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Review of the Family Sphaeriidae (Mollusca: Bivalvia) of Australia, With the Description of Four New Species

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ABSTRACT. The sphaeriid fauna of Australia includes 17 species and subspecies, seven of them belonging to *Musculium* and ten to *Pisidium*. Subgeneric classification of *Sphaerium problematicum* Gabriel and identity of *Cyclas egregia* Gould are not defined. Most of the species are endemic, but one species found near Adelaide is probably an introduced *Musculium lacustre* (Müller). All native *Musculium* species are allotted to the subgenus *Sphaerinova*; three subgenera of *Pisidium* are represented (*Afropisidium* and *Odhneripisidium* by one species each and *Euglesa* by eight species). Two anatomically distinct and probably monophyletic groups are distinguished in *Euglesa*. Four species are described as new: *Musculium quirindi* n.sp., *Pisidium (Odhneripisidium) australiense* n.sp., *P. (Euglesa) ponderi* n.sp. and *P. (E.) centrale* n.sp. Descriptions of shell and anatomy as well as the data on distribution and ecology are given for each species and an identification key is provided. Some phylogenetic and zoogeographical implications are discussed.

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The family Sphaeriidae includes the smallest freshwater bivalves (length of adult shell is from 2 to 20 mm). The group is distributed worldwide and inhabits almost all types of freshwater habitats including those (springs, small creeks and peat bogs) where no other bivalves can survive. Therefore, its investigation is important for not only understanding the structure and history of the fauna, but they may be also used in monitoring environmental conditions in some countries. At the same time, sphaeriids remain a group poorly studied in faunistic and taxonomic aspects because of their small size, cryptic mode of life (in bottom sediments) and scarcity of reliable diagnostic characters.

The first sphaeriid named from Australia, *Cyclas egregia*, was described by Gould (1846), but this species has remained dubious until now. The group was reviewed last century in Tasmania by Tenison Woods (1876) and checklisted for the whole continent by E.A. Smith (1883). South Australian and Victorian sphaeriids were reviewed in the 1930's (Cotton & Godfrey, 1938; Gabriel, 1939). Several poorly described species and a genus from New South Wales were added by Iredale (1943b). The list of Australian freshwater molluscs published in the same year (Iredale, 1943a) included 16 species of Sphaeriidae allotted to three endemic genera. Another species from South Australia was described by Cotton (1953).

Iredale and Cotton regarded the Australian sphaeriid fauna as endemic at the generic level and rather diverse. Most of the species were attributed to limited geographic areas. However, these authors failed to provide reliable diagnostic characters and their work has been strongly

criticised by later authors (B.J. Smith & Kershaw, 1979; Kuiper, 1983). As a result, in some field guides on freshwater molluscs (B.J. Smith & Kershaw, 1979, 1981) the opposite point of view was proposed: only two species of the common genera *Sphaerium* and *Pisidium* were recognised, one of them being the supposedly cosmopolitan *Pisidium casertanum* (Poli, 1791).

The most recent revision of Australian sphaeriids was published by Kuiper (1983), who recognised 12 species (three of them described as new). All the species were included in the widely distributed genera *Pisidium* and *Sphaerium*, the latter with an endemic subgenus *Sphaerinova* Iredale, 1943a. Most of the species (five *Sphaerium* and six *Pisidium*) were considered endemic; one species was identified as *P. casertanum*, a taxon widely distributed outside Australia. Kuiper's view on the group was accepted recently by B.J. Smith (1992).

Different views on the origin of the Australian fauna of sphaeriids have been published. McMichael (1967) and Starobogatov (1970) regarded it as derived from south Asia. Kuiper (1983) suggested ancient, Gondwanan origin for some Australian taxa. In the zoogeographic reviews of B.J. Smith & Kershaw (1979) and Taylor (1988), Australian sphaeriids were neglected because of insufficient knowledge of their affinities.

Despite sphaeriid research in Australia having a rather long history, many aspects of the systematics, biology and biogeography of the group need much further investigation. The status of some species and forms is not settled and there are considerable gaps in outlining distributions. Affinities of Australian taxa to each other and to those known from the other continents are poorly studied.

Since 1983, extensive collecting was carried out by the staff of the Australian Museum, Sydney in areas previously poorly studied (Northern Territory, northern Queensland, central Tasmania). Numerous samples of sphaeriids were preserved in alcohol or formalin and were consequently available for anatomical study and statistical assessment. In addition, some new sphaeriid collections were accumulated in the other Australian museums.

Quite recently, new anatomical data were obtained and successfully used for taxonomy and phylogenetic analysis of sphaeriids from different regions (Korniushin, 1992, 1995, 1998a; Dreher-Mansur & Meier-Brook, 1992). The anatomical investigation of Australian sphaeriids is of importance for understanding both the evolution of the group at the global scale and the history of the Australian freshwater fauna. Characters of shell microsculpture, especially those of shell pores, regarded as taxonomically significant by recent investigators (Dyduch-Falniowska, 1983; Kuiper & Hinz, 1984), were also not previously studied in most of the Australian species.

The aim of the present study was to obtain a better understanding of the taxonomic diversity and affinities of Australian sphaeriids by using new material and recently proposed taxonomic characters. Earlier published descriptions and diagnoses are supplemented by anatomical and some microstructural characters and several new species are described. An identification key is provided and some phylogenetic and zoogeographical problems are discussed.

Materials and methods

Material for this study was obtained mainly from zoological museums in Australia: Australian Museum, Sydney—about 250 lots; Western Australian Museum, Perth—8 lots; South Australian Museum, Adelaide—20 lots; Queen Victoria Museum, Launceston—8 lots; Tasmanian Museum, Hobart—about 40 lots. Most of the type specimens deposited in Australian and European museums were revised.

Distribution maps include all localities of the material used in this study. Collection data for the type lots and the other reference lots (those taken for statistical, microstructural or anatomical investigation) are provided, type lots marked with an asterisk (*) were not examined in this study.

The shells were studied by light microscopy and Scanning Electron Microscopy (SEM). Specimens selected for SEM were coated with gold using a Dynavac Mini Coater and examined with a Cambridge Instruments Stereoscan 120 microscope using Secondary Electron Detector and Robinson Detector (for backscatter electrons), at 18KV and a working distance 18–30 mm. When necessary, adherent material was removed from shells by treating with 25% hypochlorite bleach and cleaning by hand.

Pores were counted on SEM photographs. In those, taken at high magnification (400×) counts were made for the whole area covered; several smaller patches were separately observed in each photograph taken at lower magnification (200×). In each case, the area covered by photographing was estimated from the scale bar. Pore density was recalculated for 1 mm^2, mean values and standard deviation are provided in descriptions, when applicable.

The following shell measurements were made (Fig. 1): shell length (L), shell height (H), shell width (W), height of the hinge plate under umbo (HH), length of ligament pit (LL), length of hinge—equivalent to the distance between cusps of lateral teeth in the left valve (LH), distance of umbo from anterior (LA) and posterior (LP) margins. The following indices were calculated: relative shell height (H/L), relative hinge plate height (HH/H), relative hinge length (LL/L), position of the umbo (not in all lots) (LA/LP), relative shell width (W/H). In *Musculium*, the length of the embryonic shell LE was also measured and its relative size (LE/L) was calculated. A total of 450 specimens were measured; specimens from large lots (more than 20 specimens) were selected randomly. Basic statistical parameters (mean value and standard deviation) were calculated for each sample.

All computerised statistical treatments were made using Statistica for Windows including a standard, two-tailed test for independent samples.

Traditional designation of hinge teeth (Kuiper, 1983) is applied here: in the left valve, cardinal teeth are marked as c2 (inner) and c4 (outer), posterior lateral teeth as p3 and anterior laterals as a3; in the right valve, cardinal tooth is c3, posterior lateral teeth are p1 (inner) and p3 (outer), anterior laterals a1 and a3 respectively (see Fig. 1).

Anatomical study was based on methodology used for Palaearctic (Korniushin, 1992, 1996b) and African species (Piechocki & Korniushin, 1994; Korniushin, 1995). Characters of the mantle edge (including musculature), gills

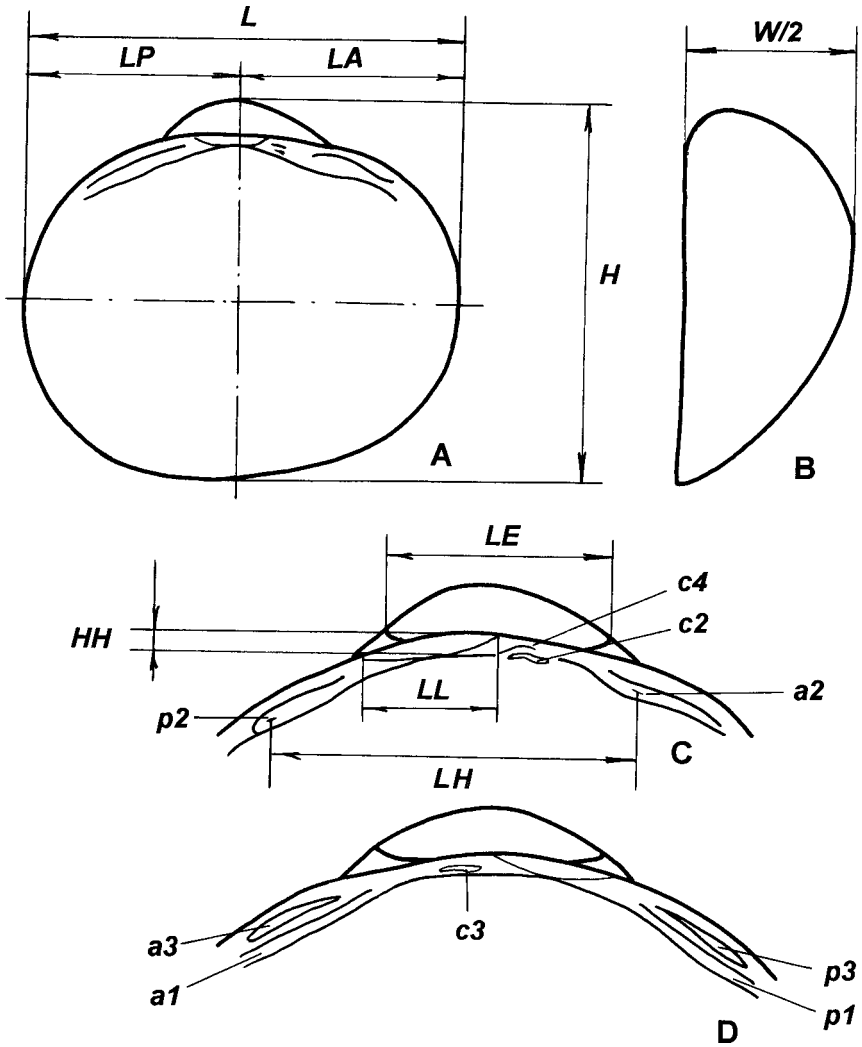


Figure 1. Shell measurements and hinge teeth designations applied in this paper: A—left valve from the inner side; B—the same valve anteriorly; C—hinge of the left valve; D—hinge of the right valve. *L*—shell length, *LP*—length of posterior part of the shell, *LA*—length of anterior part, *LE*—length of embryonic (nepionic) shell, *H*—shell height, *W*—shell width, *c2–c4*—inner and outer cardinal teeth of the left valve, *c3*—cardinal tooth of the right valve, *a1–a3*—inner and outer anterior lateral teeth of the right valve, *p1–p3*—corresponding posterior lateral teeth, *a2*—anterior lateral tooth of the left valve, *p2*—corresponding posterior lateral tooth.

(including brood pouches) and nephridia were investigated. The latter were studied *in situ*, after opening the valves. If the part of proximal duct was observed between the branches of the dorsal lobe, the type of nephridium was defined as open; in nephridia of the closed type the branches tightly adjoin each other (Fig. 2A–C). Gills and mantle were stained with Grenacher's carmine and water eosine respectively and mounted on microscope slides in Canada Balsam. The position of the outer demibranch was evaluated by counting inner demibranch filaments in front of its anterior margin (Fig. 2D, see also Korniushin, 1996a, 1997). Siphons were observed in life, whenever material was available; siphonal retractors were figured from preserved specimens (Fig. 2E). Number, size and arrangement of inner radial muscle bundles were observed in mantle preparations of *Pisidium* species and the other elements of mantle musculature were also taken into account (Fig. 2F). SEM was also used for the study of pallial structures by using critical point drying with a BIORAD CPD750.

Abbreviations of museum collections are as follows; in the text the type of the lot is indicated by the letter d (dry lot) or w (wet alcohol or formalin lot) after the collection number or museum abbreviation:

AM	Australian Museum, Sydney
IZK	Institute of Zoology, Kiev
BMNH	Natural History Museum, London
QVM	Queen Victoria Museum, Launceston
SAM	South Australian Museum, Adelaide
SMF	Senckenbergsmuseum, Frankfurt-am-Main
TMH	Tasmanian Museum, Hobart
WAM	Western Australian Museum, Perth
coln.	a particular collection in the museum, when applicable

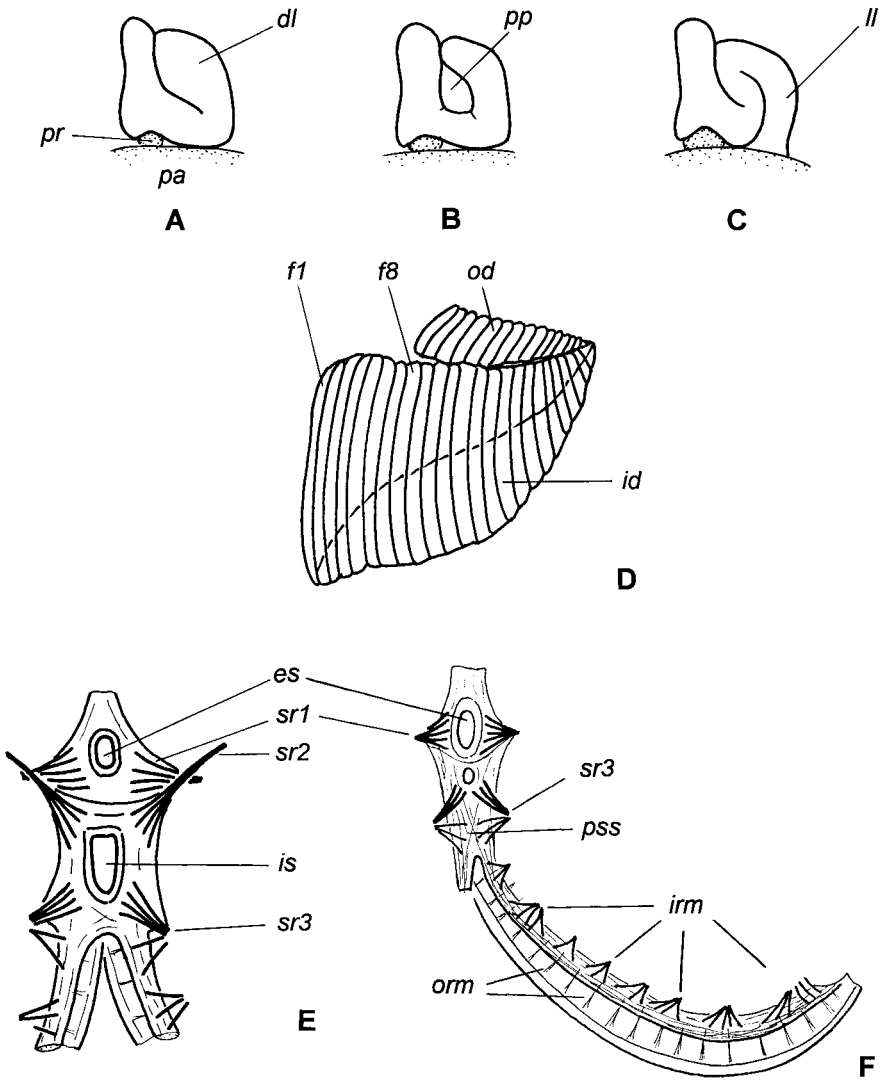


Figure 2. Principal anatomical characters: A–C—types of nephridium (dorsal view): closed (A), open (B), with visible lateral loop (C); D—diagrammatic view of ctenidium from outside, defining of the outer demibranch position (in this case it extends from the eighth filament): *f1*—first filament of the inner demibranch, *f8*—eighth inner demibranch filament, if counted from the anterior edge; E—siphons and siphonal retractors in *Musculium* (diagrammatic internal view); F—mantle edge with its musculature in *Pisidium* (diagrammatic internal view).

Collectors names are abbreviated as follows: AK, A.V. Korniushin; FWA, F.W. Aslin; GC, G. Clark; IL, I. Loch; JH, J. Hall; JW, J. Waterhouse; OG, O. Griffiths; WFP, Winston F. Ponder; WP, Warwick F. Ponder. Abbreviations of states, territories and topographic terms: NSW, New South Wales; NT, Northern Territory; Qld, Queensland; SA, South Australia; Tas., Tasmania; Vic., Victoria; WA, Western Australia; Ck, creek; Hwy, highway; Mt, mountain; NP, National Park; alt., altitude; Rd, road.

Anatomical structures, labelled on the figures:

aa anterior adductor
bp brood pouches
dg digestive gland
es exhalant siphon
g gill
irm inner radial muscles
is inhalant siphon
ldl lateral branch of the dorsal lobe
ll lateral loop
mdl medial branch of the dorsal lobe
orm outer radial mantle muscles
pa posterior adductor
pp pericardial part of nephridium
pr pedal retractor
pss presiphonal suture
sr1 retractors of the exhalant siphon
sr2 dorsal retractors of the inhalant siphon
sr3 ventral retractors of the same siphon
s excretory sac

Systematic account

Genus *Musculium* Link, 1807

Type species. *Tellina lacustris* Müller, 1774, by monotypy.

Distribution. Almost cosmopolitan (all continents except Antarctica).

Diagnosis. Shells usually thin and fragile. Umbones narrow (in comparison with *Sphaerium*), central or slightly shifted posteriorly. Hinge plate relatively narrow; tendency to hinge teeth reduction evident in many (but not all) species. Both siphons tubular. Upper (exhalant) siphon with one pair of retractor muscles, lower (inhalant) with two pairs (Fig. 2E). Outer demibranch of two lamellae, relatively small (height about 1/3 inner demibranch height), begins at 5th filament of inner demibranch (Starobogatov & Streletskaja, 1967; Korniushin, 1996a). Brood pouches multiple. Nephridia with long and narrow funnel and small excretory sac without internal valve (Dreher-Mansur & Meier-Brook, 1992).

Remarks. This genus was for a long time regarded as a subgenus of *Sphaerium*. Generic rank was applied by Starobogatov & Streletskaja (1967), Burch, (1975), Heard (1977), Dreher-Mansur & Meier-Brook (1992) and Korniushin (1996a). Shell characters were not reliable for diagnostics, while in some species they were intermediate between *Musculium* and *Sphaerium* (see also Heard, 1977). Peculiarities of reproduction and life cycle, namely late (in comparison with *Sphaerium*) formation of eggs and sperm, small size of intramarsupial larvae, higher fecundity, high growth rate and short life span were reported by Heard (1977). These characters are associated with the preference for temporary or unstable water bodies, evident in the majority of species. Validity of the genus *Musculium* was confirmed by the study of enzymes (Hornbach, 1980). However, the best generic diagnostic characters were provided by the study of nephridia (Dreher-Mansur & Meier-Brook, 1992). *Musculium* is well distinguished from *Pisidium* by larger size, median or nearly median position of the umbo, presence of two tubular siphons, two pairs of retractor muscles by the lower (branchial) siphon, outer demibranch with two lamellae and multiple brood pouches.

Cyclas tasmanica Tenison Woods, 1876 was first attributed to *Musculium* by Heard (1977). In the present study the diagnostic characters of nephridium were checked, and the diagnostic long funnel and small excretory sac without an internal valve were observed in all Australian species previously included in *Sphaerium s.l.* by Kuiper (1983).

Subgenus *Sphaerinova* Iredale, 1943a

Type species. *Sphaerium macgillivrayi* E.A. Smith, 1882 by original designation.

Distribution. Australian, but may also include taxa from New Zealand, south Asia (India) and South America (see Remarks).

Diagnosis. Shells small (length up to 9 mm, usually 7 to 8 mm) compared with that in nominate subgenus; beaks usually slightly shifted posteriorly, not protruding, prodissoconch sometimes separated by growth break line but never forming bean-shaped cap. Ligament externally visible, elevated in largest specimens. Siphons short, especially their fused part; dorsal retractor muscles of inhalant siphon markedly reduced and scars merged with those of posterior adductors. Outer demibranch 0.3 to 0.4 height of inner demibranch (depending on stage of development).

Remarks. In introducing the genus *Sphaerinova*, Iredale (1943a) distinguished it from *Sphaerium* by the narrow ligament plate and somewhat reduced cardinal teeth. However, these characters are diagnostic of *Musculium* as a whole, not just of the Australian taxa. Kuiper (1983) treated *Sphaerinova* as a subgenus of *Sphaerium* with two species, namely *S. tasmanicum* and *S. lacusedes* Iredale, 1943a, distinguished from *Musculium* (which he considered to be another subgenus of *Sphaerium*) by their externally visible ligament and by the peculiar form of the umbo (no bean shaped caps). B.J. Smith (1992) also accepted subgeneric status of *Sphaerinova* within *Sphaerium s.l.*, but included in this taxon all Australian species of the group.

The placement of *Sphaerinova* in *Musculium* is confirmed by the similarity in shell characters, peculiarities of reproduction (Heard, 1977) and, especially, by the diagnostic characters of the nephridium. Alongside the characters, provided by Kuiper (1983), it is distinguished from the nominate subgenus by the markedly reduced siphonal retractors. Short siphons were found in the two species observed alive (Figs. 6D,E, 19A,B), and the weakness of the retractors suggests that this character is common to all species. The umbo is shifted somewhat posteriorly in many of them.

Australian species observed below are considered consubgeneric because of the similarity in the main characters of the siphons, siphonal musculature and gills. In my opinion, differences in the ligament position between *M. kendricki* and *M. problematicum* vs *M. tasmanicum* and *M. lacusedes* mentioned by Kuiper (1983: 25) are not significant: all species have an externally visible ligament and the degree of its elevation evidently depends on shell size, being most pronounced in large specimens of *M. tasmanicum*, *M. lacusedes* and *M. tatiarae*.

Musculium novaezelandiae (Deshayes, 1854) from New Zealand is considered closely related to *M. tasmanicum* by many authors (Heard, 1977; Kuiper, 1983), thus it may also belong to *Sphaerinova*. Several anatomically studied species from South America and south Asia are characterised by the posterior shift of the umbo and the external ligament (Kuiper & Hinz, 1984; Subba Rao, 1989) and may be related to or possibly consubgeneric with Australian taxa.

Musculium (Sphaerinova) tasmanicum (Tenison Woods, 1876)

Diagnosis. Shell quadrangular or trapezoid, very thin and fragile, transparent. Upper (dorsal) margin almost straight, with clear angles. Umbones narrow, protruding. Internal

pores dense. Hinge plate narrow, cardinal teeth straight or slightly bent, lateral teeth normally developed.

Shell quadrangular or trapezoid, compressed, thin-walled, transparent, sometimes of red or brown colour due to staining. Dorsal margin straight or slightly curved. Anterior and posterior ends usually markedly angulated. Umbones narrow or moderately broadened, somewhat protruding, sometimes with separated prodissoconch. External surface smooth (Fig. 3C). Internal pores rather abundant (Fig. 3D). Siphonal retractors scars distinguishable but merged to posterior adductor scars. Hinge plate narrow (Table 1), especially under umbo; hinge teeth thin, cardinals straight or slightly bent; lateral teeth straight. Ligament visible from outside, somewhat protruding, ligament pit long and narrow. Shells of young specimens circular or short oval.

Anatomy. Gill and siphonal characters as in subgeneric diagnosis. Inner demibranch with three to four (rarely five) brood pouches, including up to five (usually two or three) filaments each. Nephridium usually of closed type, proportions of dorsal lobe vary.

Distribution. Northern Territory (occasionally); along the east coast and Great Dividing Range from northern Queensland to Victoria; the Murray-Darling system (apparently rare), including South Australia (lower Murray); Tasmania.

Ecology. Appears to show a preference for lentic water.

Remarks. This species is one of the most variable among Australian sphaeriids. Variability of the shell shape, position of umbo and the shape of nephridium (to a lesser extent) shows clear geographical pattern. The northern form is the most distinct in its morphological character and geographically separated from the nominate form widely distributed in the Australian mainland and Tasmania. However, morphological differences between these forms concern only a few characters, and the limits of their variation nearly overlap. Because of the geographic separation without a clear morphological gap, both forms are defined as subspecies.

