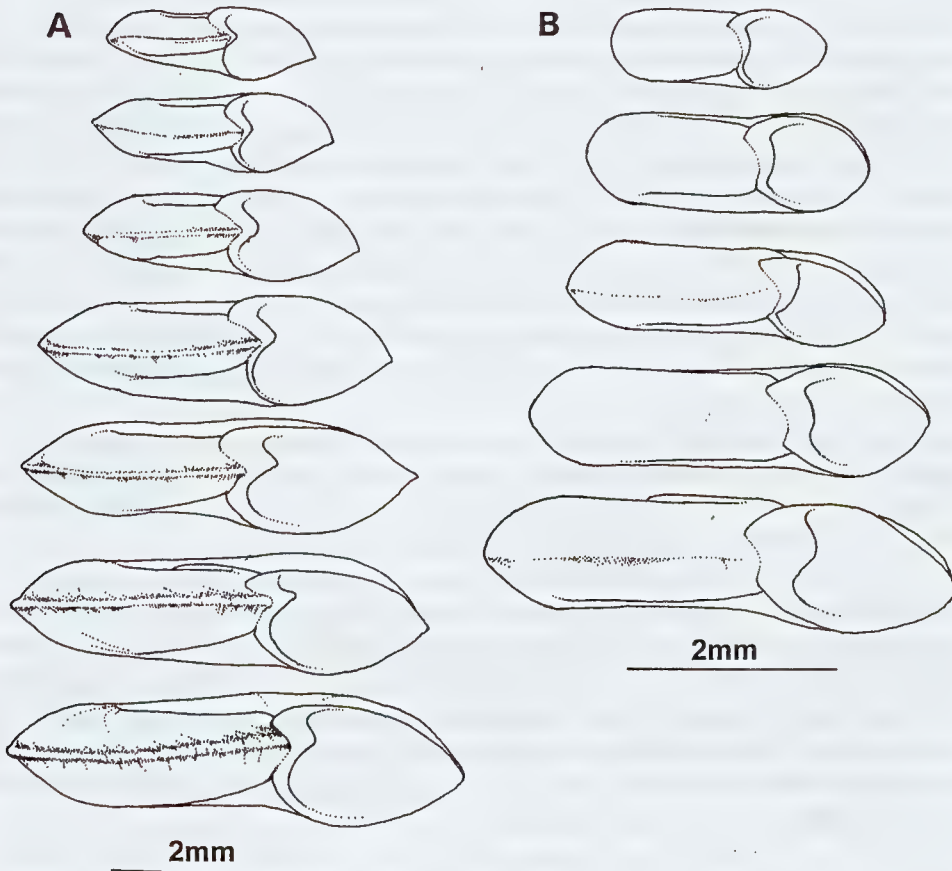
**Figure 10.**
Growth series for **(A)**, *Gyraulus edgbastonensis* sp. n., holotype (lowermost shell) and selected paratypes (AMS 144985) and **(B)**, *G. gilberti* from near Gympie, QLD (AMS 144859). *G. edgbastonensis* is usually more acutely angled over the whole size range. A further difference evident in this figure, due to the more rapid increase in height of the whorl in *G. edgbastonensis,* is that in this species the height of the penultimate whorl at the attachment of the lip is obviously less than the height of the whorl on the opposite side of the shell.

*Diagnosis: G. edgbastonensis* sp. n. is distinguished from all other described species of *Gyraulus* from Australia by the rapidly increasing, acutely angular and strongly keeled whorls, the canaliculate suture near the aperture of large specimens, whose lip may be partly detached, and the darkly pigmented body of many individuals.

*Derivation of name:* Named after the Edgbaston Homestead.

*Description of shell* (Figs 3, 5, 8-10; 20 M-O, 26 A): Whorls increase so rapidly that less than 3.5 are completed in a fully grown shell of about 4.5 mm diameter (Fig. 8), not much depressed (a/b 3 to 4) yet acutely angled (Figs 9, 10A), with prominent keel and fringe. These characters are present over the whole size range seen, which extends down to a shell diameter of 2 mm in the type material (Fig. 10A). Colour reddish brown. Left side concave, with whorls strongly curved near the suture, becoming increasingly flatter towards the periphery and slightly concave approaching the keel; inner whorls sunken within last-formed whorl. Right side nearly flat or somewhat domed, according to position of keel; whorls curved less strongly and more evenly, though descending steeply to the suture; inner whorls only a little sunken. Near the aperture of large specimens the suture is sunken (canaliculate) and the lip may be partly detached from the preceding whorl. Aperture cordate; the keel of the penultimate whorl projects prominently from the parietal margin. Microsculpture (Fig. 26A): transverse ridges are numerous, close-set, varying much in thickness, somewhat wavy, producing a wrinkled (rugose) texture; spiral sculpture less conspicuous, formed by widely-spaced striae and fine ridges, of which there are up to about 9 on the left side and about 5 on the right side of the last whorl; the thickened parts of the ridges may bear short projections of periostracum.

The keel of the holotype (Figs 10A lowermost shell; 20 M-O) is situated a little to the right of mid-whorl, but in large paratypes the keel's position varies from nearer to the right side to close to the left side, while the last whorl may be so much deflected that the aperture lies entirely to the left of the keel. Medium-sized and small specimens are more nearly planispiral, with the keel usually at mid-whorl and the lip attached on either side of it. The degree of depression and angulation varies remarkably little over the size range examined (1.9 to 4.65 mm diameter).

*Dimensions of holotype and selected paratypes* (AMS 144985):

|           | whorls | diameter (mm) | a/b  |
|-----------|--------|---------------|------|
| holotype  | 3.30   | 4.40          | 3.38 |
| paratypes | 2.95   | 4.72          | 3.73 |
|           | 3.35   | 4.65          | 3.78 |
|           | 3.10   | 4.54          | 3.72 |
|           | 3.18   | 3.96          | 3.57 |
|           | 2.80   | 3.81          | 3.53 |
|           | 3.15   | 3.27          | 3.64 |
|           | 2.65   | 2.65          | 3.41 |
|           | 2.45   | 2.40          | 3.42 |
|           | 2.35   | 2.25          | 3.50 |
|           | 2.35   | 1.92          | 3.40 |

*Anatomy:* Description based on 8 paratypes: 4 from sample AMS 144985, 2 from AMS 144987 and 2 from SAMA .D19033. Pigmentation of dark grey, a little

brownish in some animals, suffusing the head/foot and tentacles, which do not show a distinct core. Diffuse greyish black on the mantle roof, concentrated anteriorly and along the kidney margins. Kidney apparently without septa, though much folded by contraction of all the bodies examined. Intestine with only a leftwards kink or a very short posterior loop, despite the contraction of the bodies. Copulatory organ like that of *G. gilberti*, having the penis attached at the proximal end of the sheath, and the penis tip not swollen. Prostate lobes 15 to 19 in total (mean 17.2). Bursa copulatrix shape, tadpole elongate or tadpole spherical. Seminal vesicle with 6 to 9 spinous convolutions. Ovotestis lobes 18 to 26, in two approximate rows. Radula (n = 2, from AMS 144985, shell diameter 4 mm): maximum dimensions of ribbon, length 0.87 mm, breadth 0.16 mm; formula 16-1-16, with 4 or 5 additional rudimentary tooth-plates at margins; transverse rows about 150. Central tooth bicuspid, inner laterals with 3 major cusps, well separated and sharply pointed.

*Comparison with other taxa:* The depressed, acutely angular, strongly keeled shell of *G. edgbastonensis*, with rapidly increasing whorls is distinct from other species of *Gyraulus* known from Australia. Shell somewhat similar to the acutely angular form of *G. waterhousei*, found in the Sydney area, the Clarence River basin and a few other localities (Brown, 1981 and present paper), but darker in colour and with the height of the whorls increasing more rapidly, evident in profile view as the obvious increase in whorl height from the inner lip towards the periphery (Fig. 10A). *G. atkinsoni* (Johnston) of Tasmania also has acutely angled rapidly increasing whorls, but its copulatory organ is different and like that of *G. meridionalis* (present paper and Brown, 1998). The acute angulation of even the smallest shells examined of *G. edgbastonensis* is remarkable and possibly a unique character. The pigmentation of the head/foot of some individuals is almost black, and darker than any other *Gyraulus* seen during this investigation.

*Remarks:* *G. edgbastonensis* is known only from "Big Spring" and some of the other Edgbaston Springs, which belong to the Barcaldine Supergroup of Queensland artesian springs (Ponder, 1986; Ponder & Clark, 1990). These springs support a radiation of hydrobiid taxa that show the conditions to be favourable for molluscan speciation. Six species live in the Edgbaston Springs and all are found in "Big Spring" (Ponder & Clark, 1990, Table 4). It is not remarkable that an endemic species of *Gyraulus* should occur here too, and more might be expected. However, the three other samples of *Gyraulus* from this area differ conspicuously from *G. edgbastonensis*, in their lighter-coloured shell and slowly increasing whorls, which are scarcely more than obtusely angled; these snails do not seem separable from *G. gilberti* (see under that species, AMS 144984, AMS 345152 and SAMA D19030).

    Many shells in the type material, and in other samples, bear oval capsules each containing a single developing snail. Many protoconchs are visible and they are depressed and closely similar to a young *Gyraulus*. However, those dissected from capsules were found to have an operculum and are thus likely to be the young of one or more of the hydrobiids known from these springs.

*Distribution:* Western QLD; *G. edgbastonensis* sp. n. is known only from Big Spring and some of the other artesian springs near Edgbaston Homestead.

**Gyraulus (G.) essingtonensis** (Smith, 1883)
(Figs 3 and 5, shells nos 5 and 6; 4, 6, 11-14, 28 B, 32)

*Planorbis essingtonensis* Smith, 1883: 294-295, pl. 6, figs 33-35.
*Glyptanisus essingtonensis* – Iredale, 1943: 226.
*Glyptanisus coranus* Iredale, 1943 [see under *G. (G.) coranus*].
*Gyraulus essingtonensis* – Burch & Jeong, 1984: 67-84, figs 1l [shell], 13-15 [radula];
- Jung & Burch, 1990: 76 [radula]; - Smith, 1992: 269.

*Type locality:* Freshwater lagoons, Point Smith, Port Essington [Cobourg Peninsula, NT].

*Type material examined:* BMNH 41.10.12.159-167, syntypes, 12 dry shells, "purchased of Mr Gould" [in Accession Register]. BMNH 45.5.14, 9 shells, from freshwater lagoons, Point Smith, Port Essington, presented by the Earl of Derby [in the General Collection, but topotypical and possibly from the same series as the syntypes; the box label is damaged but corresponds to entry 45.5.14.32-39 in the Accession Register].

*Other material examined:* The copulatory organ and prostate gland were examined in each sample listed. Only the shell was examined in 40 other samples identified by the author as *essingtonensis* or *?essingtonensis*, from northern NT: AMS registration numbers 150821 and within the sequence 345704-345916, mostly from the Mataranka area, the Roper River and coastal region of the western Gulf of Carpentaria.

**Northern Territory**
AMS 138752 (4 wet); George Gills Range, Stokes Creek Canyon, swamp, 24°22'S 131°45'E, 26 May 1983, W.F. Ponder and W. Zeidler. AMS 138757 (50 wet); George Gills Range, eastern tributary of Stokes Creek in Hidden Valley, 24°22'S 131°45'E, 26 May 1983, W.F. Ponder and W. Zeidler. AMS 138758 (3 wet); George Gills Range, pool at entrance to Stokes Creek Canyon, 24°22'S 131°44'E, 26 May 1983, W.F. Ponder and W. Zeidler. AMS 144772 (22 wet); Cobourg Peninsula, Smith Point, lagoon behind Ranger Station, open water, weedy edge, I June 1976, W.F. Ponder, J.B. Burch and D. Fleughelman, stn 22. AMS 144773 (10 wet); locality and collectors as for 144772, 3 June 1976, stn32. AMS 144774 (70 wet); Cobourg Peninsula, Smith Point, lagoon, 3 June 1976, collectors as for 144772, stn 31. AMS 144775 (35 wet); Cobourg Peninsula, Smith Point, lagoon, open water, 3 June 1976, collectors as for 144772, stn 30. AMS 144776 (34 wet); Cobourg Peninsula, end of Smith Point, lagoon, June 1976, collectors as for 144772, stn 19. AMS 144777 (28 wet); Cobourg Peninsula, Reef Point, swamp with clear brown water, 2 June 1976, collectors as for 144772, stn 27. AMS 144778 (3 wet); details as 144777. AMS 144779 (11 wet). Cobourg Peninsula, Banteng Plain, small lagoon recently exposed to salt water, 3 June 1976, collectors as for 144772, stn 28. AMS 144780 (21 wet); black soil plain of Alligator (South) River, Arnhem
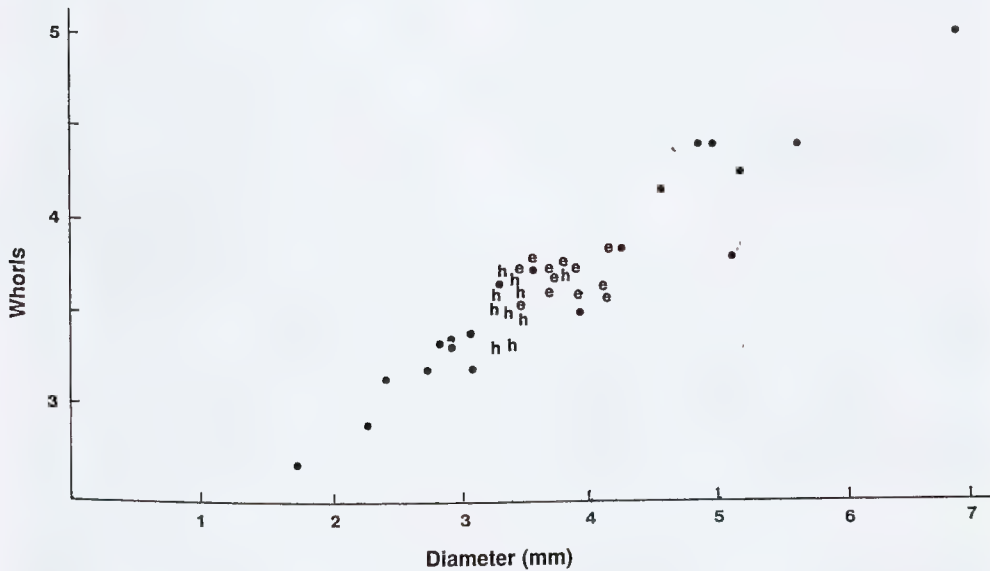
**Figure 11.**
*Gyraulus essingtonensis* and *G. hesperus*. Relationship between number of whorls and shell diameter. (e) = *G. essingtonensis*, syntypes (n = 12; BMNH 41.10.12.159-167). (●) = *G. essingtonensis* from the Cobourg Peninsula (n = 20; AMS 144774, shells less than 3.0 mm diameter; AMS 144777, shells more than 3 mm diameter). (h) = *G. hesperus*, some of the syntypes (n = 10, AMS 100594).
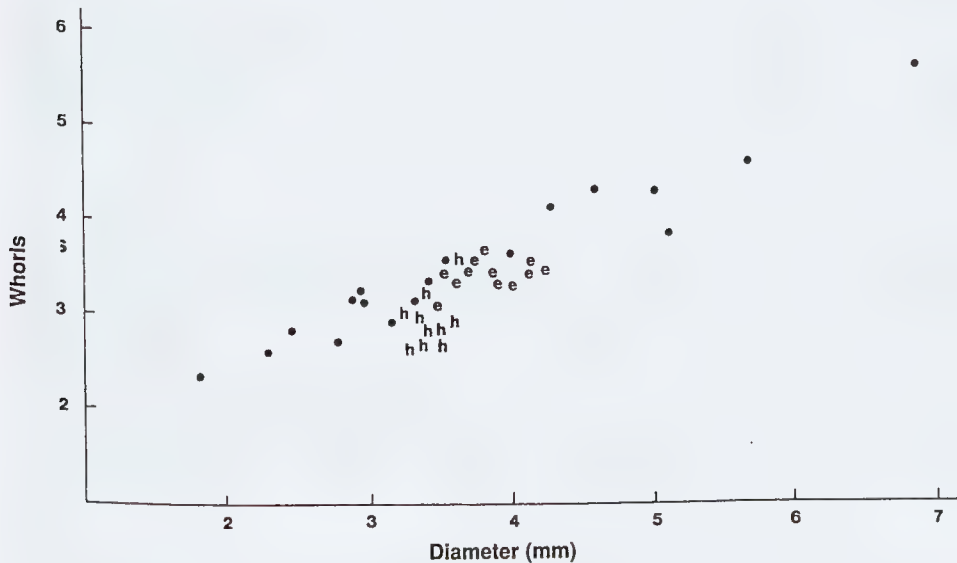


**Figure 12.** *Gyraulus essingtonensis* and *G. hesperus*. Relationship between flatness index (a/b) and shell diameter, for the same shells plotted in Fig. 11, except that n = 18 rather than 20 for *essingtonensis* from sample AMS 144777. Symbols as in Fig. 11.
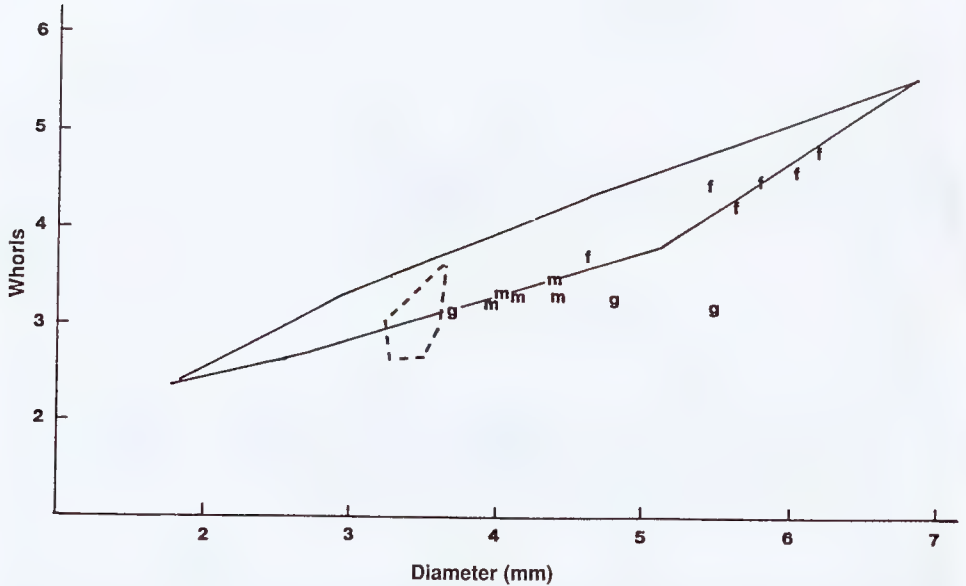
**Figure 13.**
*Gyraulus essingtonensis* compared in respect of flatness index (a/b) and shell diameter with types or representative shells of other taxa. The large polygon encloses the distribution of types and other material of *G. essingtonensis* plotted in Fig. 12. The small polygon (broken line) encloses the distribution of the syntypes of *G. hesperus* plotted in Fig. 12. (f) = *brazieri* Clessin (= *fragilis* Smith), 6 representative shells, BMNH 79.5.21.743-8. (g) = *gilberti*, 3 syntypes, BMNH 1969143. (m) = *macquariensis*, 5 syntypes, BMNH 43.9.20.55-60.

Highway, 8 June 1976, collectors as for 144772, stn 46. AMS 345700 (5 dry); Salt Creek at Roper Highway, 15°0.74′S 133°14.3′E, 19 May 1997, stn NT97/003, W.F. Ponder, V. Kessner and D.L. Beechey. AMS 345710 (40 wet); Black Jungle Springs, 13°3′S 132°9.86′E, 17 Aug 1994, stn: NT7, W.F. Ponder, G. Wilson and V. Kessner. AMS 345773 (40 wet); Leech Lagoon, between Katherine and Mataranka on Stuart Hwy, 14°38.14′S 132°37.51′E, 23 June 1996, stn: NT96/36, W.F. Ponder and D.L. Beechey. AMS 345778 (100 wet); Surprise Creek, S of Boroloola, W Gulf of Carpentaria, 16°51.39′S 137°13.02E, 24 Aug 1994, Stn NT:34, W.F. Ponder, G. Wilson and V. Kessner.

*Queensland (north-west)*
AMS 345641 (500 wet); Harris Lake, S of Burketown, on road to Normanton, 17° 48.67′S 139°33.36′E, 29 May 1997, stn NA97/070, W.F. Ponder, V. Kessner and D.L. Beechey. AMS 345645 (20 wet); Gregory River, on Riversleigh to Lawn Hill road, 19°1.11′S 138°43.56′E, 27 May 1997, stn NA97/056, collectors as for 345641.

AMS 345688 (100 wet); Billabong beside Norman River, at Gulf Development Road, 17°51.4'S 141°8.11'E, 30 May 1997, stn NA97/083, collectors as for 345641. AMS 345692 (50 wet); billabong on Burke Development Road, NW of Marlborough Yard, 16°5.46'S, 142°41.17'E, 3 June 1997, stn NA97/121, collectors as for 345641. SAMA .D19034 (5 wet); Beames Brook, 37.5 km N of Gregory Downs on road to Burketown, 27 April 1988, W. Zeidler. SAMA D19036 (13 wet); Gregory River, at ford 2 km WNW of Riversleigh Homestead, 29 April 1986, J.A. Forrest. SAMA D19037 (15 wet); Gregory River, 2 km WNW of Riversleigh Homestead, 26 April 1986, J.A. Forrest.

*Western Australia*

AMS 144782 (29 wet); Packsaddle Swamp, Kunanurra, 7 May 1978, J.C. Walker and J. Stoddart. AMS 144783 (60 wet); Perth, Coogee, Melaleuca swamp S of Troode Street, 22 Dec 1971, W.F. Ponder and G.W. Kendrick. AMS 144797 (20 wet); Murchison River, at bridge N of Geraldton, on main Northern Hwy, 7 Jan 1972, W.F. Ponder. AMS 345153 (25 wet); Murchison River, Four Mile Pool, below North West Coastal Hwy, at bridge, 27°49.66'S 114°41.5'E, 01 Sept 1989, stn 122, V. Kessner. AMS 345154 (8 wet); Pilbara region, upper part of Dales Gorge, Fortescue Falls area, 50 km SE of Wittenoom Gorge, 22o 25'S 118o 41'E, 15 Sept 1987, stn P12, W.F. Ponder and W. Edgecombe. AMS 345155 (14 wet); Pilbara region, Shay Gap Pool, 20°30'S 120°9'E, 18 Sept 1987, stn P21, W.F. Ponder and W. Edgecombe. AMS 345157 (1 wet); Pilbara region, Skull Springs, E of Nullagine, 21°53'S 121°0'E, 17 Sept 1987, stn P18B, W.F. Ponder and W. Edgecombe. AMS 345158 (4 wet); Pilbara region, first spring behind Sandfine, 19°47.25'S 121°20.75'E, 18 Sept 1987, stn P23, W.F. Ponder and W. Edgecombe. AMS 345162 (60 wet); Pilbara region, Dampier Gorge, main seepage past Asbestos Mine, near Wittenoom Gorge, 22°21'S 118°27'E, 14 Sept 1987, stn P11, W.F. Ponder and W. Edgecombe. AMS 345165 (8 wet); same details as for 345154. AMS 345419 (60 wet); Calico Springs on track to Bungle Bungles, 17°25'S 128°11'E, 11 July 1988, stn K21, W.F. Ponder. AMS 345425 (60 wet); Saddler Spring, N of King Leopold Range, on Mt Bell road, 17°9'S 125°28'E, 5 July 1988, stn K14A, W.F. Ponder. AMS 345433 (60 wet); Palm Yard Spring, Bungle Bungles National Park, 17°15'S, 128°15'E, 12 July 1988, stn K50, W.F. Ponder. AMS 345708 (5 wet); spring N of Brolga Springs, N of Ning Bing Ranges, 14°49.64'S 128°32.23'E, 28 June 1996, stn NT96/72, W.F. Ponder, A.C. Miller, D.R. Beechey and V. Kessner. AMS 345709 (100 wet); arm of Lake Argyl at Kununurra, 15°47.21'S 128°44.26'E, 28 June 1996, Stn NT96/85, collectors as for 345708. AMS 345752 (100 wet); Marglu Billabong, Parry Lagoons Nature Reserve, 20 km SE of Wyndham, July 1 1996, stn NT 96/93, W.F. Ponder and V. Kessner. AMS 345801 (20 wet); spring 9 km N of Brolga Springs, 14°49.68'S, 128°31.97'E, 29 June 1996, stn NT 96/75, collectors as for 345708. AMS 345900 (200 wet); large unnamed spring 2 km N of Brolga Springs, 14°52.86'S 128°33.65'E, 28 June 1996, stn NT96/71, collectors as for 345708. AMS 345901 (300 wet); Brolga Springs, 14o 53.64'S 128o 34'E, 29 June 1996, stn NT96/74, collectors as for 345708. AMS 345902 (200 wet); near Long Spring, N of Ning Bing Ranges, 14°53.54'S 128°38.53'E, 29 June 1996, stn NT96/77, collectors as for345708. AMS 345903 (100 wet); billabong, Point Springs, Point Spring Yard, Weber Ranges, 15°24.51'S 128°53'E, 30 June 1996, stn NT96/85, collectors as for 345708.

*Shell* (Figs.3 & 5, shells nos 5 & 6; 4, 6, 11-14):

Original description "Shell white, discoid, compressed, striated by lines of growth. Spire sunken a little below the last whorl. Volutions 4, equally convex above and beneath; the last in adult specimens carinated, not very acutely, a little below the middle. Lower surface sunken in the centre about as much as the upper. Aperture almost horizontal. Greatest diameter 5 millim., height 1¼." (Smith, 1883).

It may be added, that the syntypes are not much depressed (having a/b 3.07-3.68), their right side (upper of Smith) is distinctly more sunken than the left, the periphery varies from subangular to acutely angled with traces of a fringe, and spiral sculpture was undetectable even after careful cleaning. Rather than white, fresh shells from Smith Point are translucent and weakly corneous.

*Dimensions of selected syntypes:*

|         | whorls | diameter (mm) | a/b  |
|---------|--------|---------------|------|
| Largest | 3.85   | 4.21          | 3.45 |
|         | 3.65   | 4.14          | 3.44 |
|         | 3.60   | 4.14          | 3.42 |
| smallest | 3.55  | 3.49          | 3.07 |

The other material from the Cobourg Peninsula (234 specimens in 9 samples) includes larger and more depressed shells, to nearly 7 mm diameter with 5 whorls and a/b of 5.5. For two samples that include a wide size-range of shells, plots of whorls against diameter (Fig. 11) and a/b against diameter (Fig. 12) show the syntypes of *G. essingtonensis* occupying a central area in a continuous distribution of values, apparently for a single species. Shape of whorls more or less as described by Smith, evenly curved on either side, though usually more convex on right side; periphery rounded in small shells, becoming increasingly angular and sometimes developing a fringed keel, usually about mid-whorl. Some shells have the lip deflected to such an extent that it is attached entirely to the left side of mid-whorl. Lip commonly thin and obtusely angled, but sometimes rounded and thickened; a thickened lip is present in some specimens of only medium size, suggesting a temporary cessation of growth. Weak spiral striae present in some specimens, cutting the transverse ridges to form spiral rows of short riblets.

In the material from outside of the Cobourg Peninsula, shell shape varies widely and apparently continuously, from depressed with a keel and fringe to high-whorled with only an obtuse angle (a/b from about 3.0 to nearly 4.5). Spiral sculpture also varies widely, within and between samples, from so weak as to be scarcely perceptible on even a dry shell, to obviously striate and ridged, and sometimes reticulate. In some samples the presence of strong spiral sculpture on high-whorled shells produced a resemblance to *G. hesperus*; such specimens were classified as *G. essingtonensis* because their left side was not deeply concave and their prostate lobes were more numerous.

In samples from three areas separated from the main area of origin of the material, these shell characters were noted. WA, George Gills Range: a/b to 3.9,

subangled to distinctly keeled, spiral striae and ridges producing reticulate pattern in some individuals. WA, the eastern Pilbara: a/b to 4.5, subangled to acutely angled and fringed, spiral striae and ridges with projecting periostracum in some individuals. WA, West coast: a/b to 4.3, angle obtuse to acute, no fringe seen, spiral striae and ridges in some individuals.

*Anatomy* (Figs 28 B, 32): In specimens from the Cobourg Peninsula pigmentation was no more than a diffuse brownish grey along kidney and uterus, and more commonly the mantle was unpigmented apart from a mid-anterior brown patch (60 of 205 animals from 8 samples). Kidney non-septate (total n = 8, from 5 samples). Intestine either with posterior loop (n = 6) or without (n = 11) (total n = 17 from 6 samples). Copulatory organ as described for *G. gilberti*; penis attached at apex of sheath (total n = 11, from 6 samples). In immature snails of 2 to 4 mm diameter, from the Cobourg Peninsula, the site and mode of development of the penial stylet were as described for *G. gilberti*. Prostate of 17-22 primary lobes (mean 19.8, n = 12, from 7 samples), of which one or two may be bifid. Bursa copulatrix; shapes elongate club (n = 5) or tapering (n = 5) (total n = 10, from 6 samples). Seminal vesicle of 6 to 10 spinous convolutions (total n = 7, from 6 samples). Ovotestis of about 18 to 25 lobes in approximately 2 rows (n = 7, from 5 samples).

*Radula* (2 snails from Smith Point, AMS 144772, of about 4.5 mm diameter): maximum dimensions of ribbon 0.80 X 0.16 mm, formula 15 or 16-1-15 or 16, number of transverse rows about 225. Central tooth bicuspid, lateral/marginal teeth with 3 dominant cusps, of which the mesocone is slender, acutely pointed and about twice as long as the endocone and ectocone. Additional minor cusps, interstitial and lateral, were evident only in the few outermost teeth. Minor cusps were much more conspicuous in the radula of *G. essingtonensis* described by Burch & Jeong (1984) according to SEM. However, this material was from the Bow River in eastern WA, an area from which all the *Gyraulus* material examined during the present study is identified as *G. hesperus*.

No substantial difference from the foregoing account was detected in the soft parts of snails from the other samples listed here (at least one examined from each sample). Body pigmentation (Fig. 28 B) varied from none except in the eyes to dark greyish black in the head/foot and tentacle cores, and in the mantle along the kidney margins, in a diffuse zone on the right side following the uterus and a narrow band along the anterior margin. A brown patch varying in tint from orange to purplish was present in the mid-anterior mantle roof of some snails in many samples from Queensland, northern NT and north-eastern WA. Patch frequency reached 93% in AMS 345773, NT, Leech Lagoon, n = 40. The patch was lacking from all snails examined from George Gills Range (n = 80) and it was present in specimens from only one locality in the eastern Pilbara (AMS 345162). In all those copulatory organs mounted for microscopical examination (n = 18 from 15 localities), the penis was clearly attached to the apex of the sheath, as appeared to be so too in the unmounted copulatory organs examined from all samples. Prostate lobes 13 to 25 (Fig. 32) in snails from NT, WA and north-western QLD. The smallest number of 13 was observed in two snails from the George Gills Range, but another from here had 19.
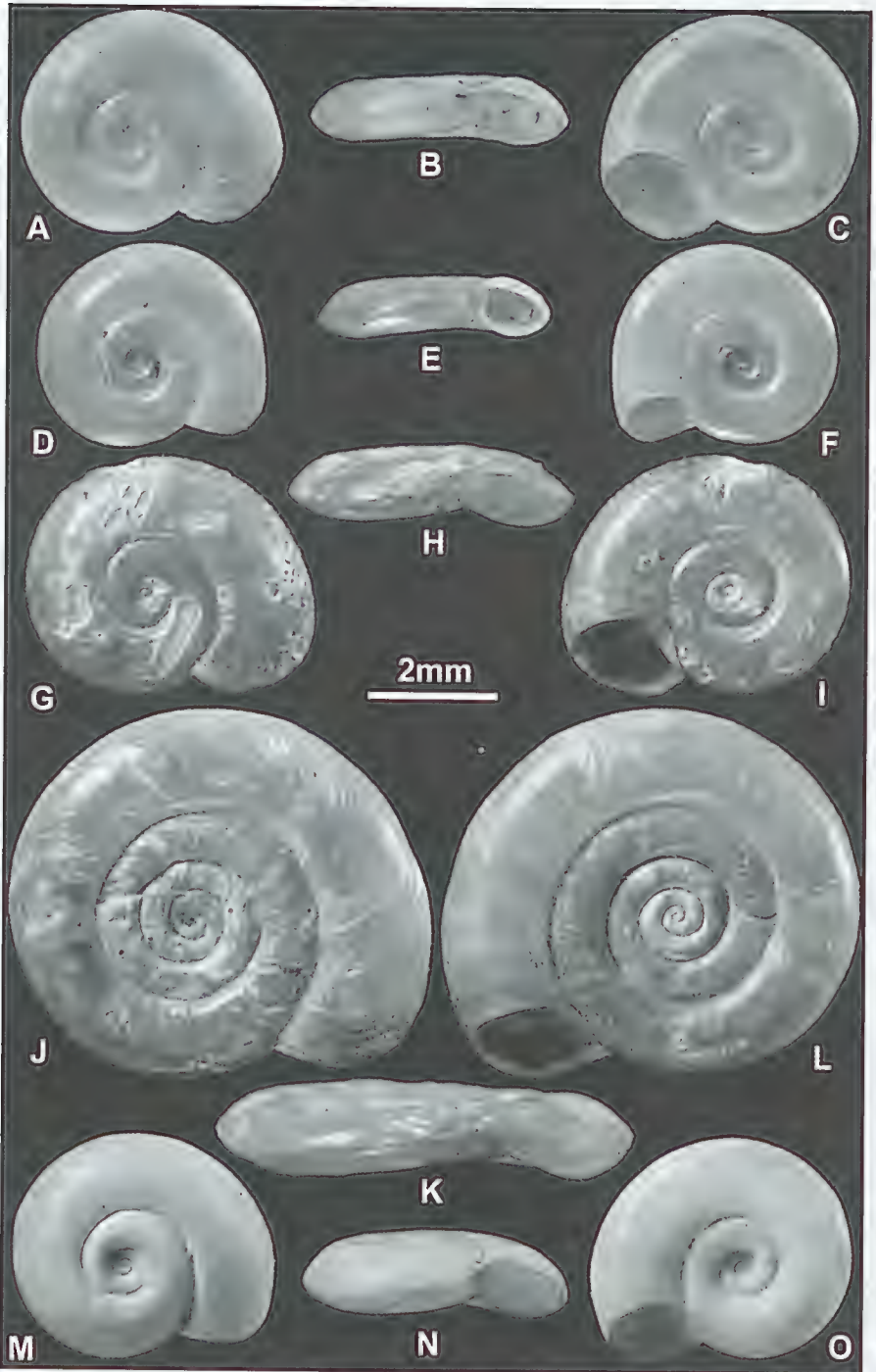
**Figure 14.**
*Gyraulus (G.) essingtonensis.* **A-F**, two syntypes, BMNH41.10.12.159-67. **G-I**, topotypical example from Smith Point, Cobourg Peninsula, AMS 144774. **J-L**, from Reef Point, Cobourg Peninsula, AMS 144777. **M-O**, from Murchison River, WA, AMS 144797.
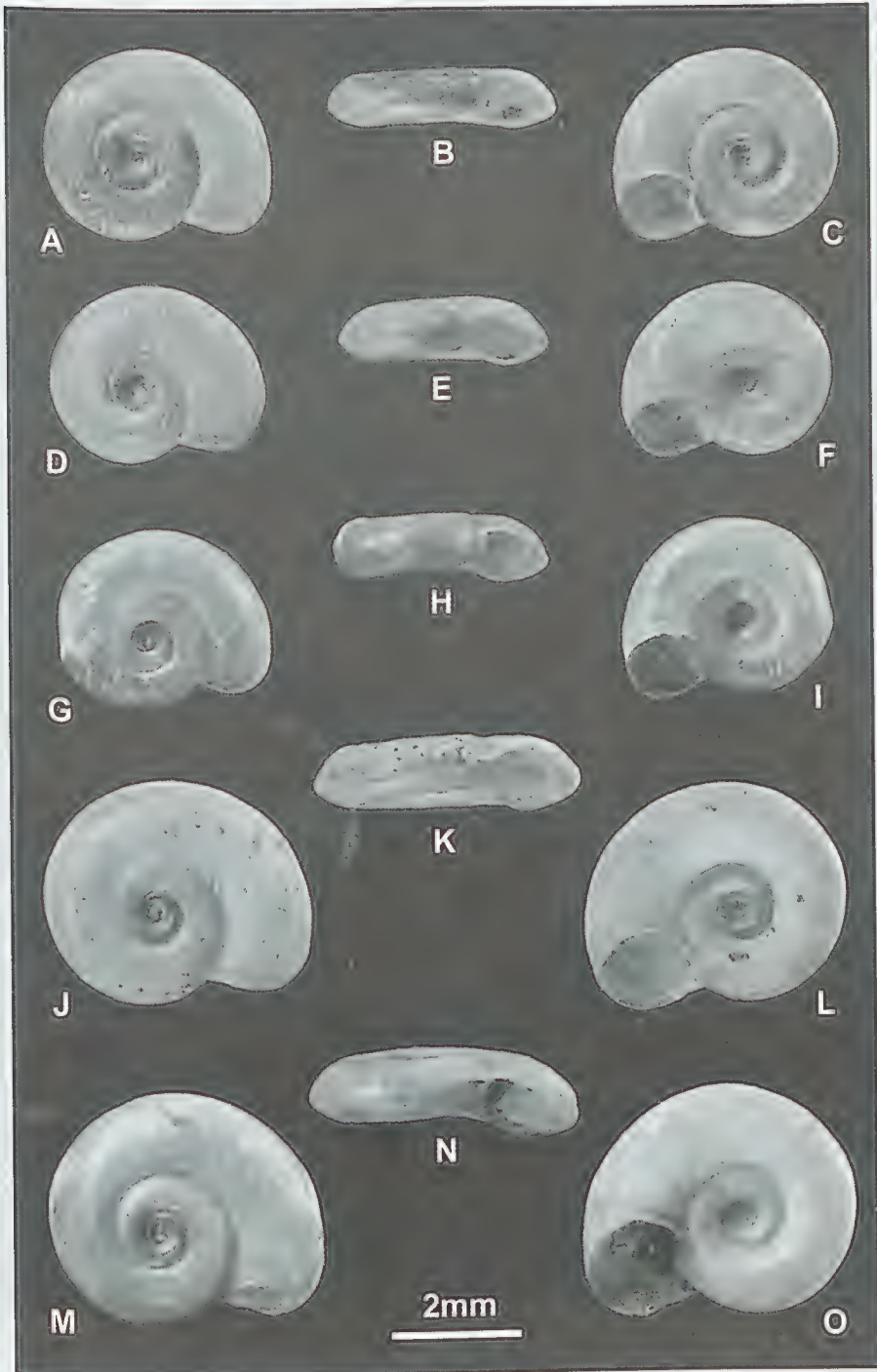
**Figure 15.**
A-F, *Gyraulus (G.) hesperus*, two syntypes, AMS 100594. **G-I**, *G. hesperus* from Timber Creek Top Springs Road, NT, AMS 144757. **J-L**, *G. (G.) coranus*, probable syntype, AMS 002153. **M-O**, *G. (G.) coranus*, syntype, SAMA D5130.

*Comparison with other taxa:* With respect to the material of *Gyraulus* from NT and WA seen by the author, *G. essingtonensis* differs from *G. hesperus* in its more depressed shell, which may be acutely angled (rather than only obtusely angled), flat or only shallowly concave left side, generally weaker spiral sculpture, and the larger number of prostate lobes (averaging about 20 rather than 15). See further under Remarks.
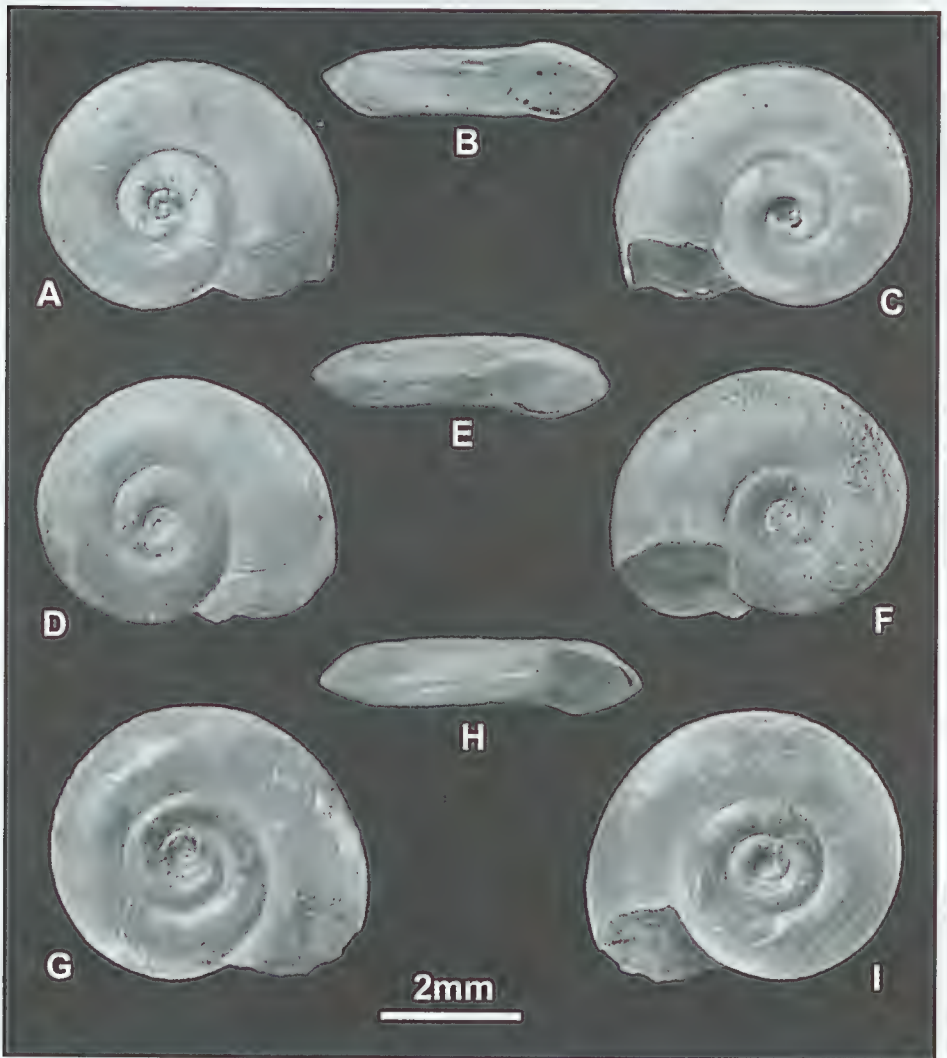


**Figure 16.**
**A-C**, *Gyraulus (G.) daemeli*, lectotype, ZMB 13223. **D-F**, *G. (G.) planissimus*, from Cape York, syntype, ZMB 18239. **G-I**, *G. (G.) planissimus*, from Rockhampton, syntype, ZMB 102385.

*Remarks:* According to the morphological data currently available it seems practicable to divide all the material of *Gyraulus* seen from NT and WA into just

the two taxa *G. essingtonensis* and *G. hesperus*. But although there are marked differences between the shell forms characteristic of these species, some lots of snails had to be classified with doubt, as variation in both shell form and number of prostate lobes appears to be continuous. Particular difficulty was experienced with some samples from north-west Queensland, in which the range of shell form was wide, yet only a few individuals appeared to be fully grown. The strongest indication of sympatric occurrence of the two species was seen in a sample from near Mataranka in NT (AMS 345700), which included a few empty shells with slowly increasing whorls resembling *G. essingtonensis* and a much larger number of complete snails most similar to *G. hesperus*. However, the whitened appearance of the *G. essingtonensis* shells suggests they are considerably older, and so there might have been a temporal succession of the two species in this habitat. Generally these two taxa appear to be geographically separated, as *essingtonensis* alone was identified in some areas that are comparatively well-sampled, e.g. Cobourg Peninsula, and the lower Ord River basin and Ning Bing Ranges area. *G. essingtonensis* was found infrequently, if at all, in the areas where most of the localities for *G. hesperus* are situated. Further evidence is needed to validate these taxa as distinct species, and to distinguish *G. essingtonensis* from taxa named from the eastern coastal region, and considered below.

When Smith described *Planorbis essingtonensis* he had for comparison material from only 4 Australian localities, according to his text, all near the east coast and situated at least 6800 km from Port Essington (disregarding material of doubtful provenance, identified as *P. obtusus* and *P. spirorbis*). Smith's characterisation of *essingtonensis* may be summarised as: more depressed than *gilberti* and *macquariensis*, more acutely keeled than *macquariensis* and less so than *fragilis* (= *P. brazieri* Clessin), lacking spiral striae which are present in both *gilberti* and *fragilis*. When variation in depression is viewed as a plot of flatness index a/b against (a) (Fig.13), the syntypes of *macquariensis* lie at or just below the lower limit of distribution of *essingtonensis*, and two syntypes of *gilberti* are further below. However, these differences are perhaps insignificant in relation to the wide range of variation attributed to *gilberti* and *macquariensis* in this paper. The representative specimens of *brazieri* Clessin (= *fragilis* Smith) are larger than any syntype of *essingtonensis*, their distribution in Fig. 13 conforms fairly closely to that of the larger specimens of *essingtonensis* now available; though the shell of *fragilis* is more acutely angled. Presence or absence of spiral sculpture is not consistent enough to serve as a character for distinguishing any of these taxa; wide variation was observed among individual shells from single collecting sites in the Cobourg Peninsula as well as from east of the Great Dividing Range.

Given this variation in shell shape and microsculpture, and since no distinguishing anatomical character was found, it could be that *essingtonensis* and *gilberti* (with its possible synonyms *brazieri*, *fragilis* and *macquariensis*) are conspecific. *G. essingtonensis* is retained here as a distinct species for three considerations: little gene-flow seems possible between the snail populations of the Cobourg Peninsula and eastern Australia, no specimen seen of *essingtonensis* is quite so acutely angular as are some eastern populations (e.g. *G. waterhousei*), and the segregation of *G. essingtonensis* allows a focused comparison with *G. hesperus*.

*Distribution:* NT – Cobourg Peninsula, Arnhem Land, Roper River basin, coast of western Gulf of Carpentaria, George Gills Range. NT/SA border – western Lake Eyre Basin, Finke River area [if *G. coranus* Iredale is conspecific]. QLD (northwest) – southern Gulf of Carpentaria region. WA – lower Ord River, Ning Bing Ranges area, Leopold Ranges, the eastern Pilbara, western coast (Coogee and Murchison River).

### *Gyraulus (G.) fragilis* of authors

*Planorbis fragilis* 'Brazier', Smith, 1883, see under *Gyraulus brazieri*.
*Planorbis fragilis* (Brazier), Smith – Tate, 1896, see under *Gyraulus coranus*.

### *Gyraulus (G.) gilberti* (Dunker, 1848)
(Figs 3 and 5, shell no. 9; 4, 6, 8-10, 13, 17 A-C, 23-29, 31, 32)

*Planorbis gilberti* Dunker, 1848: 40-41; - Sowerby, 1878: pl. 5, fig. 37a, b [non Dunker]; - Tate & Brazier, 1882: 559; - Smith, 1883: 294, pl. 6, figs 30-32; - Clessin, 1885: 186, pl. 28, fig. 5; - Tate, 1896: 216 [in remarks under *P. fragilis*], pl. 19, fig. 22; - Fielder, 1896: 140.
*Glyptanisus gilberti* – Iredale, 1943: 226; - Durie, 1953: 218, fig. 12, pl. 2.
*Gyraulus gilberti* – Brown, 1981: 73, fig. 6b; - Smith, 1992: 269.
*Planorbis macquariensis* Smith, 1883 [see under *Gyraulus macquariensis*].
*Planorbis brazieri* Clessin, 1885, new name for *Planorbis fragilis* Smith, 1883 [see under *Gyraulus brazieri*].
*Planorbis daemeli* Clessin, 1885 [see under *Gyraulus daemeli*].
*Planorbis planissimus* Clessin, 1885 [see under *Gyraulus planissimus*].
*Glyptanisus idenus* Iredale, 1943 [see under *Gyraulus idenus*].
*Glyptanisus speranus* Iredale, 1943 [see under *Gyraulus speranus*].
*Glyptanisus stabilis* Iredale, 1943 [see under *Gyraulus stabilis*].
*Gyraulus* sp. Shea, 1995: 5, fig. 13.

*Type locality:* New Holland, restricted to Brisbane district by Smith (1992, referring to Iredale, 1943).

*Type materials examined:* BMNH 1969 146, syntypes; 3 dry shells [including one figured as 'holotype' by Brown, 1981].
*Other material examined:*
**Queensland**
BMNH 59.11.9.15 (9 dry); Brisbane Water, freshwater lagoon, August 1847; Voyage of 'The Rattlesnake', specimen no. 383. AMS 144855 (7 wet); Plane Creek, 6.4 km (4 miles) S of Sarina, 9 Sept 1970, W.F. Ponder and J.B. Burch. AMS 144856 (40 wet); 129 km (80 miles) S of Sarina on the Sarina-St Lawrence Highway, 9 Sept 1970, W.F. Ponder and J.B. Burch. AMS 144857 (32 wet); 13 miles (21 km) north of Gympie on Highway 1, overflow from Curra Creek, lagoon, 3 Sept 1970, W.F. Ponder and J.B. Burch. AMS 144 859 (100 wet); 27 miles (43 km) north of Gympie on Highway 1, from lilypads in pool, 3 Sept 1970, J.B. Burch and P.H.
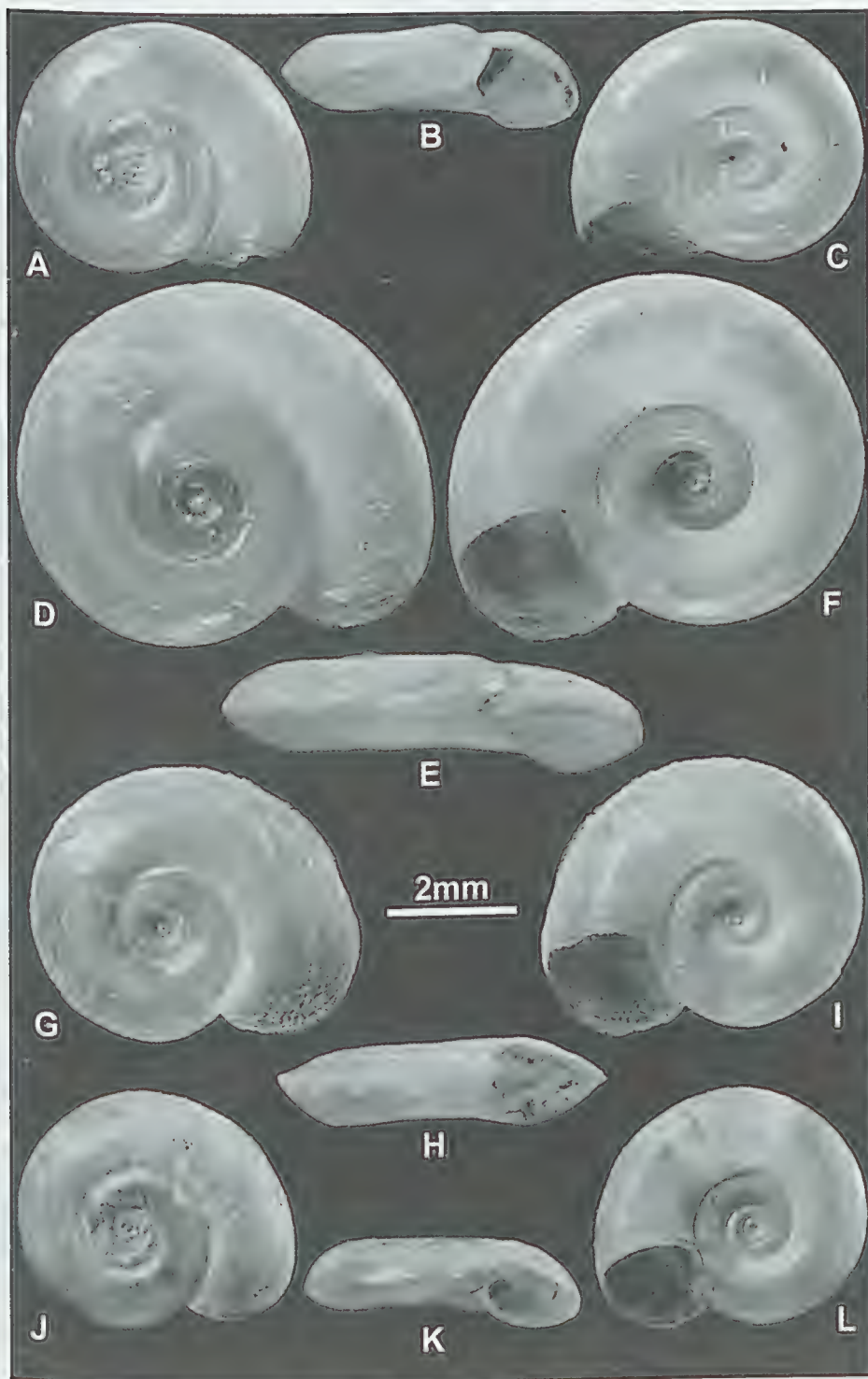
**Figure 17.**
A-C, *Gyraulus (G.) gilberti*, syntype, BMNH 1969146. **D-I**, *G. (G.) idenus*, two syntypes, AMS 033768. **J-L**, *G. (G.) macquariensis*, syntype, BMNH 43.9.20.55-60.

Colman. AMS 144860 (2 wet); Pioneer River, 26 km (16 miles) from Mackay, 30 April 1975, W.F. Ponder, J.B. Burch and P. H. Colman. AMS 144861 (23 wet); Boyne River at Gayndah (see under *G. idenus*). AMS 144864 (9 wet); Nebo Creek on Nebo-Collinsville road, 5 May 1975, collectors as for 144860. AMS 144865 (75 wet); Cooper Creek on Nebo-Collinsville road, at turn-off to Homevale, Mt Britton, 5 May 1975, collectors as for 144860. AMS 144866 (50 wet); Deacons Creek on Bruce Highway, between Maryborough and Gympie, 9 May 1975, collectors as for 144860. AMS 144867 (15 wet); Myrtle Creek on Bruce Highway, about 8 km (5 miles) N of Proserpine, 4 May 1975, collectors as for 144860. AMS 144869 (20 wet);  Lethe Brook, 5 km S of Proserpine on Bruce Highway, 30 April 1975, collectors as for 144860. AMS 144870 (6 wet);  Boggy Creek, 60 km S of Cooktown on the Cooktown-Mareeba road, 22 Oct 1975, P.H. Colman. AMS 144871 (40 wet);  Mowbray River, 4.3 km from Highway, [16°32'S 145°28'E; P.H. Colman, in litt. to author], 1 Oct 1980, P.H. Colman. AMS 144872 (16 wet); large ditch about 13 km (8 miles) S of Rockhampton on Bruce Highway, 22 July 1969, W.F. Ponder. AMS 144873 (30 wet); water hole, SW of Miriam Vale, 11 km (7 miles) NNW of Bororen, 23 July 1969, W.F. Ponder, L. Moor and B. Baker. AMS 144984 (55 wet); north of Barcaldine, about 2.3 km northeast of Edgbaston, 22° 43' 30"S 145°25' 30"E, large spring on open plain, snails from spring head in bamboos, 26 Sept 1984, W.F. Ponder and P.H. Colman [Station 72B in Ponder & Clark, 1990: Fig. 1, Appendix 1]. AMS 144989-91 (250 wet);  Belinda Spring, Salvator Rosa Section of Carnarvon Gorge National Park, 29 Sept 1984, W.F. Ponder and P.H. Colman. AMS 144992 (65 wet);  Major  Mitchell Springs, Salvator Rosa Section of Canarvon Gorge National Park, 29 Sept 1984, W.F. Ponder and P.H. Colman. AMS 144996 (35 wet); Creek NE of Julia Creek township, 19°35'S 142°15'E, 15 Sept 1984, W.F. Ponder and P.H. Colman. AMS 345152 (4 wet); Fortuna Bore, 45 km N of Aramac on Lake Dunn Road, 22°S 145° 32'E, 31 May 1981, P. DeDekker. SAMA D19030 (50 wet); artesian spring, just S of Coreena Homestead, 32 km directly due NE of Barcaldine, 23°17'S 145°24'E, 5 May 1988, stn 13, W. Zeidler [same data as for Station Z14 in Ponder & Clark, 1990, fig. 1 and Appendix 1]. SAMA D19035 (40 wet); Carnarvon Creek, Carnarvon Gorge National Park, about 3.5 km W of Rangers' HQ, 7 May 1988, W. Zeidler.

*New South Wales*
AMS 144799-802, -804, 805, -826, -828, -833 (total of 225 wet); all collecting stations in south-eastern  NSW (see under *G. macquariensis*).

*Shell* (Figs 3-6, 8-10, 13, 17 A-C, 23-25, 26 B):
Original description  (translated from the Latin) "A *Planorbis* with the shell depressed, somewhat lens-shaped, pale corneous, polished, translucent, upper surface fairly flat, umbilicate beneath; whorls 4, on both sides obtusely angled; below the middle acutely keeled; aperture oblique, sub-cordate; upper margin projecting. Diam. max. 2 ½ lines [5.3 mm]; height ¾ line [1.6 mm]. Reported from New Holland by the celebrated Mr Gilbert." (Dunker, 1848).