Table 1. Shell indices in the species of *Musculium* (mean ± SD, N—number of measured specimens, measurements shown in Fig. 1). Abbreviations: N—number specimens measured; H/L—relative shell height; HH/H—relative height of the hinge plate; LL/L—relative length of the ligament pit; LH/L—relative hinge length; LA/LP—position of umbo; LE/L—relative length of embryonic (prodissoconch) shell (not measured in *Pisidium*); W/H—relative shell width.

species and locality	N	H/L	HH/H	LL/L	LH/L	LA/LP	LE/L	W/H
Musculium tasmanicum tasmanicum								
Coomooboolaroo, Qld	3	0.81±0.016	0.21±0.002	0.20±0.008	0.58±0.029	1.23±0.066	0.21±0.023	0.63±0.009
Binnum Waterholes, SA	7	0.80±0.015	0.023±0.008	0.18±0.008	0.55±0.015	1.13±0.068	0.18±0.030	0.64±0.030
Table Cape, Tasmania	5	0.82±0.014	0.020±0.004	0.22±0.019	0.52±0.015	0.94±0.071	0.20±0.019	0.64±0.041
pooled	15	0.81±0.015	0.022±0.005	0.19±0.019	0.56±0.025	1.16±0.079	0.19±0.029	0.64±0.025
pooled, range		0.80–0.84	0.014–0.034	0.18–0.25	0.50–0.61	0.86–1.28	0.14–0.23	0.58–0.69
Musculium tasmanicum queenslandicum								
Atherton Tableland, Qld	3	0.84±0.007	0.019±0.021	0.20±0.021	0.60±0.009	1.25±0.071	0.20±0.027	0.65±0.075
Buffet Creek, NT	7	0.84±0.008	0.022±0.004	0.21±0.015	0.61±0.009	1.30±0.041	0.20±0.029	0.60±0.032
pooled	10	0.84±0.007	0.021±0.004	0.21±0.018	0.60±0.010	1.28±0.053	0.20±0.027	0.61±0.051
pooled, range		0.83–0.86	0.016–0.029	0.18–0.24	0.59–0.63	1.18–1.38	0.17–0.25	0.565–0.74
Musculium tatiarae								
Lake Eliza, SA	5	0.86±0.006	0.043±0.004	0.19±0.011	0.57±0.026	1.04±0.073	0.27±0.044	0.61±0.035
Binnum Waterholes, SA	8	0.84±0.014	0.032±0.008	0.23±0.022	0.59±0.024	1.15±0.103	0.24±0.028	0.64±0.020
Lake Torrens, SA	6	0.84±0.012	0.031±0.006	0.24±0.029	0.59±0.021	1.08±0.063	0.17±0.029	0.67±0.049
pooled	19	0.84±0.014	0.035±0.008	0.22±0.028	0.58±0.024	1.10±0.093	0.23±0.049	0.64±0.041
pooled, range		0.83–0.87	0.018–0.048	0.18–0.28	0.54–0.64	0.96–1.30	0.13–0.32	0.58–0.72
Musculium lacusedes								
pooled	5	0.78±0.038	0.035±0.006	0.20±0.025	—	1.02±0.064	0.25±0.075	0.59±0.029
Musculium kendricki								
north of Capel, WA	5	0.85±0.010	0.033±0.006	0.18±0.020	0.63±0.068	1.15±0.044	0.21±0.019	0.64±0.014
Musculium quirindi								
paratypes	5	0.81±0.014	0.037±0.003	0.19±0.013	0.57±0.016	1.54±0.096	0.21±0.035	0.71±0.034
Attunga, NSW	5	0.86±0.015	0.032±0.007	0.21±0.012	0.58±0.014	1.18±0.058	0.25±0.020	0.75±0.036
pooled	10	0.83±0.027	0.034±0.006	0.20±0.016	0.58±0.015	1.36±0.20	0.23±0.033	0.73±0.041
pooled, range		0.80–0.87	0.022–0.040	0.18–0.23	0.56–0.60	1.13–1.64	0.16–0.27	0.68–0.79

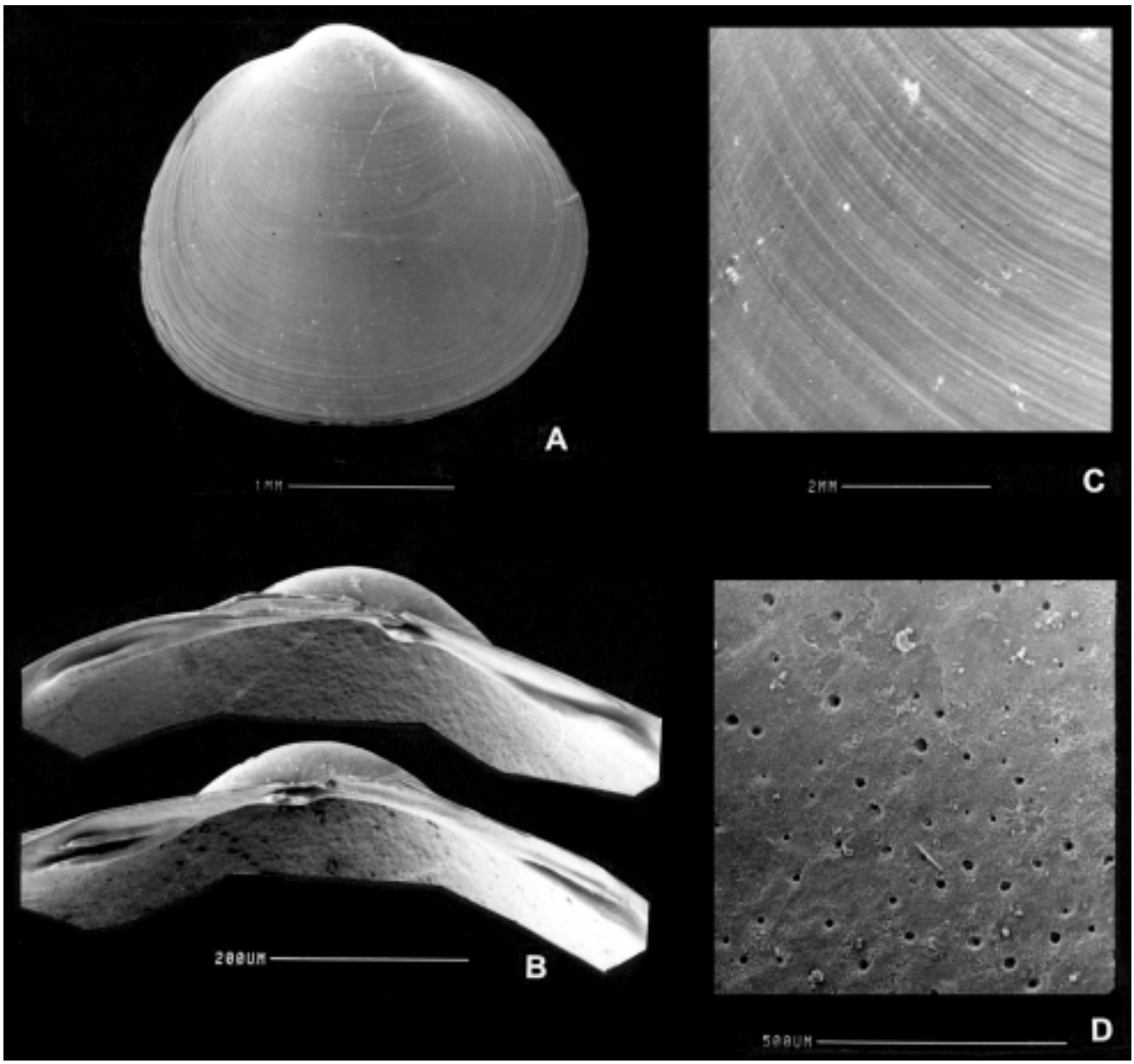


Figure 3. *Musculium tasmanicum tasmanicum* (Tenison Woods), Blue Mountains, NSW (AM, no number), shell: A—exterior view of left valve, B—hinge, C—sculpture, D—internal pores.

Musculium (Sphaerinova) tasmanicum tasmanicum

Figs. 3–8

Cyclas tasmanica Tenison Woods, 1876: 82.
Sphaerium translucidum Sowerby in Reeve, 1876: pl. 5, fig. 46; E.A. Smith, 1883: 305, pl. 7, fig. 32; Iredale, 1943a: 196.
Sphaerium macgillivrayi E.A. Smith, 1883: 305, pl. 7, fig. 34.
Sphaerinova macgillivrayi.–Iredale, 1943a: 195.
Sphaerinova victoriana Iredale, 1943a: 195.
Sphaerinova nundialis Iredale, 1943a: 195; Iredale, 1943b: 95, fig. 3.
Sphaerinova terenda Iredale, 1943b: 95, fig. 3.
Australpera bradena Iredale, 1943a: 196; Iredale, 1943b: 95, fig. 3.
Sphaerium tasmanicum.–Kuiper, 1983:19, figs. 14–29 (part: typical form and forms *terenda*, *bradena* and *nundialis*).

Type material. Possible syntypes TMH E1111/7452*, a few fragments, Swansea, east coast, Tas., revised by Kuiper (1983). *Sphaerium translucidum*, holotype and 2 paratypes BMNH 1846.10.7.144/145-6, Palmtree Ck, Qld. *Sphaerium macgillivrayi*, syntypes, 1 specimen and 1 valve, BMNH 1859.10.28-9, Penrith, NSW. *Sphaerinova victoriana* Iredale, possible syntypes, NMV F533*, 7 specimens and a valve, Tarraville, Vic., revised by Kuiper (1983). *Sphaerinova nundialis*, lectotype (Kuiper, 1983: 21) AM C109823, Nundle, NSW. *Sphaerinova terenda*, holotype AM C100522 and paratype AM C109821, Leeton, Murrumbidgee River, NSW. *Australpera bradena*, holotype AM C100521, Braidwood, NSW.

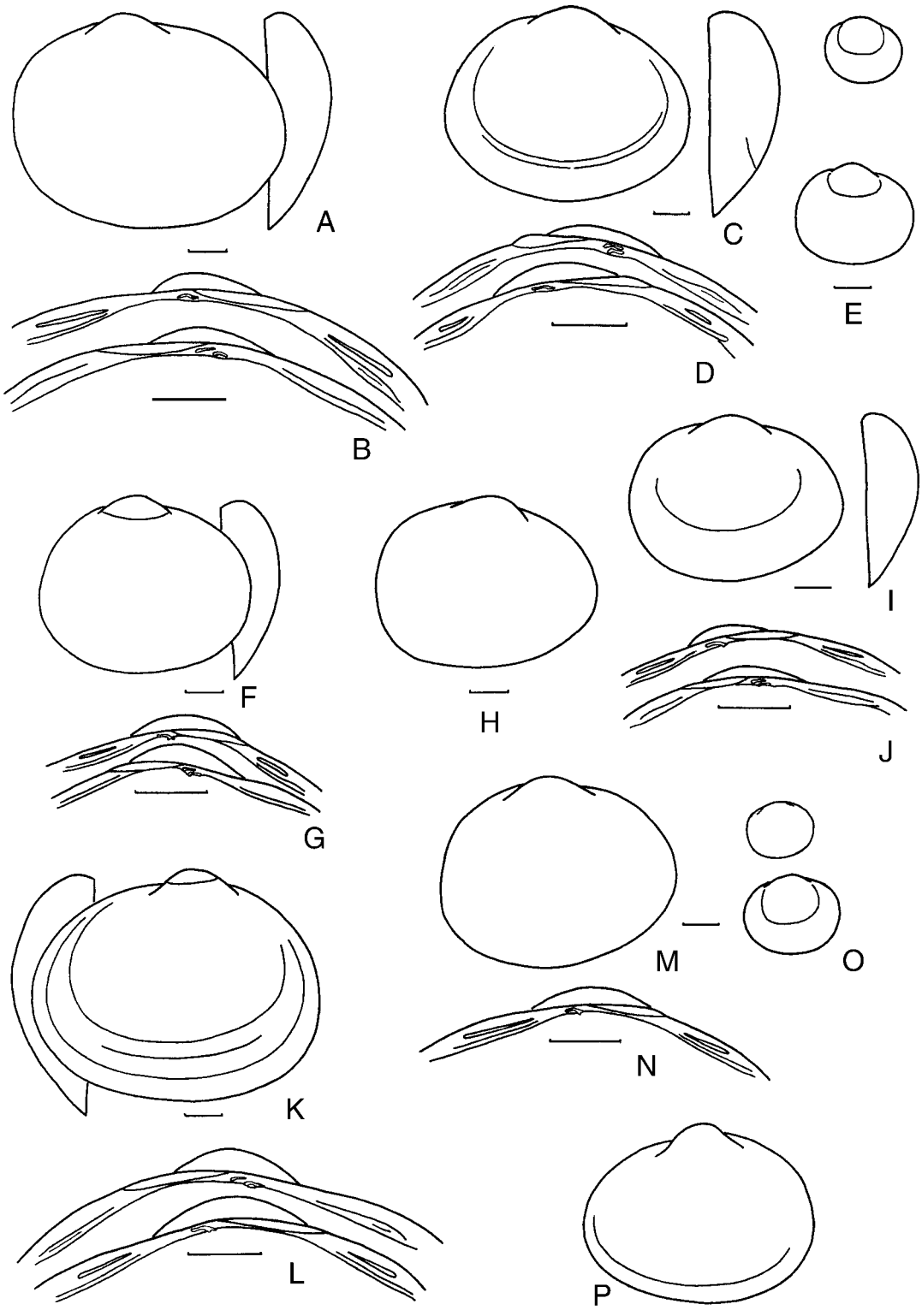


Figure 4. *Musculium tasmanicum tasmanicum*, variation of shell form: A,B—Coomooboolaroo, Qld (AM C109829), A—right valve, here and below the views from outside and hind end are provided, B—hinge; C–E—Somerset Dam, Qld (AM C135527), C—right valve, D—hinge, E—young shells; F,G—Attunga State Forest, NSW (AM, no number), right valve and hinge; H—Dubbo, NSW (AM 02832), right valve from outside; I,J—Tarraville, Vic. (SAM D19061), right valve and hinge; K,L—Binnum Waterhole, SA (SAM D19062), left valve and hinge; M–O—Table cape, Tas. (AM, no number), M—right valve, N—hinge of the right valve, O—young shells; P—Hobart, Tas. (AM C27754), left valve. Scale bars = 1 mm.

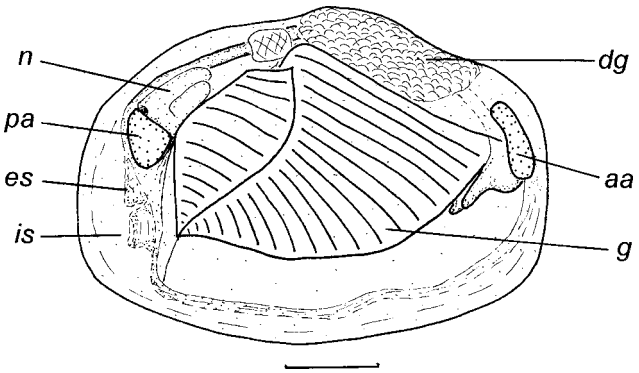
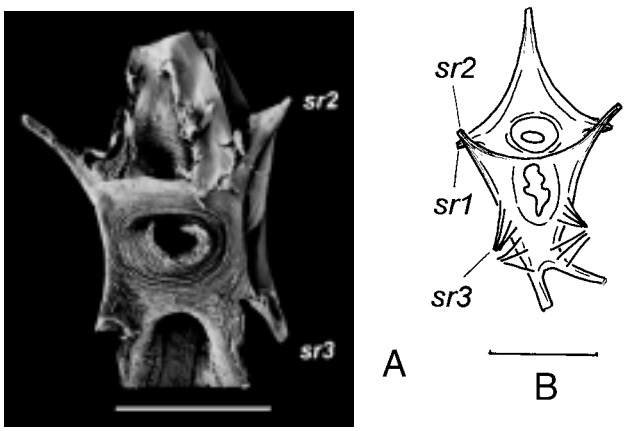
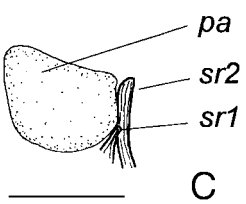


Figure 5. *Musculium tasmanicum tasmanicum*, Somerset Dam, Qld (AM C135527), gross anatomy. Scale bar = 1 mm.





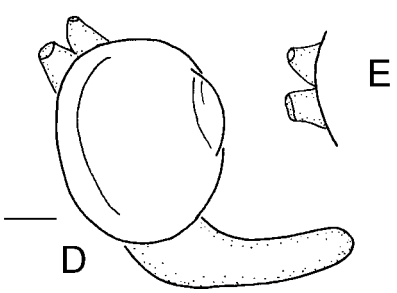
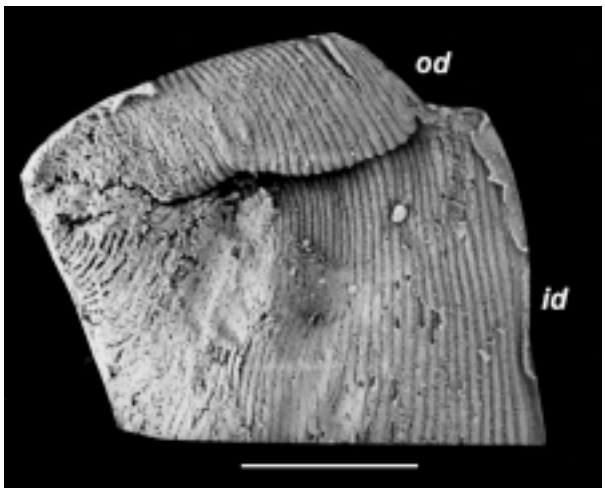


Figure 6. *Musculium tasmanicum tasmanicum*, siphons and siphonal musculature: A—Blue Mountains, NSW (AM, no number), siphons from inside; B—Somerset Dam, Qld (AM C135527), siphonal retractors from inside; C—specimen from the same lot, posterior adductor and adjacent siphonal retractors from right side; D,E—fully extended siphons in living specimens from Blue Mountains, NSW. Scale bars = 1 mm.



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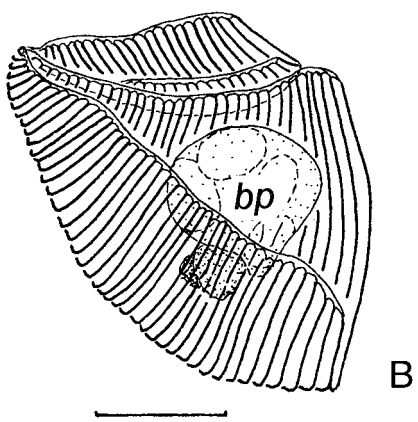

Figure 7. *Musculium tasmanicum tasmanicum*, gills: A—Blue Mountains, NSW (AM, no number), upper part of gill from outside; B—Somerset Dam, Qld (AM C135527), gill with brood pouches from inside. Scale bars = 1 mm.

Other material examined. QUEENSLAND: lagoon at Coomooboolaroo, Mt Duaringa, Dawson District (AM C109829d); east of Somerset Dam, between Mt Byron and Mt Delaney, small weedy muddy stream, coll. WFP, WP & OG, 30 September 1982 (AM C135527w); tributary of Brisbane River, 27°32'S 152°54'E, coll. WFP, WP & OG, 5 September 1982 (AMw). NEW SOUTH WALES: Attunga State Forest, 30°55'S 150°54'E, coll. IL & JW, 9 November 1985, with *M. quirindi* n.sp. (AMw); near Dubbo (AM 02832d); west end of Lake Lidell, 32°23'S 151°08'E, coll. P. McWilliamson, D. Hoese & J. Paxton, 24 November 1972 (AM C129137w); Warranwang, west of Lithgow, Blue Mountains, 33°28'S 149°59'E, on grass, moss, etc., coll. WFP & A. Korniushin, 18 August 1996 (AMw); Bora Ck at Mayfield, 35°13'S 149°47'E, coll. WFP & WP, 12 January 1981 (AM C126457w); Tuross River valley near east end of Cadger Rd, 36°09'S 149°55'E, coll. WFP, 19 January 1981 (AM C128099w); East Lakes Golf Course, Sydney, 33°56'S 151°13'E, coll. OG, 7 August 1982 (AM C315745w). VICTORIA: Tarraville, Gabbriel coln. (SAM D19061d); Loddon River at Newstead, 37°07'S 144°03'E, alt. 220 m, coll. WFP & R. Hershler, 2 February 1984 (AMw). SOUTH AUSTRALIA: Binnum Waterhole Police Paddock, Tatiara Ck, Bordertown, coll. June 1886, Tomsett coln., with *M. tatiarae* (SAM D19062d); Lower Murray River,

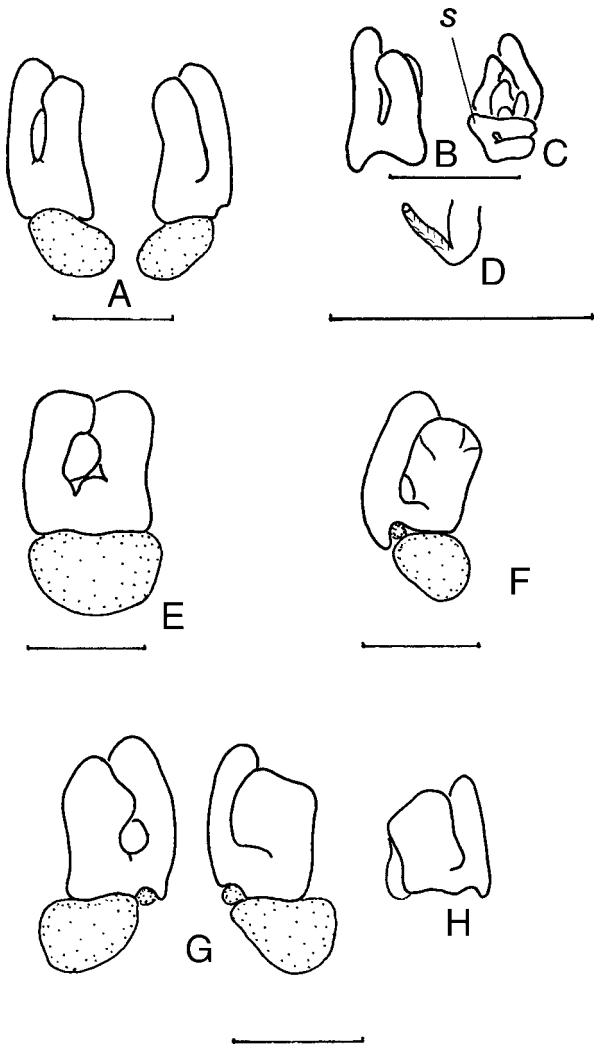

Figure 8. *Musculium tasmanicum tasmanicum*, nephridia: A—Somerset Dam, Qld (AM C135527), dorsal view; B—Brisbane River, Qld (AM, no number), dorsal view; C—ventral view of the same nephridium; D—funnel of the nephrostome of the same nephridium; E—Blue Mountains, NSW (AM, no number), dorsal view; F—Sydney, NSW (AM C315745), dorsal view; G,H—Table Cape, Tas. (AM, no number), dorsal view, two nephridia of one and the same specimen are figured in G. Scale bars = 1 mm.

Tailem, Cotton coln. (SAM D19064d). TASMANIA: swamp on Table Cape, 40°57'S 145°43'E, coll. WFP, JW & F. Hermans, 8 February 1989 (AMw); Swansea (?), Tate coln., with *M. lacusedes* (SAM D19065d); Maria Island, W. Petterd coln. (AM C27755d); Hobart, W. Petterd coln. (AM C27754d).

Diagnosis. Umbones subcentral. Upper retractors of inhalant siphon relatively strong. Dorsal lobe of nephridium broad.

Shell. Rather large, usually 7–9 mm long (largest specimen measured: L 9.7 mm, H 8.5 mm, W/2 2.5 mm), somewhat elongated. Umbones almost central (Table 1). Mean density of internal pores 342±116 per mm^2 (n = 4). Siphonal retractors scars clear.

Anatomy. Siphons of living specimens (observed in sample from Blue Mountains) rather short, less than ½ of body length; inhalant and exhalant siphons equal in length and fused only at their base. Upper retractors of inhalant siphon relatively strong (in comparison to other subspecies). Up to eight embryos per pouch. Closed type of nephridium found in 14 of 20 studied specimens, otherwise small part of pericardial tube visible. Dorsal lobe of nephridium relatively broad.

Distribution (Fig. 56). From southern Queensland to Victoria, South Australia and Tasmania; more abundant in mountainous regions.

Ecology. Found in slow flowing creeks, swamps, lakes, waterholes and ponds.

Variability. As in the species in general, shell and some anatomical characters in this subspecies show a clear geographic pattern of variation. The forms represented in southern Queensland and northern NSW (correspond geographically and morphologically to *Sphaerium translucidum* Sowerby and *Sphaerinova nundialis* Iredale respectively) are rather similar in their large (up to 8.5 mm long) elongate and angulate shells with narrow and almost central umbones (Fig. 4A–E). Only the specimens from southern Queensland were anatomically studied, and they were characterised by an elongate dorsal lobe of the nephridium (Fig. 8A,B).

The form described as *Sphaerinova bradena* Iredale is distributed in eastern NSW (along the Great Divide and East coast); it is also large, but distinguished by its relatively high, rounded or angulate, compressed shell with a narrow umbo slightly shifted posteriorly (Figs. 3, 4F,G). The embryonic part of the shell in this form is relatively small. *Sphaerium macgillivrayi* E.A. Smith from the same area is smaller and its shell has central umbones. These differences may be due to individual variation.

A peculiar form inhabits the upper catchments of the Murray-Darling system; it is characterised by its smaller size (5.5 to 6 mm long), elongate, convex shell with central umbones, relatively broad embryonic shell and presence of faint sculpture (striation) (Fig. 4H–J). *Sphaerinova terenda* Iredale (Kuiper, 1983, fig. 8) and *S. victoriana* Iredale (Fig. 4I,J) are almost identical and represent this form. The shells from the lower Murray are similar to them but somewhat larger (Fig. 4K,L).

Most of the shells from Tasmania (the nominate form) are similar to the form from eastern NSW, but have somewhat broader umbones (Fig. 4M–O). An elongate symmetrical form with markedly protruding umbones (Fig. 4P) occurs in southeastern Tasmania (Hobart).

The lots of *Musculium tasmanicum tasmanicum* represented in available collections were not numerous, therefore it was not possible to carry out the statistical analyses needed to justify the status of the forms tentatively recognised here. After examination of additional materials, some of them may eventually be elevated to the status of subspecies, in addition to *M. tasmanicum queenslandicum*.

The number of embryos per brood pouch is also variable, but no geographical pattern was observed in the material studied.

Musculium (Sphaerinova) tasmanicum queenslandicum (E.A. Smith, 1883)

Fig. 9

Sphaerium queenslandicum E.A. Smith, 1883: 305, pl. 7, fig. 33; Iredale, 1943a: 196; Kuiper, 1983: 19 (in synonymy of *Sphaerium tasmanicum*).

Type material. HOLOTYPE BMNH 1879.5.21.779, Limestone Ck, Burdekin River, Qld.

Other material examined. QUEENSLAND: Rocky Ck, Atherton, coll. F. Allen (AM C313698d); East Baratha Ck, 14 miles north of Ayr, coll. Price, September 1958 (AMd); Little Brook, 5 km south of Proserpine on Bruce Hwy, coll. WFP, J. Burch & F. Colman, 30 April 1975 (AMd); Myke Ck, crossing no. 1 on Bruce Hwy, 5 miles north of Proserpine, coll. 4 May 1975 by WFP, F. Colman & J.B. Burch (AMd). NORTHERN TERRITORY: pool at mouth of canyon, Buffet Ck, south from Gulf of Carpentaria, 17°29'S 137°38'E, coll. WFP, J. Wilson & V. Kessner, 26 August 1991 (AMw).

Diagnosis. Umbones shifted posteriorly. Upper retractors of inhalant siphon weak. Dorsal lobe of nephridium narrow, elongated.

Shell. Rather small (maximum length 6.6 mm), relatively high. Umbones evidently shifted posteriorly (Table 1). Siphonal retractors scars weak, seen as small appendages of the posterior adductor scars.

Anatomy (only specimens from the Northern Territory studied). Upper retractors of inhalant siphon weak. Up to eight (usually four to six) embryos per pouch. Nephridia of closed type, dorsal lobe of nephridium elongate.

Distribution. Northern Queensland and Northern Territory (Fig. 56).

Ecology. As in nominate subspecies. Common in Queensland (on Atherton Tableland), rare in Northern Territory: only one population found despite extensive collecting in this region. According to W. Ponder (oral communication), high water temperature seems to be a principal factor limiting the distribution of these molluscs.

Variability and taxonomic remarks. The form observed here is distinguished from typical *M. tasmanicum* mainly by its peculiar shell outline and posteriorly shifted umbo. Differences in the LA/LP index that characterise the position of the umbo are statistically significant (values of index in Table 1, $t = 4.14$, $p<0.01$), but variation ranges overlap. Some differences in anatomical characters are also notable: the northern form has weaker siphonal retractors and an elongate dorsal lobe of the nephridia, but the range of variability in these characters is not known.

Both forms of *Musculium tasmanicum* are separated geographically. However, the nearest populations from northern and southern Queensland are morphologically the most similar. While the form observed here is morphologically distinct, the differences concern only a few characters.

One specimen from the Atherton Tableland, while having the characteristic shape of this subspecies, is distinguished by its rather solid shell and broader hinge plate. While no other specimens are currently available, the status of the form remains unclear.

Musculium (Sphaerinova) tatiarae (Cotton & Godfrey, 1938)

Figs. 10–14

Sphaerium tatiarae Cotton & Godfrey, 1938: 178, fig. 181; Iredale, 1943a: 195.
Sphaerinova bursa Cotton, 1953: 21.
Sphaerium tasmanicum Kuiper, 1983: 21, figs. 41, 42 (forms *tatiarae* and *bursa*).