E. Smith (1883) remarked of the syntypes, that obtuse angulation is more conspicuous on the under (left) side than the upper side, the keel is situated below mid-whorl only in the last whorl and especially towards the aperture, and all the specimens have, to a small extent, fine spiral striae.
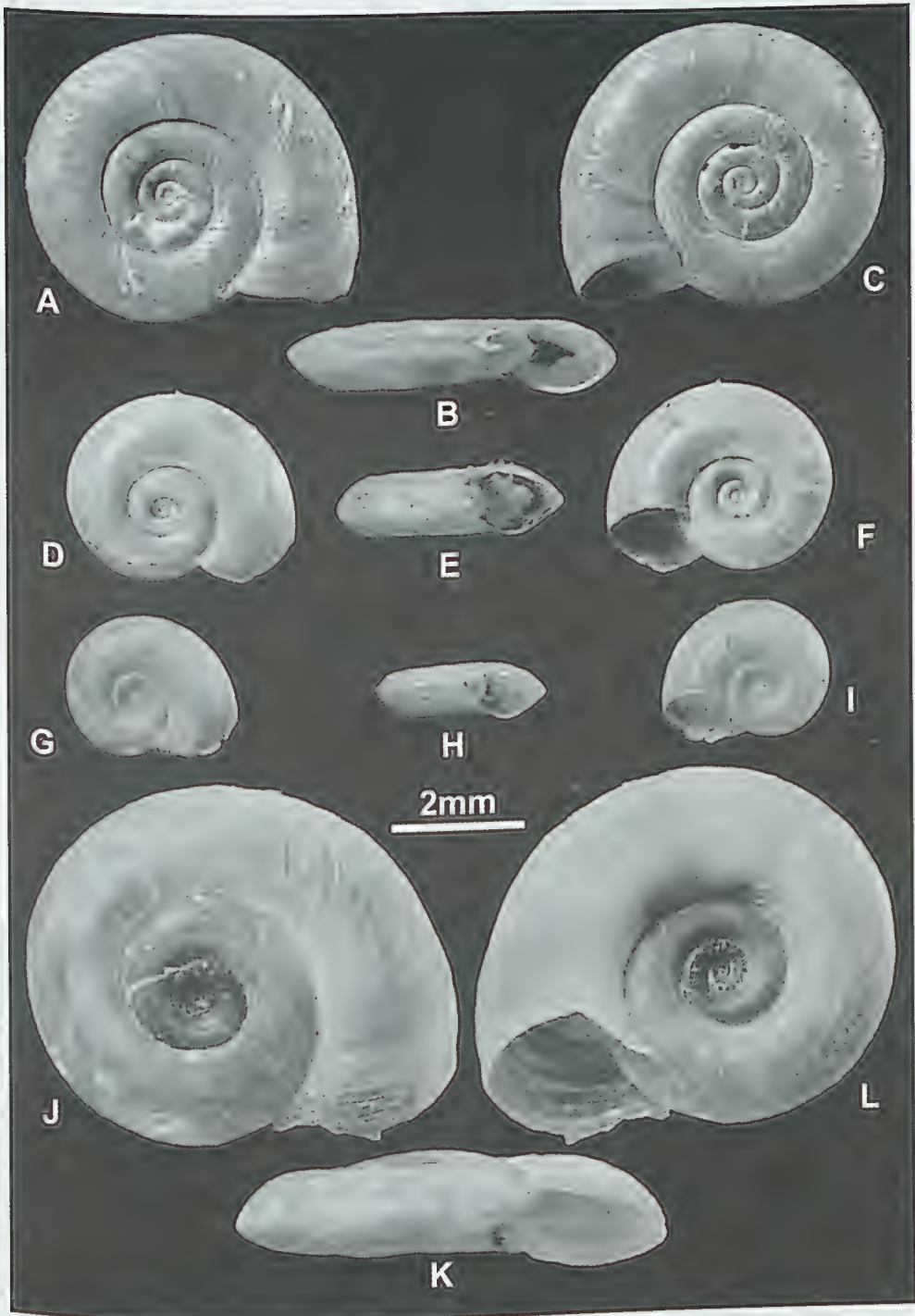
**Figure 18.**
A-C, *Gyraulus (G.) waterhousei*, from near Grafton, NSW, AMS 144815. D-F, *G. (G.) metaurus*, syntype, AMS 051737. G-I, *G. (G.) ordessus*, holotype, AMS 100621. J-L, *G. (G.) speranus*, syntype, AMS 000263

The observations may be added, that the largest syntype (Fig. 17 A-C) is about 5.5 mm diameter (lip slightly damaged), with 3.8 whorls, which increase rapidly and are high in proportion to breadth, giving a/b 3.15. This syntype's peripheral angle is keeled only in parts, and is situated a little to left of mid-whorl, with remnants of fringe; left side concave, surface of whorls strongly curved to subangular; last ¾ whorl deflected and peristome attached mostly to

left of the keel; microsculpture of weak spiral ridges on right side of whorls 1 and 2, last whorl on both sides with spiral striae, dividing the fine transverse ridges into short riblets. The two smaller syntypes are similar, with their lips more damaged. The example of *Planorbis gilberti* figured by Sowerby (1878) appears to be a different species, as pointed out by Clessin (1885), in which the keel is almost basal and the whorls are comparatively high. Clessin's own figure of *gilberti* seems derived from that of Smith (1883).

*Dimensions of syntypes:*

| whorls | diameter (mm) | a/b |
|--------|---------------|------|
| 3.8 | 5.52 | 3.15 |
| 3.50 | 4.07 | 3.13 |
| 3.85 | 4.83 | 3.20 |

The syntypes of *G. gilberti* were compared in respect of the variables shell diameter, whorls and flatness index (a/b), with the most closely topotypical material available, collected in the Gympie area of SE Queensland, (samples AMS 144857, -59, -66) and in the Carnarvon Gorge National Park (AMS 144990). Also compared were types or representative shells of *G. brazieri* (= *fragilis* Smith), *daemeli* and *planissimus*, all considered to be synyms of *G. gilberti* in the present work. The syntypes of *gilberti* have about one-half a whorl less than some shells of similar diameter, including a syntype of *planissimus* and one of *brazieri* (Fig. 23). Yet the entire distribution of values in this plot appears sufficiently compact and continuous to be acceptable for a single species, and its area would contain also all the 40 shells measured from 22 other samples identified as *G. gilberti*, comprising 13 from the coastal area of Queensland between Miriam Vale and Cooktown, 5 from Carnarvon Gorge National Park, 3 from the Barcaldine area and one from further to the north-west (AMS 144996, Julia Creek). A similarly compact distribution was given by the flatness index (a/b) plotted against diameter for the same group of shells. With regard to species named by Clessin (1885), the whorl number of the lectotype of *daemeli* (Fig. 23) is low relative to its diameter, whereas one type of *planissimus* (Fig. 23) and several of *waterhousei* (not figured) have over ¾ whorl more at about the same size. Figure 24 shows

that the syntypes of *gilberti* lie within the distribution of the syntypes of *idenus* and specimens from Gayndah (AMS 144861); this distribution too seems consistent with the view that the specimens are all conspecific. Their values for (a/b), plotted against shell diameter, gave similarly compact distributions.

The small range of variation in a/b of 3.13 to 3.20, displayed by the syntypes of *G. gilberti* is much extended among the specimens of similar size from the Gympie area, for which values vary continuously from about 3 to over

4.2 (Fig 25), usually with a corresponding increase in the acuteness of the peripheral angle, which is fringed in most large specimens. However, the extremely depressed shells from one of the Barcaldine springs (SAMA D19030, near Coreena) are angled only obtusely (Fig. 25 E). Some shells have the angle placed well towards the right side; of these some resemble *daemeli* (Fig. 25 C) while others are more like *waterhousei* as figured by Brown (1981) (Fig. 25 D). On the left side, whorl shape varies from almost evenly curved to subangled. Microsculpture (Fig. 26 B) varies widely within some samples, e.g. AMS 144859, from a combination of fine transverse ridges and spiral ridges, forming rows of short riblets, to a stronger reticulate pattern, in which spiral ridges predominate; some shells have short lamellae of periostracum projecting from spiral ridges.

The two samples from northern Queensland are puzzling. A large shell from between Cooktown and Mareeba (AMS 144870) is 5.6 mm in diameter, depressed, with a/b of 3.6 and a peripheral angle, and it resembles *G. gilberti* as known from southern Queensland. But smaller shells of 3 to 4 mm diameter in the same sample, and others from the Mowbray River (AMS 144871) (Fig. 25F), have comparatively high whorls (a/b of 2.5 to 3), with the periphery rounded or only obtusely angular and with strong spiral sculpture; such shells are more like *G. hesperus*.

*Anatomy* (Figs 27-29, 31, 32): Data for specimens from north of Gympie (AMS 144859), with shells closely similar to the syntypes of *G. gilberti*. Pigmentation on mantle (n = 9) varying from none to weak brownish-grey, concentrated above the margins of the kidney and uterus, sometimes in a narrow band along the anterior border; some animals with dark grey core in tentacles (Fig. 28 A). Kidney non-septate (n = 9). Intestine either with posterior loop (n = 6), the longest reaching back over the stomach into the digestive gland, or without (n = 4). Copulatory organ (n = 8) (Figs. 27, 29 A, B) 3 mm long at shell diameter of 4.75 mm; penis sheath two to three times length of preputium, in a well extended specimen; vas deferens enters apex of sheath; penis attached at end of sheath, penis tip not swollen; penis pore opening a short distance from the tip. Penial stylet like that commonly observed in *Gyraulus* sensu stricto (e. g. Brown, 1981, fig 5 b; Meier-Brook, 1983, fig. 26), coloured orange-brown with a slender furled blade and globular, knobbed base (the stylet of *G. meridionalis* is broader with a truncate asymmetrical base). The penial stylet is usually incompletely developed in snails of less than 3.5 mm diameter. Prostate (n = 10) (Figs 31 A, 32): mean number of primary lobes 19.7, range 17-25; mean number of terminal lobes 20.6, range 18-25. Bursa copulatrix of shape varying from club spherical (n = 1), through club elongate (n = 1) to tapering (n = 6). Seminal vesicle of 6 to 8 spinous convolutions (n = 5). Ovotestis of 25 to 30 lobes, arranged in 2 or 3 approximate rows (n = 5).

The penis was immature and lacked a fully formed stylet in permanent preparations of 5 copulatory organs from snails of about 3 mm in shell diameter from north of Gympie (AMS144859). However, some snails of the same size were fully developed. In all the immature specimens the penis sheath and preputium were clearly differentiated, as were the papilla and diaphragm. The tip of the developing penis extended no further than into the base of the papilla.

A stylet was not immediately visible, but at a magnification of X400 its outline was detectable within the penis tissue, which had a brownish tint around the stylet. The cellular lining of the penis sheath adjacent to the stylet was thickened, with a brown colour due to pigmented inclusions within the cells. It appeared that the initial cuticular structure of the stylet was laid down by the folded epithelium of the penis tip, while the lining of the penis sheath contributed to the tanning process of chitinisation.

*Radula* (n = 4; snails from north of Gympie shell diameter about 4.5 mm): maximum dimensions of ribbon, length 0.818 mm, breadth 0.182 mm; formula 18(19)-1-18(19) with one or two additional rudimentary structures at the margins, transverse rows about 135. Central tooth with two sharply pointed major cusps, and one or two small denticles on either side of the crown. Inner lateral teeth with 3 major cusps, all sharply pointed; mesocone half as long again as the endocone and ectocone. Outer lateral/marginal teeth with several small denticles lateral to the ectocone. The major cusps appeared broader and more acuminate than those of *G. essingtonensis* in SEM images (Burch & Yeong, 1984).

No difference in soft parts was evident in animals from other localities listed (n = 27 to 48, according to organ, from 14 to 19 samples), including specimens from Gayndah (AMS 144861) described under *G. idenus*, in respect of the kidney, intestine, copulatory organ, bursa copulatrix, seminal vesicle and ovotestis. Pigmentation was denser in some individuals, though distributed in the same way, and some specimens from 3 samples (AMS 144856, -65 and –72) had an orange–brown patch in the mantle mid-anteriorly (28 individuals out of 73). Prostate lobes were comparatively few in snails from Carnarvon Gorge National Park (mean terminal lobes 15.2, range 11 to 18, n = 10) as well as from the Mowbray River and near Cooktown (mean terminal lobes 16.4, range 13 to 21, n = 5). The number of prostate lobes in the remaining material ranged from 15 to 22 (mean 18.0, n = 20 from 12 samples). Thus, the overall variation in number of terminal prostate lobes was rather wide: mean 17.7, range 11-26; n = 45, from 16 sites.

*Comparison with other taxa:* see under Remarks below.

*Parasites:* Laboratory-bred *G. gilberti* originating from the Brisbane area were shown by experiments (Durie, 1953) to serve as intermediate host for the stomach fluke *Ceylonocotyle streptocoelium* (Fischoeder) (Trematoda; Paramphistomatidae), a parasite of sheep and cattle. The shell representing these snails figured by Durie is depressed, acutely angled and fringed; it resembles many of the specimens of *G. gilberti* examined during the present study. This species was later cited as intermediate host for the same parasite (transferred to *Orthocoelium*) by Boray (1982) and (Boray & Munro (1998).

*Habitat:* The present material of *G. gilberti* was collected from a wide range of streams, small rivers and pools, some associated with springs; the snails were commonly taken from aquatic vegetation. Durie (1953) provides the most

extensive account of the ecology of this snail known to me. Durie observed that it occurred frequently together with *Segnitilia alphena* [probably a species of *Helicorbis*]. Both species were found in large numbers in swamps and slow-flowing streams, usually attached to grass or water weed, throughout the coastal and subcoastal regions of the eastern and southern States. Rapid repopulation of areas where water had dried out was observed. Thousands of dead snails were found in a large swamp near Brisbane when it was completely dry in Jan 1952 and drought continued until rains fell in March 1952; by July a large population of snails was again present, and many specimens of *G. gilberti* showed by marks on the shell that they had survived the period of drought. Durie commented that these snails "have a remarkably efficient means of combatting unfavourable habitat conditions". Such an ability to survive drought is in contrast to the association in Africa between *Gyraulus* and relatively stable waterbodies (see general Discussion).
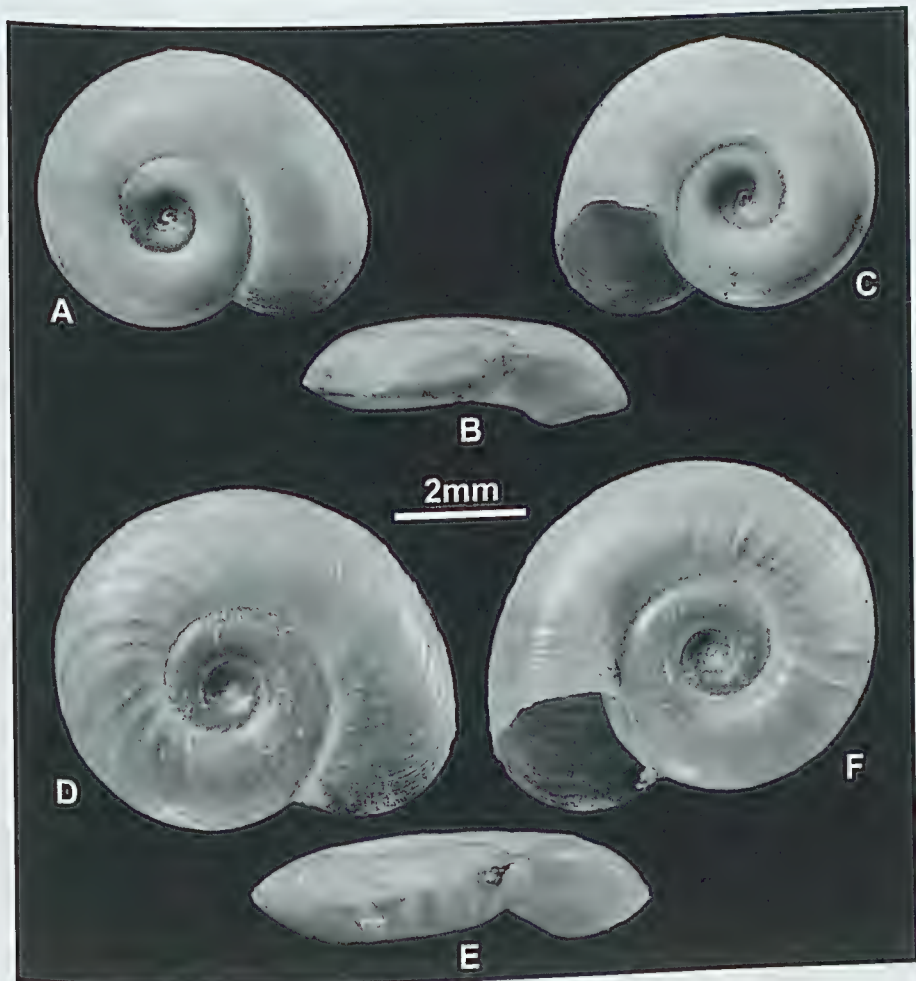


**Figure 19.**
A-C, *Gyraulus (G.) speranus*, syntype, AMS 000263. D-F, *G. (G.) stabilis*, 'holotype', AMS 100610 (probably a syntype).

*Remarks:* G. *gilberti* is the oldest named species of its genus from Australia, it predates by one year G. *convexiusculus* (Hutton, 1849) and it has line priority over G. *chinensis* (Dunker, 1848). Knowledge of the morphological variation of G. *gilberti* is important for judging which of the later described species are its synonyms. Unfortunately, no recently collected material was available from the immediate area of Brisbane, which probably includes the site of the type locality `New Holland'. Specimens with soft parts were collected most closely to Brisbane in the area from 170 to 200 km north of the present city, between Gympie and Maryborough.

According to the concept of the species adopted here, the shell of G. *gilberti* varies widely in degree of depression and angulation, and development of spiral sculpture and fringe. Of all the shell forms of G. *(Gyraulus)* seen during this study, only those of G. *hesperus* and G. *edgbastonensis* sp. n. are clearly distinct from the range of variation ascribed here to G. *gilberti*. As the range of variation in both shell and anatomy does not appear to be clearly demarcated from the variation displayed by material described under G. *isingi*, G. *macquariensis* and G. *waterhousei*, these taxa are perhaps conspecific with G. *gilberti* in addition to those listed here as synonyms.

Additional material from northern Queensland is needed in order to determine with more confidence the status of two species from Cape York, named by Clessin (1885) *daemeli* and *planissimus*, both known only from shells, and also two samples of complete snails from northern localities (AMS 144870-71, from near Cooktown and the Mowbray River). While both of Clessin's species appear unlikely to be distinguishable from G. *gilberti*, the comparatively high-whorled shells and low number of prostate lobes of the snails from the other localities suggest that they might belong to a different species, possibly G. *hesperus*.

*Distribution:* According to the present synonymy, G. *gilberti* occurs in eastern Australia, from Cape York (*daemeli, planissimus*) southwards through southern QLD (*brazieri, idenus, stabilis*) and into northern NSW (*speranus*). Most of the material reported here is from east of the Great Dividing Range; genetic relationships need to be examined to test for conspecificity with G. *gilberti* the populations in north-west QLD reported here as G. *essingtonensis* or G. *hesperus*. The distribution of G. *gilberti* possibly extends further southwards through VIC and into eastern SA, if we should include material here classified under G. *isingi*, G. *macquariensis* and G. *waterhousei* (including *caroli, metaurus* and *ordessus*).

### *Gyraulus (G.) hesperus* (Iredale, 1943)
(Figs 3 and 5, shell no. 10; 11, 12, 13, 15 A-I, 26C, 28 C, 31B and C; 32)

*Glyptanisus hesperus* Iredale, 1943: 226.
*Gyraulus hesperus* – Smith, 1992: 269.

*Type locality:* North-west Australia, Lennard River [flowing towards King Sound from the King Leopold and Oscar ranges, northwest WA].

*Type material examined:* AMS 100594, 300 dry shells registered as syntypes, from Fitzroy River, 17°31′S 123°35′E [status as syntypes questionable, since although the Fitzroy River enters King Sound and is no more than 100 km from the Lennard River, the latter locality is the only one mentioned by Iredale].

*Other material examined:*

**Northern Territory**

BMNH 41.11.24.36-50 (34 dry); Victoria River, presented by Captain Wickham. AMS 144756 (29 wet); Victoria River area, Top Springs-Timber Creek road, pond, 12.8 km west of Jasper Creek crossing, 19 May 1978, J.B, Burch and J.C. Walker, stn NT79. AMS 144757 (30 wet); Victoria River area, Top Springs-Timber Creek road, 19 May 1978, collectors as for 144756, stn NT74. AMS 144758 (1 wet); Victoria River area, Top Springs-Timber Creek road, small stream, 19 May 1978, collectors as for 144756, stn NT80. AMS 144759 (6 wet); No. 6 Bore Creek, Duncan Highway, southeast of Kunanurra, 17 May 1978, collectors as for 144756, stn NT46. AMS 144760 (12 wet); same data as for 144759. AMS 144761 (30 wet); Sydney Creek, Duncan Highway, south of Kunanurra, 16 May 1978, collectors as for 144756, stn NT42. AMS 144762 (4 wet); Duncan Highway, 9.1 km south of Nicholson/Katherine junction, 16 May 1978, collectors as for 144756, stn NT40. AMS 144763 (60 wet); Moriarty Creek, Victoria Highway, southeast of Kunanurra, 17 May 1978, collectors as for 144756, stn NT48. AMS 144764 (8 wet); data as for 144763. AMS 144765 (4 wet); Victoria Highway, 0.5 km east of West Baines River, 17 May 1978, collectors as for 144756, stn NT54. AMS 144766 (13 wet); Victoria Highway, 14.8 km east of Escarpment Creek, small stream, 18 May 1978, collectors as for 144756, stn NT64. AMS 144767 (4 wet); Crawford Creek, Victoria River Downs, 19 May 1978, collectors as for 144756, stn NT76. AMS 144768 (1 wet). Victoria River at grid ref. 413930, sheet SE52-14, 19 May 1978, collectors as for 144756. AMS 144769 (15 wet); Katherine road, 28 km east of Victoria River bridge, creek, 18 May 1978, collectors as for 144756. AMS 144781 (10 wet); Duncan Highway, 35 km south of Nicholson/Katherine road junction, creek, 16 May 1978, collectors as for 144756. AMS 345766 (1 wet); Wearyan River, W Gulf of Carpentaria, 16°10.19′S 136°45.45′E, 24 Aug 1994, stn NT31, W.F. Ponder, G. Wilson and V. Kessner. AMS 345700 (100 wet); Salt Creek at Roper Highway, 15°0.74′S 133°14.3′E, 19 May 1997, stn NA97/003, W.F. Ponder. V. Kessner and D. L. Beechey. AMS 345771 (20 wet); West Baines River at road crossing, 15°55.98′S 129°44.68′E, 2 July 1996, stn NT96/95, W.F. Ponder, A.C. Miller, D.L. Beechey and V. Kessner. AMS 345785 (30 wet); data as for 345766, stn 31B. AMS 345790 (26 wet); Dingo Springs Creek, W of Victoria River on Victoria Hwy, 15°44′S 133°59′E, 27 June 1996, stn NT96/58, W.F. Ponder. AMS 345802 (30 wet); Mulurak Rapids, Elsie Park, Roper River, 14°56.68′S 133°12.38′E, 27 Aug 1994, stn NT44, W.F. Ponder, G. Wilson and V. Kessner. AMS 345864 (50 wet); Crawford Creek, 16°16.22S 130°57.1′E, 3 July 1996, stn 96/103, W.F. Ponder, A.C. Miller, D.L. Beechey and V. Kessner. AMS 345876 (11 wet); Timber Creek, W of Victoria River on Victoria Hwy, 15°44.33′S 130°30.58′E, 27 June 1996, stn NT96/59, W.F. Ponder. AMS 345877 (60 wet); billabong beside Victoria Hwy between Timber Creek township and the WA border, 15°45.18′S 130°2.65′E, 27 June 1996, stn NT96/61, W.F. Ponder, A.C. Miller, D.L. Beechey and V. Kessner.
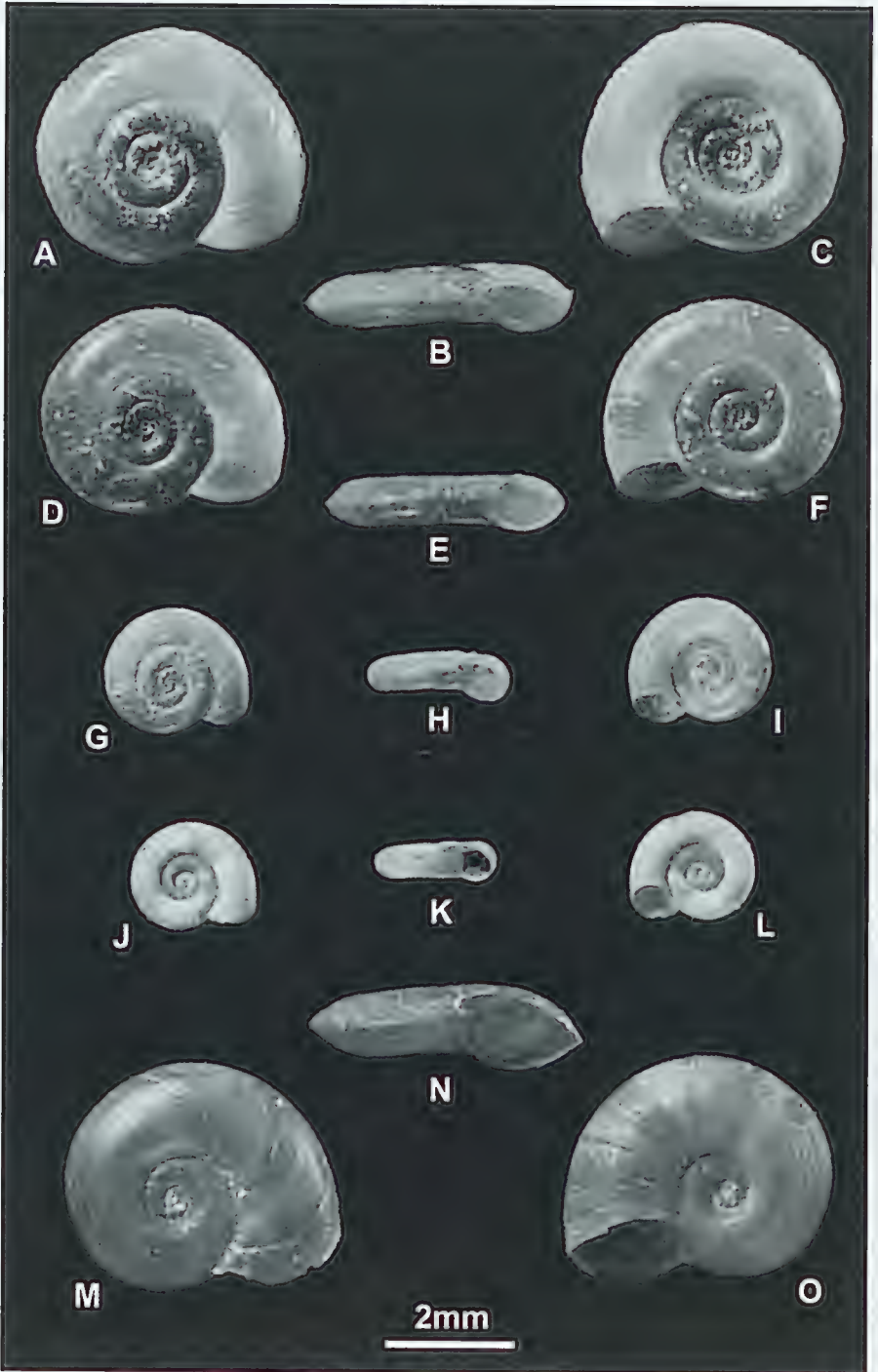
**Figure 20.**
A-F, *Gyraulus (G.) waterhousei*, two syntypes, ZMB 19019. G-I, *G. (Pygmanisus) leonatus*, syntype, AMS 051711. J-L, *G. (Pygmanisus) pelorius*, AMS 111731. M-O, *G. (Gyraulus) edgbastonensis* sp. nov., holotype, AMS 144985.
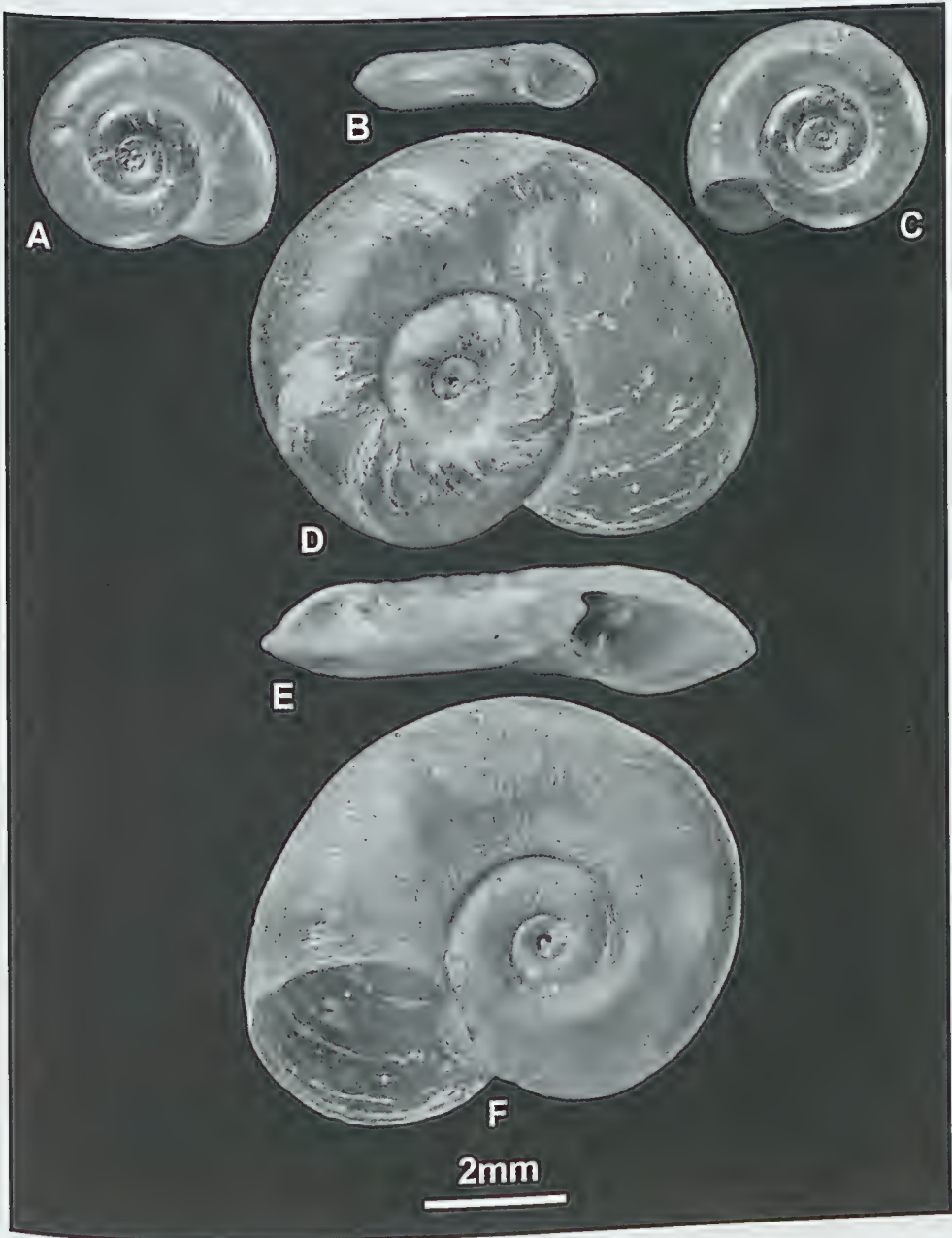
**Figure 21.**
A-C, *Gyraulus (G.) caroli*, holotype, NMV F549.  D-F, *G. (G.) isingi*, holotype, SAMA D10603.