Type material. HOLOTYPE SAM D12583, Tatiara Ck, Bordertown, SA. *Sphaerinova bursa*, holotype and paratype SAM D14453, River Torrens Lake, SA.

Other material examined. VICTORIA: Golden Ck, west of Corner Inlet, 38°45'S 146°10'E, coll. WFP, GC, R. de Keyzer & D. Beechey, 11 February 1990 (AMd); Spout Ck, 38°28'S 144°02'E, coll. FWA, 11 April 1988 (AMw); near gauge station on Mt Emu Ck, 38°19'S 142°53'E, coll. FWA, 23 April 1988 (AMw). SOUTH AUSTRALIA: Binnum Waterholes Police Paddock, Bordertown, coll. June 1886, Tomsett coln., with *M. tasmanicum* (SAM D19063d); Lake Torrens, Adelaide, coll. Major T. Cherry, with *Musculium* cf. *lacustre* (AM C42311d); Smiths Bay, Kangaroo Island, Cooper coln. (SAM D19067d); small swampy spring, east side of Lake Eliza, SE of Robe, 37°13'S 139°53'E, coll. WFP, 15 May 1984 (AMw); creek flowing in Lake George, north of Beachport, coll. IL & K. Handley, 27 February 1978 (AMw); Mt Gambier (AM C039180d). TASMANIA: Bowlers Lagoon, sample 1 in ti-tree area, coll. L. Mowra & T. Kingston, 23 September 1991 (QVM 9:12426w); Lagoon of Islands, coll. B.S. Mollison, 30 January 1965 (TMH E10977w); Rebecca Lagoon, coll. B.S. Mollison, 21 October 1963 (TMH E10980w); Lake Dulverton, coll. B.S. Mollison, October 1961 (TMH E10982d).

Material tentatively identified as *M. tatiarae*. NEW SOUTH WALES: Lake Binjie, south of Broken Hill, 33°18'S 141°48'E, 3–4 m above the current strand line, coll. J.W. Pickett, 1990 (AMd); Willow Dam, 25 miles from Griffith, 16 May 1972 (AMw). VICTORIA: Scotts Ck at Murfitt Rd Bridge, coll. FWA, 22 April 1988 (AMd); Darlot Ck, south of Ettric, 38°09'S 141°46'E, coll. A. Miller, 18 April 1994, with *P. aslini* (AM 302417d).

Diagnosis. Shell circular or short oval, solid, not transparent. Upper margin evenly curved, without angles. Umbones relatively broad, not protruding. Internal pores rare. Hinge plate broadened, cardinal teeth bent, lateral teeth normally developed.

Shell smaller than in *M. tasmanicum* (usually up to 6 mm long, some specimens 7–9 mm), circular or short oval, rather solid, white or yellow-coloured, not transparent. Dorsal margin evidently arched, merging to anterior and posterior ones without angles. Umbones of small specimens relatively broad and markedly shifted posteriorly, narrower (in relation to the whole shell) and centrally placed in larger specimens. Prodissoconch not

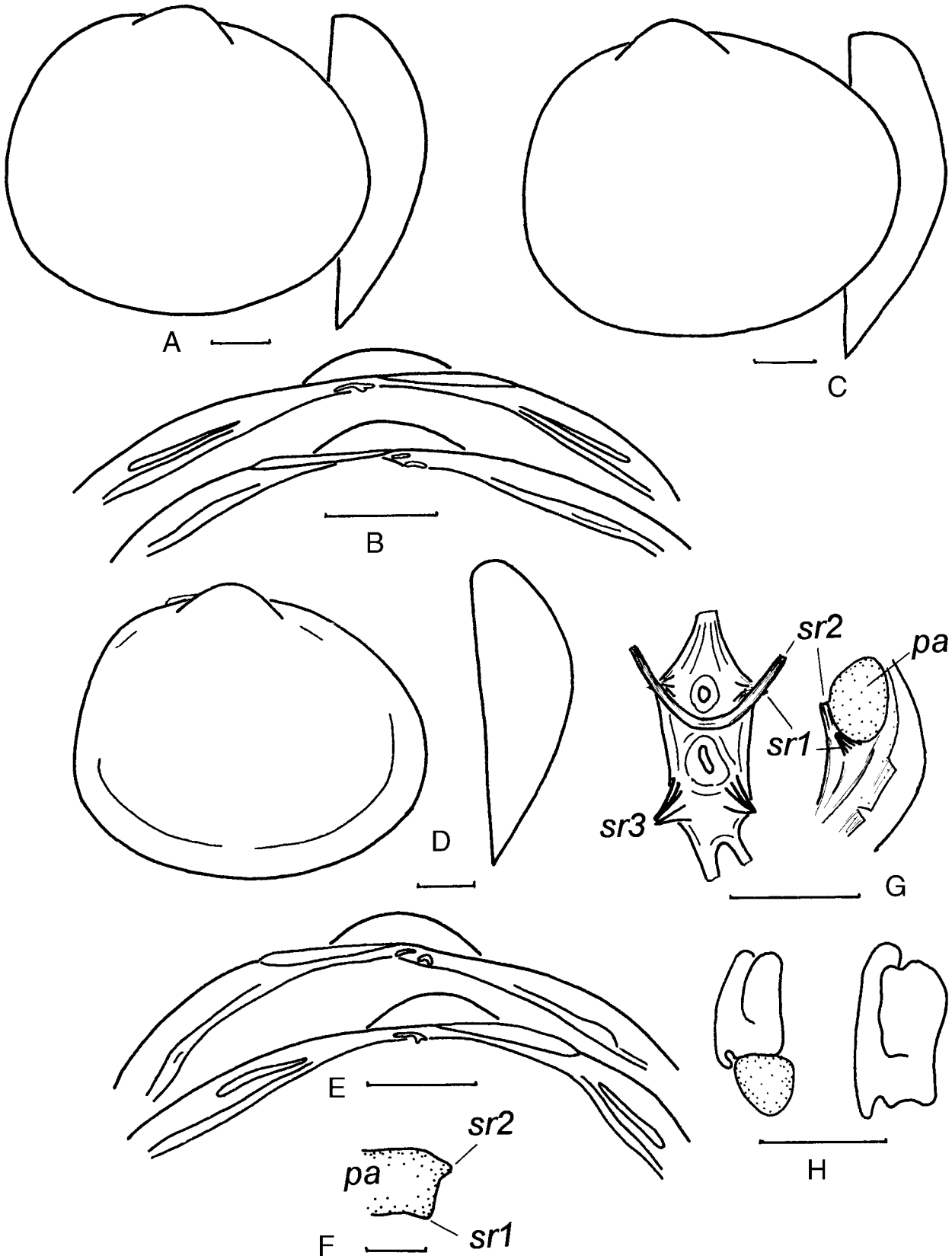

Figure 9. *Musculium tasmanicum queenslandicum* (E.A. Smith), shell and anatomy: A,B—north of Ayr, Qld (AM, no number), right valve and hinge; C—Atherton, Qld (AM C313698), right valve; D–H—Buffet Ck, NT (AM, no number), D—right valve, E—hinge, F—posterior muscle scars, G—siphons and siphonal retractors from inner side and left side, H—nephridia dorsally. Scale bars = 1 mm.

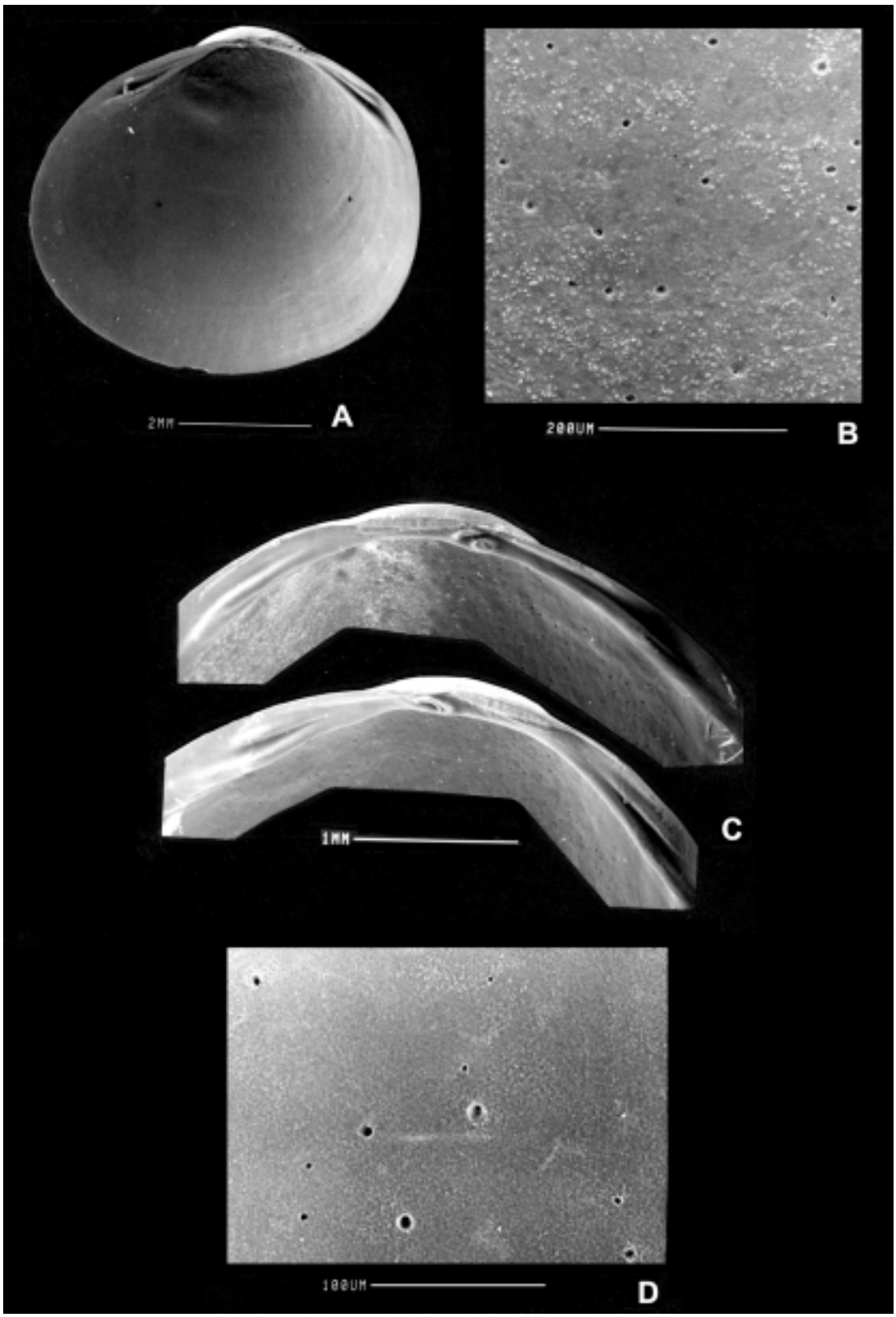

Figure 10. *Musculium tatiarae* (Cotton & Godfrey), shells: A—Bowlers Lagoon, Tas. (AM, no number), young specimen, right valve from inside; B—internal pores of the same specimen; C—Lake Eliza, SA (AM, no number), hinge; D—internal pores of this specimen.

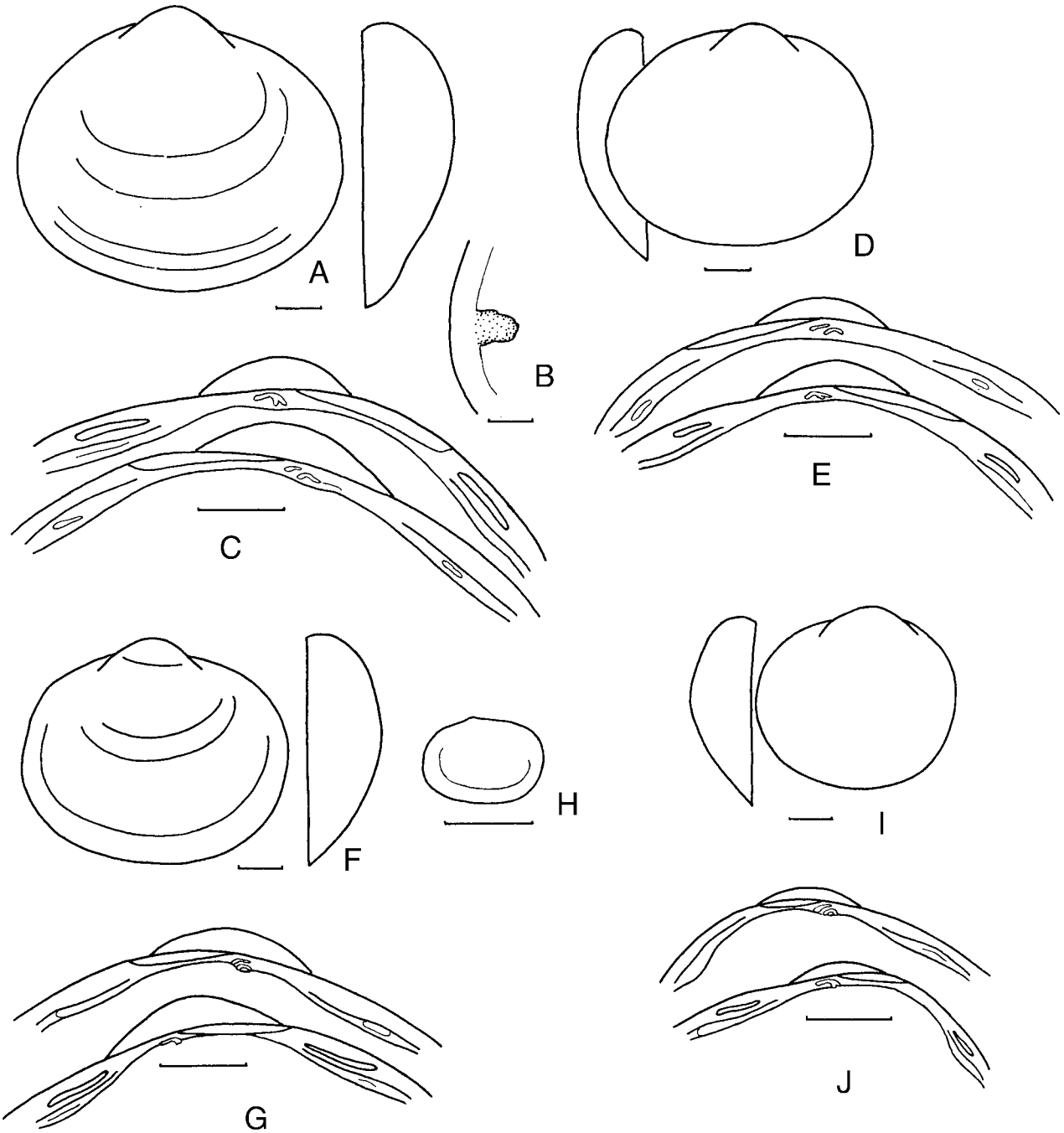

Figure 11. *Musculium tatiarae*, variation of shell form: A–C—holotype, Tatiarae Ck, SA (SAM D12583), A—right valve, B—posterior muscle scars, C—hinge; D,E—Binnum Waterhole, SA (SAM D19063), left valve and hinge; F–H—Bowlers Lagoon, Tas. (QVM 9:12426), F—right valve, G—hinge, H—young specimen; I–J—Lake Dulverton, Tas. (TMH E10982), left valve and hinge. Scale bars = 1 mm.

separated. Hinge plate relatively broad (Table 1). Surface smooth (sculpture not developed). Internal pores widely separated (density 157±62 per mm^2, n = 9). Scars of posterior adductors small, siphonal retractors scars merged to them. Ligament pit long, ligament exteriorly visible but usually not elevated. Cardinal teeth (c2 and c3) markedly bent or hooked, posterior end of c3 cleft. Lateral teeth evidently arched. Shells of young specimens elongate.

Anatomy. Characters of siphonal retractors and gills similar to those in *M. tasmanicum tasmanicum* (Figs. 12, 13). Three to four brood pouches per gill and up to seven embryos per pouch. Nephridium usually of open type (in 10 of 13 studied specimens), occasionally of closed type; dorsal lobe broad (Fig. 14).

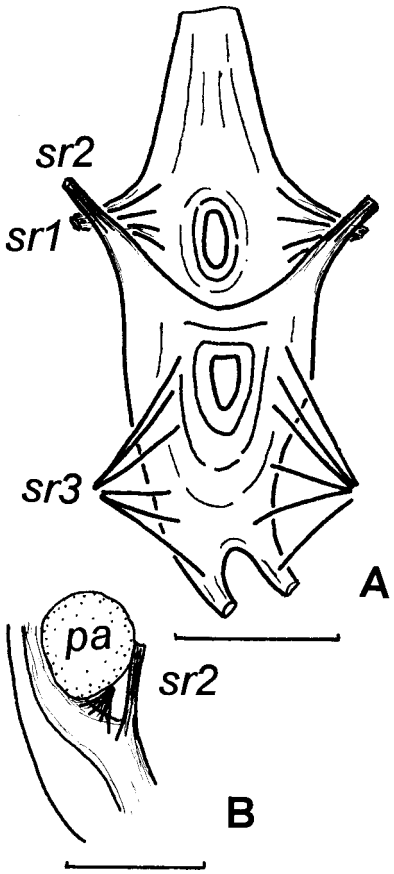

Figure 12. *Musculium tatiarae*, siphonal musculature, Bowlers Lagoon, Tas. (QVM 9:12426): A—from inside, B—from right side. Scale bars = 1 mm.

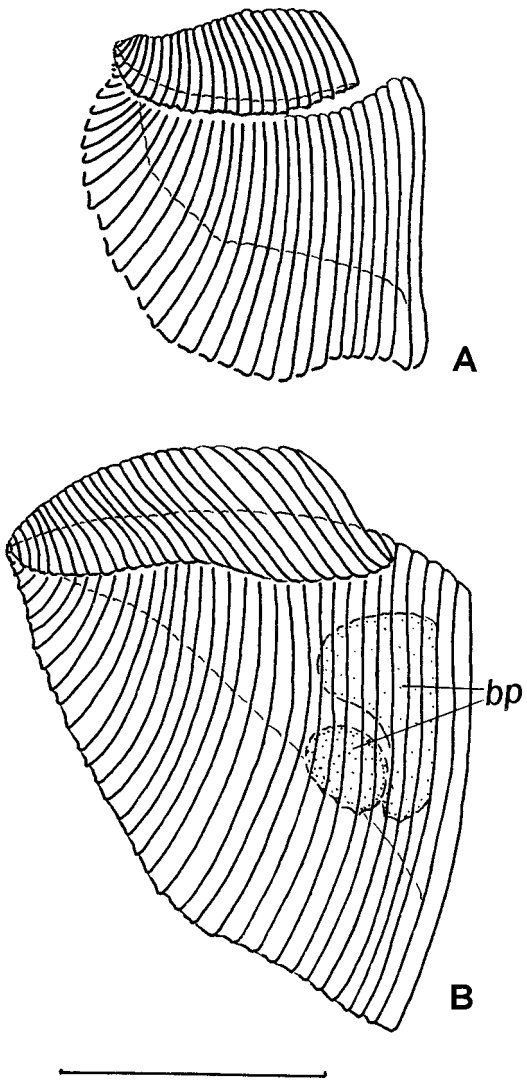

Figure 13. *Musculium tatiarae*, gills from outside: A—Lake Eliza, SA (AM, no number), young specimen; B—Lagoon of Islands, Tas. (TMH E10977), adult specimen. Scale bar = 1 mm.

Distribution. Southern Victoria, South Australia, northern Tasmania (Fig. 56). Specimens with similar characters occur in New South Wales, but their belonging to *M. tatiarae* needs confirmation.

Ecology. Most common in large lakes and lagoons. Occurs in smaller lakes, waterholes and creeks as well.

Variability. The largest shells (up to 9 mm long) are known from the area of Adelaide. Populations from the coastal lagoons of South Australia are characterised by smaller size (5 to 6 mm long), triangular or oval shell outline and posteriorly shifted umbo (Fig. 10C), as in the genus *Pisidium*. Tasmanian populations are intermediate in size and can be distinguished by circular outline and more centrally placed umbones (Figs. 10A, 11F–J).

The placement of the form from southern Victoria is not clear. It is similar to *M. tatiarae* in shell outline, shape and position of umbones (Fig. 21I–K). At the same time, it is distinguished by its narrow hinge plate, so the possibility that it may be a form of *M. tasmanicum* cannot be excluded. A very small, dwarf form was found in Darlot Ck (Fig. 21L). Some of the shells were only 3.5 mm long but contained 1–2 large embryos. The status of this form is also unclear.

Several specimens from the Murray-Darling system in New South Wales with thick shells and rather strong hinges (Fig. 21A–D) are also only tentatively identified as *M. tatiarae*.

Taxonomic remarks. The species can be distinguished from *M. tasmanicum* by the rounded shell outline, broad and posteriorly shifted umbo, broad and strongly curved hinge plate, hooked cardinal teeth and arched lateral teeth and

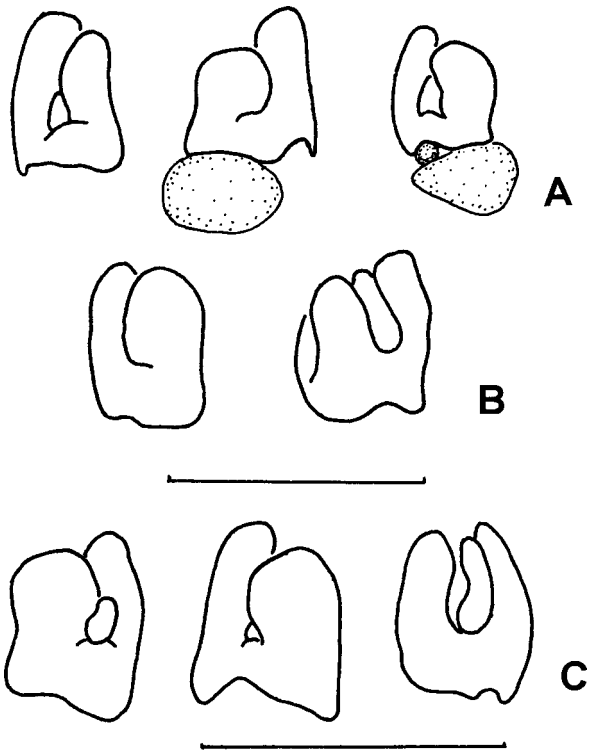

Figure 14. *Musculium tatiarae*, nephridia dorsally: A—Bowlers Lagoon, Tas. (QVM 9:12426); B—Lagoon of Islands, Tas. (TMH E10977); C—Lake Eliza, SA (AM, no number). Scale bars = 1 mm.

the widely spaced shell pores. Differences in the breadth of the hinge plate are statistically significant with $p<0.01$ (values of the index in Table 1, $t = 4.81$, $p<0.001$); the same concerns the differences in density of the internal pores ($t = 3.83$, $p<0.01$). The elongate outline of young shells is associated with the shape of the umbo (since the umbonal part of adult shell is formed in the early ontogenetic stages, the more elongate the young shell is, the broader the umbo will be). The white colour of the shell is also the distinctive character of *M. tatiarae*. Prevalence of the open nephridium type in *M. tatiarae* is also notable.

The differences in each of the characters described here are not large, but they agree well with each other. Applying several diagnostic characters, it is usually not hard to discriminate between *M. tasmanicum* and *M. tatiarae*. One lot containing both species without intermediates was found (Binnum Waterholes, Bordertown, see Figs. 9 and 23). Thus, the species distinctness of *M. tatiarae* is verified by sympatry and justified by several characters. At the same time, identification of specimens from Scotts Ck and Darlot Ck (Victoria) and Lake Binjie (southern New South Wales) as this species are tentative and require more material to determine their status.

Musculium (Sphaerinova) lacusedes (Iredale, 1943a)

Fig. 15

Sphaerinova lacusedes Iredale, 1943a: 195.
Sphaerium lacusedes.–Kuiper, 1983 (full synonymy).

Type material. Types not known, presumably they are lost, Great Lake, Tas.

Other material examined. TASMANIA: Great Lake, coll. Taffin, 2 June 1902 (TMH E5195d); Arthurs Lake, identified as *S. macgillivrayi* (SMF 87123d); South Esk River, W. Petterd coln. (AM C27756d); Swansea [sic, locality doubtful], Tate coln., with *M. tasmanicum* (SAM D19066d).

Diagnosis. Shell round or oval, thin but not transparent. Upper margin evenly curved, without angles. Umbones relatively broad. Internal pores dense. Hinge plate narrow, cardinal teeth curved, lateral teeth reduced.

Shell large (up to 9.5 mm long), round or oval, thin but not transparent, of yellowish colour. Anterodorsal margin straight, other margins merged to each other without angles, forming regular curve. Umbones central (median), prodissoconch not separated. Sculpture faint. Internal pores rather numerous, more than 400 per mm^2 (Kuiper, 1983). Hinge plate narrow. Cardinal teeth arched, c3 sometimes cleft. Lateral teeth evidently reduced, outer laterals in right valve absent. Ligament pit somewhat shorter than in *M. tasmanicum* (in relation to the shell length) (Table 1). Ligament visible from outside, elevated in large shells.

Anatomy known only from dried specimens. Dorsal retractor of inhalant siphon rather short and weak, as in *M. tasmanicum*; its scar usually merged with that of adductor, in a Frankfurt specimen (the largest one studied) it is well marked.

Distribution. Central Tasmania (Fig. 56).

Ecology. Mostly found in lakes, but at least one lot from the South Esk River is known. Apparently rare and is therefore a poorly studied species.

Taxonomic remarks. As mentioned by Kuiper (1983) and confirmed by the present study, reduction of the outer lateral teeth in the right valve is the most remarkable feature of *M. lacusedes*. This character seems to be constant. The yellowish colour of periostracum also seems to be diagnostic. However, the small number of available specimens is insufficient to reliably assess and data on morphological variability, and the data on the anatomy, distribution and ecology are still insufficient.

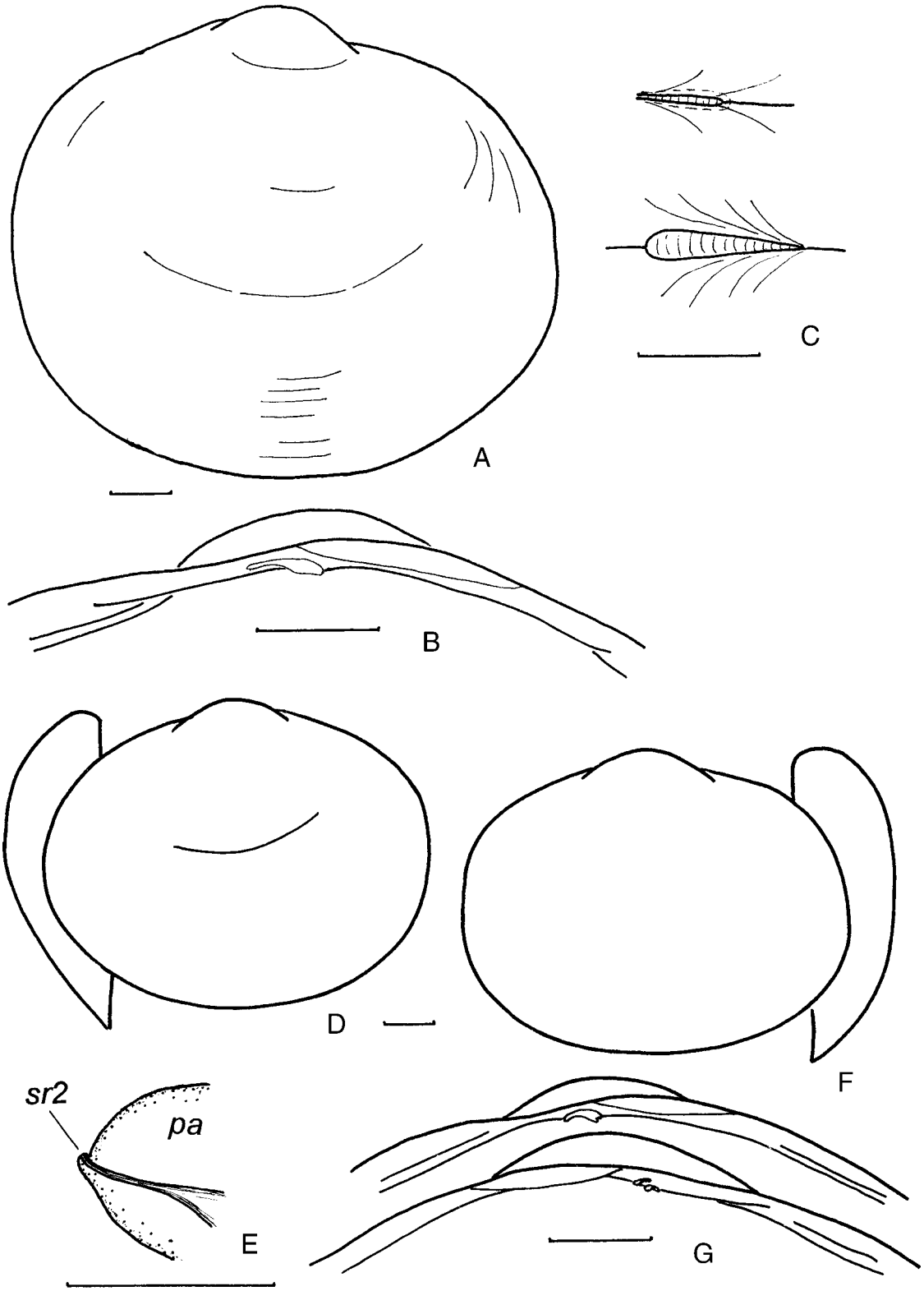

Figure 15. *Musculium lacusedes* (Iredale): A–C—Arthurs Lake, Tas. (SMF 87123), A—right valve, B—hinge of the right valve, C—ligaments of the young and the larger shell, from the dorsal side; D,E—Great Lake, Tas. (TMH E5195), D—left valve, E—dried muscles and their scars; F,G—South Esk River, Tas. (AM C27756), right valve and hinge. Scale bars = 1 mm.

Musculium (Sphaerinova) kendricki (Kuiper, 1983)

Fig. 16

Sphaerium kendricki Kuiper, 1983: 25, fig. 44–46.

Type material. HOLOTYPE WAM 649-74a, drain through Roselea nursery across North Beach Rd, Osborne Park, 31°54'S 115°50'E, WA. PARATYPES WAM 649-74b, 22 specimens, ZMA K-21018 to ZMA K-21023*, 6 specimens; same data as holotype.

Other material examined. WEST AUSTRALIA: drain from Herdsmans Lake, Perth, coll. G.P. Whitley, 27 December 1944, det. S.M. Slack-Smith (WAM 107/126-44d); Lake Monger, Lederville, coll. D. Edward, 23 November 1958, det. J. Kuiper (WAM 1053-66d); muddy lake near Jeloup turnoff, north of Capel, coll. J. Goodsell, 29 February 1976 (WAM 106-96d); Lake Nowergup 31°38'S 115°44'E, coll. F. Cheal & B. Robson, 9 November 1989, det. S.M. Slack-Smith (WAM 105-96w).

Diagnosis. Shell circular or short oval, solid, not transparent. Upper (dorsal) margin almost straight, with angles. Umbones broad, not protruding. Internal pores rare. Hinge plate broadened, cardinal teeth curved, lateral teeth normally developed.

Shell medium-sized (up to 8.2 mm long), circular or short oval, flat, rather solid, not transparent, of white colour. Dorsal margin long, slightly curved, with faint angles at anterior and posterior ends. Ventral margin evenly curved. Umbones central, relatively broad, not protruding, prodissoconch not separated. Sculpture: fine concentric striations. Scars of posterior adductors small, siphonal retractor scars merged to them. Internal pores rare. Hinge plate rather broad (Table 1). Ligament pit short and narrow, hinge relatively long. Ligament visible from exterior but not elevated. Cardinal teeth: c3 curved, deeply cleft on its posterior end, c2 curved or arched, c4 straight or slightly arched.

Anatomy. Siphonal retractors weak. Dorsal retractor of lower (inhalant) siphon short and weak. Outer demibranch relatively small. Two brood sacs and three generations of young, with one to five embryos each, found in single dissected specimen. Nephridium of closed type; lateral loop visible from outside.

Distribution. Southwestern Australia (Fig. 56).

Ecology. Lakes and lagoons.

Taxonomic remarks. Position of this species in the subgenus *Sphaerinova* is indicated by the following anatomical characters: nephridium with small excretory sac (generic character of *Musculium*), small outer demibranch, weak upper retractors of the lower siphon (subgeneric characters of *Sphaerinova*). It is distinguished from other Australian *Musculium* species by the peculiar shell outline, longer hinge (relatively large distance between the cusps of lateral teeth) and shorter ligament. The outline of the nephridium is also peculiar.

Musculium kendricki is similar to *M. tatiarae* in its solid shell, white colour and rather strong hinge teeth.

Musculium (Sphaerinova) quirindi n.sp.

Figs. 17–20

Sphaerium tasmanicum.–Kuiper, 1983: fig. 15.

Type material. HOLOTYPE AM C350024, shell dry, animal wet, Quipolly Ck, on Quirindi-Breeza Rd, NW of Quirindi, coll. WFP & AK, 19 September 1996. PARATYPES AM C350025d&w; 15 specimens, same data as holotype.

Other material examined. NEW SOUTH WALES: Attunga State Forest, 30°55'S 150°54'E, coll. IL & JW, 9 November 1985, with *M. tasmanicum* (AMw); Peel River, Tamworth, Musson coln. (AM C109829d); Kings Ck, tributary of McIntyre River, east of Inverell, 29°49'S 151°23'E (AM C109825d); Bell River, 19 km NW of Molong, coll. WFP and AK, 15 September 1996 (AM, 1 empty valve).

Diagnosis. Shell oval, solid, not transparent. Upper margin evenly curved, without angles. Umbones relatively broad, protruding. Internal pores dense. Hinge plate broadened, cardinal teeth arched, lateral teeth normally developed.

Shell medium-sized or small (Table 2), oval, rather inflated, solid and not transparent, white or yellowish. Holotype measurements: L 5.5, H 4.5, W/2 1.65 mm. Largest specimen measured: L 6.5, H 5.5, W/2 1.9 mm. Upper margin slightly curved, merging to anterior and posterior

Table 2. Measurements (mm) of paratypes of *Musculium quirindi* n.sp.

	L	H	HH	LL	LH	LA	LE	W/2
paratype	6.20	5.00	0.175	1.30	3.50	3.75	1.00	1.85
paratype	4.75	3.90	0.150	0.90	2.75	2.95	1.00	1.35
paratype	4.85	3.90	0.150	0.85	2.75	3.00	1.05	1.45
paratype	4.60	3.85	0.125	0.85	2.75	2.75	1.00	1.30
paratype	3.85	3.10	0.125	0.75	2.15	2.25	1.00	1.05

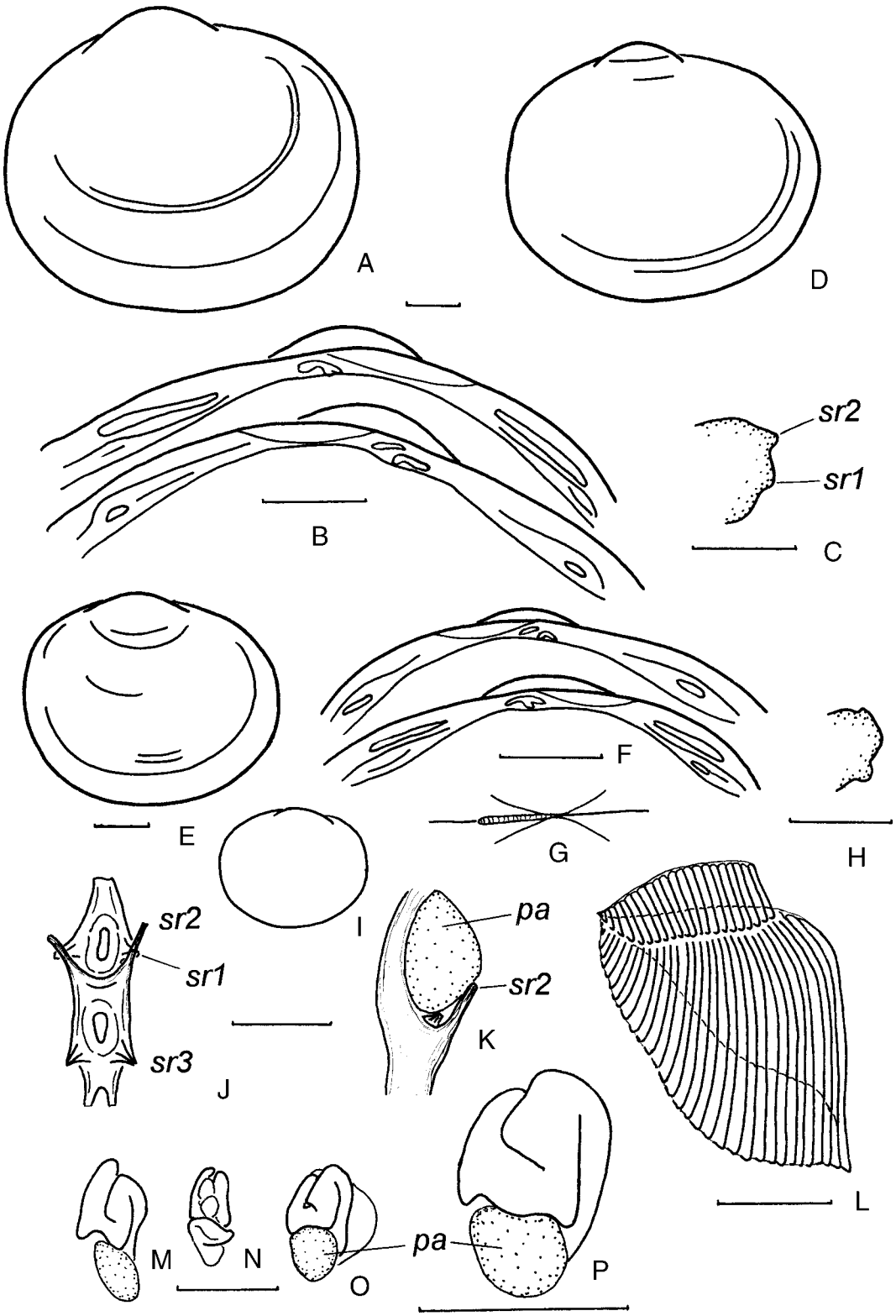

Figure 16. *Musculium kendricki* (Kuiper), shell and anatomy: A–C—Herdsmans Lake, WA (WAM 107/126-44), A—right valve, B—hinge, C—siphonal muscle scars; D—Lake Monger, WA (WAM 1053-66), elongated form, right valve; E–P—Lake Nowergup, WA (WAM 105-96), E—right valve, F—hinge, G—ligament dorsally, H—posterior muscle scars, I—shell of a young specimen, J—siphons and siphonal muscles from inside, K—the same, side view, L—gill from outside, M,O,P—nephridia dorsally, N—nephridium ventrally. Scale bars = 1 mm.

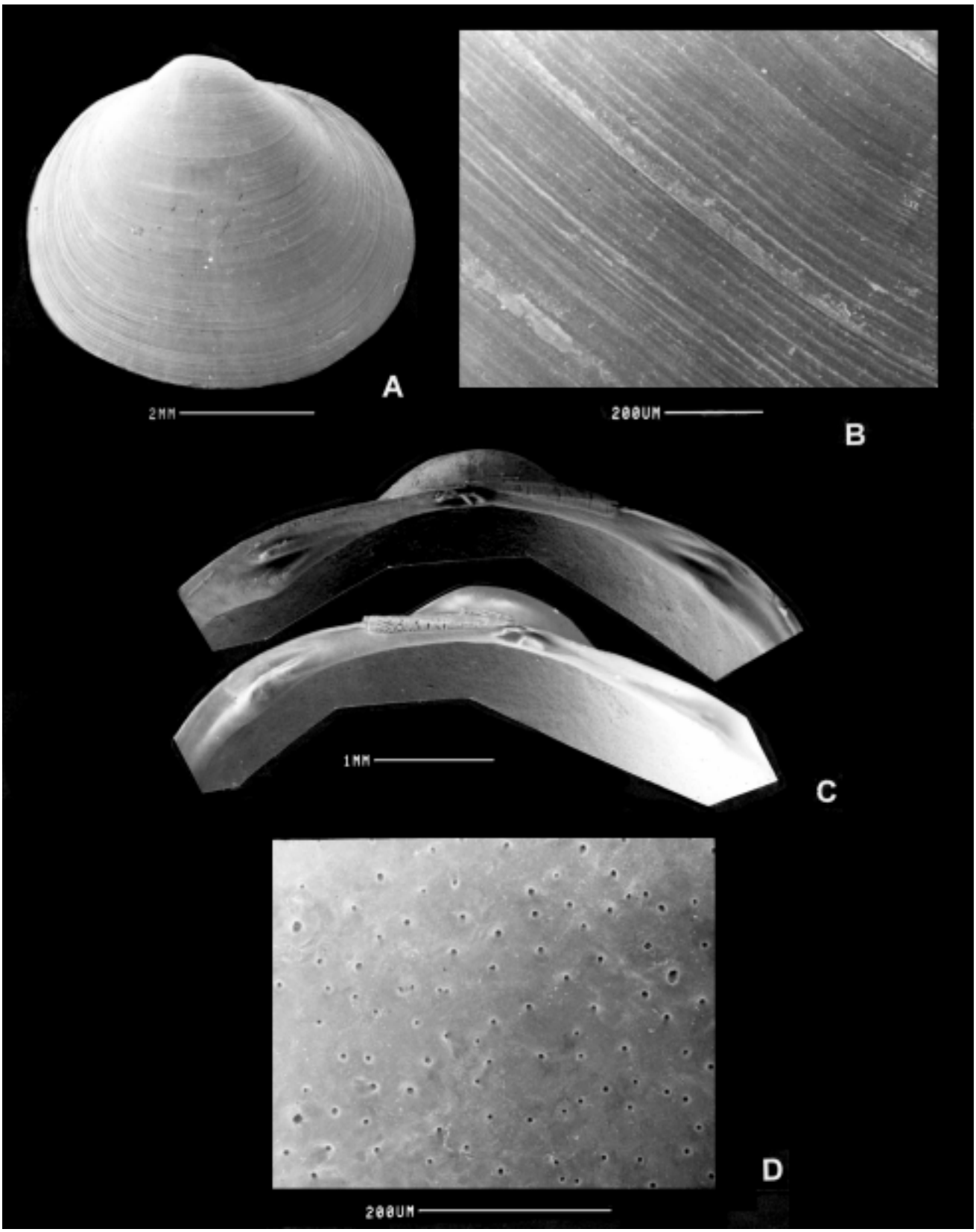

Figure 17. *Musculium quirindi* n.sp., type specimens, shells: A—right valve of the holotype (AM C350024) from outside, B—sculpture of the same specimen, C—hinge of the paratype (AM C350025), D—internal pores of the same specimen.

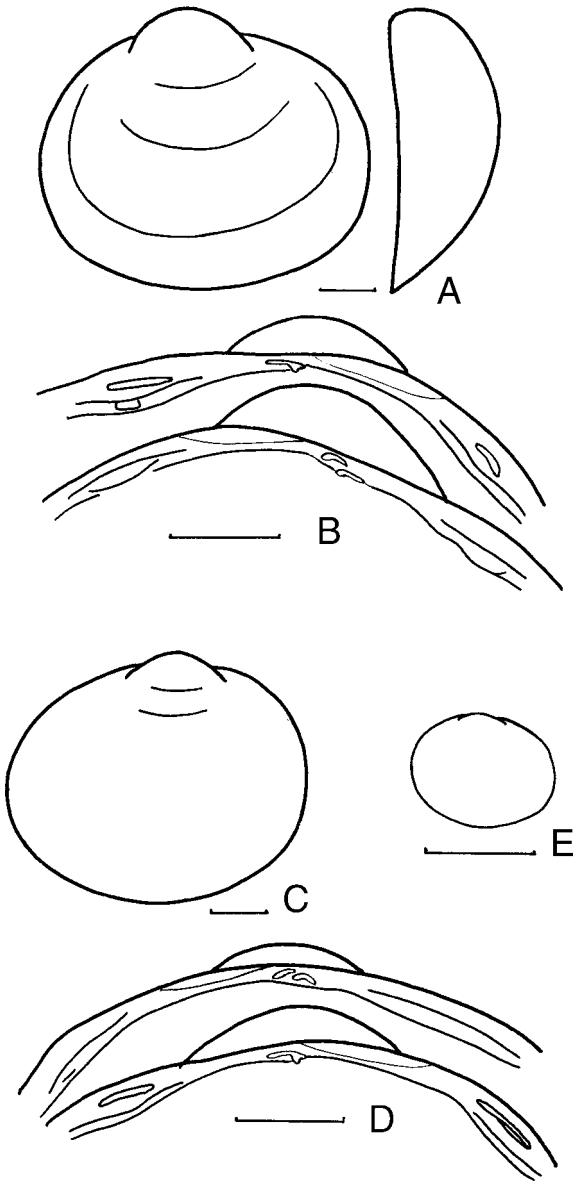

Figure 18. *Musculium quirindi*, variation of shell form: A,B—Attunga State Forest, NSW (AM, no number), right valve and hinge; C–E—Kings Ck (AM C109825), C—left valve, D—hinge, E—shell of a young specimen. Scale bars = 1 mm.

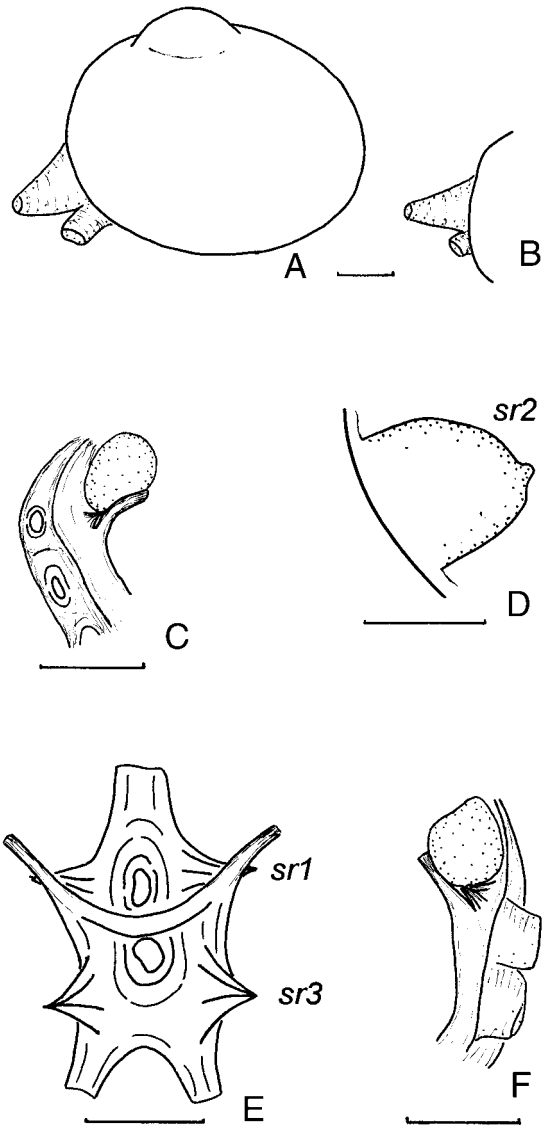

Figure 19. *Musculium quirindi*, siphons and siphonal musculature: A–E—paratypes (AM 350025); A,B—extended siphons of living specimens, C—siphonal muscles, side view, D—posterior muscle scars; F—Attunga State Forest, NSW (AM, no number), side view of siphons and siphonal muscles. Scale bars = 1 mm.

ones without angles. Posterior margin broad, truncated, anterior one narrow, somewhat elongate. Ventral margin slightly curved. Umbones submedian, in some specimens shifted posteriorly; protruded. Prodissoconch not separated. Internal pores numerous (643±35 per mm^2, n = 4). Scars of adductor muscles relatively large, those of siphonal retractors marked but not separated. Hinge plate relatively broad (Table 1, 2). Ligament pit long, ligament exteriorly visible but usually not elevated. Cardinal teeth arched, that of right valve cleft on its posterior end. Lateral teeth straight, thick, somewhat swollen. Young shells circular or short oval.

Anatomy. Upper (exhalant) siphon of living specimens markedly longer than lower one (only type lot observed, Fig. 19A–E). Dorsal retractors of inhalant siphon short but rather strong (in comparison with *M. tasmanicum*). Outer demibranch as in *M. tasmanicum*. Two to four brood pouches per gill with three to eight embryos each. Nephridia of open type, with short, broad dorsal lobe (Fig. 20).

Distribution. All studied lots are from the western slope of the Great Dividing Range, northeastern NSW (Fig. 56).

Ecology. Inhabits creeks, seems to prefer swift flow and thick vegetation.

Etymology. Named after the town nearest to the type locality—Quirindi.

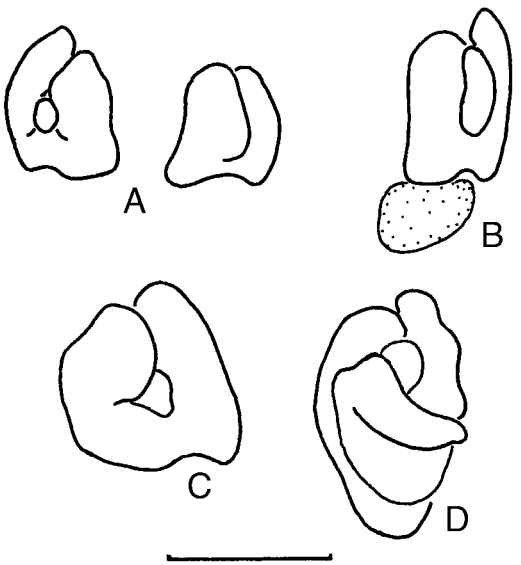

Figure 20. *Musculium quirindi*, nephridia: A,B—Attunga State Forest, NSW (AM, no number), dorsal view (two nephridia of one and the same specimen are figured in A); C,D—paratypes, dorsal and ventral views. Scale bars = 1 mm.

Variability and taxonomic remarks. Shell outline, position of umbo and hinge details are subject to individual variation. The new species is similar to the form of *M. tasmanicum* distributed in the upper Murray catchment but differs from it in its solid shell and strong hinge. These characters were also evident in the population from Attunga State forest living in sympatry with *M. tasmanicum*. The open type of nephridium (Fig. 20), rare in *M. tasmanicum*, is seen in this species. The new species is distinguished from *M. tatiarae* by its small, elongate and inflated shell as well as by its dense shell pores.

Musculium (?Sphaerinova) problematicum (Gabriel, 1939)

Fig. 21E–H

Sphaerium problematicum Gabriel, 1939: 128, pl. 4, fig. 36; Kuiper, 1983: 24, fig. 43 (full synonymy).

Type material. HOLOTYPE NMV F529*, Murray River, Merbein, Victoria. PARATYPES SAM D15675, 1 specimen; paratypes AM C63917, 2 specimens, NMV F584*, 21 specimens, same data as holotype.

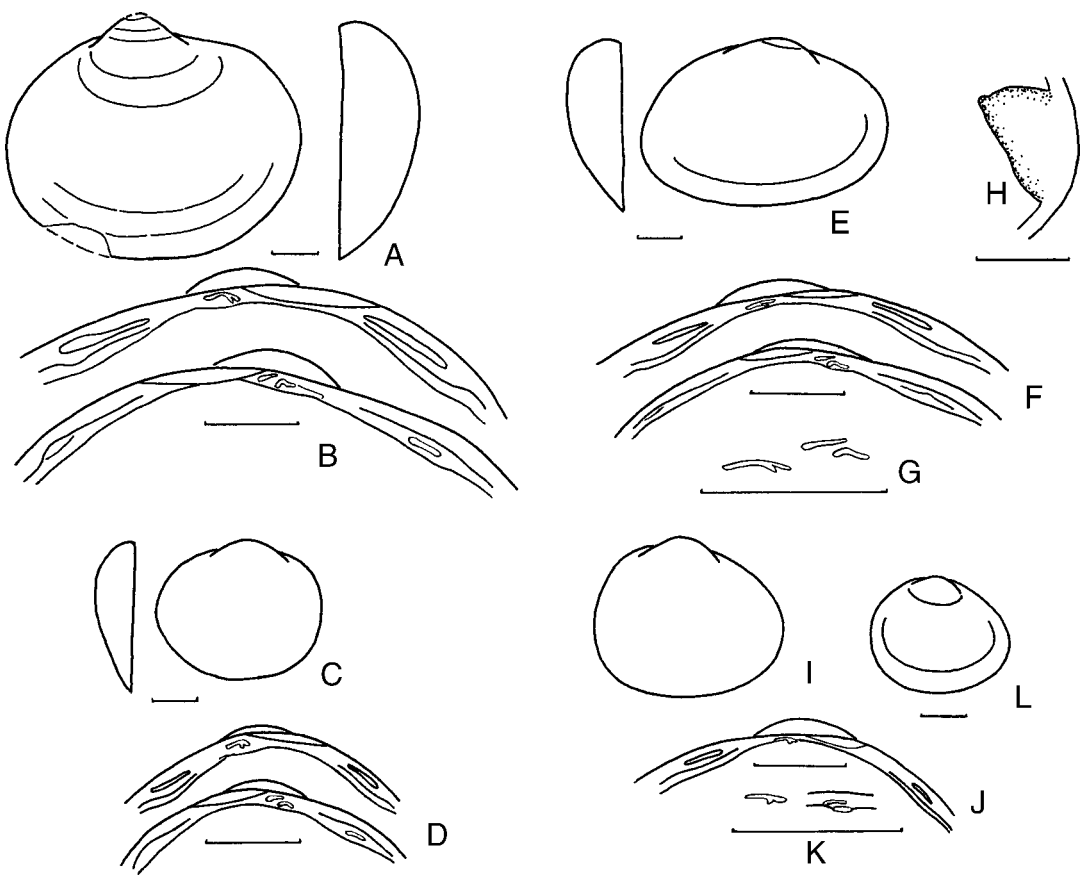

Figure 21. The forms of *Musculium* with undefined species status, shells: A,B—*Musculium* cf. *tatiarae*, near Griffith, NSW (AM, no number), right valve and hinge; C,D—*Musculium* cf. *tatiarae*, Lake Binjie, NSW (AM, no number), left valve and hinge; E–H—*M. problematicum* (Gabriel), paratype (AM C63917), E—right valve, F—hinge, G—cardinal teeth, H—posterior muscle scars; I–K—*Musculium* cf. *tatiarae*, Scotts Ck, Vic. (AM, no number), I—right valve, J—hinge of the right valve, K—cardinal teeth; L—*Musculium* cf. *tatiarae*, Darlot Ck, Vic. (AM C302417), right valve. Scale bars = 1 mm.