AMS 345879 (23 wet); Creek on road to Limestone Gorge, Gregory National Park, 13 km from Victoria Highway, 15°51.83'S 130°91'E, 3 July 1996, stn NT96/101, collectors as for 345877.

*Queensland (north-west)*

AMS 345636 (1000); waterhole on Eight Mile Creek, on Karumba to Chillagoe road, 17°28.66'S 141°10.6'E, 1 June 1997, stn NA97/094, W.F Ponder, V. Kessner and D.L. Beechey. AMS 345639 (1000); billabong, 17°21'S, 138°40.21'E [between Burketown and the NT border], 25 May 1997, stn NA97/045A, collectors as for 345636. AMS 345644 (50 wet); Macadam Creek, E of Gregory Downs Station, 18°38.4'S 139°11.45'E, 27 May 1997, stn NA97/059, collectors as for 345636. AMS 345646 (20 wet); mudhole, 17°15.21'S 138°40.21'E [between Burketown and the NT border], 25 May 1997, stn NA97/045B, collectors as for 345636. AMS 345648 (30 wet); Nicholson River at Doomadgee, 17°57.64'S 138°51.06'E, 25 May 1997, stn NA97/047B, collectors as for 345636. AMS 345687 (40 wet); data as for AMS 345636. AMS 345690 (1 wet); waterhole and stream between Adels Grove and Lawn Hill Stn Homestead, 18°39.15'S 138°33.65'E, 26 May 1997, stn NA97/051, W.F. Ponder and V. Kessner. AMS 345695 (15 wet); Nicholson River at Escott, 17°44.46'S 139°25.09'E, 28 May 1997, stn NA97/065, W.F. Ponder, V. Kessner and D.L. Beechey. AMS 345699 (3 wet); Brannigan Creek on Karumba to Normanton road, 17°28.66'S 141°10.6'E, 31 May 1997, stn NA97/093, collectors as for 345695. AMS 345701 (100 wet); mudhole about 1 km E of Karumba, 17°29.66'S 140°50.6'E, 31 May 1997, stn NA97/088, collectors as for 345695.

*Western Australia*

AMS 144784 (8 wet); Forbes Beach, Ord River, Kunanurra, 6 May 1978, J. Stoddart and J.C. Walker. AMS 144785 (14 wet); North branch of Ord River, Wyndham-Halls Creek road, 13 May 1978; J.B. Burch, J. Stoddart and J.C. Walker. AMS 144786 (80 wet); tributary of Ord River, Great Northern Highway, west of Mount Ransford, 13 May 1978, stn WA27 [17°29'S 128°00'E, P.H. Colman, in litt. to the author], collectors as for 144785. AMS 144787 (90 wet); 26.8 km north of Froghollow, Great Northern Highway, small creek, 10 May 1978, stn WA12 [17°12'5 128°07'E, P.H. Colman , in litt. to author], J.B. Burch and J.C. Walker. AMS 144788 (1 wet); 141 km north of Halls Creek, Great Northern Highway, stream, 10 May 1978, stn WA13, J.B. Burch, J. Stoddart and J.C. Walker. AMS 144789 (2 wet); data as for 144788. AMS 144790 (8 wet); data as for 144788. AMS 144791 (35 wet); data as for 144788. AMS 144792 (9 wet); Froghollow Creek, Wyndham-Halls Creek road, 13 May 1978, J.B. Burch, J. Stoddart and J.C. Walker. AMS 144793 (12 wet); Cheese-tin Creek, Wyndham-Halls Creek road, 7 May 1978, J. Stoddart and J.C. Walker. AMS 144795 (1 wet); Mary River, Halls Creek-Fitzroy Crossing road, 11 May 1978, J.B. Burch, J. Stoddart and J.C. Walker. AMS 151057 (16 wet); spring SE of Fitzroy Crossing, 5.6 km N of Great Northern Hwy in Emmanuel Range, 18°47'S 126°5.5'E, 28 May 1986, stn PC59, P.H. Colman. AMS 345159 (3 wet); Pilbara region, Millstream N.P., top end of Lily Pool/Crystal Pool, 21°35.67'S 117°4'E, 14 Sept 1987, stn P7A, W.F. Ponder and W. Edgecombe [more material in 345161]. AMS 345160 (14 wet); Pilbara region, Millstream N.P., Fortescue River, top end of Palm Pool, 21°34.33'S 117°3.17'E, 14 Sept 1987, W.F. Ponder and W. Edgecombe. AMS 345161 (25 wet); data as for 345159, but from bottom end of pool. AMS 345163 (4 wet); Pilbara region, Millstream N.P., Pilbara Springs, upper site in Deep Reach Pool, 21°37.25'S 117°6.5'E, 13 Sept 1987, stn P14A, W.F. Ponder and W. Edgecombe. AMS 345164 (1 wet); Pilbara region, Millstream N.P., data as for 345160. AMS

345224 (60 wet); springs near "Date Palms", Bungle Bungles N.P., 17°17′S 128° 26′E, 12 July 1988, stn 27, W.F. Ponder. AMS 345230 (60 wet); Elimberie Spring, Oscar Plateau, Kimberley area, 17°40′S 125°3′E, 1 July 1988, stn K5, W.F. Ponder, G.E. Barnes, N.C. Lee. AMS 345421 (40 wet); "Fowl Yard", Osmond Creek, large pool, Bungle Bungles N.P., 17°16′S 128°30′E, 12 July 1988, stn K26, W.F. Ponder. AMS 345429 (100 wet); Catjuput Creek, Windjana Gorge, Leopold Downs road, 17°43′S 125°19′E, 1 July 1988, stn K7, W.F. Ponder. AMS 345436 (100 wet); Pillara Spring, Pillara Range, SE of Fitzroy Crossing, 18°20′S 125°48′E, 7 July 1988, stn K9, W.F. Ponder. AMS 345438 (22 wet);  Lennard River Gorge, Kimberley, riverbed beyond upper pool, 17°11′S 125°12′E, 7 July 1988, stn K18, W.F. Ponder. AMS 345751 (70 wet); unnamed spring at treeline near Haley's Spring, N of Ning Bing Ranges, 14°53.59′S 128°39.84′E, 30 June 1996, stn NT96/80, W.F. Ponder, A.C. Miller, D.L. Beechey and V. Kessner. AMS 345909 (17 wet); Six Mile Bore, tributary of Tunnel Creek, SE of Napier Ranges, 17°41′S 125°15′E, 1 July 1988, stn K6, W.F. Ponder.
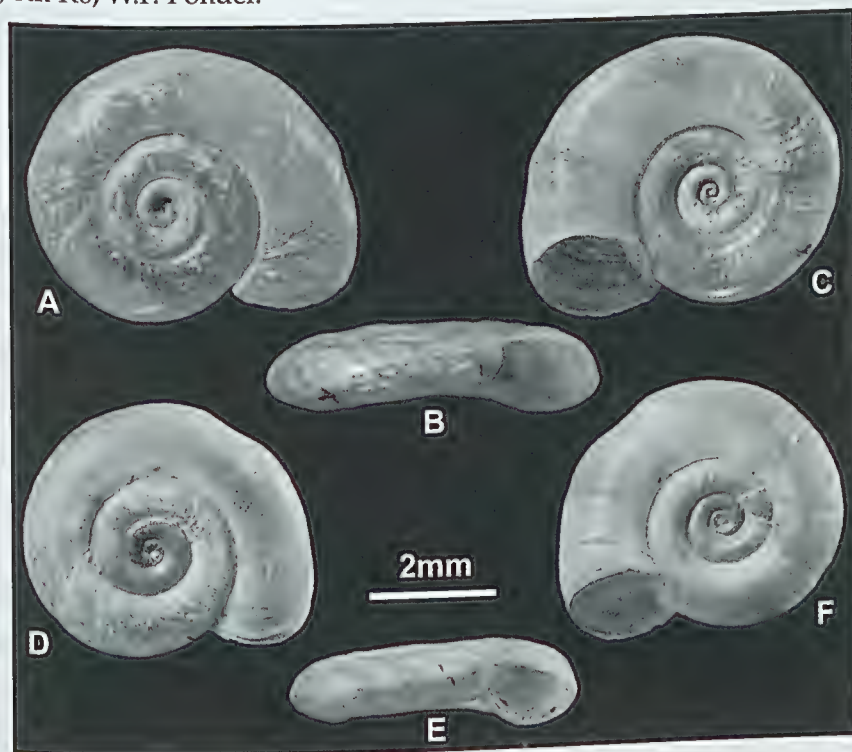


**Figure 22.**
**A-C,** *Gyraulus (G.) isingi*, from Moro Springs, N Flinders Ranges, SA, AMS 144848. **D-F,** *G. (G.) parvus*, holotype, SAMA D14131.

*Shell* (Figs 3, 5, 11-13, 15 A-F):
Original description "Specimens from the Lennard River, North-west Australia, are smaller than the preceeding [*Glyptanisus essingtonensis*], more tightly coiled, deeper, mouth smaller, strongly keeled medially, finely concentrically striate throughout, growth lines obsolete. The shell measures 4 mm in breadth, 1.5 mm in depth." (Iredale, 1943).

The observations may be added, that compared to the syntypes of *essingtonensis*, the syntypes of *hesperus* (Fig. 15 A-F) are generally more deeply concave on the left side, and the last whorl increases more rapidly, so that only 3.5 whorls may be completed at a diameter of 3.5 mm (Fig. 11). Further, *G. hesperus* is less depressed; mean a/b is 2.9 for 10 large syntypes, range 2.6-3.5 (Figs 12, 13). However, some syntypes have the left side hardly at all concave, but variation appeared continuous. Iredale's words "strongly keeled medially" are rather misleading, as a keeled appearance is seen in only some shells, in which a slender ridge runs along the periphery, which may be scarcely even subangular. Some of the smaller syntypes lack any angle at all, and no fringe was seen on any of these shells. The angle is strongest in the last half whorl of large specimens. Iredale's description also fails to convey the nature of the sculpture, which is comparatively strong, both transversely and spirally; numerous fine growth ridges are intersected by spiral striae and conspicuous spiral ridges, of which about 8 to 18 are irregularly spaced on either side of the syntypes whose dimensions are given below. The spiral ridges may be nodular and the sculpture is reticulate in some shells.

*Dimensions of syntypes* (10 selected larger ones):

|          | whorls | diameter (mm) | a/b  |
|----------|--------|---------------|------|
| Largest  | 3.74   | 3.71          | 3.49 |
|          | 3.59   | 3.56          | 2.90 |
|          | 3.63   | 3.49          | 2.59 |
|          | 3.50   | 3.49          | 2.78 |
|          | 3.49   | 3.42          | 2.64 |
|          | 3.33   | 3.42          | 2.81 |
|          | 3.71   | 3.38          | 3.18 |
|          | 3.61   | 3.31          | 2.61 |
|          | 3.53   | 3.31          | 2.93 |
|          | 3.32   | 3.27          | 2.93 |

Of the other material listed here, the snails collected most closely to the type locality are from the Lennard River Gorge (AMS 345438). Their shells closely resemble syntypes in form and sculpture, but there is wide variation among other samples from the King Leopold/Napier/Oscar ranges. Large shells from Windjana Gorge (AMS 345429) are unusually depressed (a/b nearly 4.0 at about 4 mm diameter) and thus resemble *G. essingtonensis*, but have stronger spiral sculpture. Shells from Pillara Spring (AMS 345436) are exceptionally high-whorled (a/b only 2.7 at 4 mm diameter), but these are practically devoid of spiral sculpture.

The shells in the remaining materials from WA and NT resemble the syntypes in having whorls that are high, not fringed, and angled only obtusely if at all; the left side may be deeply concave and often there is coarse spiral sculpture of nodular ridges (Fig. 26 C). Commonly the flatness index (a/b) is less than 3.0 for shells that appear fully-grown. The degree of concavity depends on how far the last whorl is deflected leftwards, and this is greatest in the larger

shells. Angulation tends to increase with growth; small to medium sized shells are usually curved evenly at the periphery. Spiral sculpture is well developed in small shells; it may become obsolete near the lip of large ones.

The snails from Millstream National Park (NT) are included in *G. hesperus* with some doubt, as the angle when present is situated near the left side rather than nearly medianly, some specimens are distinctly keeled and the spiral ridges may bear projecting processes of periostracum. The material from north-west QLD is highly varied in respect of peripheral angulation and development of fringe and spiral sculpture, but all these shells have the whorls increasing more rapidly than in the shells from this area identified as *G. essingtonensis*.

*Anatomy* (Figs 28 C; 31 B, C; 32): The most closely topotypical specimens (AMS 345438) were disappointing in having their bodies deeply retracted, making dissection difficult and the number of lobes could not be counted in several prostate glands examined, which were small and apparently immature. Two copulatory organs from these snails were mounted for microscopical examination, which showed the penis to be attached at the end of the sheath. In the entire material examined the only apparent difference from *G. essingtonensis* was the smaller number of prostate lobes. Pigmentation was commonly almost lacking apart from in the eyes, but varied continuously to a much darker state, in some samples the head/foot and tentacle cores were dark grey, and there was diffuse black along the kidney margins, in a zone on the right side of the mantle roof, and in a narrow band along the anterior margin. A brown patch in the mid-anterior mantle roof was present in some or all the snails examined from each of 21 samples (335 out of 640 animals examined). Patch frequency reached 100% in AMS 345785 (Wearyan River, n = 25) and AMS 345877 (Timber Creek, n = 30). The brown patch was lacking in 25 samples (n = 310 individuals). Kidney non-septate, so far as could be determined from the contracted state of most of the organs; in the 8 kidneys examined microscopically, any undulations at the margins appeared to caused by folds rather than by septa. Intestine either with a posterior loop of varying length or without any loop. Copulatory organ as described for *G. gilberti*, with penis attached at end of sheath (n = 41 organs examined microscopically, from 33 samples). In immature animals (from Moriarty Creek, SE of Kununurra) the site and mode of development of the penial stylet were as described for *G. essingtonensis* and *G. gilberti*.

Prostate lobes (Figs 31 B, C; 32) 8 to 20 mean 14.8 (n = 39 from 28 samples). Bursa copulatrix highly varied in shape, from tadpole (n =6) through club (n = 20) to tapered (n = 7) (total n = 33, from 29 samples). Seminal vesicle of about 5 to 10 convolutions, spinous. Ovotestis of 20 to 30 lobes, in approximately two rows though often indistinct.

*Comparison with other taxa:* The typical form of *G. hesperus* differs from *G. essingtonensis* and all other known species of Australian *Gyraulus* in its high, rounded or only obtusely angled whorls and strong spiral sculpture. The left side of fully-grown shells is more or less deeply concave. The mean number of nearly 15 prostate lobes is considerably less than in *G. essingtonensis* (mean about 20).

*Remarks:* Although the shell forms typical of *G. hesperus* and *G. essingtonensis* are readily distinguishable, variation in both shell and number of prostate lobes appears to be continuous and some samples had to be classified with doubt (e.g. *G. hesperus*; AMS 345429 and 345436, as noted under 'Shell' and see further under Remarks for *G. essingtonensis*). In the one sample in which both the two shell forms were present and appeared clearly distinct (AMS 345700, NT, near Mataranka), the *G. essingtonensis* lacked bodies (see further under Remarks for that species). Substantiation is needed of the present identifications of *G. hesperus* from the Gulf of Carpentaria region, in NT and north-west QLD. This material shows wide variation in shell shape and sculpture.

*Distribution:* NT–W Gulf of Carpentaria (Wearyan River), Roper River (Mulurak Rapids) and most frequently found in Victoria River basin. QLD (north-west) – southern Gulf of Carpentaria region. WA – Ning Bing Ranges (near Haley's Spring), upper Ord River basin, SW Kimberley area and the western Pilbara (Millstream N.P.)

### *Gyraulus (G.) idenus* (Iredale)
(Figs 3 and 5, shell no. 11; 17 D-I; 24)

*Glyptanisus idenus* Iredale, 1943: 226 [under *G. gilberti*].
*Gyraulus idenus* (Iredale) – Smith, 1992: 269 (as synonym of *G. gilberti*).

*Type locality:* Eidsvold, Queensland.

*Type material examined:* AMS 033768 syntypes; 34 dry shells, presented by Dr T.L. Bancroft, 1912.

*Additional material:* AMS 144861, QLD, Boyne River at Gayndah, under bridge, 23 wet, 25 April 1975, W.F. Ponder, J.B. Burch and R.M. Colman.

*Shell* (Figs 3 and 5, shell no. 11; 17 D-I; 24):
Original description "they [specimens from Eidsvold, Queensland] differ from Smith's account [of *Planorbis gilberti*] in their larger size, more descending mouth, more flattened base, less sunken spire, and fine sculpture. The shell measures 7 mm in breadth by 2 mm in height." (Iredale, 1943).
    The syntypes range in diameter from about 2.5 mm to nearly 7 mm, with up to 4.3 whorls (Figs 3, 24), rather rapidly increasing. Periphery angled over entire size range and keeled in large specimens; most with remains of fringe. Keel situated about mid-whorl or closer to right side. The largest syntype (Fig. 17 D-F) is the most depressed, with a/b = 4.57 (Fig. 5, shell no. 11). Right side more or less domed, more flattened in those specimens having the keel near to this side, inner whorls only slightly sunken. Left side concave; last whorl increasing rapidly, strongly curved to sub-angled, somewhat descending and most so in the largest syntype, in which the apertural lip is attached entirely on the left side of the keel. Microsculpture generally strong, comprising numerous transverse ridges, wider spaced spiral ridges (sometimes weakly nodular and

with periostracal bristles) and spiral striae; the overall appearance may be reticulate.

*Dimensions of selected syntypes:*

|         | whorls | diameter (mm) | a/b  |
|---------|--------|---------------|------|
| Largest | 4.17   | 6.8           | 4.57 |
| Others  | 4.29   | 5.9           | 4.10 |
|         | 3.89   | 6.0           | 3.35 |
|         | 3.90   | 5.5           | 3.97 |
|         | 3.94   | 5.8           | 3.84 |
|         | 3.48   | 4.2           | 3.14 |
|         | 2.93   | 3.1           | 2.59 |
|         | 2.79   | 2.4           | 2.57 |

The shells from Gayndah (AMS 144861) reach nearly 6 mm in diameter and resemble closely the medium-sized syntypes in their general shape, rate of whorl increase (Fig. 24), acute peripheral angle, strongly curved left surface of the whorls and microsculpture.
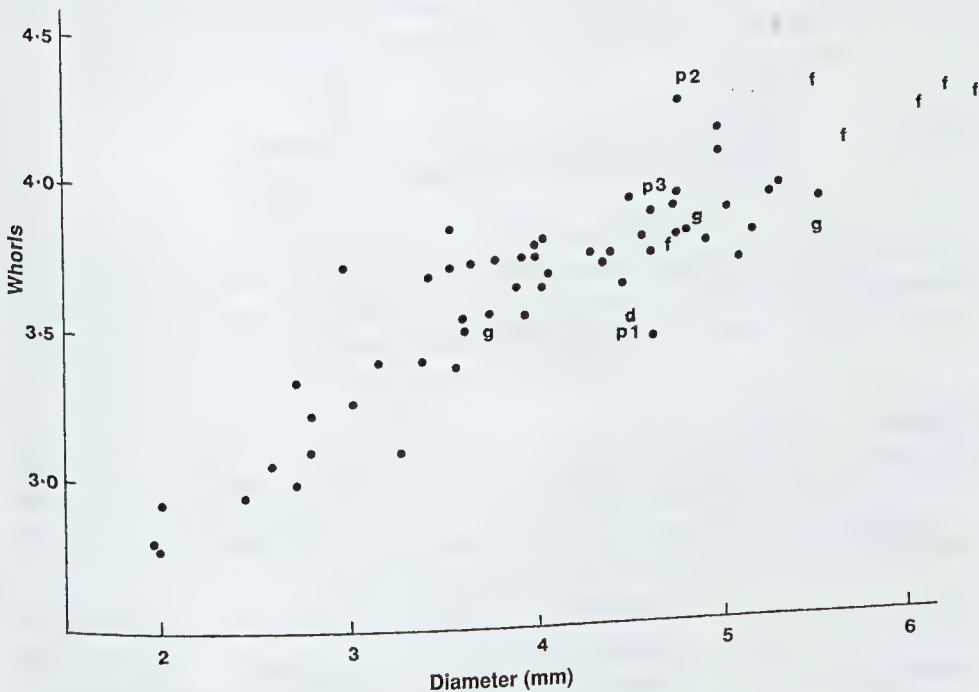


**Figure 23.**
Relationship between number of whorls and shell diameter for some of the samples identified in this paper as *G. gilberti*, all from south-east QLD: Gympie-Maryborough area (AMS 144857, n = 10; AMS 144859, n = 19; AMS 144866, n = 10) and Belinda Spring in Carnarvon Gorge National Park (AMS 144990, n = 15).
Also plotted are types or representative shells: d = *daemeli*, lectotype; f = *brazieri* (*fragilis* Smith), BMNH 79.5.21.743-8 (n = 6); g = *gilberti*, syntypes (n = 3); p1 = *planissimus*, syntype from Cape York; p2 and p3 = *planissimus* syntypes from Rockhampton.

*Anatomy:* Description based on 2 specimens (AMS 144861). Body pigmentation almost lacking; pale brownish-grey band along mantle border, grey tentacular cores. Kidney margins straight. Copulatory organ about 3.0 mm long, from shell diameter 5.0 mm. Penis tip only slightly swollen. Prostate lobes 18 and 20. Bursa copulatrix; elongate club shape. Ovotestis; 20 and 30 lobes, mostly in two rows. Seminal vesicle of 6 to 8 convolutions, spinous. In these respects and other anatomical features, no significant difference from *G. gilberti* was detected.
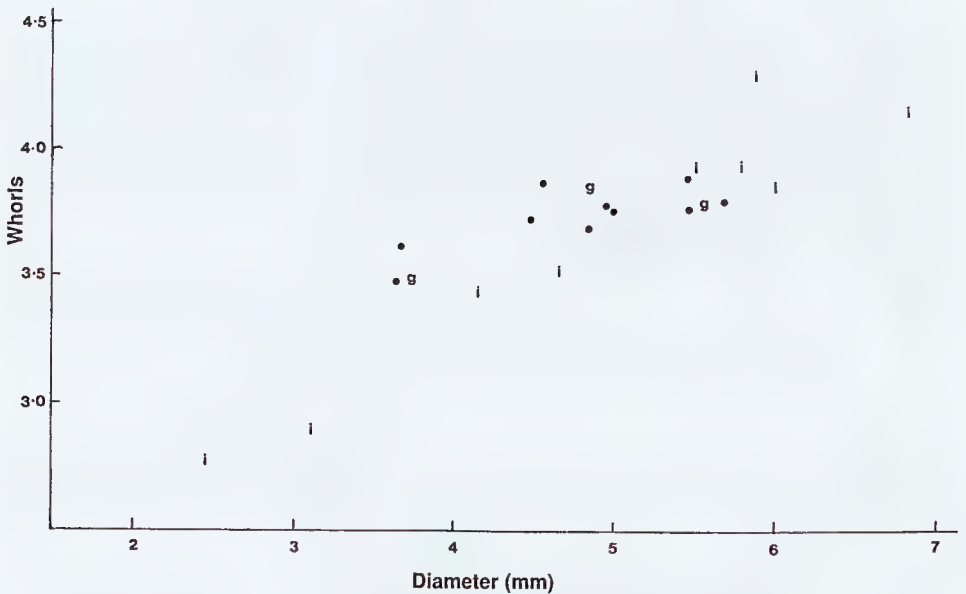


**Figure 24.**
Relationship between number of whorls and shell diameter for snails from the Boyne River at Gayndah, south-east QLD (AMS 144861, n = 10), representing *G. idenus* (here treated as a junior synonym of *G. gilberti* ). g = *gilberti* syntypes (n = 3); i = *idenus* syntypes, n = 9.

*Comparison with other taxa:* Iredale characterised *idenus* by comparison with *G. gilberti* as described by Smith (1881). The differences he described are commented on here in the light of comparisons between syntypes of both taxa. Iredale was rightly impressed by the large size of *idenus*. At 6.8 mm diameter, the biggest syntype is one of the three largest shells of *Gyraulus* from Australia known to me, with one of 6.9 mm from the Cobourg Peninsula (AMS 144777) and one of 6.3 mm from near Sarina, Queensland (AMS 144855). However, the plot of diameter against number of whorls (Fig. 24) for syntypes of *idenus* and *gilberti* (5.5 mm maximum) appears to conform to a continuous growth series. The 'more descending mouth' is evident in only the largest syntype of *idenus*,

which has the lip deflected entirely to the left of the keel, but the other syntypes have the lip attached more medially, enclosing the keel as in *gilberti*. I could find no basis for ascribing to *idenus* a 'more flattened base'. I am not sure whether Iredale's 'less sunken spire' is on the left or the right side of the shell; the degree of concavity on the left side appeared similar in the syntypes of the two taxa, the right side is somewhat flatter in those examples of *idenus* where the keel is situated towards to same side. Far from being 'finer' than in *gilberti*, the sculpture is stronger in most syntypes of *idenus*.

*Remarks:* *G. idenus* has not been previously figured. Syntypes of 5 to 6 mm in diameter are so like the largest syntype of *gilberti* that their conspecificity appears highly likely. Particular points of resemblance are rate of whorl increase, degree of peripheral angulation, depth of concavity on the left side and the subangle on the left surface of the last whorl. Although microsculpture is much stronger on some of the *idenus* syntypes, others are hardly more strongly sculptured than the largest syntype of *gilberti*. The alcohol-preserved specimens from Gayndah, situated about 25 km south-east of Eidsvold, were the most closely topotypical material of *G. idenus* available. It is reasonable to take their anatomy as representative of that taxon, in view of the close similarity between their shells and the syntypes. Since neither shell nor anatomy seems to provide any distinctive character, I concur with Smith (1992) in regarding *G. idenus* as a junior synonym of *G. gilberti*.

### *Gyraulus (G.) isingi* (Cotton & Godfrey, 1932)
(Figs 3 and 5, shell no. 12; 21 D-F; 22 A-C, 33)

*Planorbis isingi* Cotton & Godfrey, 1932: 162, pl. 3, figs 9,10.
*Plananisus isingi* – Iredale, 1943: 225; Cotton, 1943: 148, pl. 18, figs 13,14.
*Gyraulus isingi* – Smith & Kershaw, 1979: 262, as synonym of *Gyraulus tasmanicus* Tenison-Woods; - Brown, 1981: 73-76, fig. 9a, partim, only material from Mayne Creek, east of Port Fairy, Victoria); - Smith, 1992: 269.
*Glyptanisus caroli* Iredale, 1943: 225.
*Pygmanisus parvus* Cotton, 1943: 148, pl. 18, figs 11, 12; - Smith, 1992: 272. [See under *G. (Pygmanisus)*]

*Type locality:* South Australia, Point McLeay, Lake Alexandrina. Recorded by Cotton & Godfrey (1932) also from the rivers Torrens and Murray, Lake Albert at Meningie, Riverton and Valley Lake, Mount Gambier.

*Type material examined:* SAMA D10603, holotype.

*Other material:*
**South Australia**
AMS 144848-9 (100 wet); Moro Springs in Moro Gorge, small creek in gorge among reeds, 30°41'S 139°12'E, 11 May 1981, W.F. Ponder, B. Jenkins and W.F. Ponder jun., stn 37A. AMS 144850 (25 wet); Valley Lake, Mount Gambier, amongst freshwater vegetation, 26 Feb 1978, E.K. Yoo and K. Handley. AMS

345910 (2 wet); Ewens Ponds, S of Mt Gambier, large deep pond, 38°1.617'S 140°47.333'E, 16 May 1984, stn 1, W.F. Ponder. AMS 345913 (2 wet); data as for 345910 except "near outflow, stn 4". SAMA .D19039 (4 wet); Ewens Ponds and Eight Mile Creek, 21 April 1979, "W.Z. and A.G." SAMA D19040 (1 wet); Weetootla Spring, about 5 km E of Grindell Hut, Gammon Ranges [in N Flinders Ranges], 30°20'S 139°15'E, 3 Sept 1981, W. Zeidler [more material in SAMA D19048]. SAMA D19041 (2 wet); Moro Spring, Big Moro Gorge, 14 km W of Wertaloona Homestead, N Flinders Ranges, 11 May 1981, W. Zeidler. SAMA D19042 (10 wet, no bodies); "Fossil Cave", sinkhole SE of Tantanoola (south-eastern SA), 26 Jan 1981, P. Horne and M. Nielson. SAMA D19043 (1 wet); Roonka Station, Blanchetown, at edge of Cumbunga Creek, 12 May 1973. SAMA D19045 (22 wet); Pool 300 m below Moro Gorge Pool, Flinders Range, 5 Sept 1982, H. Anderson. SAMA D19046 (3 wet); Campsite waterhole, 300 m down from Moro Gorge Waterhole, N Flinders Ranges, 5 Sept 1992, H. Anderson. SAMA D19047 (70); Moro Spring, about 20 km SW of Wertaloona Homestead, N Flinders Ranges (extreme W end), 2 Sept 1981, W. Zeidler. SAMA D19048 (40 wet); data as for SAMA D19040.

*Victoria*
BMNH ETD3455 (6 wet); Mayne Creek, 3 miles E of Port Fairy, 2 Nov 1970, B.J. Smith [part of material reported on by Brown, 1981]. AMS 144842 (1 wet); Warribee River at road bridge, 14 March 1975, C. Wallace. AMS 144843 (1 wet); Hopkins River at Allansford, E of Warrnambool, pool beside river, 18 Aug 1973, W.F. Ponder and R. Burn. AMS 144845 (10 wet); Moyne River on Princes Highway, E of Port Fairy, sluggish deep pool, 5 March 1977, W.F. Ponder and E.K. Yoo. AMS 144846 (2 wet); Scotts Creek N of Port Campbell, 5 March 1977, W.F. Ponder and E.K. Yoo. AMS 144847 (3 wet); 3 miles E of Strathdownie, S of Castleton, roadside pool, 20 Feb 1978, I. Loch, E.K. Yoo and K. Handley. AMS 345435 (1 wet); Spring Creek, at Woolsthorpe Road, 38o 10.46'S 142o 27.55'E, 8 April 1988, stn FA126, F.W. Aslin. AMS 345893 (4 wet); Gauge station, 100 m E of road bridge over Mt Emu Creek, 38o 17.47'S 142o 53.2'E, 23 April 1988, stn FA195, F.W. Aslin. SAMA D19038 (6 wet); Cundies River, 6 km S of Cobden, on road to Port Campbell, 3 Dec 1981, W. Zeidler.

*Shell* (Figs 3 and 5, shell no. 12; 21 D-F; 22 A-C):
Original description "Planorbid, depressed, thin; yellow, mouth whitish; axial growth lines, regular; whorls four, obtusely keeled; columella convex, following the curvature of the penultimate whorl; umbilicus wide, very shallow. Type – height 2, diam.major 7.3, minor 6 mm" (Cotton & Godfrey, 1932).

The observations may be added that the holotype (Fig. 21 D-F) is unusually large, its last whorl is flattened on the left side near the periphery but strongly curved and nearly subangular near the suture, and no spiral sculpture was evident on either side. However, spiral striae are well developed in shells of similar shape though smaller size (to 3.5 mm) from Valley Lake, Mount Gambier (AMS 144850), which is a locality given by Cotton & Godfrey. These shells are consistently acutely angular at about mid-whorl peripherally, even in the smallest shell of 1.8 mm diameter, which has spiral rows of short bristles. Spiral sculpture is strong also in the single shell from Blanchetown (SAMA

D19043), which of all the collection sites is situated most closely to the type locality; this large shell closely resembles the holotype in shape.

*Dimensions:*

|  | whorls | diameter (mm) | a/b |
|---|---|---|---|
| Holotype | 3.67 | 7.45 | 4.25 |
| AMS 144850, Valley Lake, Mt Gambier | 3.10 | 3.46 | 3.61 |
| SAMA D19043, Blanchetown | 3.86 | 5.42 | 3.40 |

There is no shell so large as the holotype in the other material from SA. Though few (8 in three lots) the shells from Ewens Ponds, south of Mt Gambier, vary widely in degree of depression, angulation and sculpture, some having well-developed spiral ridges. The shells from the isolated collecting sites in the North Flinders Ranges have their whorls increasing less rapidly than in the holotype; a large individual from Moro Springs (AMS 144848) (Fig. 22 A-C) completes 4 whorls at diameter of about 5 mm, whereas the holotype has about this number of whorls at the much greater diameter of over 7 mm. Shells from both the Moro Gorge and Weetoota Spring (SAMA D19040) are mostly only obtusely angular; both fringe and spiral sculpture are weak or entirely lacking.

The shells from Victoria have a maximum diameter of about 5 mm. Their angle is commonly acute, but such shells may be not much depressed, having a/b little more than 3 (AMS 144843 and 144847). Spiral sculpture and peripheral fringe were present in at least some shells from each locality except Mayne Creek.

*Anatomy:* There was apparently no difference of significance from materials of *Gyraulus (Gyraulus)* from elsewhere in eastern Australia apart from *G. meridionalis*. In snails from Valley Lake, Mount Gambier (n = 4 ) pigmentation was entirely lacking apart from weak eyespots; kidney apparently non-septate, though much contracted; intestine with right-angled bend or short posterior loop; copulatory organ with long penis attached at end of penis sheath; prostate lobes 13 to 18; bursa copulatrix of spherical to elongate tadpole shape; seminal vesicle of 6 to 8 spinous convolutions; ovotestis lobes about 25, poorly defined. The snail from Blanchetown differed only in having grey to black pigmentation, on the right side of the mantle roof, along the kidney margins, along the anterior border of the mantle, and in the tentacle cores.

In the other material, pigmentation was commonly grey to black as in the specimen from Blanchetown; the anterior mantle roof usually lacked a brown patch or one was only weakly developed (in 10 out of 40 bodies examined in AMS 144848, Moro Spring). The same form of copulatory organ was observed in 15 further samples, by either external or microscopical examination (11 permanent preparations). Prostate lobes 12 to 19 (mean 16; n = 12 from 11 samples).

*Comparison with other taxa:* Following their original description of *Planorbis isingi*, Cotton & Godfrey remarked "Rather variable. Most nearly related to the Tasmanian *P. atkinsoni* Johnston, but flatter, smaller, whorls less acutely angled, mouth wider but not so high." It must be added that the holotype of *isingi* is

actually considerably larger than the maximum diameter of 5 mm given for *atkinsoni* by Johnston (1879), and it is not so "flat" as the largest shell of nearly 5 mm diameter and a/b nearly 5 in possible type material of *atkinsoni* (Tasmanian Museum, Hobart, Reg. No. E879). In its most distinct form, *G. atkinsoni* has the keel situated towards the right side and the outer lip is deflected towards the same side (Brown, 1998); this form was not seen in the present material of *G. isingi*. *G. atkinsoni* also differs in having the penis attached far from the base of the penis, as it is in *G. meridionalis*. The same penial morphology is found in *G. tasmanicus* (Tenison-Woods, 1876) (Brown, 1998), which therefore cannot be a senior synonym of *G. isingi* as believed by Smith (1992). Accordingly, *G. isingi* can be distinguished from *G. meridionalis*, the only other taxon of *Gyraulus (Gyraulus)* recognisable in SA and VICT by, its usually less depressed and less acutely angled shell, the lack of a distinct orange-brown patch in the mid-anterior mantle roof, and the distal attachment of the penis that is evident externally as a swelling in the comparatively short penis sheath.

*Parasites:* Boray (1982) names *G. isingi*, as well as *G. gilberti*, as an intermediate host for the stomach fluke *Orthocoelium streptocoelium*.

*Remarks:* The fundamental assumption in this concept of *G. isingi* is that its penial morphology is like that of most species of *Gyraulus* known from mainland Australia, e.g. *G. gilberti*, rather than like that of *G. meridionalis*. Although this is known to be so for specimens of *G. isingi* from Valley Lake, Mt Gambier, one of the localities given in the original description, confirmation is needed from topotypical material. Since *G. isingi* does not appear to differ in any clear respect of shell or anatomy from the range of variation among the specimens from New South Wales and Queensland described here under *G. gilberti* and *G. macquariensis*, it is maintained as a distinct species with considerable doubt.

*Distribution* (Fig. 33): SA, south east (Cotton & Godfrey, 1932; Cotton, 1943; present paper), VIC (Brown, 1981, Mayne Creek only; present paper).

***Gyraulus (G.) macquariensis*** (Smith, 1883)
(Figs 3 and 5, shell no. 14; 13; 17 J-L)

*Planorbis macquariensis* Smith, 1883: 295, pl. 7, figs 4-6; - Clessin, 1885: 189-190, pl. 28, fig. 4.
*Plananisus macquariensis* – Iredale, 1943: 225.
*Gyraulus macquariensis* – Brown, 1981: 76, fig. 9b (in comments under *G. isingi*); - Smith, 1992: 269.

*Type locality:* Macquarie River, New South Wales.

*Type material examined:* BMNH 43.9.20.55-60, syntypes, 6 dry shells, presented by Revd D. Landsborough. These shells are taken to be the syntypes because they were mounted on a card and seem likely to correspond to the 6 specimens indicated in the registration number. In a tube within the same box are another 5 shells, which resemble the others in size and shape.
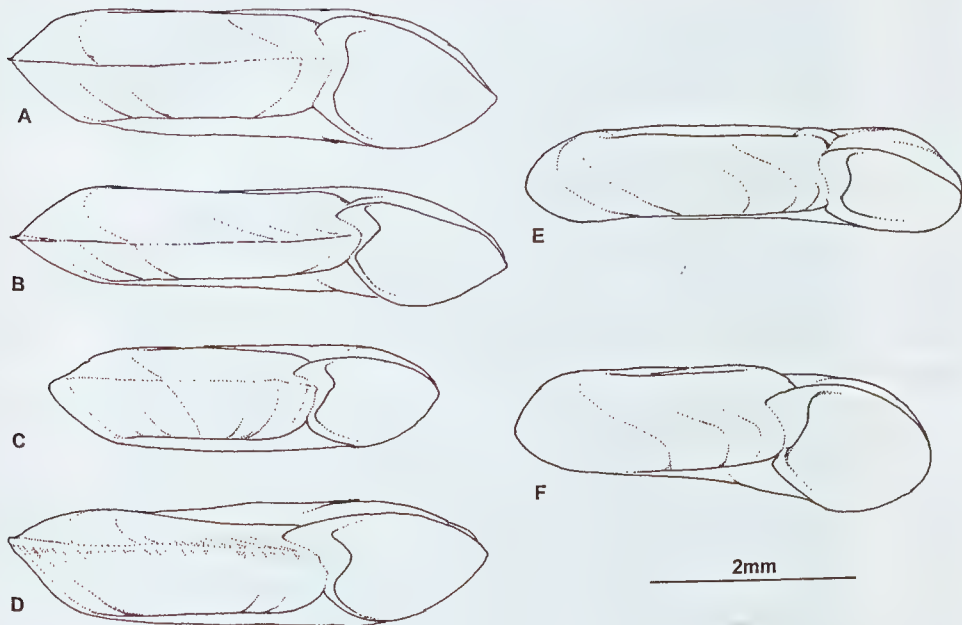
**Figure 25.**
*Gyraulus gilberti*. A-D, Shells from near Gympie, south-east QLD, representing range of variation in depression and position of keel. **A**, High-whorled example (a/b = 3.10). **B**, Extremely depressed example (a/b = 4.26). **C**, Keel situated towards right side, example resembling *daemeli* Clessin. **D**, Keel situated towards right side, example approaching the form of *waterhousei* Clessin described by Brown (1981). (A) and (D) from sample AMS 144859; (B) and (C) from sample AMS 144857. **E**, From one of the Barcaldine springs, south-west QLD, this shell is depressed (a/b = 4.20) but only obtusely angled (SAMA 19030). **F**, From Mowbray River, northern QLD, high-whorled shell (a/b = 3.14) that approaches the shape of *G. hesperus* (AMS 144871).

*Other material examined*: Listed here is all the available material of *G. (Gyraulus)* from southern New South Wales except for 3 samples (AMS 89355, -144814 and –144839) which are listed under under *G. waterhousei* together with samples from the Clarence River Basin in north-eastern NSW.
AMS 144799-800 (9 wet, segregated from *G. (Pygmanisus)* by Brown); NSW, Guinea Creek, N of Badja Forest road, off Tuross road, 18 Jan 1981, stn 84, W.F. Ponder and W.F. Ponder jun. AMS 144801 (6 wet, segregated from *G. (Pygmanisus)* by Brown); NSW, Guinea Creek on Badja Forest road, just off Nimmitabel road, 36°12'S 149°28'E, stn 35, W.F. Ponder and W.F. Ponder jun. AMS 144802 (8 wet); NSW, Big Badja River at Boggy Plain, 36°08'S 149°28'E, 18 Jan 1981, stn 32, W.F. Ponder and W.F. Ponder jun. AMS 144804 (40 wet); NSW, Undoo Creek at Oak Valley, on Countegany-Cooma road, 36°11'S 149°26'E, 18 Jan 1981, W.F. Ponder and W.F. Ponder jun. AMS 144805 (6 wet); NSW, Numeralla River, E of Numeralla, E of Cooma, 36°12'S 149°20'E, 18 Jan 1981, stn 87, W.F. Ponder and W.F. Ponder jun. AMS 144826 (150 wet, segregated from *G.*

*(Pygmanisus)* by Brown); NSW, creek 5.5 km north-west of Adaminaby, Snowy Mountains Highway, 35°59'S 148°44'E, 1 Nov 1980, stn 20, W.F. Ponder and J. Hall. AMS 144828 (23 wet); NSW, 1.7 km W of Adaminaby, on Snowy Mountain road, 36°00'S 148°42'E, swampy pool, 1 Nov 1980, W.F. Ponder and J. Hall. AMS 144833 (6 wet); NSW, Carrabungla Creek, on road 18 km W of Taralga, 26 Sept 1975, stn 40, J.B. Burch, M.S. Burch and D. Fleughelmans.

*Shell* (Figs 3, 5, shell no. 14; 13, 17 J-L):
Original description "Shell smaller than *P. essingtonensis,* not quite so compressed, more sunken in the umbilical region, less acutely keeled and corneous. Whorls 3 1/2. Aperture not so narrow perpendicularly as in the above-named species, and scarcely as horizontal. Greatest diameter 4  1/3 millim., height 1 1/3" (Smith, 1883).
It may be remarked in regard to Smith's description, that although the syntypes of *macquariensis* are a little less depressed they are scarcely less acutely keeled or angular at the periphery. No difference in colour in colour was evident when syntypes of the two species were compared after cleaning. As remarked by Smith, in comparison with *G. gilberti* the left (lower) side of the last whorl is not subangled and spiral striae are generally lacking (though traces present on inner whorls). The syntypes of *macquariensis* lie close to the syntypes of *essingtonensis* and *gilberti* in plots of whorls (Fig. 3) and (a/b) (Figs 5, 13) against diameter, illustrating the similarity in form.

*Dimensions of syntypes* (excluding one damaged):

| whorls | diameter (mm) | a/b |
|--------|---------------|------|
| 3.70 | 4.43 | 3.25 |
| 3.70 | 4.40 | 3.45 |
| 3.70 | 4.03 | 3.31 |
| 3.65 | 4.07 | 3.27 |
| 3.60 | 4.00 | 3.17 |

All other shells measured conformed to distributions plotted for *G. gilberti,* in respect of whorls and (a/b). Unfortunately no material was available from the catchment of the Macquarie River, the type locality for *Planorbis macquariensis,* which rises in the Blue Mountains west of Sydney and flows northwestwards to join the Darling or Barwon River. The most closely topotypical sample (AMS 144833) is from near Taralga, situated about 70 km south-west of the headwaters of the Macquarie River. Compared with the syntypes, these shells are more depressed, with a/b to 4.29, but appeared conspecific; spiral sculpture is extremely weak or lacking as in the syntypes. In other samples listed under Additional Material spiral striae were detectable in most specimens that were sufficiently cleaned, being strongest in samples AMS 144805 and 144826. A particularly close resemblance to syntypes of *macquariensis* was observed in some shells from near Gundagai in southern NSW (AMS 144814) and, interestingly, from the Clarence River Basin (samples listed under *G. waterhousei*).
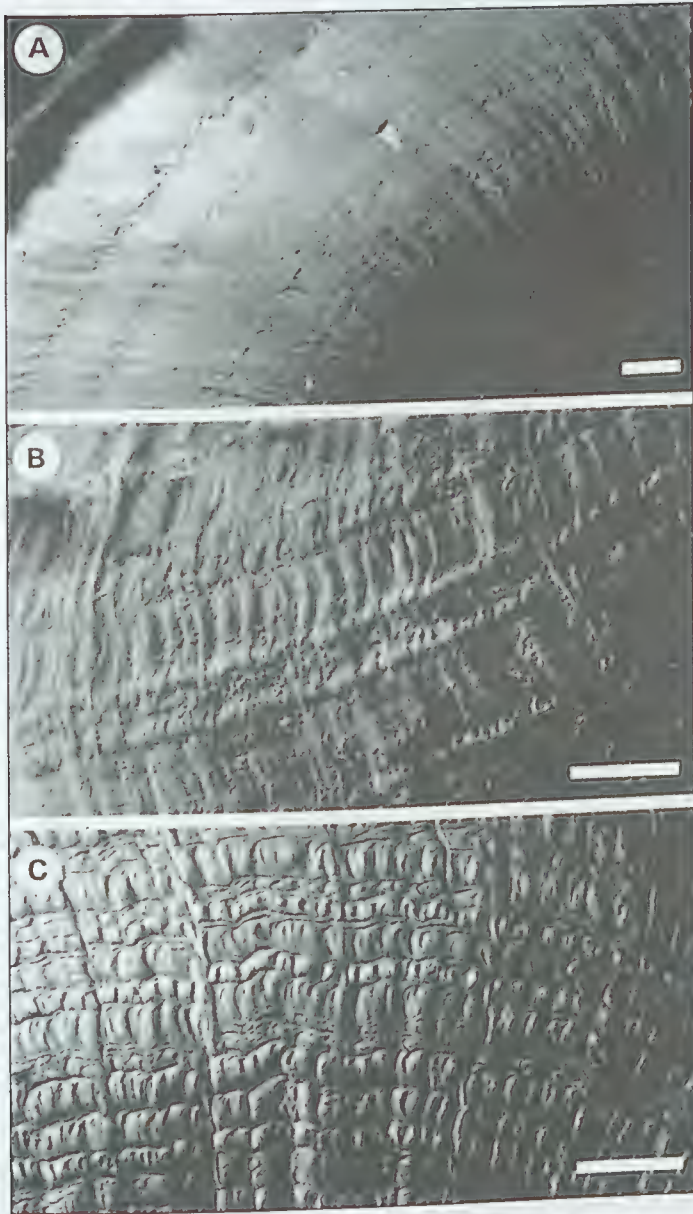
**Figure 26.**
Scanning electronmicrographs of sculpture on last whorl of shells. **A**, *Gyraulus edgbastonensis* sp. n., paratype. **B**, *G. gilberti*, from near Gympie, QLD, AMS 144589. **C**, *G. hesperus*, from between Halls Creek and Wyndham, WA, AMS 144791. Scale bars represent 0.10 mm.

*Anatomy:* Pigmentation varying from none evident except in eye spots to diffuse brownish grey on right side of mantle roof; some specimens with narrow dark band along mantle border, grey-black edging to uterus and kidney, and grey tentacle cores (total n = 10, from 8 samples). Kidney non-septate (total n = 8,

from 7 samples). Intestine either with posterior lobe (n = 6) or without (n = 4) (total n = 10, from 7 samples). Copulatory organ as described for *G. gilberti* (total n = 12, from 7 samples). Prostate of 14 to 18 primary lobes, of which some bifid, giving maximum of 21 terminal lobes (n = 6, from 7 samples). Bursa copulatrix shape varying from narrowly tapered to spherical club and elongate tadpole (n = 10, from 7 samples). Seminal vesicle of about 5 to 8 spinous convolutions (total n = 7, from 6 samples). Ovotestis lobes about 14 to 25 in two approximate rows. There appeared to be no significant difference from *G. gilberti*.
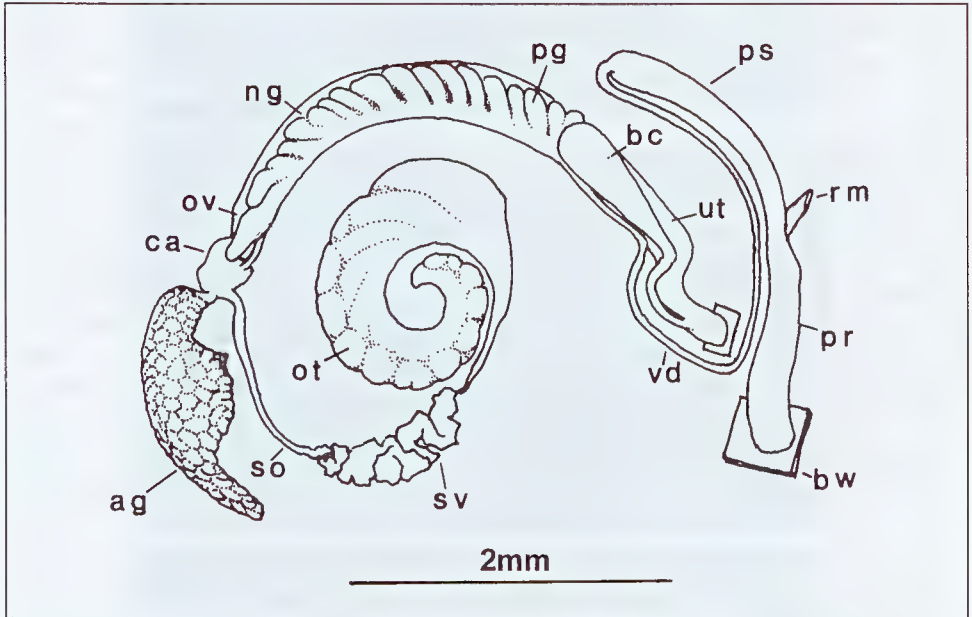


**Figure 27.**
Reproductive organs of *Gyraulus gilberti* from near Gympie, QLD, AMS 144859; animal with shell diameter 4.75 mm. Labelling: **ag**, albumen gland. **bc**, bursa copulatrix. **bw**, body wall. **ca**, carrefour. **ng**, nidamental gland. **ot**, ovotestis. **ov**, oviduct. **pg**, prostate gland lobes. **pr**, preputium. **ps**, penis sheath. **rm**, retractor muscle. **so**, sperm-oviduct. **sv**, seminal vesicle. **ut**, uterus. **vd**, vas deferens.

*Remarks:* On consideration of the ranges of variation observed in shell and anatomy, the material here taken to represent *G. macquariensis* could not be readily separated from specimens from north-eastern NSW described under *G. waterhousei*, from Queensland described under *G. gilberti* or from Victoria/South Australia described under *G. isingi*. Therefore it seems that all these taxa may be conspecific, with *G. gilberti* the senior name.

*Gyraulus (G.) meridionalis* (Brazier, 1875).
(Fig 29 C-E, 33)

Synonymy for Australian mainland only; for Tasmania see Brown, 1998.
*Gyraulus meridionalis* – Smith & Kershaw, 1979: 89 [probably only in part if any; the identification was according to shell only].

*Gyraulus tasmanicus* – Smith & Kershaw, 1979: 88 [probably only in part if any; the identification was according to shell only].
*Gyraulus isingi* – Brown, 1981: 73-76, Figs 1d, 8a, 10 [in part, excluding material from Mayne Creek near Port Fairy].

*Type locality:* Tasmania, Circular Head; in accordance with designation of lectotype by Brown (1998).
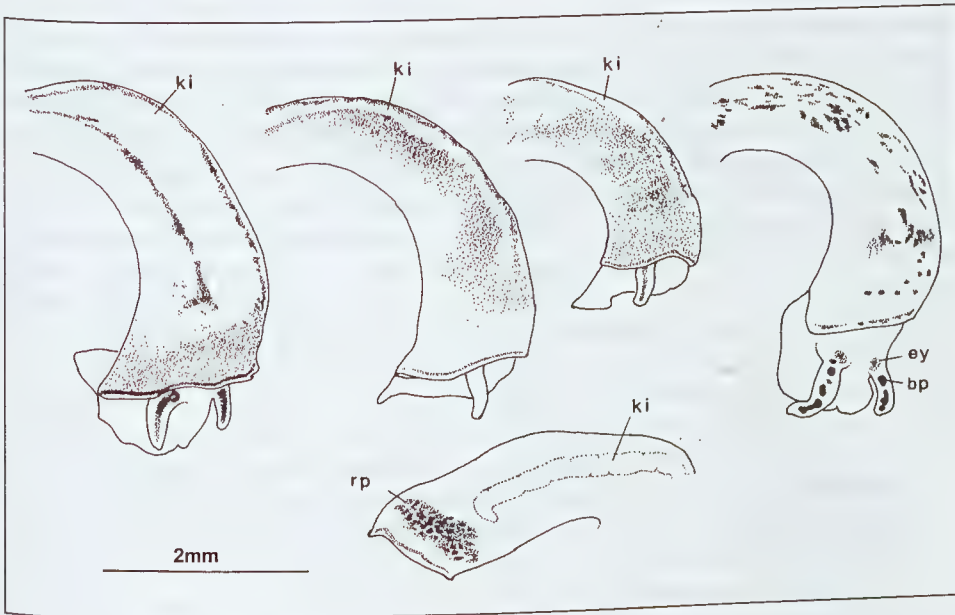


**Figure 28.**
Pigmentation of anterior mantle roof and tentacles. **A**, *Gyraulus gilberti* from near Gympie, QLD (AMS 144859), dark individual. **B**, *G. essingtonensis* from George Gills Range, NT (AMS 138752). **C**, *G. hesperus* from tributary of Ord River, WA (AMS 144786). **D**, *G. chinensis* from near Picaninnie, SA (SAMA D19044). **E**, *G. gilberti* from near Colinsdale, QLD (AMS 144865) showing position of reddish-brown patch in the mid-anterior mantle roof (this body was otherwise unpigmented apart from a narrow grey band along the mantle border). Labelling: **bp**, black patches in tentacles. **ey**, eye. **ki**, kidney. **rp**, reddish-brown patch.

*Type material examined:* AMS 100598, lectotype (designated by Brown, 1998); AMS 100598, 38 paralectotypes (dry) from Circular Head; QVM 9:116, 2 paralectotypes (dry) from Tasmania, Ouse River.

*Other material examined:* All lots except AMS 345894, Barwon River, identified according to microscopical examination of copulatory organ. BMNH ETD3455 (5 wet); VIC, 10 miles (16 km) E of Warrnambool, 1 Nov 1970, B.J. Smith. BMNH ETD3455 (18 wet); VIC, Camperdown Scenic Road, swamp, 1 mile (1.6 km) from turn-off, 22 Aug 1970, K.N. Bell. AMS 302519 (24 wet); VIC, upper part of Darlot

Creek, Condah Swamp, 38°0.87'S 141°49.92' E, 18 Feb 1984, stn Vic 28, G.A. Clark
and A.C. Miller. AMS 345894 (2 wet); VIC, Barwon River at Gauge Station, 200
m upstream of Pollocksford road bridge, 38°8.783' S 144°11.35' E, 12 April 1988,
stn FA143, F.W. Aslin. AMS 345896 (45 wet); VIC, Cotters Lake, Wilsons
Promontory N.P., 38°56.23'S 146°15.17'E, 12 Dec 1988, stn EV31, J.H. Waterhouse
and G.A. Clark. AMS 345897 (11 wet); VIC, data as for AMS 345896. AMS 345911
(50 wet); SA, south-east end of Bool Lagoon, 37°8.93'S 140°40.4'E, 17 May 1984,
stn 13(1A), W.F. Ponder.