Only several lots from the type locality are available. These specimens differ from the other species by their elongate shell outline. However, they are similar to the species of *Sphaerinova* observed above in the shape of the muscle scars and ligament, and therefore the species may be tentatively included in that subgenus. Its status cannot be defined because of the scarcity of material and, given the variability of shell outline in species of *Musculium*, one cannot exclude the possibility that *M. problematicum* is just a local form of *M. tasmanicum*.

Subgenus *Musculium* s.str.

Type species. *Tellina lacustris* Müller, 1774, by monotypy.

Distribution. Europe, northern and eastern Asia, North America.

Diagnosis. Shell medium-sized (usually 8–10 mm long). Beaks median, definitely prosogyrous (bent anteriorly), protruded, with clearly separated prodissoconch usually forming a bean-shaped cap. Ligament not visible from exterior. Siphons long, dorsal retractors of branchial siphon normally developed, with their scars well marked as appendages of posterior adductor scars or separated.

Taxonomic remarks. Detailed characteristics of this subgenus are given in many reviews (Heard, 1977; Korniushin, 1996b). A short description of the type species and figures of a closely related or possibly conspecific taxon that is geographically nearest to Australia is provided below.

Musculium (Musculium) lacustre (Müller, 1774)

Figs. 22, 23

Sphaerium haasi C. Boettger, 1915 (SMF 1552w).

Material examined. Kiev, Ukraine, coll. AK, May 1997 (IZK); Dobo, Ins. Wammer, Aru, holotype of *Sphaerium haasi* C. Boettger, 1915 (SMF 1552w).

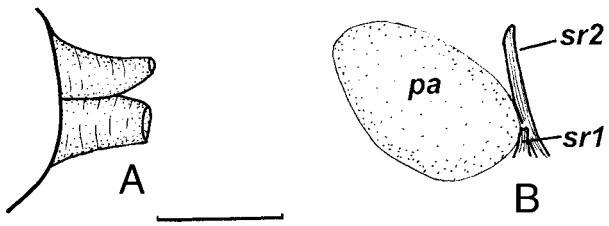

Figure 22. *Musculium lacustre* (Müll.), Kiev, Ukraine (collection of the author), siphons and siphonal muscles: A—extended siphons of the living specimen, B—posterior adductor and siphonal retractors, side view. Scale bar = 1 mm.

Diagnosis. Shell short oval, inflated, thin and fragile, transparent. Upper margin usually forming angles. Umbones median, with marked caps. Ligament not visible from exterior. Siphonal retractors strong, upper retractors of branchial siphon long. Nephridia usually of closed type.

Remarks. Very thin shell and marked caps of *Sphaerium haasi* (Fig. 23) evidently indicates that it belongs to the genus *Musculium* and has close affinity with *M. lacustre*. Presence of the latter species in Southeast Asia is suggested by recent reports (Morton, 1985). However, the forms from this region have some peculiarities in shell and anatomical characters and may represent closely related, but distinct species (Korniushin, in press). Extended discussion on this matter is beyond the scope of this paper.

Until now, *M. lacustre* or any other species of the nominate subgenus, were not recorded from Australia. In the course of this study, several specimens with large shells and strong siphonal retractors were found. They were so different from the common Australian *Sphaerinova* species, that their belonging to an introduced species of *Musculium* s.str., most probably to *M. lacustre*, is suggested.

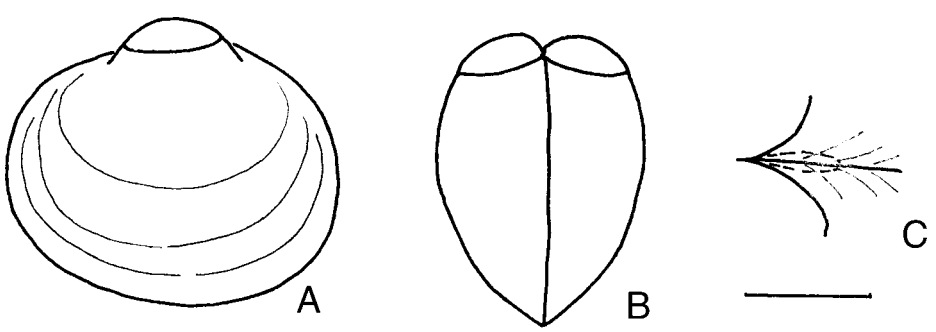

Figure 23. *Musculium lacustre*, Aru Islands (holotype of *Sphaerium haasi* C. Boettger, SMF 1552): A—lateral and B—anterior view of the shell, C—ligament dorsally. Scale bars = 1 mm.

Musculium (Musculium) cf. *lacustre* (Müller, 1774)

Fig. 24

Material examined. SOUTH AUSTRALIA: Lake Torrens, Adelaide, coll. Major T. Cherry, with *Musculium tatiarae* (AM C42311d, adult shell); Sturt River, Coromondel Valley, area of Adelaide (SAM D19068w, young specimens).

Shell large (length 11.5 mm, height 9.4, breadth 5 mm), rectangular, flat. Upper margin almost straight. Umbones narrow, shifted anteriorly and prosogyrous. Prodissoconch separated. Sculpture: fine striation and irregular folds. Hinge plate narrow, cardinal teeth: c2 short, triangular, c4 long, straight, c3 curved, not cleft. Lateral teeth long, posterior ones sharply bent, almost making right angle.

Anatomy. Only young specimens studied. Siphonal retractors strong, upper retractor of inhalant siphon long, attached to shell apart from posterior adductor. Three broods found in gills: free larvae and two brood pouches with two to four larvae in each. Nephridium of open type; dorsal lobe elongate.

Remarks. Identification of this very interesting form is tentative, because only one full-grown shell is available. This shell is similar to the large European forms of *M. lacustre*, particularly in the narrow protruding umbone and the separated prodissoconch (cap). The form from the Aru Islands assigned above to *M. lacustre* is much smaller. The specimens described

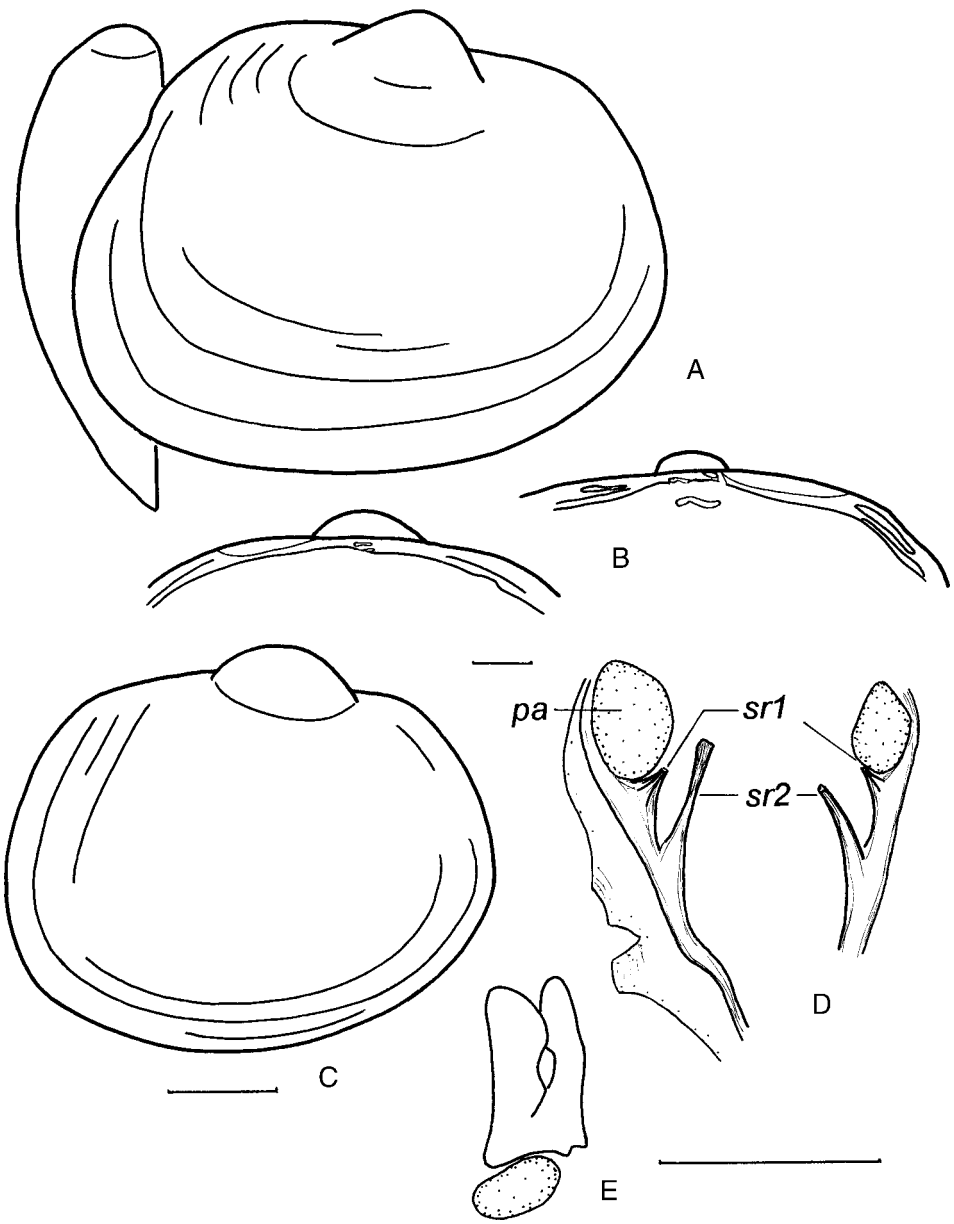

Figure 24. *Musculium* cf. *lacustre* (Müll.), shell and anatomy: A,B—Lake Torrens, Adelaide, SA (AM C42311), A—right valve, B—hinge; C–E—younger specimens from Sturt River, SA (SAM D19068), C—right valve, D—side view of posterior adductor and siphonal retractors, E—nephridium dorsally. Scale bars = 1 mm.

here show some similarity to the North American *M. transversum* (Say, 1829) in their straight upper margin and long lateral teeth, as well as in the long and strong upper retractors of the inhalant siphon, but the latter species has a much more elongated shell and broader umbone. Another similar species is known from the Amur River; it is included in the latest review of Palaearctic sphaeriids (Korniushin, 1996b) as *Paramusculium limanicum* (Moskvicheva, 1986), but further revision is necessary.

Musculium transversum was successfully introduced into England (Ellis, 1978). While both of the Australian localities of *Musculium* s.str. are situated near Adelaide, its introduction also seems probable. However, until more material is studied, the species cannot be identified with certainty and sources of introduction are not clear.

Incertae sedis

Cyclas egregia Gould, 1846

Cyclas egregia Gould 1846: 86.
Sphaerium egregium.–Kuiper, 1983: 24 (full synonymy)

Type material. Types not found, Hunter River, NSW.

None of the recent reviewers (Kuiper, 1983) cites the type specimens of this species. They are not listed in the malacological collection of the Museum of Comparative Zoology (Cambridge, Massachusetts), from which they were requested. In all probability, the types are lost. According to the original description (Gould, 1846), the species is characterised as very similar to *Sphaerium corneum* (Linneaus, 1758) but larger and with a more prominent ligament. The shell length should actually be about 20 mm (7/8 of an inch).

Sphaeriids with these characters have never otherwise been seen in Australia, and E.A. Smith (1883) doubted that original material was really Australian. However, it seems quite possible that Gould dealt with specimens of corbiculids, which are rather frequent in the large rivers (including the Hunter River). Specimens of juvenile *Corbicula* are quite often misidentified as sphaeriids.

Genus *Pisidium* Pfeiffer, 1821

Type species. *Tellina amnica* Müller, 1774 by subsequent designation (Gray, 1847).

Distribution. Cosmopolitan.

Diagnosis. Shell of medium size or small (usually up to 5 mm long, in some species 7–10 mm). Umbones placed posteriorly. Only exhalant siphon tubular; inhalant mantle opening without tubular extension or absent, only one pair of its retractors (ventral) present, other pair reduced. Outer demibranch with ascending lamella only (Korniushin, 1996b), or absent. Only one brood pouch in each gill. Nephridium with long funnel and small excretory sac without internal valve (Dreher-Mansur & Meier-Brook, 1992).

Remarks. The subgeneric division which is accepted by most reviewers after Kuiper (1962), is based on characters of gills, siphons and ligament. Subsequently, two major groups were distinguished by the type of brood pouch (Meier-Brook, 1970). New data encouraged some recent investigators (Adler, 1994; Korniushin, 1996b) to divide *Pisidium* into several genera. The number and composition of the new genera are, however, still controversial. Therefore, *Pisidium* is conservatively treated here as a single genus. The subgeneric divisions are based on those of Kuiper (1962), Zeissler (1971) and Burch (1975), with some nomenclatorial changes made below.

Subgenus *Afropisidium* Kuiper, 1962

Type species. *Pisidium lepus* Kuiper, 1957 = *P. pirothi* Jickeli, 1881 by original designation.

Distribution. South America, major part of Africa, south and Southeast Asia, Australia and New Zealand.

Diagnosis. Ligament external, elevated over dorsal margin. Only one (exhalant) siphon present; inhalant opening merged with pedal slit due to loss of presiphonal suture; ventral pair of siphonal retractors well developed, placed at posterior end of pedal slit. Outer demibranch absent. Brood pouch localised dorsally, formed by 7 to 20 filaments (depending on size of animal). Lateral loop of nephridium clearly visible from dorsal side.

Pisidium (Afropisidium) aslini Kuiper, 1983

Figs. 25–27

Pisidium aslini Kuiper, 1983: 35, fig. 65–69.

Type material. HOLOTYPE NMV F31522*, left bank at junction of Moleside Ck, Glenelg River, Vic. PARATYPES NMV F31533*, AM C135461, SAM*, WAM*, TMH E13349*, SMF 129900, about 200 specimens altogether, same data as holotype.

Other material examined. VICTORIA: Darlot Ck south of Ettric, 38°09'S 141°46'E, with *M. tatiarae* (?) (AM C302417d). TASMANIA: Greys Ck at Dunns Rd, SW of Smithton, 40°53'S 144°59'E, alt. 55 m, coll. WFP, JH & WP, 23 January 1982, with *P. tasmanicum* (AM C315738, from AM C135191w); Wandle River at Murchison Hwy, rock and gravel substrate, coll. WFP, JH & WP 23 January 1982, with *P. tasmanicum* (AM C135192w); tributary of Duck River, south of Roger River Township on Trowutta Rd, 41°00'S 145°03'E, coll. J. Clark & A. Miller, 8 February 1995 (AMw).

Diagnosis. Shell small compared to other species of the subgenus. Surface finely striated, sculpture more pronounced around umbo. Hinge plate narrow, cardinal teeth straight. Inner radial mantle muscles weak, forming six to eight bundles. Nephridia of the open type.

Shell very small (maximum 2.5 mm long), oval, moderately or strongly convex, thin, transparent or subtransparent. Margins evenly curved, without angles. Umbones rather broad, located in posterior 2/5 to 1/3 of shell length (Table 3). Sculpture: fine concentric striae, more pronounced around umbo. Pore density about 350 per mm^2. Mantle line usually poorly defined, mantle muscles scars elevated over mantle line but not separated from it. Hinge plate narrow, especially before and after cardinal teeth. Ligament pit short

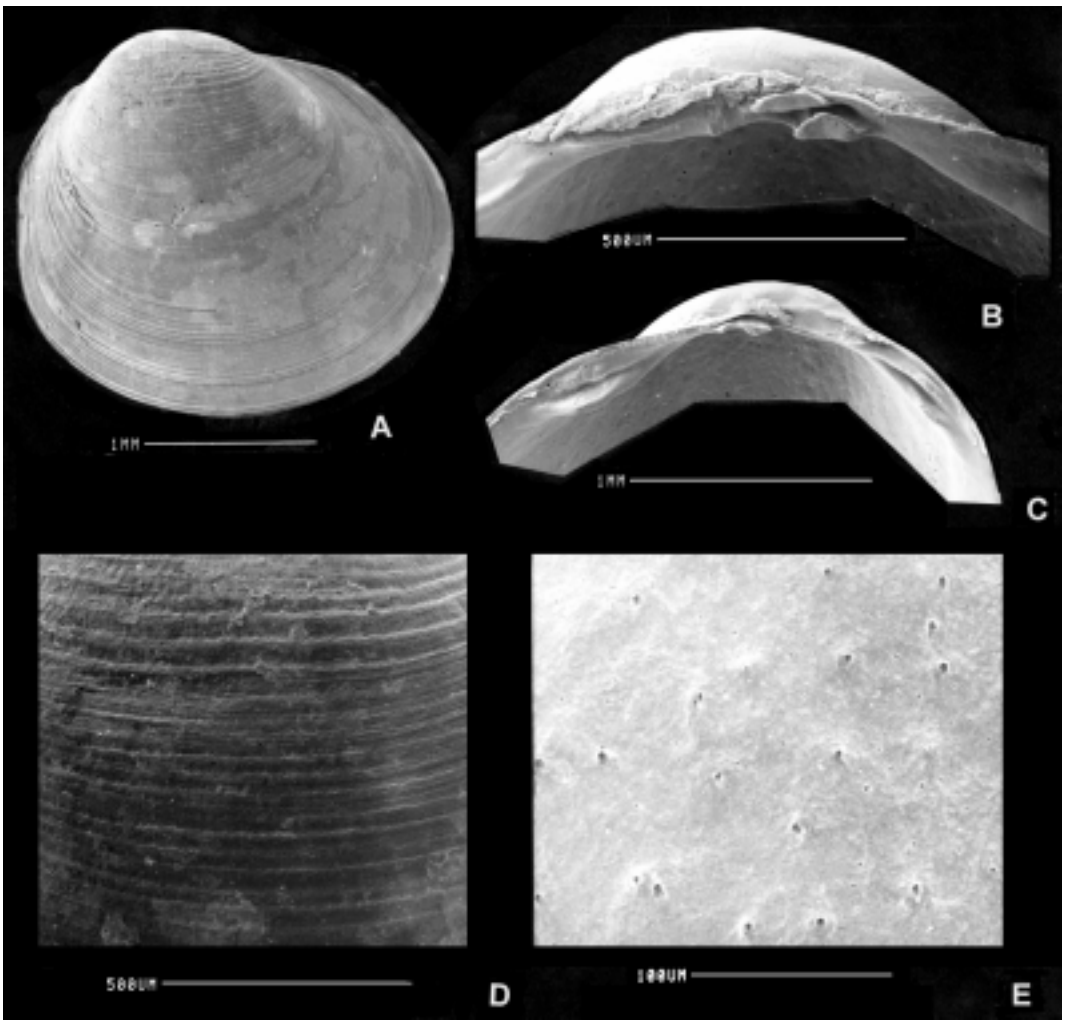

Figure 25. *Pisidium aslini* Kuiper, Wandle River, Tas. (AM C135192), shell: A—right valve from outside, B—hinge, C—sculpture, D—internal pores.

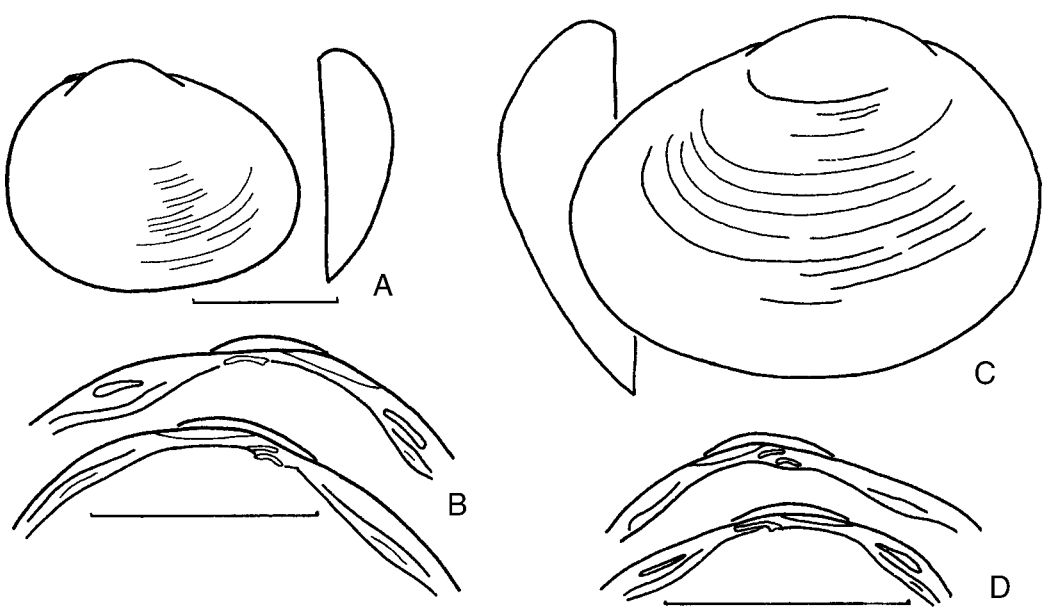

Figure 26. *Pisidium aslini* from Victoria, shells: A,B—paratype (AM C135461), right valve and hinge; C,D—Darlot Ck, Vic. (AM C302417), left valve and hinge. Scale bars = 1 mm.

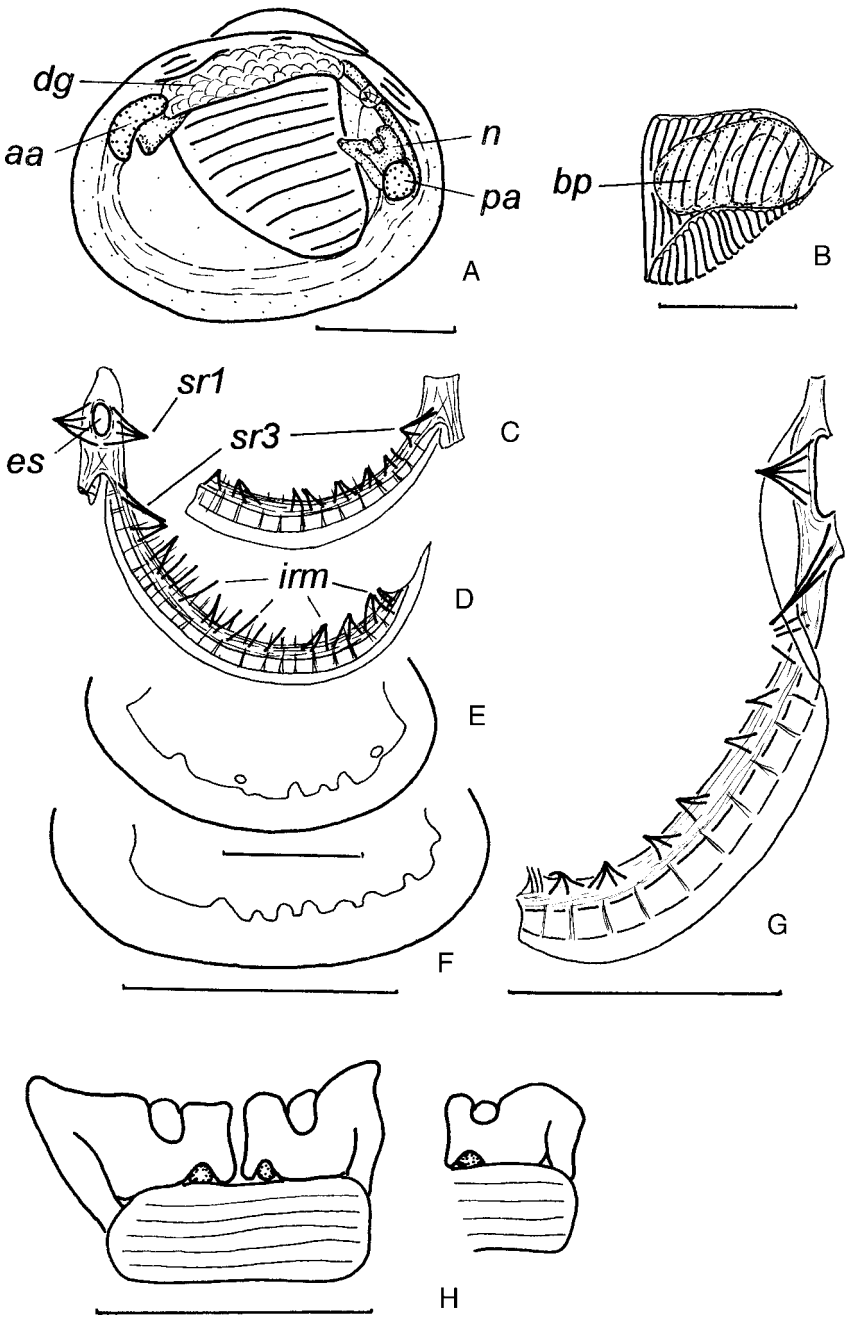

Figure 27. *Pisidium aslini*, Wandle River, Tas. (AM C135192), anatomy: A—gross anatomy; B—ctenidium with a brood pouch from inside; C,D,G—mantle muscles; E,F—mantle muscle scars; G—nephridia dorsally. Scale bars = 1 mm.

(Table 3), ligament markedly elevated. C2 in smaller specimens straight, in larger ones bent in middle, c4 straight, c3 slightly bent and thickened at posterior end. Lateral teeth moderately thick, rather short; a3 definitely shorter than a1, p1 and p3 of almost equal length.

Anatomy. Studied only in specimens from Greys Ck and Wandle River, Tas. Mantle edge rather narrow. Inner radial mantle muscles short (not much longer than outer radial muscles) and weak, six to eight bundles distinguishable.

Brood pouch placed dorsally and formed by seven filaments. Not more than two larvae found in each gill of gravid specimens.

Nephridia of open type with broad dorsal lobe, lateral loop clearly visible from dorsal side.

Distribution. While Kuiper (1983) mentioned only one locality—Glenelg River—this species is also known to occur in a few other localities in southern Victoria and northern Tasmania (Fig. 57C).