*Shell:* In the lectotype series and other Tasmanian material described by Brown
(1998) the periphery varied from subangled to acutely angled with keel and
fringe; the flatness index (a/b) reached 5.4 in the most depressed specimens.
Spiral sculpture was commonly present, of rows of riblets formed by spiral
striae intersecting fine transverse ridges. The shells of specimens previously
reported as *G. isingi* have an acute angle situated a little towards the left side,
with a keel and fringe (Brown, 1981, figs 1d and 8a); spiral sculpture is not
evident, but the surfaces are extensively eroded. Similarly in the newly
identified AMS material the shells are much depressed, acutely angled with a
conspicuous blunt keel, and spiral sculpture is usually of only weak striae.

*Dimensions of large specimens:*

|  | whorls | diameter (mm) | a/b |
|---|---|---|---|
| BMNH ETD 3455, near Warnambool | 3.58 | 4.00 | 3.95 |
| BMNH ETD3455, Camperdown Scenic Road | 2.97 | 3.10 | 4.0 |
| AMS 302519 | 3.33 | 3.89 | 4.93 |
| AMS 345894 | 3.60 | 4.84 | 4.20 |
| AMS 345896 | 3.34 | 3.38 | 4.20 |
| AMS 345911 | 3.34 | 3.89 | 4.93 |

*Anatomy* (Fig. 29 C-E): Observations reported on the material previously
determined as *G. isingi* by Brown (1981, fig. 10) referred to an "unusual"
structure of the copulatory organ, in which the penis "had a short free-hanging
part". This seemed attributable to sexual immaturity, "but if found to be fully
grown such specimens might be considered a distinct species" (Brown, 1981, p.
75). In 1998, permanent preparations stained with safranin were made of a
copulatory organ from each of these samples (earlier preparations were
unstained). Then it was clearly seen that the organ resembled that of *G.
meridionalis* from Tasmania (Brown, 1998) in having a short stout penis, attached
at a considerable distance from the end of the penis sheath and having a
distinctly swollen tip. All the penial stylets examined in this material were
colourless, and apparently not yet fully chitinised (Brown, 1981, fig. 10).

In the AMS material examined subsequently, the copulatory organ (Fig.
29 C-E) is likewise similar to that of *G. meridionalis* from Tasmania, in both the
fleshy structure and the stylet, which is brown and appears fully formed. The 3

stylets examined microscopically differed consistently from those of all other taxa of *Gyraulus* known from the Australian mainland, in having the blade broader in proportion to its length, and the base asymmetrical with a lateral projection (Fig. 29 E). As in Tasmanian material the vas deferens is inserted subterminally on the penis sheath, the penis is attached some distance from the proximal end of the sheath, and the penis tip is swollen. The penis tip figured here has two overlapping folds, which partly enclose the penis pore and the groove leading towards the stylet.

Body pigmentation is lacking (eyes inconspicuous) except for an orange patch in the mid-anterior mantle roof in almost all snails in the samples AMS 302519, 34596-7 and 345911. This orange patch was observed too in *G. meridionalis* from Pipers Lagoon Creek in Tasmania (Brown, 1998, p. 124). Kidney with straight margins and without septa; any septa-like structure seemed due to contraction. Posterior loop of intestine, short to long. Prostate lobes 8 to 16 (mean 12; n = 5). Bursa copulatrix shape spherical to elongate club. Seminal vesicle with 5 to about 9 spinous convolutions. Ovotestis lobes 20 to 25 in two approximate rows.

*Comparison with other species:* The copulatory organ of *G. meridionalis* differs conspicuously from that of any other taxon of *Gyraulus* known from the mainland of Australia, in the subterminal (rather than terminal) insertion of the vas deferens, the distal position (rather than proximal) of attachment of the penis, the marked swelling of the penis tip and the form of the penial stylet (comparatively broad with splayed base). The shells of the material collected in Victoria are much depressed, acutely angular and strongly keeled, and in these respects they lie at the extreme of variation observed in this study. Comparable forms are the most depressed examples of *G. waterhousei* (sensu Brown, 1981, fig. 6a and present paper) and *G. edgbastonensis* sp. n.. Some of the shells from Victoria approach the form of *G. atkinsoni* (Johnston, 1879; Brown, 1998) of Tasmania, which is perhaps not a distinct species but an extremely depressed form of *G. meridionalis*. However, in typical *atkinsoni* the last whorl is deflected far towards the right side, whereas it is usually deflected to the left in the specimens from Victoria.

*Remarks:* The distinctive characters of the copulatory organ of *G. meridionalis* possibly justify recognition of a subgenus *Plananisus* Iredale. Although this species is reported to be widely distributed in south-eastern mainland Australia as well as in Tasmania (Smith & Kershaw, 1979, 1981; Smith, 1992), the present records are the first for the mainland to be based on anatomical examination and comparison with Tasmanian examples. As snails with the characteristic penial morphology were found in only 7 of the samples of *Gyraulus* from the SE mainland (out of a total of 29, from Victoria and south-eastern SA), it appears that the mainland distribution of this species is much less extensive than previously supposed. A wide distribution in the SE mainland has been attributed also to *G. tasmanicus* (Tenison-Woods) (Smith & Kershaw, 1979; Smith, 1992), but this taxon appears to be a junior synonym of *meridionalis* (see Brown (1998).

*Distribution* (Fig. 33): Identified in accordance with penial structure, *G. meridionalis* is known only from Tasmania (Brown, 1998), southern VIC and south-east SA.

### *Gyraulus (G.) metaurus* (Iredale, 1943)
(Figs 3 and 5, shell no. 16; 18 D-F)

*Glyptanisus metaurus* Iredale, 1943: 225-226; - Smith, 1992: 270, in synonymy of *Gyraulus waterhousei* Clessin.

*Type locality:* Armidale, NSW.

*Type material examined:* AMS 051737, 20 dry shells from Armidale, labelled 'probable syntypes'.

*Shell* (Figs 3, 5, 18 D-F):
Original description: "specimens differ in lack of concentric striation, while the growth lines are very notable. The shell measures 3 mm in breadth by 1 mm in height, the medial keel only prominent on the last whorl, the umbilicus wide, the mouth fairly large, oblique, and thin" (Iredale, 1943).

Some of the putative syntypes (Fig. 18 D-F) differ from Iredale's description in having spiral sculpture, of striae and ridges, and the growth ridges do not appear remarkable in comparison to the other material of *Gyraulus* examined in this study. Last whorl obtusely angular at beginning, becoming acute to keeled nearer the lip, its surface strongly curved near the suture, much flatter towards the periphery. Neither umbilicus nor aperture appeared distinctive.

*Dimensions:*

|              | whorls | diameter (mm) | a/b  |
|--------------|--------|---------------|------|
| large syntype | 3.65   | 3.60          | 3.33 |

*Remarks:* Following Smith (1992) I place *metaurus* in the synonymy of *G. waterhousei*, though with doubt, for although the sides of the last whorl are flattened towards the angle and spiral ridges are present on some syntypes, none of them has the angle near enough to the right side to produce the form of *waterhousei* described by Brown (1981).

### *Gyraulus (G.) ordessus* (Iredale, 1943)
(Figs 3 and 5, shell no. 17; 18 G-I)

*Glyptanisus ordessus* Iredale, 1943: 225; - Smith, 1992: 270, as synonym of *Gyraulus waterhousei*.

*Type locality:* Chichester Dam, Hunter River district, NSW.

*Type material examined:* AMS 100621, syntype, dry shell [labelled 'probable holotype']
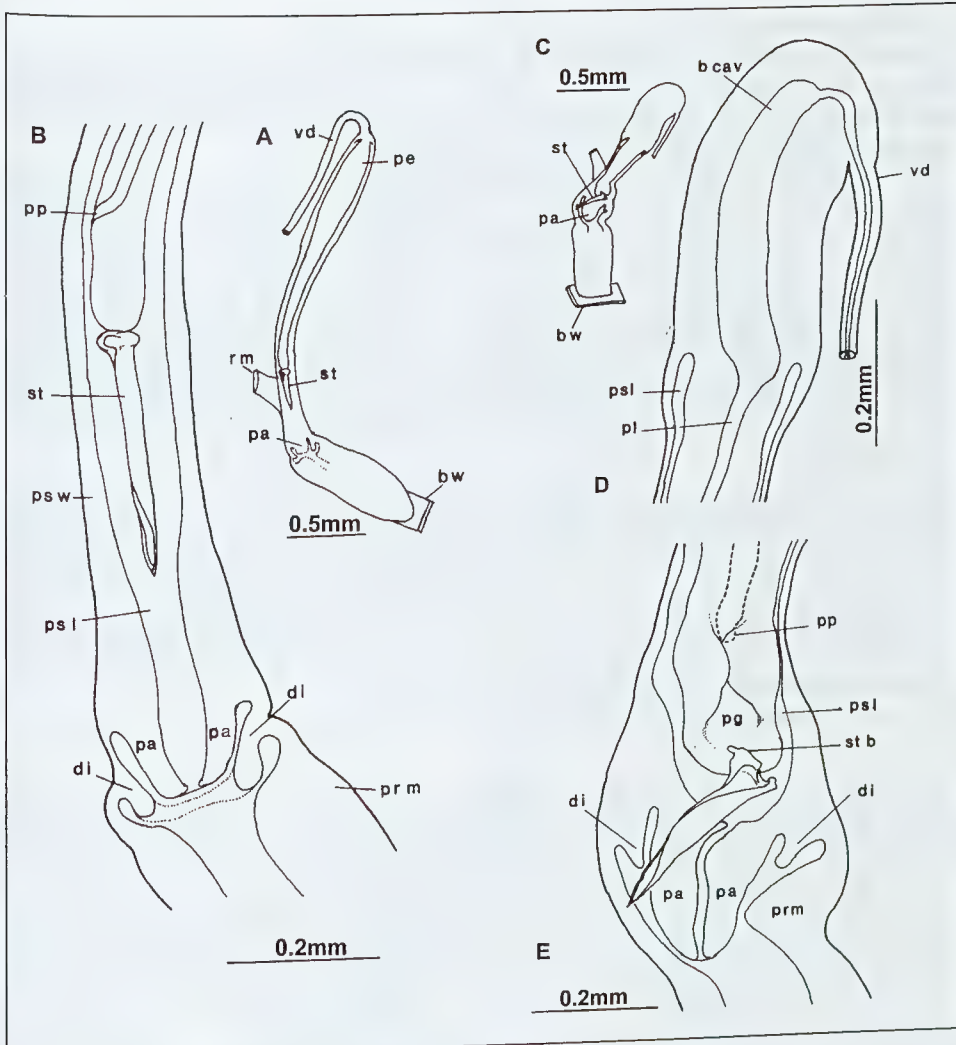
**Figure 29.**
Copulatory organs of Australian *Gyraulus* drawn by camera lucida from stained permanent preparatios. Internal structures shown as seen through external walls. **A, B,** *G. gilberti* from near Gympie, QLD (AMS 144859), shell diameter 4.75 mm, whole copulatory organ and the middle portion at greater magnification. In this well-extended organ there was no sign of the groove usually evident between the penis pore and the stylet. **C, D, E,** *G. meridionalis* from Bool Lagoon, SA (AMS 345911), shell diameter 3.90 mm; whole copulatory organ, with views at greater magnification of the proximal end of the penis sheath and of the middle region. The stylet appears to have broken through the tissue at the base of the papilla and is projecting into the preputium. The penis pore (pp) opens at the proximal end of two overlapping folds, which enclose the penial groove (pg).
Labelling: **bcav,** bulbous cavity in penis sheath. **bw,** body wall. **di,** diaphragm. **pa,** papilla. **pe,** penis. **pf,** penial folds. **pg,** penial groove. **pl,** lumen of penis. **pp,** penis pore. **prm,** muscle pillar in preputium. **psl,** lumen of penis sheath. **psw,** wall of penis sheath. **rm,** retractor muscle. **st,** stylet. **stb,** base of stylet, with lateral projection. **vd,** vas deferens.

*Shell* (Figs 3, 5, 18G-I):

Original description: "a species of the strongly keeled series, the keel median, spire sunken, upper [right] side of whorl round, lower side only subkeeled, sculpted, in addition to the fine growth lines, with distinct concentric striae, measuring 3 mm long by 1 mm in height" (Iredale, 1943).

The type examined (Fig. 18 G-I) corresponds well to Iredale's description. Being less than 3 mm in diameter and but little depressed (a/b = 2.66) it probably is not full grown. Left side of last-formed whorl strongly curved to subangular. Microsculpture conspicuous on both sides, the numerous fine transverse ridges being divided into rows of riblets by spiral striae and ridges, of which about 6 are oustandingly strong on the last whorl. This sculpture, the position of the keel towards the right side and the flattening of the right surface of the whorl are characters reminiscent of *Gyraulus waterhousei* as described by Brown (1981).

*Remarks:* G. *ordessus* is the type species of *Glyptanisus* named by Iredale (1943) to accommodate a group of strongly keeled species, with the surface conspicuously spirally sculptured. He did not specify how *ordessus* differed from the other members. In respects described above, the syntype examined resembles G. *waterhousei* as described by Brown (1981), and like Smith (1992) I classify *ordessus* as a synonym of that species.
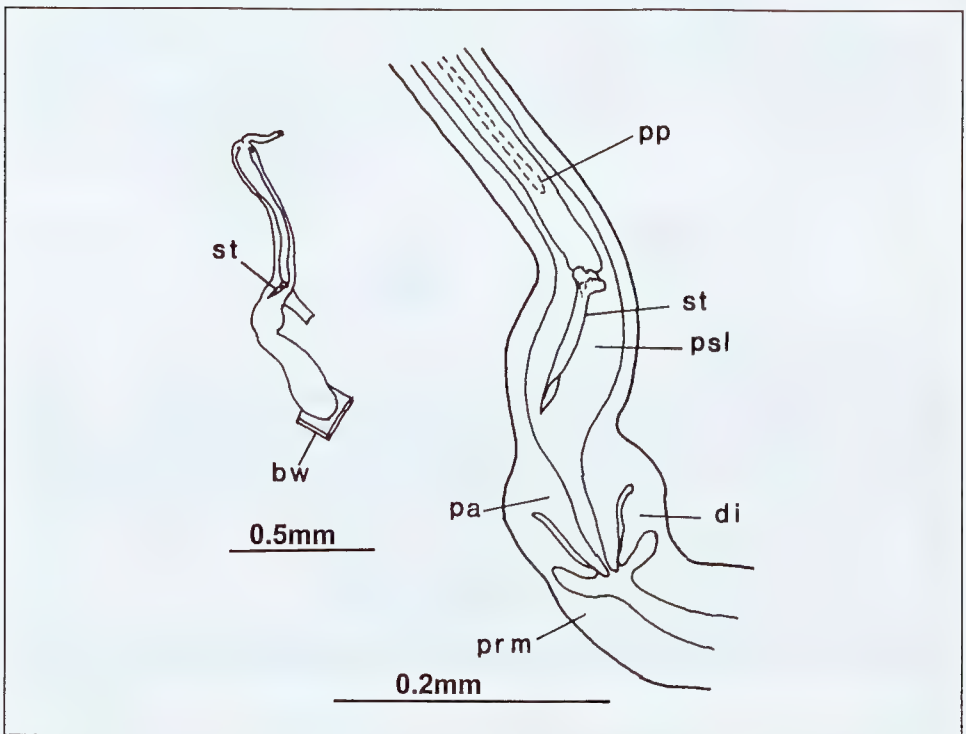


**Figure 30.**

G. *(Pygmanisus) scottianus* from Snowball Road, NSW (AMS 144809), shell diameter 2.8 mm, whole copulatory organ and middle portion at greater magnification. Labelling: see Fig. 29.

### *Gyraulus (G.) parvus* (Cotton, 1943)
(Figs 3 and 5, shell no. 18; 22 D-F)

*Pygmanisus parvus* Cotton, 1943: 148, pl. 18, figs 11,12; - Smith, 1992: 272.

*Type locality:* River Torrens, South Australia.

*Type material examined:* SAM D14131, Holotype, dry shell.

*Shell* (Figs 3, 5, 22 D-F):
Original description " Diameter 5 mm. Height 1.25 mm. Shell small, whorls rounded, aperture rounded, sculpture of growth lines only, otherwise typical of the genus and resembling the genotype, *Pygmanisus scottianus* from Launceston, northern Tasmania" (Cotton, 1943).

It may be added that the holotype (Fig. 22 D-F) is definitely subangled at about mid-whorl; a few weak spiral striae were visible at magnification X25; transverse ridges numerous and irregular, several stronger varices indicate interruptions to growth in a seasonal habitat.

*Dimensions of holotype:*

| whorls | diameter (mm) | a/b |
|--------|---------------|------|
| 3.96   | 4.90          | 3.96 |

*Remarks:* The large size of the holotype, compared to other taxa of *G. (Pygmanisus)* and its subangled periphery suggest that it is more likely a species of *Gyraulus (Gyraulus)*. There is a resemblance to *G. caroli* (Iredale) from Portland, Victoria, of which the holotype has an angle only a little more distinct. In both these shells the whorls increase distinctly less rapidly than in some lots included here under *G. isingi*, but not much more slowly than in specimens from Narribee River (AMS 144842) and Moro Springs (AMS 144848). Some of the lots included under *G. gilberti* and *G. macquariensis* include similar shells. Considering the close proximity of their type localities, `Pygmanisus' parvus is best classified as a junior synonym of *Gyraulus isingi*, and in any case *G. parvus* (Cotton) is a junior homonym of *Gyraulus parvus* (Say, 1817).

### *Gyraulus (G.) planissimus* (Clessin, 1943)
(Figs 3 and 5, shell no. 20; 16 D-I; 23)

*Planorbis planissimus* Clessin, 1885: 165-166, pl. 24, fig. 7 (non *Planorbis planissimus* Mousson, 1869, nomen nudum); - Smith, 1992: 277 (under species incertae cedis).
*Glyptanisus planissimus* (Clessin) – Iredale, 1943: 226.

*Type locality:* Clessin gave two localities in Queensland that are about 1600 km apart – Cape York (registration numbers 18239 and 13223) and Rockhampton.

*Type materials examined:* ZMB 18239, syntype, dry shell, Cape York; ZMB 102385, syntypes, 2 dry shells, Rockhampton.

*Shell* (Figs 3 and 5, 16 D-I, 23):

Original description: Translated from the German "Shell: very depressed, lightly striated, thin, horn-coloured, moderately convex above, slightly sunken at centre; underside concave at centre; 4 whorls, increasing moderately fast; acutely keeled near the middle (keel lying only a little towards the upper side); separated by a moderately deep suture; the last one twice as wide as the penultimate: the whorls are somewhat more swollen above the keel than below it; aperture strongly oblique, wide, broadly lanceolate; peristome sharp, margins joined. . . Diameter 4.5 mm, height 0.8 mm" (Clessin, 1885).

The syntype from Cape York (Fig. 16 D-F) is moderately depressed (a/b = 3.97 mm), with an acute angle at mid-whorl, bearing remnants of a fringe. Its right side is nearly flat and only shallowly sunken, with the whorls almost evenly curved. Left side moderately sunken, last whorl strongly curved to subangular near beginning. Last half-whorl deflected towards left side, most of peristome attached to that side of the angle. Microsculpture of transverse ridges intersected by spiral striae, and on the right side near the lip are fine spiral ridges. The two shells from Rockhampton are similarly angular, though one (Fig. 16 G-I) is considerably more depressed (a/b = 4.33) and its angle is near the the right side, which is correspondingly flattened and a little concave near the angle, thus approaching the form of *G. waterhousei*. Parts of this shell have strong sculpture, transverse and spiral, from which filaments of periostracum project on the right side.

*Dimensions of type material:*

|              | whorls | diameter (mm) | a/b  |
|--------------|--------|---------------|------|
| Cape York    | 3.50   | 4.44          | 3.97 |
| Rockhampton  | 4.33   | 4.76          | 4.01 |
|              | 3.91   | 4.66          | 4.33 |

*Comparison with other taxa:* Clessin (1885) compared *planissimus* only with *essingtonensis*, which he distinguished by its less acute keel; the syntypes of *essingtonensis* do indeed have a comparatively obtuse angled and they are treated here as representatives of a distinct species. Since Clessin had specimens of both *planissimus* and *daemeli* from Cape York, it is surprising that he did not publish any comparative remark; the lectotype of *daemeli* is the less depressed of these two shells, but viewed together they appeared conspecific. Compared with the syntypes of *G. gilberti*, the types of *planissimus* are to a varying extent more depressed, have the whorls less strongly curved on the left side and have stronger microsculpture.

*Remarks: G. planissimus* is a taxon of some historical importance, since of the 4 species of *Gyraulus* from Australia named by Clessin (1885) this one is the most senior, by virtue of page-priority. Unfortunately no comparative material recently collected from Cape York was available. Since the two localities given by Clessin are some 1600 km apart, the homogeneity of the type material might

be questioned, but the differences described above did not seem sufficient to preclude conspecificity. One syntype from Rockhampton and the lectotype of *daemeli* show a certain resemblance to *G. waterhousei*, as described by Brown (1981), in being angled towards the right side, which is correspondingly flattened. Both this form of shell and the medianly angled form of *planissimus* from Cape York are present in samples from southern Queensland here identified as *G. gilberti*, of which *planissimus* apparently is a junior synonym.
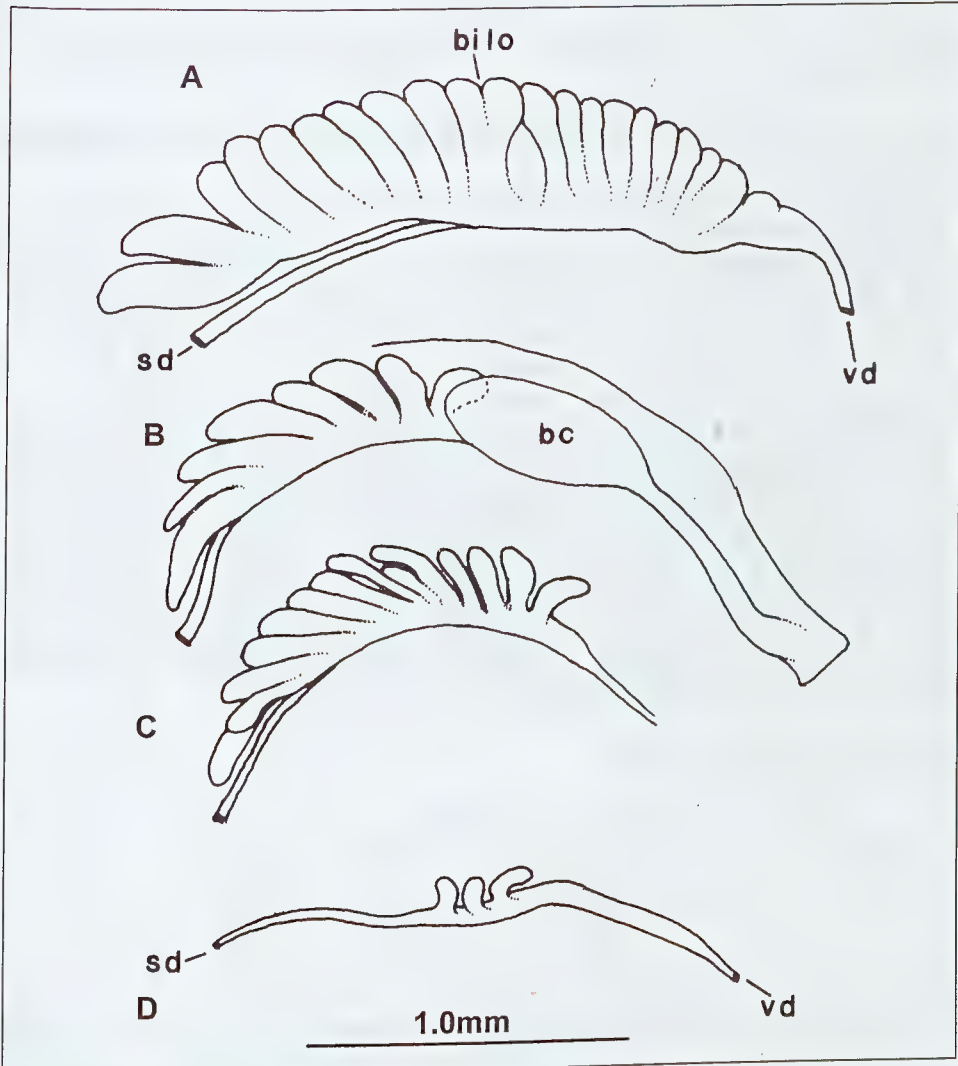


**Figure 31.**
Prostate gland and bursa copulatrix. **A**, *Gyraulus gilberti* from near Gympie, QLD (AMS 144859), animal with shell diameter 4.0 mm; one lobe is bifid and is immediately proximal to a short interstitial lobe. **B, C**; *G. hesperus* from Crawford Creek, NT (AMS 345864), shell diameters 3.7 mm and 3.3 mm; the bursa copulatrix is of the elongate tadpole shape. **D**, *G. (Pygmanisus) scottianus* from Snowball Road, southern NSW (AMS 144809), shell diameter 3.2 mm. Labelling: **bc**, bursa copulatrix. **bilo**, bifid lobes. **sd**, sperm duct. **vd**, vas deferens.

*Gyraulus (G.) speranus* (Iredale, 1943)
(Figs 3 and 5, shell no. 21; 18 J-L; 19 A-C)

*Glyptanisus speranus* Iredale, 1943: 227; - Smith, 1992: 270 (in synonymy of *Gyraulus waterhousei* Clessin).

*Type locality:* Narrabri, Namoi River, NSW.

*Type material examined:* AMS 000263, syntypes, 45 dry shells, presented by C. T. Musson, 1891.

*Other material examined:* BMNH 94.6.5.221-226, 6 dry shells from Narrabri, presented by J.H. Ponsonby.

*Shell* (Figs 3, 5 , 18 J-L, 19 A-C):
Original description: "shows a tightly coiled sunken apex, recalling *Segnitilia* from above, strongly keeled medially, upper and lower surfaces somewhat subkeeled above and below, the concentric striation obscured by growth lines. Breadth, 5 mm; height, 1.75 mm" (Iredale, 1943).
    It may be remarked that the apex is actually not much like that of *Helicorbis* (=*Segnitilia*), being more sunken and less tightly coiled than in that taxon. The largest syntype (Fig. 18 J-L) is strongly depressed, with (a/b) of 4.25, smaller specimens (Fig. 19 A-C) are considerably higher, with (a/b) between 3.0 and 3.5. Whorls of syntypes are strongly curved to subangular near the suture and most strongly so on the left side. Left surface of whorl nearly flat as it approaches the keel, which bears traces of a fringe. Largest syntype has coarse irregular transverse ridges on last whorl and only weak spiral striae, but most of the smaller specimens have strong spiral sculpture of striae and ridges. The shells from Narrabri (BMNH, presented in 1894), resemble the syntypes are possibly are from the same series.

*Dimensions of selected syntypes:*

|         | whorls | diameter (mm) | a/b  |
|---------|--------|---------------|------|
| Largest | 4.20   | 6.84          | 4.27 |
|         | 3.63   | 4.95          | 3.23 |
|         | 3.67   | 4.00          | 3.04 |
|         | 3.07   | 2.70          | 2.34 |

*Comparison with other taxa:* Iredale did not give specify any character by which he distinguished *speranus* from other taxa of *Gyraulus*. There is a general resemblance in size and shape to the syntypes of *G. idenus*, which however are mostly more depressed, more acutely angled, less concave on the left side, with the whorls on that side less strongly curved near the suture. The smaller specimens of both taxa have strong spiral microsculpture. Compared with the syntypes of *G. gilberti*, the biggest example of *speranus* is more depressed, but smaller specimens are closely similar in degree of depression, strength and position of keel and shape of aperture.

*Remarks:* There is some resemblance between *G. speranus* and *G. waterhousei* as described by Brown (1981) in the shape of the left side of the whorls and the strong spiral sculpture. Although *speranus* was placed in the synonymy of *waterhousei* by Smith (1992), I prefer to treat it as a junior synonym of *G. gilberti*.

## *Gyraulus (G.) stabilis* (Iredale)
(Figs 3 and 5, shells nos 22, 23; 19 D-F)

*Glyptanisus stabilis* Iredale, 1943: 226 (under *G. daemeli*).
*Gyraulus stabilis* – Smith, 1992: 270.