Table 3. Shell indices in the species of *Pisidium* (mean±SD, N - number of measured specimens, measurements shown in the Fig.1)

species and locality	N	H/L	HH/H	LL/L	LH/L	LA/LP	W/H
Pisidium aslini							
pooled, Tas.	9	0.82±0.022	0.054±0.007	0.20±0.013	0.57±0.026	1.45±0.165	0.74±0.049
pooled, range		0.77–0.84	0.044–0.063	0.18–0.21	0.54–0.63	1.24–1.72	0.66–0.80
Pisidium australiense							
pooled	6	0.86±0.018	0.046±0.011	0.13±0.015	0.57±0.014	1.36±0.058	0.70±0.047
pooled, range		0.85–0.90	0.032–0.065	0.12–0.17	0.55–0.59	1.31–1.47	0.67–0.79
Pisidium etheridgei							
northern NSW	4	0.83±0.006	0.041±0.018	0.21±0.014	0.50±0.030	1.28±0.106	0.67±0.057
Mt. Kaputar, NSW	10	0.81±0.019	0.049±0.010	0.22±0.015	0.52±0.038	1.22±0.616	0.63±0.040
Bobundara Ck, NSW	12	0.81±0.015	0.045±0.008	0.19±0.015	0.51±0.028	1.29±0.062	0.58±0.048
Alpine Ck, NSW	3	0.84±0.005	0.038±0.007	0.20±0.009	0.47±0.028	1.23±0.148	0.64±0.032
Morwell Rv trib., Vic.	5	0.84±0.019	0.042±0.002	0.23±0.013	0.53±0.025	1.33±0.095	0.67±0.038
Chinaman's Ck, Vic.	20	0.83±0.013	0.058±0.007	0.23±0.019	0.57±0.015	1.15±0.077	0.62±0.030
Urquart Ck, Tas.	3	0.83±0.018	0.055±0.012	0.21±0.008	0.53±0.003	1.28±0.072	0.65±0.081
Lake Butters, Tas.	14	0.81±0.017	0.039±0.007	0.17±0.022	0.52±0.016	1.23±0.072	0.54±0.048
Lake Sorell, Tas.	5	0.81±0.015	0.050±0.014	0.20±0.011	0.51±0.012	1.30±0.090	0.63±0.043
pooled	76	0.82±0.020	0.048±0.010	0.21±0.048	0.53±0.035	1.24±0.096	0.61±0.065
pooled, range		0.77–0.86	0.020–0.074	0.14–0.28	0.45–0.62	0.99–1.43	0.47–0.74
Pisidium hallae							
Barrington Tops, NSW	20	0.78±0.016	0.046±0.009	0.22±0.020	0.51±0.014	1.25±0.062	0.58±0.032
Blue Mountains, NSW	12	0.77±0.016	0.057±0.008	0.21±0.012	0.51±0.016	1.25±0.093	0.67±0.034
Warburton, Vic.	5	0.77±0.008	0.047±0.001	0.22±0.012	0.48±0.028	1.28±0.079	0.66±0.040
Ben Lomond Rv, Tas.	5	0.79±0.007	0.046±0.011	0.20±0.018	0.51±0.031	1.41±0.113	0.64±0.010
Franklin Rv, Tas.	7	0.77±0.013	0.051±0.006	0.21±0.011	0.49±0.024	1.34±0.079	0.67±0.041
pooled	49	0.78±0.015	0.050±0.009	0.21±0.016	0.50±0.022	1.29±0.092	0.63±0.055
pooled, range		0.73–0.82	0.026–0.071	0.18–0.27	0.46–0.55	1.15–1.54	0.52–0.74
Pisidium kosciusko							
Lake Albino, NSW	13	0.81±0.021	0.037±0.011	0.19±0.017	0.53±0.027	1.21±0.074	0.61±0.054
range		0.79–0.86	0.016–0.054	0.17–0.22	0.49–0.58	1.04–1.34	0.49–0.68
Pisidium tasmanicum							
Morwell Rv trib. Vic.	18	0.84±0.025	0.050±0.009	0.20±0.024	0.51±016	1.34±0.140	0.70±0.045
Deep Ck, Vic.	10	0.82±0.009	0.051±0.009	0.18±0.011	0.52±0.016	1.36±0.079	0.64±0.039
Frasers Ck, Vic.	7	0.84±0.014	0.046±0.007	0.21±0.016	0.55±0.021	1.22±0.128	0.63±0.034
Nora Rv, Tas.	4	0.85±0.018	0.051±0.005	0.26±0.029	0.52±0.031	1.13±0.038	0.71±0.023
Wandle Rv, Tas.	10	0.83±0.018	0.052±0.010	0.19±0.013	0.56±0.025	1.28±0.118	0.71±0.034
type lot? Tas.	3	0.82±0.004	0.050±0.015	0.19±0.010	0.53±0.003	1.30±0.059	0.64±0.034
Lake Dulverton, Tas.	4	0.85±0.016	0.046±0.011	0.18±0.010	0.52±0.014	1.35±0.151	0.54±0.293
Ben Lomond Rv, Tas.	3	0.86±0.013	0.042±0.004	0.16±0.008	0.51±0.022	1.31±0.110	0.66±0.026
pooled	58	0.84±0.018	0.050±0.009	0.20±0.026	0.53±0.026	1.31±0.120	0.68±0.048
pooled, range		0.80–0.90	0.033–0.071	0.15–0.33	0.48–0.60	1.05–1.60	0.57–0.77
Pisidium fultoni							
Lake Butters, Tas.	13	0.83±0.015	0.043±0.005	0.21±0.014	0.56±0.021	1.26±0.093	0.56±0.032
Lake Malbena, Tas.	10	0.83±0.020	0.044±0.011	0.21±0.019	0.58±0.033	1.23±0.077	0.56±0.023
pooled	23	0.84±0.018	0.043±0.011	0.21±0.016	0.57±0.027	1.25±0.087	0.56±0.028
pooled, range		0.80–0.86	0.031–0.064	0.19–0.24	0.51–0.62	1.09–1.48	0.52–0.63
Pisidium carum							
Gympie, Qld	6	0.82±0.006	0.061±0.004	0.18±0.018	0.56±0.038	1.12±0.039	0.61±0.041
Caboolture, Qld	6	0.81±0.019	0.065±0.005	0.19±0.016	0.54±0.036	1.13±0.57	0.60±0.035
Molong Ck, NSW	9	0.83±0.014	0.067±0.009	0.19±0.019	0.55±0.020	1.10±0.067	0.63±0.037
Carnarvon, NSW	4	0.81±0.006	0.055±0.004	0.18±0.016	0.57±0.024	0.97±0.018	0.58±0.008
Loddon Rv, Vic.	20	0.83±0.012	0.056±0.006	0.19±0.017	0.56±0.031	1.11±0.054	0.60±0.036
pooled	45	0.82±0.015	0.060±0.008	0.19±0.018	0.56±0.030	1.10±0.066	0.60±0.037
pooled, range		0.79–0.86	0.042–0.081	0.16–0.24	0.47–0.61	0.95–1.28	0.54–0.71

Table 3. Continued.

species and locality	N	H/L	HH/H	LL/L	LH/L	LA/LP	W/H
Pisidium ponderi							
Bindi Brook, NSW	5	0.82±0.009	0.052±0.010	0.21±0.027	0.53±0.016	1.13±0.027	0.65±0.046
Tia Rv, NSW	10	0.84±0.009	0.047±0.007	0.21±0.014	0.56±0.027	1.13±0.050	0.67±0.030
type lot, NSW	11	0.83±0.017	0.052±0.009	0.21±0.021	0.55±0.010	1.28±0.146	0.73±0.070
pooled	26	0.83±0.029	0.050±0.009	0.21±0.019	0.55±0.021	1.20±0.127	0.70±0.060
pooled, range		0.80–0.86	0.037–0.073	0.17–0.25	0.50–0.58	1.04–1.54	0.60–0.87
Pisidium centrale							
pooled	8	0.81±0.011	0.056±0.014	0.19±0.016	0.57±0.015	1.07±0.063	0.56±0.039
range		0.79–0.83	0.034–0.078	0.17–0.22	0.56–0.60	1.00–1.17	0.49–0.60

Ecology. Inhabits creeks, is often associated with *P. tasmanicum*, in Darlot Ck it is found together with *Musculium tatiarae*.

Variability. The form from Tasmania (Fig. 25) has definitely higher and more inflated shells with weaker sculpture than the typical form (Fig. 26).

Taxonomic remarks. The placement of *Pisidium aslini* in the subgenus *Afropisidium* is based on there being an externally visible ligament (Kuiper, 1983). Principal anatomical characters (absence of inhalant mantle opening and outer demibranch, upper position of brood pouch, dorsally visible lateral loop of nephridium) are shared by two other subgenera, namely *Neopisidium* Odhner and *Odhneripisidium* Kuiper.

In shell characters, *Pisidium aslini* differs from the other species of *Afropisidium* by its smaller size, being similar to the smallest species of *Neopisidium* and *Odhneripisidium*. It is also characterised by the extreme reduction of mantle musculature and peculiar configuration of the nephridium: while in the other *Afropisidium* species the lateral loop is bent (with some portion lying transversely) and the dorsal view of nephridium is S-shaped, in *P. aslini* the lateral loop is almost straight, stretching parallel to the body axis (Fig. 27G).

The Tasmanian form of *P. aslini*—on which the anatomical description is based—differs from the typical Victorian one in its more convex shell, somewhat protruding umbo and less-pronounced sculpture, and may represent a distinct subspecies or even a species. However, more material is needed in order to define its status.

Subgenus *Odhneripisidium* Kuiper, 1962

Type species. *Pisidium stewarti* Preston, 1909 by original designation.

Distribution. Central and southern part of Eurasia, Sunda Archipelago, northern Australia, occasionally in North Africa, and (probably) in Papua New Guinea (Kuiper, 1983).

Diagnosis. Ligament introverted (Kuiper, 1962), stretching toward ventral side of hinge plate. Anatomical characters as in *Afropisidium*.

Pisidium (Odhneripisidium) australiense n.sp.

Figs. 28, 29

Type material. HOLOTYPE AM C350022d&w, gold coated for SEM, Dowah Ck upstream from the junction with Freshwater Ck, Crystal Cascades, W of Cairns, 16°58'S 145°41'E, Qld, in quiet corners of swift creek, coll. WFP, 30 September 1980. PARATYPES AM C350023w, 6 specimens, one valve gold coated for SEM, same data as holotype.

Other material examined. QUEENSLAND: Broomfield Ck at Innisfail-Japoon Rd, 17°44'S 145°56'E, small boulders and gravel, coll. WFP, 28 September 1980 (AMw&d); Douglas Ck at Palm Hwy west of Cairns, on stones and leaves in pools, coll. WFP, 28 September 1980 (AMw&d); Dowah Ck, coll. WFP, 30 September 1980 (AMw&d).

Diagnosis. Shell small, with fine broad-spaced ribs. Hinge plate narrow, cardinal teeth curved. Inner radial mantle muscles weak, about five bundles are clearly distinguishable. Nephridia of closed type.

Shell very small (Table 4, largest specimen examined: 2.17 mm long), tetragonal, rather flat, thin, sub-transparent. Upper margin straight, with more-or-less clear angles at its extremities, front margin oblique, curved on its low extremity, ventral margin slightly

Table 4. Measurements (mm) of *Pisidium (Odhneripisidium) australiense* n.sp.

	L	H	HH	LL	LH	LA	W/2
holotype	2.17	1.86	0.059	0.29	1.20	1.31	0.74
paratype	2.08	1.87	0.088	0.25	1.22	1.19	0.62
paratype	2.03	1.75	0.071	0.27	1.20	1.16	0.62
paratype	1.85	1.57	0.067	0.27	1.08	1.06	0.57
paratype	1.75	1.49	0.097	0.29	0.99	1.01	0.52

curved, back margin truncate. Umbones at posterior 2/5 of shell length (Table 3), narrow, flat (not protruded). Sculpture: fine but clear broad-spaced concentric ribs. Internal pores numerous: 861 per mm^2 (one measurement). Mantle line and adductor scars clear, several mantle muscles scars elevated over mantle line but not separated from it. Hinge plate narrow near ligament, broadened around cardinal teeth. Ligament pit triangular, somewhat elongate in comparison with other species of subgenus. Cardinal teeth: c2 strongly curved, triangular, c4 slightly curved, lying parallel to the upper margin of hinge plate, C3 hooked, with posterior end swollen. Lateral teeth short, moderately swollen, inner and outer laterals of right valve approximately same size.

Anatomy. One siphon. Inhalant mantle opening merged with pedal slit, but retractors well developed (Fig. 29E). Mantle edge rather narrow. Inner radial mantle muscles weak, forming five well-distinguished bundles. Outer demibranch absent. Brood pouch placed dorsally, formed

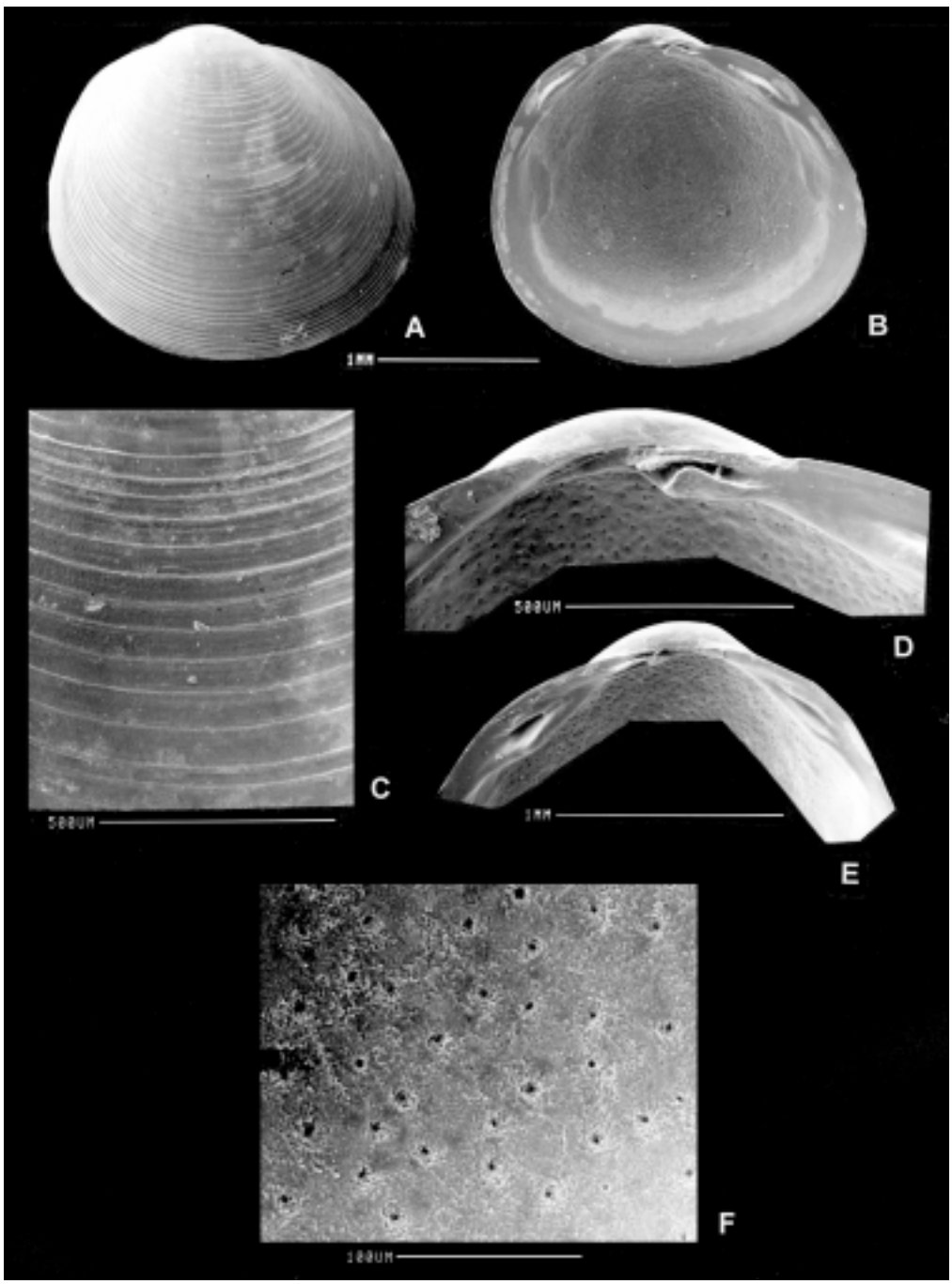

Figure 28. *Pisidium australiense* n.sp., type specimens, shell: A—right (from outside) and B—left (from inside) valves of the holotype (AM C350022); C—sculpture of the holotype, D—hinge (left valve of the holotype, right valve of the paratype); E—internal pores of the paratype (AM C350023).

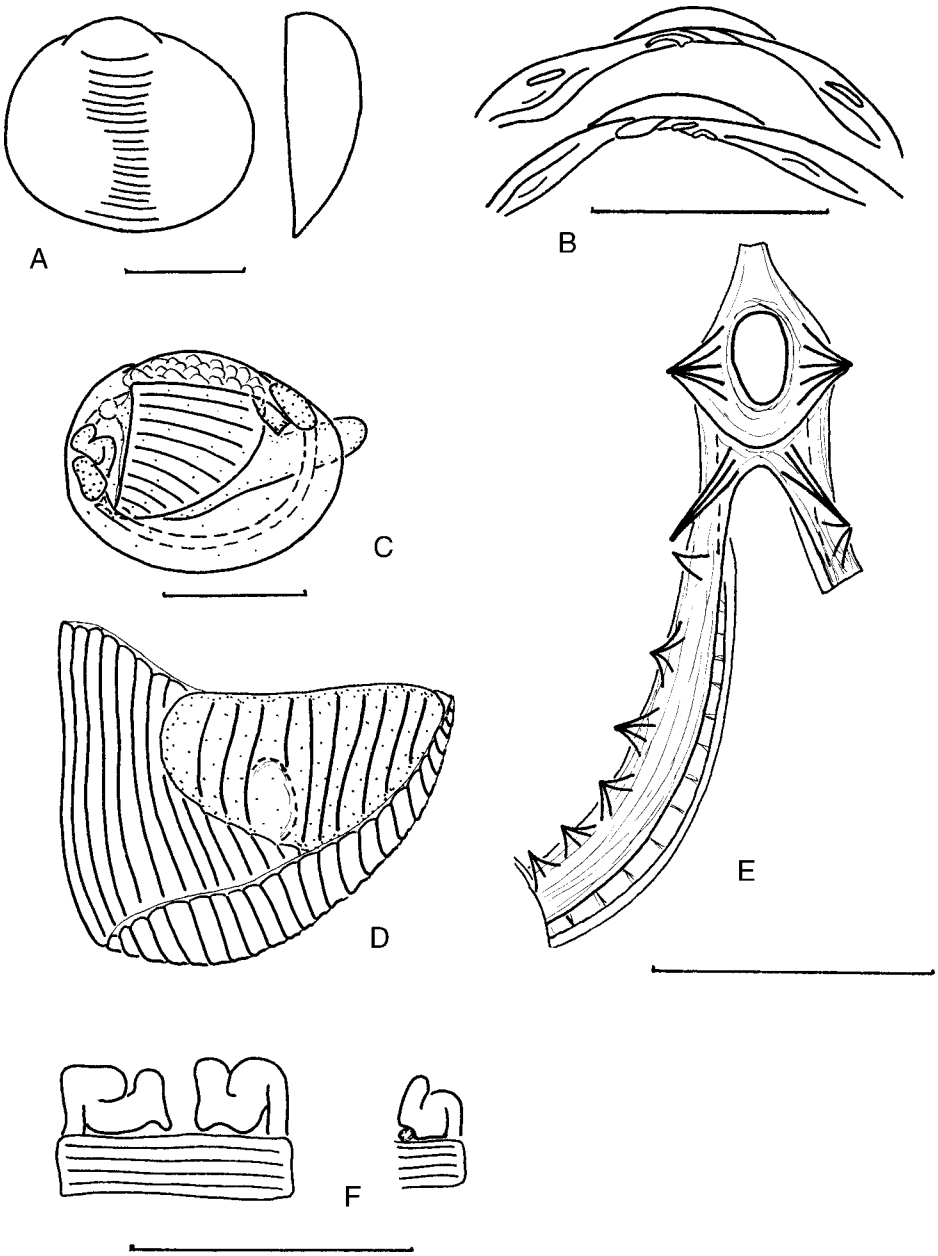

Figure 29. *Pisidium australiense*, paratypes (AM C350023), shell and anatomy: A—right valve, B—hinge, C—gross anatomy, D—ctenidium, E—mantle muscles, F—nephridia dorsally. Scale bars = 1 mm.

by seven to twelve filaments and containing two to six embryos. Nephridia of closed type, with clearly visible lateral loop (Fig. 29F).

Distribution. Known from several localities in northern Queensland, near Cairns (Fig. 57A).

Ecology. Inhabits springs and small creeks that are well shaded by trees with the bottom covered by leaves and vegetation.

Etymology. This species name is based on the country locality.

Taxonomic remarks. The presence of *Odhneripisidium* in Australia was suspected by Kuiper (1983), but this is the first species of the group to be described from the continent. A species of *Odhneripisidium* from New Guinea is mentioned, but not described, by him (Kuiper, 1983). Geographically nearby species inhabit the Sunda Archipelago (Indonesia) and New Britain (Kuiper, 1965, 1967). The new species is similar in shape to *P. dammermani* Odhner, 1940 from Sumba but differs in its regular concentric sculpture. *Pisidium sundanum* Rensch, 1934 from Java also has coarse sculpture, but is larger. The new species differs from *P. novobritanniae* Kuiper, 1967 (from New Britain), by having a rounded shell and more pronounced sculpture.

Subgenus *Euglesa* Leach in Jenyns, 1832

Type species. *Euglesa henslowiana* Leach in Jenyns, 1832 (= *Pisidium personatum* Malm, 1855), by monotypy.

Distribution. Cosmopolitan.

Diagnosis. Ligament enclosed, but not introverted. Inhalant opening of mantle and outer demibranch present. Brood pouch in low position (near upper edge of ascending lamella) and formed usually by four to five filaments, in largest specimens by six to seven filaments.

Remarks. While species of this group are distinguished from *Pisidium* s.str. (*P. amnicum* group) by the size and position of their brood pouch (Meier-Brook, 1970), many reviewers (e.g., Zeissler, 1971; Burch, 1975) consider it subgeneric. There has also been discussion concerning the name for this group. While the oldest name in consideration is *Euglesa* Leach, first published in synonymy by Jenyns (1832) and validated by publishing Leach's original manuscript (Leach, 1852). Despite the quite obscure diagnosis, there are no formal objections to this name, and it is widely used in Russian literature since Pirogov & Starobogatov (1974). The other names in use are *Cymatocyclas* Dall, 1903 (Zeissler, 1971), *Cyclocalyx* Dall, 1903 (Burch, 1975) and *Casertiana* Fagot, 1892 (Adler, 1994).

Pisidium (Euglesa) etheridgei E.A. Smith, 1883

Figs. 30–33

Pisidium etheridgei E.A. Smith, 1883: 306, pl. 7, fig. 35.
Australpera mena Iredale, 1943b: 95, fig. 3.
Pisidium casertanum.–Kuiper, 1983 (full Australian synonymy).
Pisidium carum.–Kuiper, 1983: fig. 54.

Type material. LECTOTYPE BMNH 1878.2.15.5 (Kuiper, 1983: 31), Yan-Yean Reservoir, Plenty District, Vic. PARALECTOTYPES BMNH, the same number and data as holotype, 4 specimens.

Australpera mena, lectotype (Kuiper, 1983: 32) AM C63905 and 4 paralectotypes AM C151006, Armidale, NSW.

Other material examined. QUEENSLAND: 1.5 km section of Gap Ck, off Glengallan Ck, Cunninghams Gap, Cunningham Hwy., 33 km E of New England Hwy, Qld, 28°03'S 152°23'E, alt. 720–680 m, on leaves in pools, coll. WFP, J. Stanisic & OG, 16 March 1981 (AM C313608d). NEW SOUTH WALES: Scrub Yard Ck NW of Little Mt Spirabo, 29°19'S 152°07'E, alt. 1045 m, coll. WFP, 1981 (AM 128706d); Unumgar State Forest, 28°25'S 152°41'E, coll. WFP, 1981 (AM C128678d); Dawsons Spring, Mt Kaputar, 30°17'S 150°09'E, alt. 1343 m, in sedges from spring source, coll. P. Colman, 8 November 1983 (AM C140422d); Solomons Ck, Erlen Bog State Forest, Glen Allen, 36°44'S 149°30'E, coll. WFP & JH, 14 February 1983 (AMw); 1/2 km north of Alpine Ck on Snowy Mountains Hwy, Mt Kosciusko NP, small swampy creek, coll. WFP & JH, 1 November 1980 (AM C126962d); Bobundara Ck at road crossing, 29 km south of Cooma on Myalla Rd, 36°30'S 149°07'E, alt. 900 m, coll. GC, 4 November 1990, with *Pisidium ponderi* n.sp. (AM C315743w). VICTORIA: Chinamans Ck, Wilsons Promontory NP, 38°55'S 146°24'E, alt. 80 m, in leaves, coll. WFP, A. de Keyzer & GC, 14 February 1990 (AM 315741w); tributary of Kinchington Ck near Bruarong, 36°25'S 146°50'E, alt. 540 m, coll. JW & GC, 6 December 1988 (AMw); tributary of Morwell River, 38°11'S 146°20'E, coll. WFP & GC, 20 February 1987 (AMw). SOUTH AUSTRALIA: Larrakin Lagoon, Kangaroo Island, Cotton coln. (SAM D3587d); Evens Ponds, near Mt Gambier, sediment near outflow (AMw); Portland-Nelson Rd, 38°11'S 141°19'E, coll. WFP, 15 May 1984 (AMw). TASMANIA: Launceston (AM C109827), identified by Kuiper as *P. carum*; Thirteen Mile Ck, tributary of Hazelwood River at Mt Cleveland-Corinna road junction, flowing large steam, coll. WFP, WP & JH, 24 January 1982 (AM C135175w), north of Ben Lomond Rd near Legges Tor Pond with small stream inflow, coll. WFP, WP & JH, 18 January 1982, (AM 135189w); tributary of East Gawler River, near Castra Rd, coll. 19 January 1982 by WFP & JH (AM C135196w); Lake Malbena, 41°57'S 146°16'E coll. JW, 3 February 1988, with *P. fultoni* (AMw); Lake Butters, 41°48'S 146°26'E, coll. JW, 5 February 1988, with *P. fultoni* (AMw); channel between Lake Sorell and Lake Crescent, 42°08'S 147°10'E, coll. S. Clark & A. Miller, 10 February 1995 (AMw); Urquart Ck, New River Lagoon, 43°30'S 146°34'E, coll. JW, 15 February 1988 (AMw).

Diagnosis. Shell short oval or quadrangular, moderately convex. Surface irregularly striated. Pores moderately dense. Hinge plate relatively narrow. Cardinal teeth arched or bent. Presiphonal mantle suture elongated. Inner radial mantle muscles form five to seven strong bundles. Outer demibranch small, strongly shifted posteriorly.

Shell rather small, but larger than in other species of *Pisidium* (sometimes more than 5 mm long), short-oval or quadrangular, moderately convex, usually of moderate thickness, but in some populations rather thin and fragile. Mean value of height index (H/L) for population not less than 0.81, typically 0.83–0.84 (Table 3). Margins rounded, sometimes with obtuse angles at extremities of upper margin. Most extended point of front margin approximately at level of horizontal median plane. Umbones broad, not protruding, considerably shifted posteriorly (placed at posterior 0.45 of shell length). Surface irregularly striated. Pores density variable between populations, usually not exceeding 450 per mm^2; mean value 254±107 (n = 20). Scars of most anterior muscle bundles always separated from mantle line, posterior scars sometimes merged with latter.

Hinge plate of moderate and even breadth. Ligament pit rather long and narrow. Cardinal teeth: c2 arched or bent in middle point, c4 straight or slightly arched, obliquely placed behind c2, c3 also bent or arched, thickened and cleft on posterior end with two parts adjoining each other. Lateral teeth narrow, not swollen, outer lateral teeth in right valve almost of same length as inner ones.

Anatomy. Mantle edge thick and broad. Presiphonal suture apparently elongate, 1/5 to 1/4 length of pedal slit (Figs. 33H–M, 34A). Mantle musculature well developed. Inner radial mantle muscles long (longer than outer radial ones), strong, number of bundles variable (five to seven) due to their merging or splitting.

Outer demibranch small (Figs. 33B–F, 34B), anterior edge placed at 11th to 14th filament of inner demibranch in most populations except several where outer demibranch greatly reduced; mean value for pooled data 12.8±0.38 (n

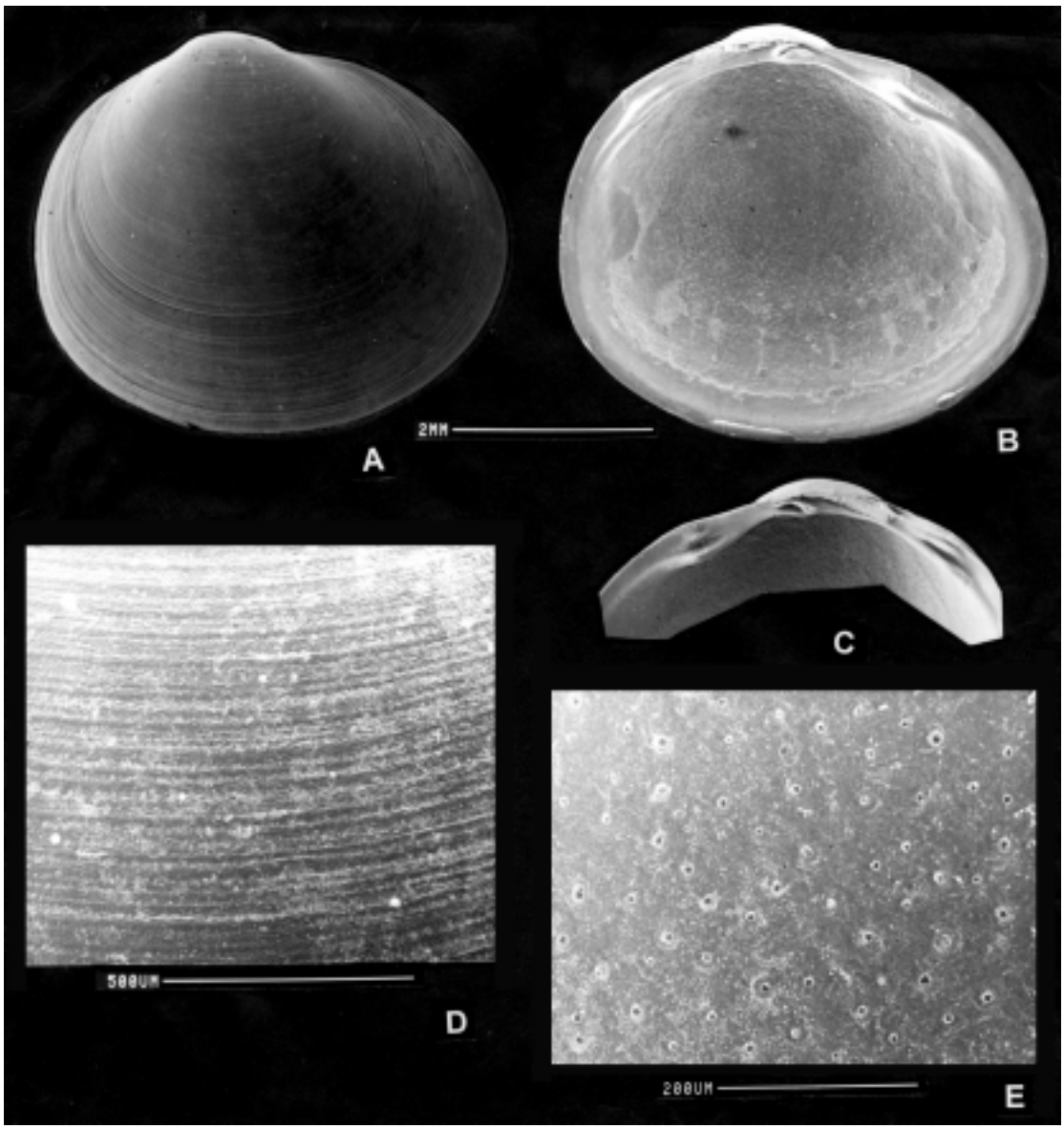

Figure 30. *Pisidium etheridgei* (E.A. Smith), Chinamans Ck, Wilsons Promontory, Vic. (AM C315741), shell: A—right valve from outside, B—left valve from inside, C—hinge of the right valve, D—sculpture, E—internal pores.

= 41). The brood pouch formed by four to seven filaments, five-filament pouches found most often. Number of offspring extremely variable: from one to ten in each demibranch, usual number four to eight.

Nephridium of closed type; dorsal lobe rectangular (Fig. 33G).

Distribution (Fig. 57B). The most southern part of Queensland, eastern NSW and Victoria along the Great Dividing Range, southeastern South Australia (including Kangaroo Island) and Tasmania. It is recorded for the Murray system by Gabriel (1939), but no material from that area has been seen and therefore these records need checking. A wider distribution in Queensland seems probable given the paucity of collections from that state.

Variability. This is one of the most variable species of *Pisidium*. Variability of shell characters have a geographic pattern, but differences between local forms are not as clear as in *Musculium tasmanicum*. The form typified by the type of *Australpera mena* Iredale, occurring in southern Queensland and northern NSW, is characterised by a rounded or oval shell with a rather high hinge plate and coarser sculpture (Fig. 32A–D). Specimens from Mt Kaputar (Fig. 32E,F) share these characters but are distinguished by their larger size (the largest specimen: L 5.7, H 4.6, W/2 1.6 mm) and numerous embryos per pouch (up to 10).

In many specimens from southern New South Wales (Snowy Mountains) and mountains of Victoria sculpture is weak, umbones are strongly shifted posteriorly, and hinge

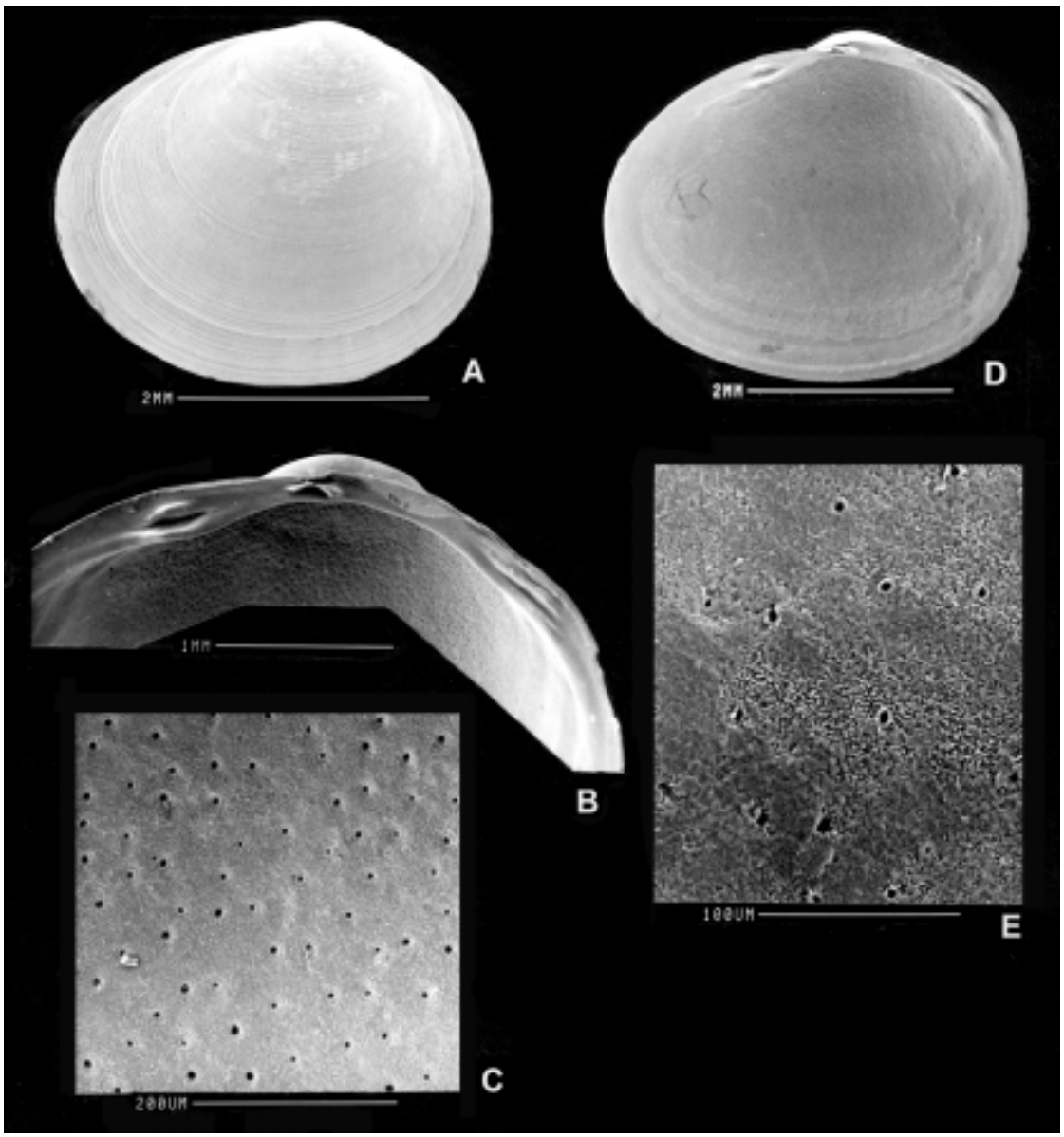

Figure 31. *Pisidium etheridgei*, shells: A–C—Bobundara Ck, NSW (AM C315743): A—left valve from outside, B—hinge of the right valve, C—pores; D,E—Lake Malbena, Tas. (AM, no number), D—right valve from inside, E—internal pores.

plate is rather narrow. Specimens with extreme outer demibranch reduction (anterior edge at 18th to 20th inner demibranch filament) were found in Bobundara Ck near Cooma (Figs. 31A–C, 33C). Another interesting abnormality observed in this area was irregularity of filament growth causing fusion of the filaments in the anterior part of the gill.

In the coastal area of Victoria and southeastern South Australia, an angulate, compressed form (the nominate one) with a strong hinge is the most common. Specimens characterised by circular and rather convex shells with a narrower hinge plate as well as by the concentration of the muscle bundles were also found here (Figs. 32G,H, 33K). In these characters, they are similar to *P. tasmanicum*, though differing in their larger size; their taxonomic placement is therefore disputable.

Tasmanian populations differ from those from the mainland in having more convex shells with broad, protruding umbones (Fig. 32I,J), some populations have large specimens (about 5.5 mm long). The characters of this form are the most pronounced in samples from southeastern Tasmania, where *P. etheridgei* looks like large *P. tasmanicum* (Fig. 32K). A peculiar form inhabits the lakes of central Tasmania, together with *P. fultoni*. This form is elongate, with a thin and fragile shell, narrow hinge plate (Fig. 31D,E) and incubates only a few embryos (one or two per pouch). The latter peculiarity is shared by *P. fultoni* associated with *P. etheridgei* in many Tasmanian lakes.

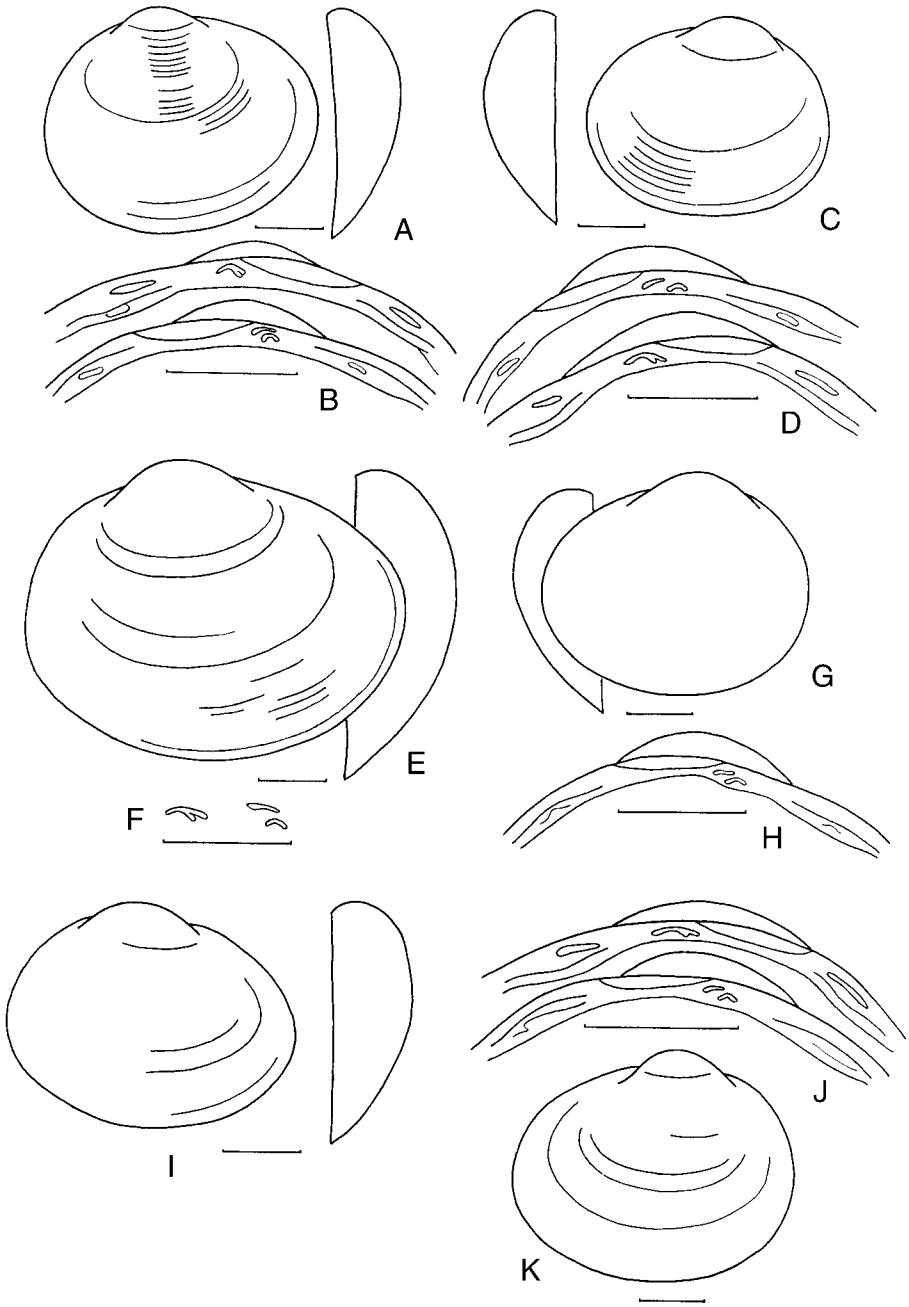

Figure 32. *Pisidium etheridgei*, variation of shell form: A,B—Gap Ck, southern Qld (AM C313608), right valve and hinge; C,D—Mt. Spirabo, NSW (AM C128706), left valve and hinge; E,F—Mt. Kaputar, NSW (AM C135175), E—right valve, F—cardinal teeth; G,H—tributary of Morwell River, Vic. (AM, no number), left valve and hinge of the left valve; I,J—Thirteen Mile Ck, Tas. (AM C135175), right valve and hinge; K—Urquart Ck, Tas. (AM, no number), left valve. Scale bars = 1 mm.

Ecology. Most frequent in creeks and small rivers. In South Australia and Tasmania it also inhabits lakes and lagoons.

Remarks. The affinity of *P. etheridgei* to the Eurasian *Pisidium casertanum* Poli, 1791 is controversial: some authors since E.A. Smith (1886) considered the Australian species distinct (Iredale, 1943a,b; Boettger, 1961), but Kuiper (1983) synonymises it with *P. casertanum*. These two species are certainly difficult to distinguish using shell characters. However, the shell of *P. casertanum* is usually triangular or subtriangular (the most extended point of the front margin is below the horizontal median plane), while in *P. etheridgei* the shell is oval or tetragonal. The umbones of the latter species are on average more central, placed perpendicular to the long axis of the shell. Because of the placement of the

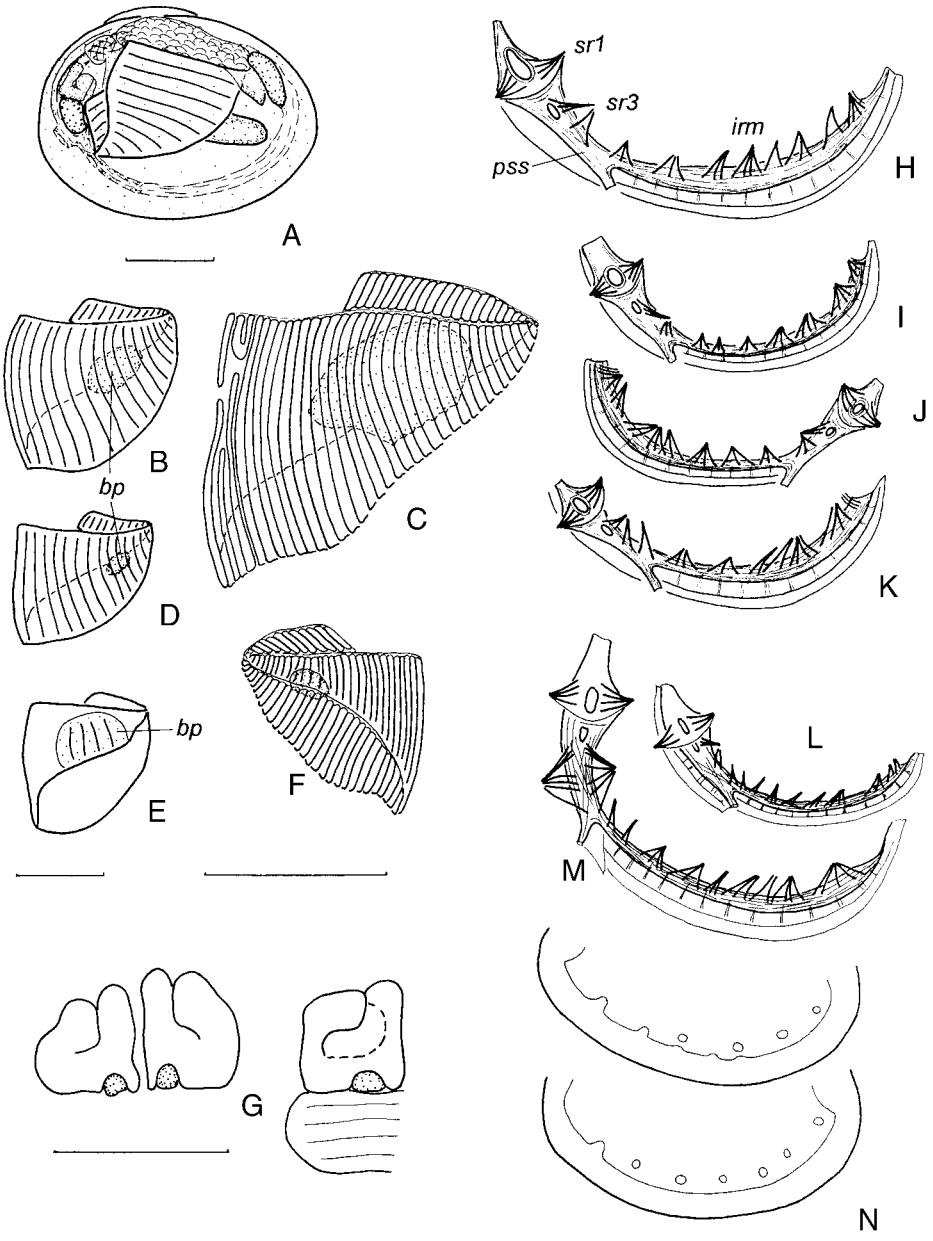

Figure 33. *Pisidium etheridgei*, anatomy: A—gross anatomy, Thirteen Mile Ck, Tas. (AM C135175); B–F—gills, B—Mt Kaputar, NSW (AM C135175), C—Bobundara Ck, NSW (AM C315743), specimen with abnormalities in filament growth, D—Chinamans Ck, Wilsons Promontory, Vic. (AM C315741), E–F—Thirteen Mile Ck, Tas. (AM C135175); G—nephridia dorsally, Thirteen Mile Ck, Tas.; H–M—musculature of the mantle edge, H—Mt Kaputar, NSW, I–J—Bobundara Ck, NSW, K—tributary of Morwell River, Vic.; L,M—Thirteen Mile Ck, Tas.; N—mantle muscle scars, Thirteen Mile Ck, Tas. Scale bars = 1 mm.

umbones and the similar form and position of the anterior and posterior lateral teeth, the shell of *P. etheridgei* is almost symmetrical, as mentioned by E.A. Smith (1883). In *P. casertanum*, the umbones are strongly shifted and bent towards the hind end of the shell, the posterior lateral teeth are shorter than the anterior ones and the shell is markedly asymmetrical. In addition, in *P. etheridgei* the ligament pit is long, the posterior lateral teeth are thin and lie parallel to each other and the margin of the hinge plate, the outer and inner laterals are almost equal in length, whereas in *P. casertanum*, the laterals tend to be swollen and lie obliquely, outer laterals are shorter than the inner ones and form an acute angle with them. On the average, *P. casertanum* is characterised by the rather high density of the internal shell pores (up to 1000 per mm^2) (Korniushin, 1996b), their been markedly lower in *P. etheridgei*. However, the best diagnostic character is the markedly elongate presiphonal suture in *P. etheridgei*.

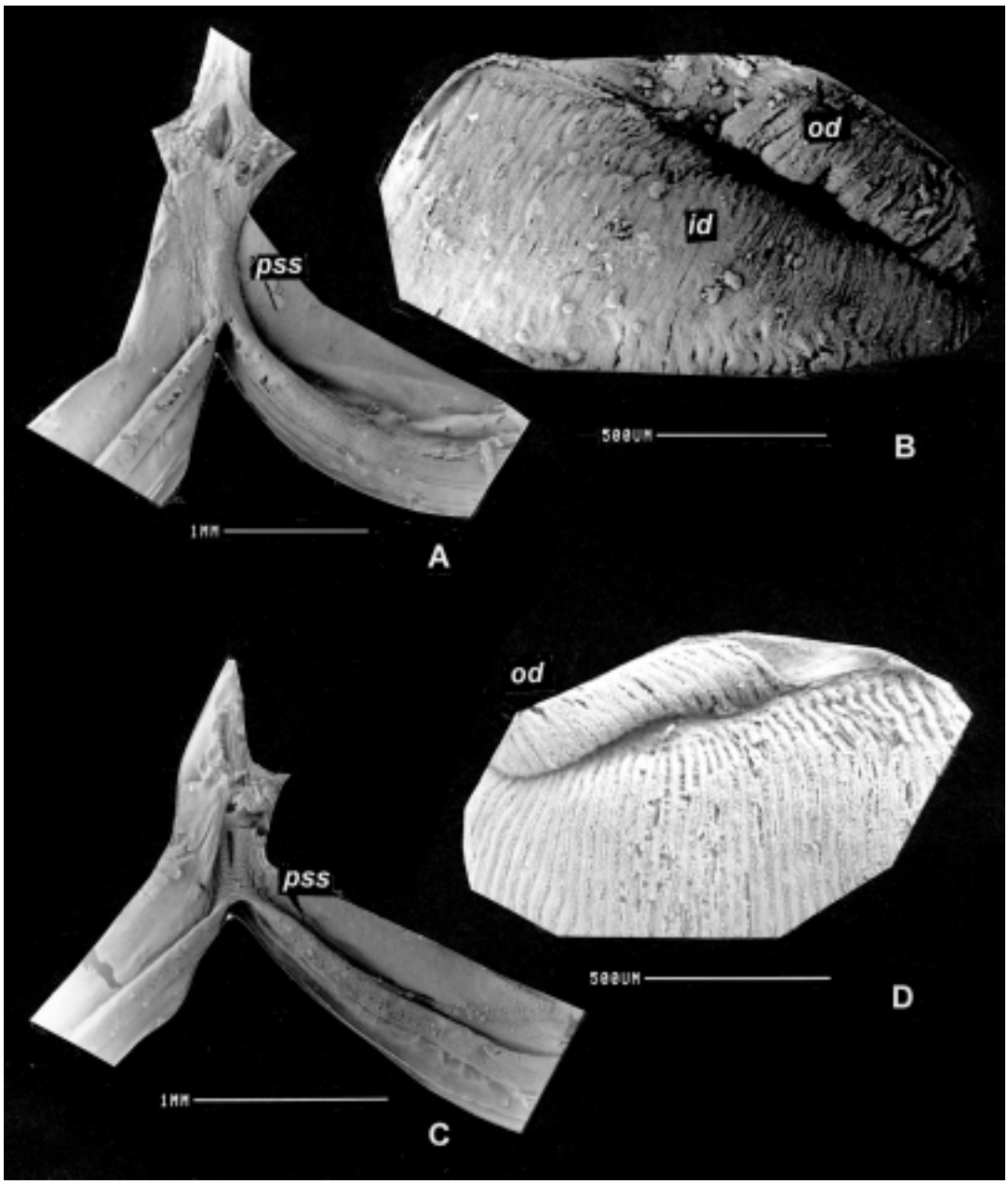

Figure 34. Soft body structures of some *Pisidium etheridgei* in comparison with *P. carum*: A—*Pisidium etheridgei* (E.A. Smith), Solomons Ck, NSW (AM, no number), part of the mantle edge; B—upper part of ctenidium from the same specimen; C,D—*P. carum*, Molong Ck, NSW (AM, no number), mantle edge and ctenidium.

Similar elongation of the presiphonal suture was observed in *Pisidium floresianum* Rensch, 1934 (Fig. 35) from the Flores Island and New Guinea. This species is also similar to *P. etheridgei* in its median position of the umbo and in the form of the hinge teeth. Another species similar to *P. casertanum* but with a more pronounced elongation of mantle suture, is known from the Amur River (East Russia) under the name *P. khurbaense* (Zatravkin, 1987) (Korniushin, 1996b).

***Pisidium (Euglesa) hallae* Kuiper, 1983**

Figs. 36–38

Pisidium hallae Kuiper, 1983: 33, fig. 78–81.

Type material. HOLOTYPE AM C126964, Yarrangobilly River at Cave Rd, off Snowy Mountains Hwy, 35°23'S 148°30'E, NSW. PARATYPES AM C135457, 23 specimens examined by this study; other paratypes in BMNH (no number)*, SMF 192901*, ZMA K23050*, same data as holotype.