*Type locality:* Lilysmere Lagoon, Burdekin River, QLD,

*Type material examined:* AMS 100610, syntype, a dry shell labelled 'holotype' [not strictly a holotype, since Iredale referred to 'specimens', and Smith (1992) refers to 150+ paratypes AMS C111757, which lot comprises about 800 shells, I. Loch in litt. to author, June 1998].
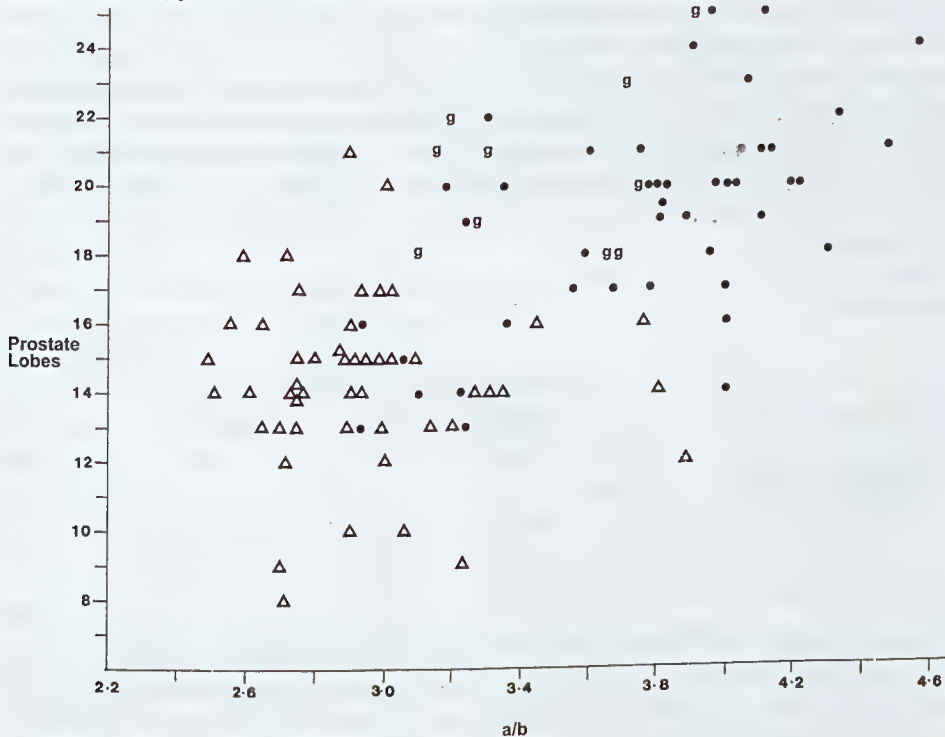


**Figure 32.**
Number of terminal prostate lobes plotted against shell flatness index (a/b) of individual snails. *Gyraulus essingtonensis* (●); n = 44, representing 34 samples). *G. gilberti* (g); n = 10, from near Gympie, AMS 144859. *G. hesperus* (△); n = 50 representing 35 samples. The two specimens of *essingtonensis* with the least number of prostate lobes (13) are from the George Gills Range, NT; the two *hesperus* with the highest number are from Pillara Spring, WA (20) and near Burketown, QLD (21). Although the smallest number of lobes observed in this sample of *gilberti* was 18, there were as few as 11 in other snails identified as this species.

*Additional material examined:* Possibly from the same series as the 'holotype': BMNH 86.7.26.227-36, 53 dry shells, Lilliesmere [sic] lagoons, Burdekin River, presented by J. Brazier; BMNH 87.5.19.85-96, 12 dry shells, Lillesmere [sic] lagoons, Burdekin River, presented by J. Brazier.

*Shell* (Figs 3, 5, 19 D-F):
Original description: "Specimens . . . are larger and flatter than *daemeli*, and in addition to a very fine concentric striation shows [sic] marked growth ridges, giving the shell a distinctive striped appearance. The shell measures 7 mm in breadth by 2 mm in height" (Iredale, 1943).

In conformity with Iredale's description of 'flatter', (a/b) for the 'holotype' (AMS) (Fig. 19 D-F) is 3.58, compared to 3.32 for the lectotype of *daemeli*. However, such a difference between conspecific individuals could easily result from allometric growth, for *stabilis* is nearly 2 mm greater in diameter. Spiral striae are fine on some areas but strong in other parts where they intersect close-set transverse ridges. Superimposed on this almost reticulate pattern are evenly spaced transverse corrugations with milky areas between (the growth ridges and stripes of Iredale). Peripheral angle acute, with remains of fringe, situated a little towards the right side as in *daemeli*. From their appearance the additional specimens (BMNH) could be from the same series as the 'holotype'. The large shells are similarly depressed, acutely angled and, to a varying degree, keeled and fringed; some have corrugations like the 'holotype' though weaker and without lighter areas between. The smaller shells in these series are also acutely angled, but much less depressed, with only weak microsculpture.

*Dimensions:*

|                     | whorls | diameter (mm) | a/b  |
|---------------------|--------|---------------|------|
| 'holotype' (AMS)    | 3.96   | 6.40          | 3.58 |
|                     |        |               |      |
| BMNH 87.5.19        |        |               |      |
|   largest | 4.07   | 5.96          | 3.23 |
|                     | 3.98   | 5.64          | 3.90 |
|   smallest| 3.59   | 4.58          | 3.14 |

*Remarks:* Iredale's description of *Glyptanisus stabilis* applies particularly to the large 'holotype' (AMS), in which the distinctive corrugation and light banding are apparently due to aberrant growth in the last whorl. These characters are not present in the smaller shells of the additional material (BMNH). There may be some doubt about the type locality, since according to I. Loch (in litt, to author, June 1998) a Lilysmere Lagoon does not appear to be known on the Burdekin River, while there is a Lilymere Lagoon near Rockhampton. The recently collected material obtained most near to the Burdekin River (AMS 144867, 144869, from Proserpine), includes shells of similar shape but lacking corrugation and banding; these samples are here identified as *G. gilberti* of which *G. stabilis* appears to be a junior synonym.

## *Gyraulus (G.) waterhousei* (Clessin)
### (Figs 3 and 5, shell no. 24; 18 A-C; 20 A-F)

*Planorbis waterhousei* Clessin, 1885: 225, pl. 28, fig. 2; - Gabriel, 1939: 122-123, pl. 3, figs 29, 29a,b [non *waterhousei* Clessin according to Iredale, 1943; see *Gyraulus caroli*].
*Glyptanisus waterhousei* – Iredale, 1943: 225.
*Gyraulus waterhousei* – Brown, 1981: 71-73, figs 1c, 6a, 7; - Smith, 1992: 270; - Shea, 1995: 5, fig. 14.
*Glyptanisus metaurus* Iredale, 1943: 225-226.
*Glyptanisus ordessus* Iredale, 1943: 225.
*Gyraulus gilberti* - Brown, 1998: fig. 12 C.

*Type locality:* Clarence River [presumably the river of that name in northern NSW].

*Type material examined:* ZMB 19069, syntypes; 6 dry shells,.

*Other material examined:* Samples listed below comprise some regarded as topotypical from the Clarence River or its basin in the vicinity of Grafton, and samples from Sydney and elsewhere that include specimens closely resembling *G. waterhousei* as described by Brown (1981). Other samples from NSW and QLD listed under *G. gilberti* also include some specimens that to a lesser degree show characters of the latter form.
### Queensland
National Museum of Wales, Cardiff, Accession No. 55.158 (3 dry, ex Melvill-Tomlin collection), no further data of locality.
### New South Wales
NMV F83085 (6 dry); NSW, Clarence River, *Planorbis waterhousei* ded. C.J. Gabriel, 1937. AMS 89355 (2 wet); NSW, Eastern Creek on Great Western Highway, between Parramatta and Penrith, sluggish creek rather heavily polluted, 9 Oct 1969, W.F. Ponder and P.H. Colman [specimens additional to those from this site identified by Brown, 1981]. AMS 144814 (9 wet); NSW, 3.2 km S of Gundagai, billabong beside Hume Highway, 19 Jan 1970, W.F. Ponder and P.H. Colman. AMS 144815 (60 wet); NSW, 18.5 km NE of Grafton on Princes Highway, pool N of road, on weed, 18 Oct 1972, W.F. Ponder and P.H. Colman. AMS 144829 (7 wet). NSW, Red Rock swamp in Red Rock National Park [about 30 km S of Grafton], 24 May 1977, B.V. Timms. AMS 144830 (8 wet); NSW, Blue Lagoon in Red Rock National Park, 20 Aug 1976, B.V. Timms. AMS 144831 (1 wet); NSW, Dune lake 5 km S of Evans Head, 23 May 1977, B.V. Timms. AMS 144839 (4 wet); NSW, Cattai Creek, off Cattai Ridge Road between Marayla and Glenorie (NW of ;Sydney], 6 May 1973, W.F. Ponder and J.B. Burch. AMS 144840 (1 dry); NSW, Cowan pond near Grafton, 16 Oct 1976, A.D. O'Brien. AMS 144841 (8 wet). NSW, Southgate near Grafton, marshland pasture, 10 Feb 1982, Dept Agriculture Regional Veterinary Laboratory. BMNH ETD3953 (18 wet); NSW, Grafton, 1984, J. Walker.

*Shell* (Figs 3 and 5, shell no. 24; 18 A-C; 20 A-F):

Original description (from the German): Shell very depressed, horn-coloured, finely striated; thin-walled, similarly shaped on either side; upper [right] side slightly sunken in middle, underside shallowly concave; whorls 4, increasing moderately rapidly, separated by deep sutures, strongly keeled in middle; last whorl twice as wide as penultimate one; aperture oblique, narrowly heart-shaped; peristome acute, margins connected, lip a little expanded. Diameter 4.5 mm, height 0.7 mm (Clessin, 1885).

It may be remarked that syntypes (Fig. 20 A-F) correspond to Clessin's descriptive text, but his figure exaggerates the depression; values for (a/b) calculated in this study range from 3.5 to 4.3, rather than 5.3 calculated from Clessin's figure. All the syntypes seen have a distinct peripheral angle, situated medially or a little to the left side; the larger ones are keeled with remnants of a fringe. Whorls evenly curved on left side, somewhat flatter to the right of the angle. Spiral sculpture is weak and evident in only some syntypes, which have fine spiral striae and rows of riblets, confined almost entirely to the left side.

*Dimensions of syntypes:*

| whorls | diameter (mm) | a/b |
|--------|---------------|------|
| 4.34 | 4.25 | 4.29 |
| 4.16 | 3.93 | 4.21 |
| 4.24 | 3.89 | 4.05 |
| 3.89 | 3.02 | 3.88 |
| 3.74 | 3.02 | 3.60 |
| 3.54 | 2.91 | 3.53 |

Shells of *G. waterhousei* from near Sydney identified by Brown (1981) differ from the syntypes in being even more depressed and more strongly keeled, and having the keel situated closer to the right side, which is correspondingly more flattened. The surface of the last whorl on both sides may undulate, being strongly curved to subangled near the suture and shallowly concave towards the periphery. Some shells have strong spiral sculpture, with up to 8 widely-spaced spiral ridges on the right side of the last whorl, which may bear short lamellae or bristles of periostracum.

The material considered here as topotypical for *waterhousei* comprises a total 100 specimens from the Clarence River and its lower basin, which mostly resemble the syntypes, though some have stronger sculpture of striae and riblets. Some shells from Grafton (Fig 18 A-C), Clarence River (NMV), and Blue Lagoon in Red Rock N.P. (AMS 144830) are somewhat more depressed (a/b to 5.7 in the latter sample) and more like *waterhousei* as figured by Brown (1981), though lacking strong spiral ridges.

*Anatomy:* Observations for specimens from the Clarence River basin and Red Rock National Park (AMS 144815, -29, -30 and –40). Pigmentation (n = 16) of mantle roof lacks a distinct pattern and is no stronger than a diffuse brownish grey; mantle border with distinct dark band in animals from Grafton (BMNH

ETD), in which the tentacles had a distinct dark core; cluster of reddish-brown granules in median area of mantle near the anterior border in all 13 specimens examined from AMS 144815. Kidney: no septa observed. Intestine; posterior loop short or lacking. Copulatory organ (n = 9) up to 2.7 mm long at shell diameter of 6 mm; penis attached at proximal end of sheath, penis tip not swollen. Prostate lobes 18 to 26 (n = 5). Bursa copulatrix tapering or spherical club-shaped. Seminal vesicle of 6 to 8 convolutions, swollen and spinous. Ovotestis of 20 to 30 lobes, in two approximate rows. Earlier studied specimens from near Sydney (Brown, 1981, figs 7, 12 C) had fewer prostate lobes (up to 15) and the penis tip appeared swollen. A recent re-examination of these permanent preparations suggested that the apparent difference in the penis could be due to variation in the contraction of tissue.

*Comparison with other taxa:* Clessin (1885) distinguished *G. waterhousei* only from *G. gilberti*, commenting that although in both species the keel is near the middle of the whorl, *waterhousei* is much more depressed. Another obvious difference between the syntypes of these taxa is that the whorls of *waterhousei* increase less rapidly and are more numerous at the same overall diameter (Fig. 3). Thus the biggest syntype of *waterhousei* is 4.25 mm in diameter with 4.3 whorls, whereas at 5.52 mm diameter a syntype of *gilberti* has only 3.8 whorls. Differences have been noted above, between the syntypes of *waterhousei* and the even more depressed shells identified as this species by Brown (1981). Iredale (1943) commented that the shell figured by Gabriel (1939) from Portland, Victoria as *waterhousei* was not that species, differing in the more rounded whorls, and named it as a distinct species *G. caroli*, which is here considered to be a probable synonym of *G. isingi*.

*Parasites:* Boray (1982) reported "*G. waterhousei (Glyptanisus gilberti)*" as an intermediate host for the stomach fluke *Orthocoelium streptocoelium*.

*Remarks:* Since *G. waterhousei* (Clessin) is the most senior name for a strongly depressed species of *Gyraulus* from eastern Australia, this name was adopted by Brown (1981) for depressed specimens from near Sydney, though with some doubt, as these shells differed from Clessin's description in having the keel situated towards the right side of the whorl instead of medianly, and in having strong spiral sculpture, which was not mentioned by Clessin. Subsequent examination of the syntypes showed that they do indeed differ in these respects from *G. waterhousei* of Brown (1981). However, the latter form is approached by some of the specimens here regarded as topotypical, and it seems not unlikely that *waterhousei* of Brown and of Clessin are conspecific. Possibly *G. waterhousei* and *G. gilberti* belong to a single biological species, as no anatomical difference was evident, and the wide variation among shells classified here as *G. gilberti* suggests that the *waterhousei* form lies at an extreme of a continuous range. Yet, the strong depression and acute angulation makes *waterhousei* one of the most distinct forms of *G. (Gyraulus)* found on the Australian mainland. A comparable taxon, found in Tasmania, is *G. atkinsoni* (Johnston), which might be either a distinct species or an extreme variant of *G. meridionalis* (Brazier) (Brown, 1998).

Treating *waterhousei* as a valid species will, I hope, encourage further investigation of its morphology, distribution and ecology. Like Smith (1992) I include as synonyms *metaurus* and *ordessus*, both named by Iredale. Of the further synonyms listed by Smith, *caroli* Iredale is here placed under *G. isingi* and *speranus* Iredale under *G. gilberti*.

*Distribution:* According to the present treatment, *G. waterhousei* occurs in eastern NSW and possibly is present in southern QLD. The most depressed and angular form is known only from the areas of Sydney and the Clarence River Basin.

### Subgenus *Gyraulus (Pygmanisus)* Iredale, 1943

*Pygmanisus* Iredale, 1943: 224.
*Type species: Planorbis scottiana* Johnston, 1879, Tasmania, by original designation.

Shell small, less than 4 mm in diameter, with rounded whorls, spiral sculpture weak or lacking. Kidney septate with undulate margins (clearly so in some specimens examined, though not clearly determinable in poorly preserved or much contracted animals). Penis like that of *Gyraulus* sensu stricto, having a miniature style of the furled dagger-like type. Prostate lobes 0 to 3, if present they are irregular and widely spaced. Ovotestis neither convoluted nor spinous. Similar to *Gyraulus (Torquis)* Dall, 1905, of North America and Eurasia (Meier-Brook, 1983) in the rounded whorls of the shell and the septate kidney, but in that subgenus a considerably higher number of prostate lobes (range 6 to 17) is reported (Meier-Brook, 1983, Table 2).

### G. *(Pygmanisus) leonatus* (Iredale, 1943)
(Figs 3 and 5, shell no. 13; 20 G-I)

*Pygmanisus leonatus* Iredale, 1943: 224; - Smith & Kershaw, 1979: 262, as synonym of *Gyraulus scottianus* (Johnston); - Smith, 1992: 272.

*Type locality:* The several localities cited in original description are: Canberra and in south-eastern NSW (Yass, Goulburn and Cooma).

*Type material examined:* AMS 51711, syntypes, 2 shells from Canberra, collected and presented by A. McKay, 1926; AMS 51720, syntype, a shell from Yass, 15 Aug 1925; AMS 51719, syntypes, 20 shells from Goulburn.

*Shell* (Figs 3, 5, 20 G-I):
Original description "Specimens . . . differ from the Tasmanian species [*G. (P.) scottianus*] in smaller size, flatter spire and less developed sculpture. The shell measures 2 mm in breadth by 0.75 mm in height, sculpture of growth lines dominant. Shells from Cooma seem even less" (Iredale, 1943).
      It may be added that the syntypes have the last whorl very strongly curved, almost subangled, on the left side. Transverse ridges are numerous and

irregular; spiral sculpture undetectable or present only as faint rows of riblets on parts of some shells from Goulburn.

*Dimensions of large syntype from Canberra:*

| whorls | diameter (mm) | a/b |
|--------|---------------|------|
| 3.37 | 2.33 | 3.50 |

*Remarks:* Iredale's reasons for distinguishing *leonatus* do not seem adequate, since the diameter of the largest syntype is comparable to the 2.5 mm given by Johnston for *scottianus*, the spire [presumably the right side] is shaped similarly in type material of both taxa, and the transverse sculpture of *leonatus* is no weaker than that of *scottianus*. Accordingly, I consider *G. (P.) leonatus* to be a junior synonym of *G. (P.) scottianus*.

**Pygmanisus parvus Cotton, 1943**
(Figs 3 and 5, shell no. 18; 22 D-F)

Taxon treated in this paper as a junior synonym of *G. isingi*; see under *Gyraulus (Gyraulus)*.
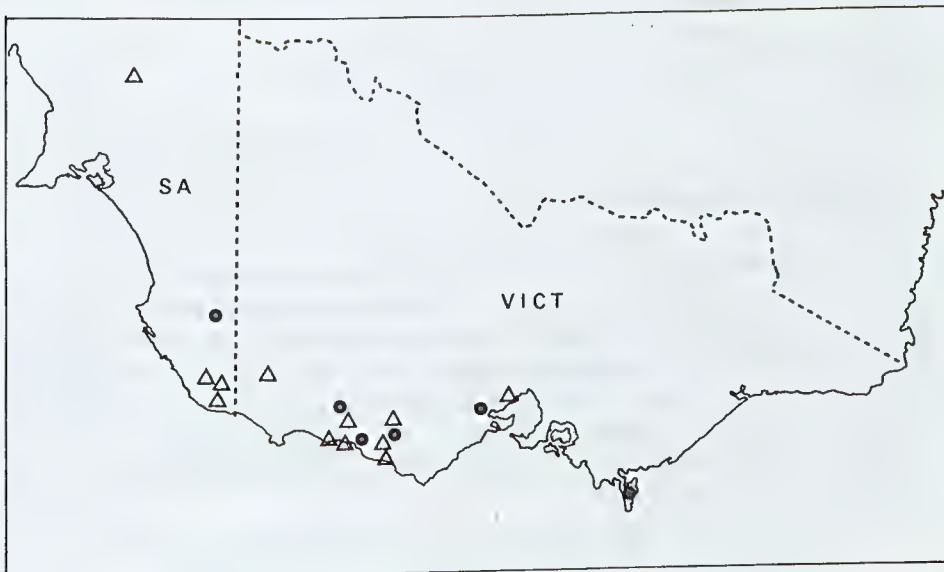


**Figure 33.**
*Gyraulus isingi* (△) and *G. meridionalis* (●). Geographical distribution of collections identified in the present paper. Identification of *G. meridionalis* is according to the structure of the copulatory organ; this species also occurs widely in Tasmania. Additional material of *G. isingi* was identified from the North Flinders Ranges in SA.

### G. *(Pygmanisus) pelorius* (Iredale, 1943)
(Figs 3 and 3, shell no. 19; 20 J-L)

*Pygmanisus pelorius* Iredale, 1943: 224; - Smith, 1992: 272, as synonym of *Pygmanisus leonatus* Iredale.

*Type locality:* Armidale, New South Wales.

*Type material examined:* 3 lots labelled 'probable syntypes'; AMS 51770, 8 shells; AMS 111731, 1 shell (with additional label 'lectotype'); AMS 100762, 18 shells [this last lot is not G. *(P.) pelorius*, see below].

*Shell* (Figs 3, 5, 20 J-L):
Original description "A different species [from *Pygmanisus leonatus*] occurs at Armidale, N.S.W., of fewer whorls, but still rounded, the mouth also rounded, the spire more sunken, the sculpture of growth lines only, the shell measuring 2 mm in breadth by 0.5 mm in height" (Iredale, 1943).

One lot of the supposed syntypes (AMS 100762) cannot be Iredale's *pelorius*, since they differ considerably from his description, in being distinctly angled at the periphery, having fine spiral striae and reaching the much greater diameter of 3.3 mm; these shells appear to be small to medium-sized specimens of a species of G. *(Gyraulus)*, probably G. *gilberti*. The other probable syntypes conform well to Iredale's description.

*Dimensions:*

|                          | whorls | diameter (mm.) | a/b  |
|--------------------------|--------|----------------|------|
| AMS 111731               | 3.09   | 2.04           | 3.15 |
| AMS 51770 (largest shell)| 3.03   | 2.04           | 3.08 |

*Remarks:* The differences by which Iredale distinguished *pelorius* from *leonatus* seem trivial. The number of whorls does not appear different when allowance is made for the larger size of *leonatus*; the more sunken spire (right side) of *pelorius* is due to the last whorl being less deflected towards the left side; most of the examined syntypes of *leonatus* also had only transverse ridges. I therefore follow Smith (1992) in treating *pelorius* as a junior synonym of *leonatus*, according to line priority, and the latter taxon is here considered to be a synonym of G. *(P.) scottianus*.

### Gyraulus *(Pygmanisus) scottianus* (Johnston, 1879)
(Figs 3 and 5, *leonatus* and *pelorius*; 20 G-L, 30, 31 D, 34)

*Planorbis scottiana* Johnston, 1879: 26
*Gyraulus scottianus* - Smith & Kershaw, 1979: 87
*Gyraulus (Pygmanisus) scottianus* – Brown, 1998: 141, figs 8,9,10,12,15, 17D-I,18A,B and 19.
*Gyraulus sp. 1* of Meier-Brook, 1983: 81, 98.

*Gyraulus sp.* Shea, 1995: 5, fig 15a-e.
*Pygmanisus leonatus* Iredale, 1943: 224 [see under that taxon].
*Pygmanisus pelorius* Iredale, 1943: 224 [see under that taxon]
*Pygmanisus parvus* Cotton, 1943: 148, pl. 18, figs 11, 12 [see under that taxon]
*Pygmanisus scottianus* - Smith, 1992: 272

*Type locality:* Launceston, Tasmania.

*Type material examined:* SAM D16180, syntype, 1 shell, , with old label "R.M.J. coll. co-type".

*Other material examined:*
**Queensland**
AMS 144995 (100 wet); W of Injune and N of Mount Hutton, on north side of Injune-Taroom road, 25°49'S 148°47'E, spring, 2 Oct 1984, W.E. Ponder and P.H. Colman.
**New South Wales**
BMNH ETD3953 (11 wet); Grafton, received in Sept 1984 from J. C. Walker. AMS 144800 (11 wet, sorted from juvenile *Gyraulus (G.) sp.* by Brown); Guinea Creek on road N of Badja Forest road, off Tuross road, small swampy creek, 36°11'S 149°28'E, 18 Jan 1981, stn 84, W.F. Ponder and W.F. Ponder jun. AMS 144801 (6 wet, sorted from juvenile *Gyraulus (G.)* by Brown); Guinea Creek on Badja Forest road, just off Nimmitabel road, isolated pools, 36°12'S 149°28' E, 18 Jan 1981, stn 25, W.F. Ponder and W.F. Ponder jun. AMS 144806 (1 wet); Mongarlowe River on The Clyde road E of Braidwood, small weedy stream, 35°26'S 149°56'E, 13 Jan 1981, W.F. Ponder and W.F. Ponder jun. AMS 144809 (8 wet); Snowball road, swampy creek, 35°55'S 149°35'E, 17 Jan 1981, stn 75, W.F. Ponder and W.F. Ponder jun. AMS 144810 (2 wet); Rushes Creek, 32 miles (51.5 km) southwest of Cooma towards Jindabyne, 1 Sept 1973, W.F. Ponder and W.F. Ponder jun. AMS 144826 (100 wet, sorted from *Gyraulus (G.)* by Brown); 5.5 km north west of Adaminaby on Snowy Mountains Highway, creek, 35°59'S 148°44'E, 1 Nov 1980, stn 20, W.F. Ponder and J. Hall. AMS 144833 (2 wet, sorted from *Gyraulus (G.)* by Brown); Carrabungla Creek on road 11 miles (17.7 km) W of Taralga, 26 Sept 1975,stn 40, J.B. Burch, M.S. Burch and D. Fleughelman. AMS 144838 (50 wet); Glenfield, Sydney, 33°55'S 150°54'E, 24 Feb 1975, N. Campbell. AMS 303885 (35 wet); Near Pipe Clay Point, Jamieson Park, Narrabeen lagoons, Sydney; temporarily filled creek, 30 Oct 1994, P.H. Colman and M. Shea.
**Victoria**
AMS 144844 (3 wet); 56 miles (90 km) S of Melbourne on Bass Highway, E side of Western Port Bay, roadside ditch, 17 Aug 1973, W.F. Ponder and B.J. Smith.

*Shell* (Figs 3 and 5, *leonatus* and *pelorius*; 20 G-L):
Original description "Shell discoidal, very minute, thin, pale horny, somewhat flattened above and below; whorls 4, depressedly rounded, finely transversely striated, regularly increasing; suture moderately sunk; aperture obliquely raised, roundly lunate; peristome simple. Diam. max. 2½ mil., min. 2 mil., height ½ mil." (Johnston, 1879).

The whorls of the single syntype seen, figured by Brown (1998, fig 18 A, B), increase regularly, and are entirely rounded and lack spiral sculpture.

*Dimensions of syntype:*

| whorls | diameter (mm) | a/b |
|--------|---------------|-----|
| 3.0 | 2.2 | 3.61. |

Little variation was observed by Brown (1998) in 420 specimens from 5 localities in Tasmania (Brown, 1998): shell diameter to 3.1 mm with 3.7 whorls, shape either entirely wholly planispiral or last whorl deflected towards the left side, fine spiral striae present in some specimens. No significant difference was apparent in the material reported here; maximum diameter 3.2 mm with a/b 4.12 (AMS 144809); spiral striae lacking or present in varying strength, sometimes deep enough to cut the transverse grooves and make a reticulate pattern. Lip strongly thickened in some specimens (Shea, 1995, *Gyraulus sp.*, figs 15 d, e).
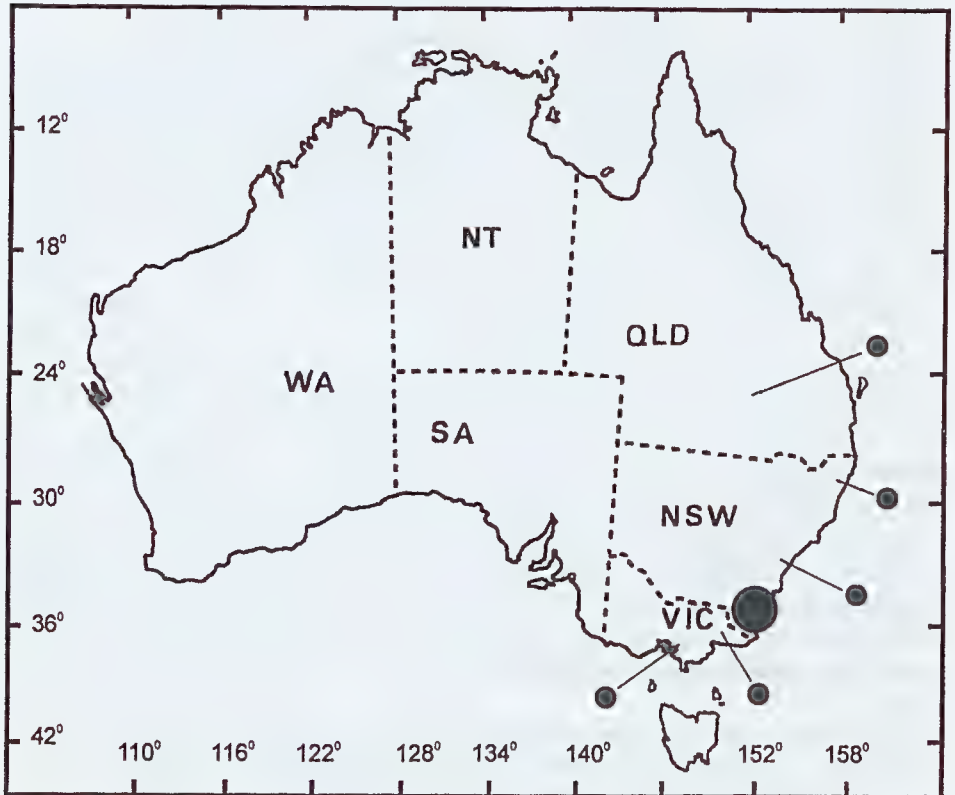


**Figure 34.**
*G. (Pygmanisus) scottianus.* Geographical distribution of collections identified in the present paper. This species also occurs in Tasmania. Most of the localities of origin are in the area of south-eastern NSW indicated by the large spot. Smaller spots represent single sites: QLD (Injune), NSW (Sydney and Grafton), VIC (Western Port Bay, Melbourne and Benambra near Corryong [*Gyraulus sp. 1* of Meier-Brook, 1983, material not seen by present author]).

*Anatomy* (Figs 30, 31 D): Due to a combination of poor preservation and damage to internal organs by larval parasites, anatomical data were obtained for comparatively few sexually mature snails. Pigmentation either lacking apart from eyespots or a light dusting of black or greyish brown on mantle roof and in head/foot, most dense between tentacles (n = 16 from 7 samples). Kidney appearing septate with undulating margins in some preparations (AMS 144838, confirmed by C. Meier-Brook, in litt. to the author, 5 March 1998), AMS 303885 and144844; total n = 7). In other preparations the kidney septa were less clear, or hardly detectable, though this may have been due to poor preservation (AMS 144995, -144800, -144809; total n = 6). Intestine either with posterior loop (n = 4), the longest extending as far as stomach, or with merely a leftwards bend (n = 4). Copulatory organ (Fig. 30) with penis attached at end of the penis sheath; penis pore subterminal, penis tip only a little swollen, stylet of the dagger-like form with bulbous base (n = 4, from AMS 144995, -144809, -303885). Prostate (Fig. 31 D); 3 short well-separated lobes in one animal (AMS 144809), but no lobe at all could be detected in 4 other animals (AMS 144800, -144844, -144995, -303885). Bursa copulatrix slender, elongate club-shaped to tapering, of mature appearance with orange-brown contents (n = 8 from 5 samples). Seminal vesicle represented by a thickened part of the hermaphroditic duct, with papillae or low tubercles but neither convoluted nor spinous (n = 5 from 4 samples). Ovotestis of 8 to 12 indistinct lobes (n = 6 from 5 samples). In all these respects the anatomy did not appear to differ from that of material of *G. scottianus* from Tasmania (Brown, 1998).

*Comparison with other species:* The shell of *G. (Pygmanisus) scottianus* (including as synonyms *G. leonatus* and *G. pelorius*) is distinguished from all other species of *Gyraulus* found in Australia by its smaller size, more slowly increasing and entirely rounded whorls, and weak microsculpture. Major distinctive anatomical characters are: kidney septate (though septa may not be visible in poorly preserved material), prostate lobes lacking or only few, seminal vesicle neither convoluted nor spinous.

*Habitat:* All collecting sites for *G. (P.) scottianus* were small waterbodies, including a spring, a roadside ditch and most frequently pools in small creeks and streams. The level of water in these places probably varies widely according to rainfall. A creek near Pipe Clay Point, Sydney (AMS 303885) was virtually dry for months before rain fell the week before snails were collected, from under dead leaves (P.H. Colman in litt. to the author, Oct 1984). Thus this species is well able to survive prolonged disappearance of surface water; yet it is versatile enough to be found in lakes as well as small waterbodies in Tasmania (Brown, 1998).

*Parasites:* The intermediate hosts in Australia of the stomach fluke *Calicophoron calicophorum* (Trematoda: Paramphistomatidae) are reported to be *Pygmanisus pelorius* by Boray (1982) and *Gyraulus scottianus* by Boray & Munro (1998).

*Remarks:* Meier-Brook (1983, pp. 81, 98) reported a small "*Gyraulus* sp. 1", from Benambra, E Victoria, having a shell diameter of only 2.5 mm, only 2 prostatic

diverticula and a "miniature edition" of the normal penial stylet, rather than one of the hobnail form. This taxon appears to correspond well to G. *(P.) scottianus.*

G. *(P.) scottianus* seems to be the only taxon needed to accommodate all populations of small *Gyraulus* with rounded whorls, found in SE Australia and having a septate kidney and few if any prostate lobes. This taxon is well differentiated within the Australian fauna of *Gyraulus* and could be viewed as one of the more distinctive lineages to have evolved within Australia. However, distinctive character states in the shell and kidney are shared with G. *(Torquis)* of N America and W Europe, and this in combination with the restricted distribution of G. *scottianus* in Australia suggests the possibility that it could be descended from specimens of G. *(Torquis)* introduced since European settlement (Brown, 1998, p. 147). Molecular data may be needed to decide this question. Meanwhile, the great reduction in the number of prostate lobes in G. *scottianus* (0 to 3) compared to the minima of 6 lobes observed in both G. *(T.) laevis* and G. *(T.) parvus* (Meier-Brook, 1983, Table 2), seems a good reason to think that G. *scottianus* had an independent origin in Australia.

*Distribution* (Fig. 34): Most of the material of G. *(P.) scottianus* recorded here is from the area of south- eastern NSW extending from the coast inland to Taralga and Adaminiby. One locality is in southern QLD (Injune) and one in VIC (Western Port Bay, south-east of Melbourne). Another possible record for VIC is Benambra (*Gyraulus sp. 1* of Meier-Brook, 1983). Apart from the addition of a record for QLD, the present data conform to the range given by Smith & Kershaw (1979), "Great Dividing Range of central and eastern Victoria and southern N.S.W." G. *scottianus* is perhaps more widely distributed than appears, as it may be overlooked due to its brief periods of activity in seasonally filled water bodies. Widespread in Tasmania (Smith & Kershaw, 1981; Brown, 1998).

**Taxa of discoidal Planorbidae recorded for Australia but probably in error**

*Planorbis obtusus* Deshayes ms of Smith, 1883

*Planorbis obtusus* Deshayes, Sowerby, 1878: *Planorbis*, pl. 5, fig 39 a,b; - Smith, 1883: 295-296.

*Material examined:* 4 dry shells, from 'Adelaide', BMNH without registration number, ex Cuming collection, one figured by Sowerby, 1878.

*Shell:* Larger than any known species of *Gyraulus.* Smith (1883) rightly commented that none is so acutely keeled as Sowerby's figured shell. Near the left side there is an obtuse angle, which in parts bears a low keel; aperture nearly rounded; transverse ridges numerous, close-set, nearly regular; spiral striae weak, only evident on inner whorls.

*Dimensions of largest shell:*

| whorls | diameter (mm) | a/b |
|--------|---------------|------|
| 5.18 | 12.9 | 4.40 |

*Remarks:* These shells appear to be *Planorbis planorbis* Linnaeus, of the Palaearctic region, and their locality of origin is doubtful. If they do represent an early introduction of this snail to Australia, the colony seems to have soon failed, as there appears to be no other local record of this species.

### *Anisus spirorbis* (Linnaeus, 1758)

*Planorbis spirorbis* Mueller – Smith, 1883: 296.

*Material examined:* 4 dry shells, from 'North Australia', BMNH without registration number, ex Cuming collection.

*Shell:* All are much depressed; whorls numerous, increasing slowly, flattened on the left side, lacking spiral sculpture.

*Dimensions of large specimen* (about one-quarter of last whorl missing): whorls 5.63, diameter 6.0 mm, a/b 4.60.

*Remarks:* Smith (1883) referred to two tablets holding several specimens of *Planorbis spirorbis* in the Cuming collection and labelled North Australia. The shells examined in the present study are in one box, and they conform to *Anisus spirorbis* or perhaps another species of this Palaearctic genus (for a recent account see Gloer & Meier-Brook, 1994). The Australian origin attributed to these specimens is probably wrong; there is no other record of *Anisus* from Australia.

## Discussion
### Taxonomy
The present anatomical observations confirm my earlier conclusions (Brown, 1981, 1998), that the small discoidal species of the *Planorbis* tribe found in Australia belong to *Gyraulus* rather than to the African *Afrogyrus* and *Ceratophallus*, despite similarities in the shell. The quantity and geographical coverage of Australian material dissected are now so extensive that it seems unlikely that either of these African taxa will be found in Australia. It has also become apparent from observations reported here, that *Gyraulus* from Australia are not classifiable in *G. (Caillaudia)*, to which Meier-Brook (1983) assigned the two species most widely distributed in tropical Africa, on account of the low number (3 to 12) and irregularity of their prostate lobes. All the Australian species may be classified either in *Gyraulus* sensu stricto, having more numerous prostate lobes, or *G. (Pygmanisus)*, which has very few if any prostate lobes and a distinctive septate kidney. The taxon '*Gyraulus sp. 1*' from Australia, in which Meier-Brook (1983, p. 98) observed only 2 prostate lobes, reminding him of

*G. (Caillaudia)*, is here treated as a synonym of *G. (P.) scottianus*, which seems likely to have evolved within Australia.

A major contribution of this study is to show from anatomical observations that the two species widespread in Tasmania (Brown, 1998), *G. meridionalis* and *G. scottianus*, are present on the Australian mainland, though they occur only in restricted south-eastern areas. These two species are clearly differentiated, from each other as well as from all other *Gyraulus*. *G. scottianus* is currently given subgeneric rank as *Pygmanisus*, and the same status may be merited by *G. meridionalis* (=*tasmanicus*) as the type species by synonymy of *Plananisus* Iredale. *G. meridionalis* conforms to *Gyraulus* s. s. of Meier-Brook (1983, p. 99) in its general anatomy, but differs in the penis being attached distally rather than at the proximal end of the penis sheath. At present I am reluctant to recognise another subgenus within *Gyraulus*, not only because the definitions of the currently recognised subgenera are not enirely satisfactory, but also in view of the need for more information about copulatory organ morphology of the genus in south-east Asia generally.

It is difficult to define clearly by morphological characters most of the species-group taxa Australian mainland, because of continuous variation in features of the shell and anatomy, and a lack of clear geographical patterns in the variation. Conchological variation bedevils the definition of genus-group taxa. The generic division made by Iredale (1943) according to whether the whorls are acutely angular (*Glyptanisus* Iredale) or no more than obtusely angular (*Plananisus*) is unsatisfactory, since whorl shape varies widely between and within populations. There are, however, four comparatively distinct forms of shell: small with slowly increasing rounded whorls in *G. (Pygmanisus) scottianus*; large, depressed and keeled (several taxa, e.g. *G. edgbastonensis* sp. n. and *G. waterhousei*); high-whorled with strong spiral sculpture (*G. hesperus*); high-whorled and angled (*G. mienanus*). The segregation of taxa with small round-whorled shells into *G. (Pygmanisus)* is well supported by anatomical characters. Unfortunately, no clear divisions are evident in the wide range of shell form displayed by *Gyraulus* s.s. in mainland Australia. Among the keeled taxa in this group, the most distinctive is *G. edgbastonensis* sp. n., found only in a few isolated artesian springs in south-western Queensland. *G. waterhousei* is also acutely keeled and is found most frequently in a restricted area of eastern Australia, but its validity as a species is questionable, as this shell form sometimes occurs apparently as an individual variant in populations of more or less obtusely angled snails. The very different group of populations of *Gyraulus* s. s., identified here as *G. hesperus*, living in northeast WA and northwest NT is characterised by a high shell, with more or less rounded whorls and strong spiral sculpture. Though distinct locally, this shell form is apparently connected by intermediate variation to the more depressed *G. essingtonensis*. *G. mienanus* is known only from Great Lake in Tasmania; there is no freshwater lake of comparable size and age in mainland Australia, and no lacustrine adaptation was evident in *Gyraulus* from mainland lakes.

The contribution of the anatomical features studied to species-level taxonomy within *Gyraulus* s. s. was small, apart from the clear characterisation of *G. meridionalis* provided by the copulatory organ. There was no clear

discontinuity in the widely variable number of prostate lobes, though the number was lower on average in populations from NT and WA identified as *G. hesperus*. The mantle pigmentation of *Gyraulus* indigenous to Australia appears to be uniformly diffuse, lacking any pattern, and is often very weak; the only population with a distinct pattern seen in this study is identified as *G. chinensis* and regarded as an introduction.

This study contributes to a better understanding of *Gyraulus* in Australia, by clarifying the conchological characters of taxa described originally from the shell alone, and by presenting extensive data for pigmentation, the copulatory organ and kidney. My observations on *Gyraulus* from Tasmania (Brown, 1998) led me to emphasise two aspects where a better understanding would be of fundamental importance for the taxonomy of this genus in Australia:

1) The relationship between *G. meridionalis* and *G. gilberti*.

2) Relationships between *G. scottianus*, the later-named species of *G. (Pygmanisus)* found on the mainland and *G. (Torquis)* of North America and Eurasia.

Observations now presented on the copulatory organ show *G. meridionalis* to be entirely different from *G. gilberti* and the several mainland taxa that may be its synonyms. According to morphological data, the single species *G. (P.) scottianus* could comprise all of the small round-whorled taxa of *Gyraulus* found in Australia, and this species seems quite likely to have evolved independently of *G. (Torquis)*. There remain important questions of species-level taxonomy that seem unlikely to be answered by morphological data alone, at least from features so far studied. Still unresolved is the fundamental question of how many taxa should be placed in the synonymy of the first-named Australian *Gyraulus*, *G. gilberti*. To determine boundaries between the biologically distinct species in this group of snails, morphological data probably need to be supplemented by evidence from molecular genetics.

## Development of the penial stylet

Although this study did not include a detailed investigation of the development of the immature stylet, observations reported here are relevant to previous authors' views on the growth of the stylet. Meier-Brook, 1983, 20) suggested, according to observations by himself and Hubendick (1958), that "possible differences in the site and mode of stylet formation . . . may prove to suggest other differences on the subgeneric level". Two patterns of development were distinguished by Meier-Brook. For some species, e.g. *G. acronicus* (Ferussac) of Europe, "In the early stages of development there is no clear distinction between the future penis sheath and the preputium. The developing penis with the stylet, which is formed in its definitive size (Hubendick, 1958; Meier-Brook, 1964) extends distally to near the male genital pore" and "during further growth of the whole copulatory organ the penis tip and stylet then gradually withdraw, before differentiation of papilla and diaphragm takes place". A different pattern of development was distinguished by Meier-Brook (1983, 20) in *G. (Torquis) parvus* and *G. (T.) laevis* (Alder), whose stylet was not recognisable until later in the growth of the animal. In these species "chitinous material" was seen in the distal internal wall of the penis sheath, and the process of chitinisation of the stylet

appeared to involve transfer of material from the penis sheath to the stylet. The site and mode of stylet formation observed in the present study for *G. essingtonensis, G. gilberti* and *G. hesperus* conform to the second pattern of development. The penis was contained wholly within the penis sheath while the stylet was forming, and this process occurred after differentiation of the penis sheath, preputium, papilla and diaphragm. The diffuse brown colour in the cellular lining of the distal penis sheath, which seemingly supplies material for the tanning of the stylet chitin, as implied by Meier-Brook, was sometimes strong enough to be visible externally. Since this pattern of development was observed in Australian species belonging to *Gyraulus* s. s., it is not a characteristic of the subgenus *Torquis*.

### Ecology and parasites

The large number of localities known for *Gyraulus* and the numerous specimens obtained indicate that these snails are among the most abundant freshwater gastropods in mainland Australia, occurring wherever there are habitable waterbodies, these ranging from seasonal rainpools to large lakes. There appears to be a difference between Australia and Africa in the type of habitat usually occupied by *Gyraulus*. In mainland Australia these snails are commonly found in waterbodies that are subject to wide fluctuations in water level, and they have been observed to reappear after the complete disappearance of surface water (see under *G. gilberti* and *G. scottianus*). In contrast, the two species of *Gyraulus* widely distributed in Africa are associated with comparatively stable waterbodies (Brown, 1994); *G. costulatus* with slowly flowing streams, dams and lakes in the tropical region, and *G. connollyi* with rivers and streams in the southern temperate region. Neither of these African species is found in habitats that dry out regularly, though such waterbodies may support large populations of other Planorbidae (Brown, 1994, Table 9.1, biotopes 4 and 5, *Bulinus* and *Ceratophallus*).

It is interesting that the transmission of paramphistome trematodes in Australia is reported to depend on *Gyraulus* as the intermediate host (Boray, 1982; Boray & Munro, 1998), whereas in Africa, where this group of parasites is also widespread, this snail is not known to play any part in the life cycle (Brown, 1998, Table 6.1).

### Zoogeography

"Presently the analysis of freshwater biogeography in Australia is hampered by poorly resolved taxonomy and lack of distributional data for many taxa" (Ponder, Wells & Solem, 1998, p. 84). This weakness is remedied to some extent by observations on *Gyraulus* presented here, from which it appears highly likely that all planate small species of Planorbidae found in Australia, apart from *Helicorbis*, are *Gyraulus*. The 4 species of *Planorbis* listed as incertae cedis by Smith (1992) are shown here to belong to *Gyraulus*. No evidence has been found for the presence in Australia of any of the planate genera of Planorbidae found in Africa apart from *Gyraulus*. Nor do the *Gyraulus* faunas of Australia and Africa show any close relationship since they are classified in different subgenera, and the present study provided no evidence in support of the

suggestion (Meier-Brook, 1983, p. 98) that the African subgenus *G. (Caillaudia)* might occur in Australia.

Several systems of faunal regions in Australia have been proposed according to the distribution of non-marine molluscs, mostly land snails and especially freshwater bivalves. However, the validity of such concepts of discrete 'fluvifaunulae' may be doubted (Wells, in Ponder et al., 1998, p. 81), and Ponder (in Ponder et al., 1998) reviewed distribution patterns of freshwater molluscs without attempting to relate them to concepts of faunal regions. Yet there is one named faunal region, the Peronian Region (Smith & Kershaw, 1979), that does seem meaningful in relation to *Gyraulus*. This region comprises the south-eastern mainland and Tasmania, and the distribution patterns defining it are evident in many groups of organism, reflecting the effects of the Bass Strait as a major barrier to disperal. This sea barrier separated Tasmania from Victoria about 40 m years ago, allowing independent evolution of the Tasmanian fauna and flora. Subsequent dispersal between these areas has been possible across land bridges formed during periods of lower sea-levels, most recently during the Pleistocene (Ponder & Wells, 1998, p.77). These periods provided opportunities for species evolved in Tasmania to disperse into the area of presentday Victoria, possible examples being *Gyraulus meridionalis* and *G. scottianus*, discussed further below.

The major distributional patterns to emerge from our present knowledge of *Gyraulus* in Australia are:

(1) The restriction of *G. (Gyraulus) meridionalis* and *G. (Pygmanisus) scottianus* to Tasmania and limited areas of the south-eastern mainland. In most of the vast area of Australia occupied by *Gyraulus* s. s. the copulatory organ is very different from that of *G. meridionalis* and is like that found in *Gyraulus* s. s. worldwide. This usual type of copulatory organ has not been observed in any specimen of *Gyraulus* s. s. from Tasmania. Since *G. meridionalis* is widespread in Tasmania, but comparatively rare on the mainland, it is perhaps the case that *G. meridionalis* evolved in Tasmania and then spread to the mainland, where it may be increasing its range. Or it could be that the distribution of *G. meridionalis* on the mainland is decreasing, perhaps due to competition from other species of *Gyraulus*, and that Tasmania provides a refuge for *G. meridionalis* and other taxa with its distinctive form of copulatory organ. *G. scottianus* has a larger distribution than *G. meridionalis* on the mainland, though it is still confined to the south-east, living usually in seasonal waterbodies liable to long periods of dryness, where there may be less competition from other species of *Gyraulus*.

(2) The occurrence of populations having the most depressed and acutely angular forms of shell only in SW Queensland (*G. edgbastonensis* sp. n.) and to the east of the Great Dividing Range (*G. waterhousei* sensu Brown, 1981).

(3) The occurrence of populations whose shell whorls are high, rounded or only obtusely angled, and strongly sculptured (*G. hesperus*), predominantly in NW Queensland and Northern Territory.

Since there is no taxonomic evidence of any link with the *Gyraulus* of Africa, the Australian fauna of *Gyraulus* seems related most closely to the fauna of SE Asia. Fossils attributable to *Gyraulus* are known from Miocene deposits in Australia (Ponder, 1998, p. 84), and the genus could have reached Australia

through land bridges that existed intermittently over a long period of time. A likely route seems to have been via New Guinea (Meier-Brook, 1983, pp. 97-98), which has been connected to Australia most recently during the Pleistocene when sea levels were lower during several glaciations, the latest about 20 000 years ago (Ponder & Wells, 1998, p. 77). Probably it was in the more distant past that *Gyraulus* colonised Australia, as the recent fauna shows little if any similarity at the species level to the fauna of New Guinea or of SE Asia as a whole. Meier-Brook (1983, p. 97) suggested that his taxon '*Gyraulus sp. 2*' from Australia could be a sister species to *G. brongersmai* of New Guinea, because of similarity in the shell, but additional evidence is needed to support this view; Meier-Brook's taxon is here treated under *G. chinensis*, which could have been introduced through human agency. The mantle of *Gyraulus* living in New Guinea, so far as it is known from observations on *G. convexiusculus* by Brown (1981), has a distinct pattern of pigmentation. This seems to be a common species in New Guinea; it was placed by Meier-Brook (1983) in the *G. chinensis* rassenkreis, which occurs throughout southern Asia and everywhere has a more or less patterned mantle. Only a single lot of patterned snails was seen by the present author in extensive material from Australia, and this population seems likely to represent an introduction of *G. chinensis* by human agency. No specimen of *Gyraulus* from Australia has been seen with either of the two most distinctive anatomical characters reported for *Gyraulus* from eastern Asia, namely a penis pore in the middle or proximal half of the penis (*G. malayensis* Meier-Brook, 1983) and a large balloon-like bursa copulatrix (*G. eugyne* Meier-Brook, 1983). No species with either the small shell form or the reduced number of prostate lobes seen in *G. (Pygmanisus)* has been reported from New Guinea or elsewhere in SE Asia, and neither has any species with a copulatory organ like that of *G. meridionalis*. Such dissimilarity between the *Gyraulus* faunas of Australia and SE Asia, suggests that the Australian fauna has evolved independently for a long time.

**Phylogeny**

In summarising his views on the evolution of *Gyraulus*, Meier-Brook commented (1983, p. 98) "The large area of S and E Asia plus the Malaysian Archipelago and Australia harbours only one subgenus although extensive speciation (=differentiation) occurred". Here Meier-Brook referred to a provisional subgenus *Gyraulus* sensu stricto, whose monophyletic status he doubted.

The distinctness and diversity of *Gyraulus* in Australia is now more impressive, for the anatomical data presented in this paper support recognition of an additional subgenus *G. (Pygmanisus)*, and a third subgenus should perhaps be recognised for *G. meridionalis* and related species with their distinctive copulatory organ. Yet despite diversity in some anatomical characters, the mantle pigmentation of *Gyraulus* in Australia is almost universally weak and lacking in pattern, in contrast to the generally patchy pigmentation in New Guinea and SE Asia (Meier-Brook, 1983, pp. 82, 86). This implies that non-patchy pigmentation was already a character of the one or more species that colonised Australia and gave rise to the recent species. A non-

patchy ancestral species perhaps originated from *G. chinensis*, the species postulated by Meier-Brook (1983, fig. 112, upper cladogram) as the stem from which arose the other species known in SE Asia. Such an origin for a non-patchy species would have involved a reversal in the character state, since according to Meier-Brook's scenario for the evolution of *Gyraulus*, patchy pigmentation is a synapomorphy for all the species in SE Asia

The morphological diversity displayed by *Gyraulus* in Australia is due to apomorphies in the shell, kidney, prostate gland and copulatory organ. Apomorphies in the shell are: strong spiral striae and reticulate sculpture (in *G. hesperus*), strong depression with an acute keel (in *G. atkinsoni*, *G. edgbastonensis* sp. n. and *G. waterhousei*), modifications of shell shape under lacustrine conditions (in *G. mienanus*), reduction in size (in *G. scottianus*). In the kidney, the development in Australia of septa and undulate margins (in *G. scottianus*) has apparently proceeded independently of their occurrence in other parts of the world (see Remarks under *G. scottianus*). Likewise in the prostate gland, the reduction in the number of lobes in *G. scottianus* seems to have occurred independently of reduction seen in other taxa (see Remarks under *G. scottianus*). In the copulatory organ the distinctive characters of the penis sheath and penis are synapomorphies for *G. meridionalis* and related taxa found in Tasmania; these character states are unique in the entire genus. Clearly the extremely depressed and keeled form of shell has evolved independently in different Australian lineages, since *G. atkinsoni* of Tasmania has the same copulatory organ structure as *G. meridionalis*, whereas *G. waterhousei* and *G. edgbastonensis* sp. n. have the different type of copulatory organ found in *G. gilberti* and all other taxa of *Gyraulus* known from the mainland apart from *G. (Pygmanisus)*.

The main conclusions to emerge from the morphology of *Gyraulus* in mainland Australia, and in Tasmania (Brown, 1998) are:

(1) The Australian fauna comprises two highly distinctive taxa, *G. (Pygmanisus)* and *G. meridionalis* (currently classified in *Gyraulus* sensu stricto, but which with related species may deserve subgenric status), and a complex of species-group taxa of *Gyraulus* s.s., which mostly are poorly defined morphologically and whose taxonomy would probably benefit from molecular analysis.

(2) The origin of the Australian fauna of *Gyraulus* lies entirely in SE Asia, though these two areas seem to have no recent species in common, and the distinctiveness of the Australian fauna indicates a long history of independent evolution.

(3) The fact that mantle pigmentation is patchy in all *Gyraulus* known from SE Asia, whereas it is non-patchy in all the indigenous Australian taxa, suggests that the development of non-patchy pigmentation was an early step in the evolution of the Australian fauna, preceding the development of distinctive character states in the shell, kidney, prostate gland and copulatory organ.

thanks are due to Winston Ponder, who made available an outstandingly large amount of material from the collection of the Australian Museum, Sydney, much of it collected by himself over many years. I appreciate the hard work and care taken in the preparation of specimens by all the collectors named in the text. I am indebted to correspondents who took time and trouble to answer my questions. Photographic images of shells and scanning electronmicrographs of microsculpture were produced in The Natural History Museum, London, by Harry Taylor and Viv Tuffney. For many years I have enjoyed correspondence about *Gyraulus* with Claus Meier-Brook and I am indebted to him for examining preparations of kidneys from *G. scottianus*. I am grateful to the Medical Research Council of the U.K for financial support.

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BOOK REVIEW

*Evolutionary Biology of the Bivalvia*
edited by *E.M. Harper, J.D. Taylor* and *J.A. Crame*

published by:
the Geological Society of London (Special Publication 177). 2000; 494 pp.
Hardback; price £99 Sterling.

Despite the implication of the title, this book is not a textbook, but a collection of 32 papers selected from among those presented at a meeting on the Biology and Evolution of the Bivalvia held at Cambridge, England, in September 1999. The editors and publishers are to be congratulated for such rapid publication after the meeting. The papers published here report the latest research from some of the most respected bivalve specialists. The book includes papers on classification, form and function, biogeography, ecology and phylogeny. It has two comprehensive indices, one for subjects and the other for taxa.

Owing to the diversity of the subjects, it is not possible to give more than a cursory review of what the volume contains. A feature of the book is the extensive editorial introduction which succeeds very well in tying the diverse papers together. The editors provide a short summary of each paper which gives the reader a good idea of the main thrust of each paper before going on to tackle the abstracts of the papers, or the papers themselves. DNA studies and cladistic analyses are a feature of a number of papers and the former in particular has proved to be and will continue to be a very powerful tool in sorting out relationships at all levels of classification.

The higher classification of the Bivalvia is dealt with in a number of papers. Molecular biological techniques are now being applied to molluscs and two such studies are included here. On the basis of these and other work reported it appears that the superfamilial and much of the ordinal classification of the bivalves hitherto based on shell morphology and anatomy has validity. Only the Myoidea seem to have a polyphyletic origin and should not be regarded as an order. It would seem that we are very close to common agreement on bivalve classification.

Two papers report studies undertaken in Australia on sperm morphology which can be used to provide phylogenetic characters. On the basis of sperm morphology, Arcoidea and Limopsoidea are not as closely related as previously supposed, whereas Ostreoidea and Limoidea are, as also Pterioidea, Pinnoidea and Pectinoidea. The sperm of giant clams supports a close relationship with cardiids confirming previous studies that the family Tridacnidae should not be regarded as a family but as a subfamily of the Cardiidae.

Pectinid eyes are the subject of another paper. Contrary to popular belief, they do not seem to used to avoid predators. Just what is their function, has yet to be discovered.

A particularly interesting study of function and form in lucinids indicated that they harbour sulphide-oxidising, chemosymbiotic bacteria and have adapted their internal structures to separate oxygen rich water for respiration

from sulphide bearing water used by the resident bacteria for chemosynthesis. Evidence of these features is present on fossil lucinids extending back to at least the Silurian.

A biogeographical paper analysing latitudinal and longitudinal gradients of taxa shows that gradients are not uniform as previously thought. Of particular interest to Australians is the revelation of the high biodiversity of Australia, regarded as a biodiversity 'hot spot'. Such broad brush studies rely very much on the literature for local faunal lists to provide data for analysis, the quality of which can vary. This is starkly demonstrated by a local study on the Florida Keys which found after on site collecting and searching through museum collections that only 73% of the fauna had been reported in the literature.

This is a book for the specialist but given the cost will only be found in institutional libraries.

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