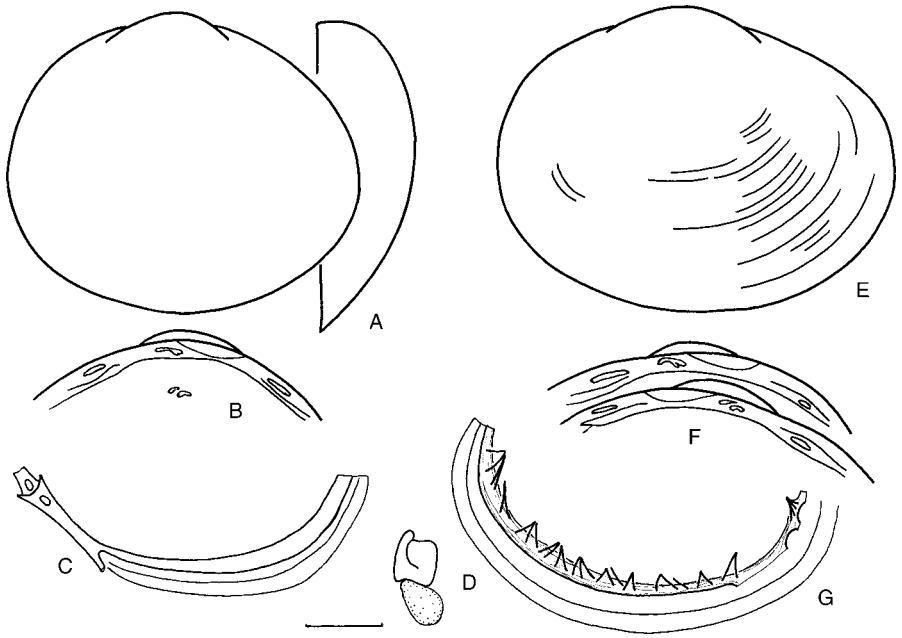

Figure 35. *Pisidium floresianum* Rensch, shell and anatomy: A,B—paratype, Flores Island (SMF), A—right valve, B—hinge of the right valve and cardinal teeth from the left one, C—mantle edge, D—nephridium (dorsally); E–G—Papua New Guinea (AM, no number), E—shell, F—hinge, G—dried mantle edge. Scale bar = 1 mm.

Other material examined. NEW SOUTH WALES: Four Mile Ck tributary, Ponderosa Forest Park, Nundle State Forest, 31°28'S 151°15'E, coll. WFP, 23 February 1988 (AM C315744w); swamp on Boggy Swamp Ck tributary, beside Pheasant Ck Rd, 2.5 km east of Thunderbolts Trail, Barrington Tops, 31°53'S 151°32'E, coll. WFP, 28 March 1985 (AM C314821w); Burraga Swamp, Barrington Tops NP, coll. WFP, 11 January 1982 (AM C135201w); Warranwang, west of Lithgow, Blue Mountains, 33°28'S 149°59'E, on grass, moss, etc., coll. WFP & AK, 18 August 1996 (AMw); the area of Kanangra-Boyd NP, coll. 1992 (AM C307115, AM C307128, AM C307130, AM C307133); Jinny Brothers Ck, 25 km south of Cooma, 36°27'S 149°07'E, coll. 4 November 1990 (AMw). VICTORIA: Mt Donna Buang Rd, 1.4 km from Warburton, 37°44'S 145°42'E, coll. WFP, JW & GC, 21 January 1987 (AMw). TASMANIA: tributary of Brid River near Springfield, 41°13'S 147°29'E., coll. WFP & R. Kershaw, 16 March 1975 (AMw); Ben Lomond Rivulet, 41°55'S 147°29'E, alt. 180 m, coll. WFP, JW & GC, 2 February 1987 (AMw); Franklin River, 42°31'S 145°45'E, coll. JW, 23 March 1988 (AMw).

Diagnosis. Shell elongate oval, moderately convex. Surface smooth. Pores rare. Hinge plate relatively narrow. Cardinal teeth arched or bent. Presiphonal mantle suture elongated. Inner radial mantle muscles form five to seven strong bundles. Outer demibranch small, strongly shifted posteriorly.

Shell. small (largest specimen: L 4.5, H 3.5, W/2 1.2 mm), oval, elongate, moderately convex, thin and fragile, subtransparent, periostracum usually of white or yellowish colour. Mean value of height index (H/L) for population not exceeding 0.78 (Table 3). All margins rounded, merging to each other without angles. The most extended point of front margin at level of horizontal median plane. Umbones broad, not protruding, considerably shifted posteriorly. Sculpture formed only by irregular growth lines. Pores relatively rare: mean density 239±43 per mm^2 (n = 5). Scars of muscle bundles separated from mantle line.

Hinge plate of younger specimens relatively narrow, in large shells somewhat broadened in area of ligament. Ligament pit long and narrow. C2 bent at middle point, in large specimens strongly curved (arched). C4 straight or slightly bent, placed obliquely behind c2. C3 strongly curved, thickened and cleft on posterior end with 2 branches adjoining each other. Lateral teeth rather short, parallel to margin of hinge plate; p2 terminating abruptly, with almost vertical hind edge, p1 and p3 narrow, almost of equal length.

Anatomy (Fig. 38). Mantle as in *P. etheridgei*. Presiphonal suture elongate, usually little more than 1/5 length of pedal slit. Pedal slit with six to seven long, strong muscle bundles; merging or splitting of latter also possible.

Outer demibranch strongly reduced and shifted posteriorly; usually beginning at 12th to 15th filament of inner demibranch (mean value for pooled data 13.3±2.3, n = 45).

Brood pouch formed by four to seven filaments, with four to seven embryos inside.

Nephridia of same shape as in *P. etheridgei*.

Variability. The species is less variable than *P. etheridgei*. Specimens from Tasmania have more protruded umbones then those from the mainland and are similar in this character to *P. tasmanicum* (see Figs. 75 and 85). The pattern of variability in the mantle muscle arrangement is not clear: most of the Tasmanian specimens are distinguished by the strong concentration of mantle muscles (five or six very

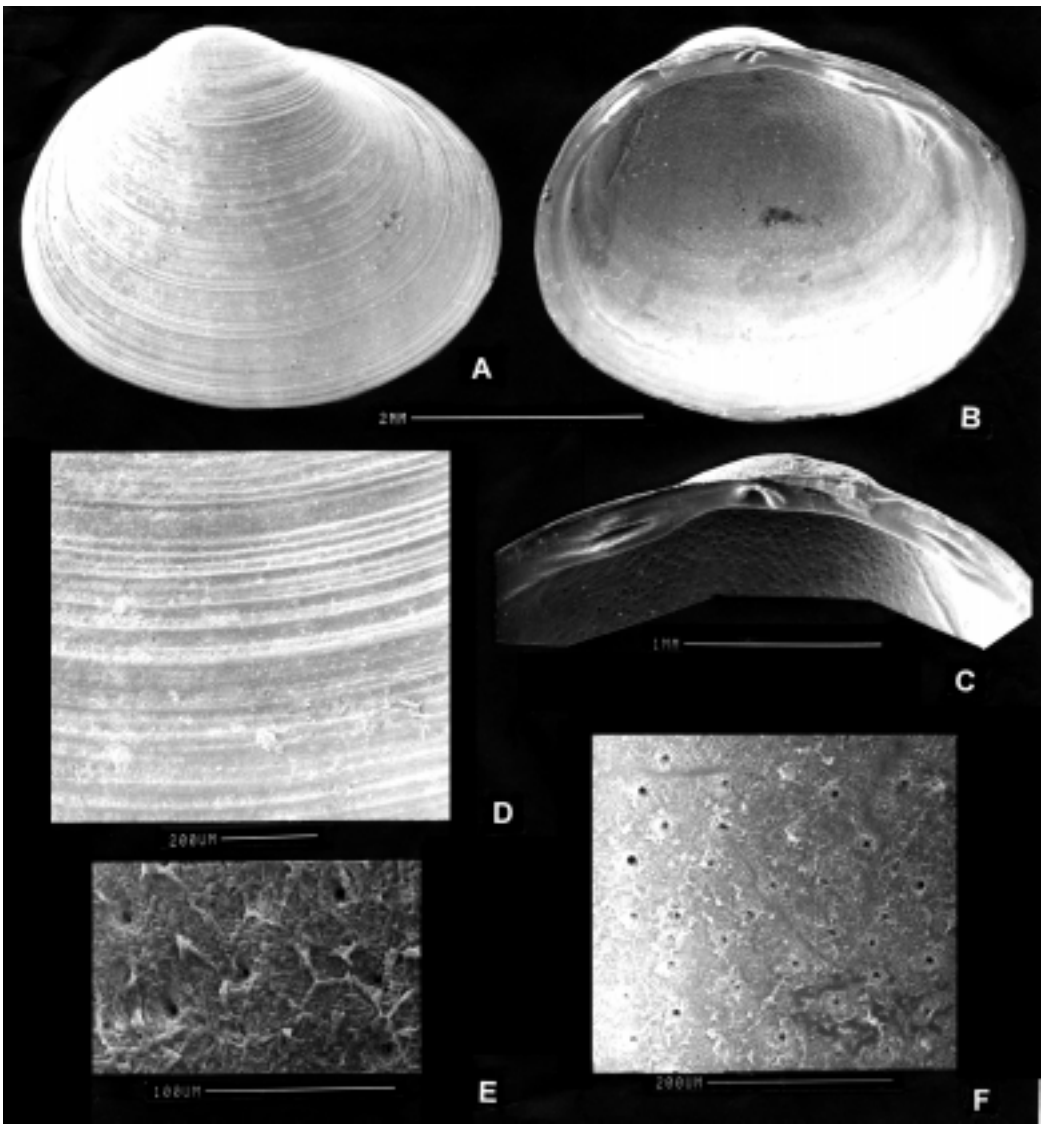

Figure 36. *Pisidium hallae* (Kuiper), Blue Mountains, NSW (AM, no number), shell: A—right valve from outside, B—left valve from inside, C—sculpture, D—hinge of the right valve, E,F—internal pores under different magnifications.

strong bundles), in New South Wales such specimens occur alongside those having many muscle bundles (up to ten) but are otherwise identical.

Generally, individual and interpopulational variability of the outer demibranch position is limited, but in some populations the outer demibranch is very strongly reduced, looking like a narrow stripe and beginning at 17th to 22nd filament of the inner demibranch. Specimens with the greatly reduced outer demibranch were found in the Snowy Mountains near the locality where a form of *P. etheridgei* with reduced outer demibranch was also found.

Distribution (Fig. 57B). This species is found along the Great Dividing Range in New South Wales and Victoria and in several localities in Tasmania.

Ecology. Swamps, springs and creeks.

Remarks. *Pisidium hallae* is most similar in shell and anatomical characters to *P. etheridgei*. It can be recognised mainly by its elongate shell (Kuiper, 1983). However, the height index (H/L) slightly overlaps *P. etheridgei*, and only large series can be identified reliably. The two species are well separated geographically, but contact zones in northern NSW, Snowy Mountains, Victoria and Tasmania are apparent. However, the two species were found together only in one locality (Alpine Ck). *Pisidium etheridgei* and *P. hallae* are clearly closely related species and a further investigation is needed to confirm reproductive isolation between them and explain the mechanism of this isolation.

Presence of *P. hallae* in Franklin River needs to be confirmed (available specimens are similar to *P. tasmanicum* and may represent a peculiar form of the latter species).

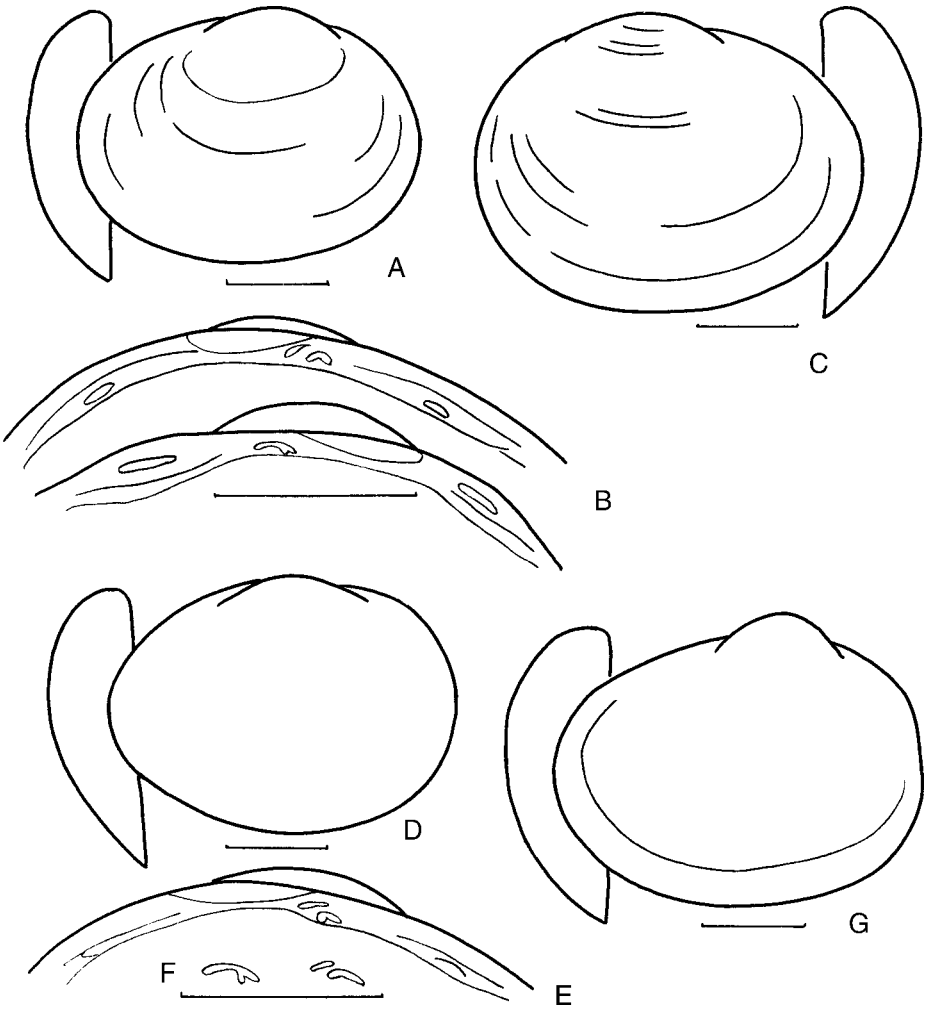

Figure 37. *Pisidium hallae*, shells: A,B—Nundle State Forest, NSW (AM C315744), left valve and hinge; C—Barrington Tops, NSW (AM C314821), right valve; D,F—Warburton, Vic. (AM, no number), left valve and hinge of the left valve, cardinal teeth of right and left valves; G—Ben Lomond Rivulet, Tas. (AM, no number), left valve. Scale bars = 1 mm.

Pisidium (Euglesa) kosciusko (Iredale, 1943a)

Figs. 39, 40

Glacipisum kosciusko Iredale, 1943a: 197.
Pisidium kosciusko.–Kuiper, 1983 (full synonymy).

Type material: HOLOTYPE AM C100523d, Blue Lake, Mt Kosciusko, NSW. PARATYPES AM C20790, AM C21790, about 40 specimens, same data as holotype.

Other material examined: NEW SOUTH WALES: Lake Albina at south end, depth 2 m, Mt Kosciusko NP, coll. B.V. Timms, 8 February 1977 (AM C315739w).

Diagnosis. Shell circular or short oval, moderately convex. Surface irregularly striated. Pores rare. Hinge plate very narrow. Cardinal teeth straight or slightly bent. Presiphonal mantle suture slightly elongated. Inner radial mantle muscles form five to seven strong bundles. Outer demibranch small, strongly shifted posteriorly.

Shell: Small (largest specimen 4.3 mm long), circular or short oval, flat or moderately convex, thin, subtransparent. Upper margin arched, angles at its extremities not clear, other margins evenly curved. Umbones low and broad, not protruding. Sculpture faint, represented by irregular striae; larger specimens with pronounced lines of growth breaks. Internal pores relatively rare, mean density 258±114 per mm^2 (n = 6).

Hinge plate narrow. Ligament pit elongate. C2 and c4 almost straight, parallel to each other; c2 shorter than c4; c3 slightly bent at middle point, cleft on posterior end. Lateral teeth narrow, outer laterals in right valve somewhat shorter than inner.

Anatomy. Mantle edge moderately broad. Presiphonal suture slightly elongate (about 1/5 length of pedal slit). Inner

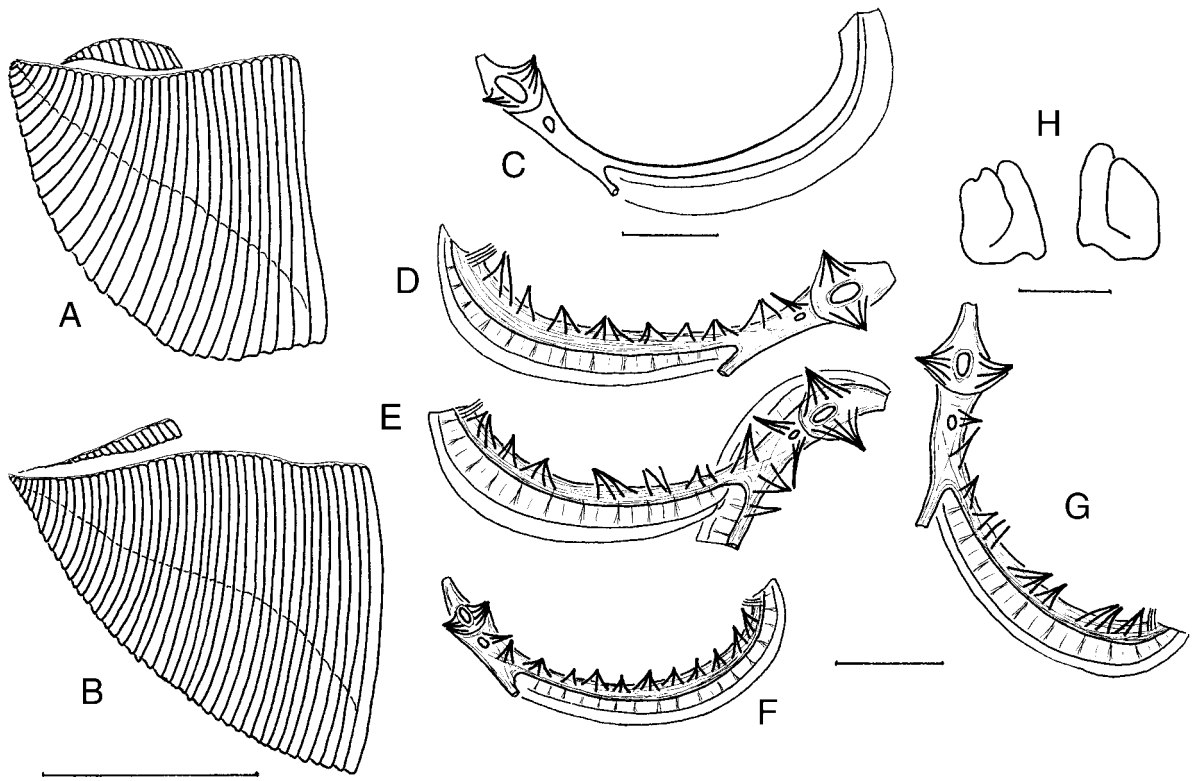

Figure 38. *Pisidium hallae*, anatomy: A,B—gills, A—Warburton, Vic. (AM, no number), B—Jinny Brothers Ck, NSW (AM, no number), a specimen with strongly reduced outer demibranch; C–G—mantle edge, C,D—Barrington Tops, NSW (AM C314821), E—Blue Mountains, NSW (AM, no number), F—Jinny Brothers Ck, NSW, G—Ben Lomond Rivulet, Tas. (AM, no number); H—nephridia dorsally, Barrington Tops, NSW. Scale bars = 1 mm.

radial mantle muscles weaker than in *P. etheridgei*, forming seven bundles along pedal slit.

Outer demibranch strongly reduced and placed against 12th or 13th filament of inner demibranch (mean value 12.8±0.5, n = 4). Brood pouches not found.

Nephridium of closed type, with rectangular dorsal lobe.

Distribution. Known from the area of Mt Kosciusko, Snowy Mountains, New South Wales.

Ecology. Abundant in two alpine lakes; Kuiper (1983) mentioned also several lots from creeks and pools.

Remarks. This species is the most similar to *P. etheridgei*. It differs from the latter having a very thin hinge plate, parallel cardinal teeth and the outer lateral teeth being shorter than the inner ones.

However, the mentioned characters considerably vary within the studied populations. This species occupies a very specialised habitat, where it replaces *P. etheridgei*. The probability of speciation in these small alpine lakes is rather low, while no other endemic species of molluscs are known from them. Therefore *P. kosciusko* may prove to be only a peculiar form of *P. etheridgei*.

Pisidium (Euglesa) tasmanicum Tenison Woods, 1876

Figs. 41–44

Pisidium tasmanicum Tenison Woods, 1876: 82; Kuiper, 1983: 26 (part: full synonymy, only Tasmanian localities).

Type material: POSSIBLE SYNTYPES TMH E112 (Kuiper, 1983), 43 valves, ?Browns River, Tas.

Other material examined: VICTORIA: east branch of Barwon River, on Seven Bridges Rd, 38°29'S 143°44'E, alt. 140 m, coll. FWA, 16 April 1988 (AM C317041w); Deep Ck east of Foster, South Gippsland, coll. GC, 11 January 1992 (AMw); Frasers Ck, Wilsons Promontory, 39°04'S 146°20'E, coll. JW & GC, 11 December 1988 (AMw); tributary of Morwell River, 38°31'S 146°20'E, coll. WFP & GC, 10 February 1987 (AMw). TASMANIA: North Esk River on Blessington Rd 1.2 km west of Musselboro Rd, east of Launceston, 41°30'S 147°25'E, alt. 315 m, coll. WFP, JH & WP, 18 January 1982 (AM C135155w); Geales Ck on a side track off NW side of Bass Hwy, 40°53'S 145°02'E, coll. WFP, WP & JH, 22 January 1982 (AM C135169w); Wandle River at Murchison Hwy, rock and gravel substrate, coll. WFP, WP & JH, 23 January 1982 (AM 135192w); Ben Lomond Rivulet, 41°55'S 147°29'E, alt. 180 m, coll. WFP, JW & GC, 2 February 1987,

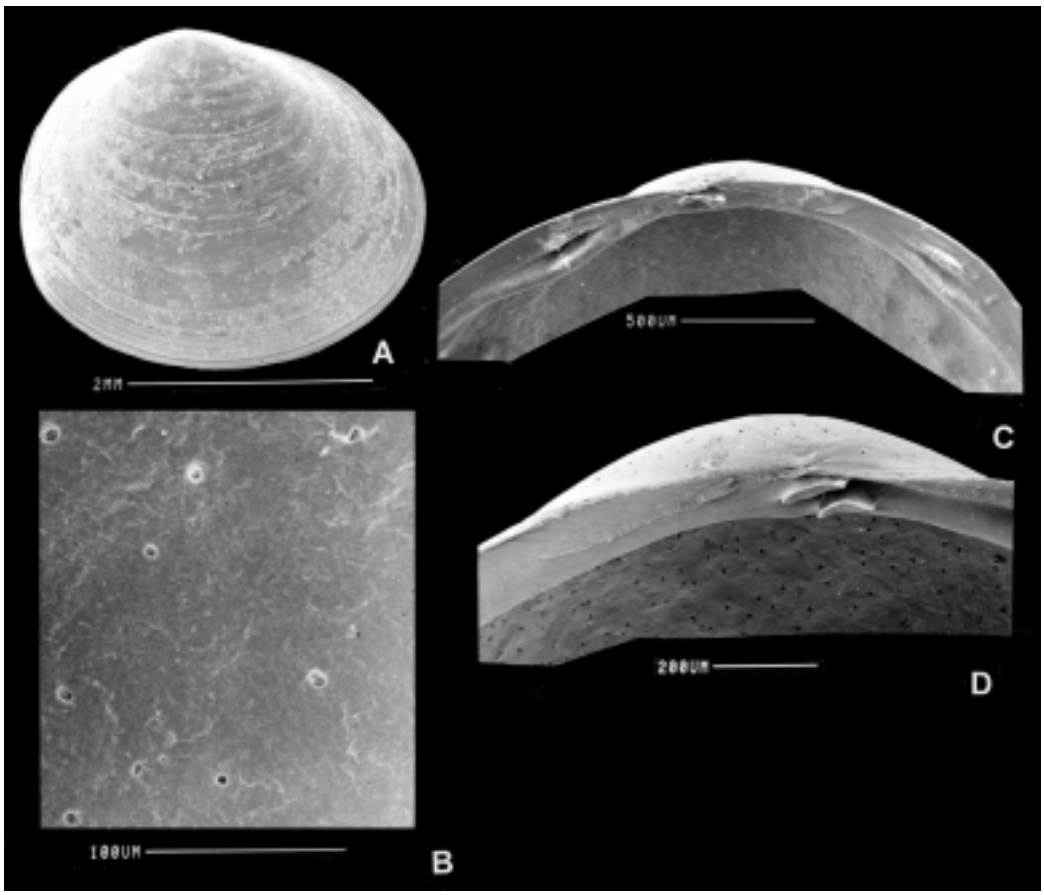

Figure 39. *Pisidium kosciusko* (Iredale), Lake Albino, Mt Kosciusko, NSW (AM C315739), shell: A—right valve from outside, B—pores, C—hinge of the right valve, D—cardinal teeth of the left valve.

with *P. hallae* (AMw); Nora River, tributary of Bird River, 25 km off Queenstown, 42°18'S 145°36'E, coll. S. Clark & A. Miller, 9 February 1995 (AMw); Lake Dulverton, R. Tate coln., undated, identified as *P. dulvertonensis* (SAM D19060d).

Diagnosis. Shell rounded or subtriangular, markedly convex. Surface irregularly striated. Pores of moderate density. Hinge plate narrow. Cardinal teeth slightly bent. Presiphonal mantle suture short or slightly elongated. Inner radial mantle muscles form four to six strong bundles. Outer demibranch small, strongly shifted posteriorly.

Shell: Small (largest specimen: L 3.6, H 3.1, W/2 1.2 mm), rounded or subtriangular, convex, thin and fragile, subtransparent, periostracum white, reddish or brownish. Upper margin short, usually marked by angles at its extremities. Hind margin obtuse, anterior one straight and oblique, with most extended point below horizontal median plane. Umbones moderately broad, protruding, definitely shifted backwards. Sculpture: clear, irregular striations and folds; coarser striae around umbones. In some populations sculpture reduced and shell almost smooth. Internal pores of moderate density: 310±84 per mm^2 (n = 8). Anterior muscle scars separated from mantle line.

Hinge plate short and narrow, arched. Ligament pit short. c2 slightly bent at middle point; c4 straight or slightly bent, almost parallel to margin of hinge plate; c3 thin, bent, cleft on its hind end. Lateral teeth short, outer ones in right valve shorter then inner.

Anatomy (Fig. 44). Mantle edge moderately broad. Presiphonal suture short or slightly elongate, 1/6 to 1/7 length of pedal slit, but in some specimens more elongate (1/5 length of the pedal slit). Mantle musculature strong, inner radial muscle bundles long but reduced in number. Four to six bundles visible at each side of pedal slit, strongest bundle second from anterior.

Anterior edge of outer demibranch placed at 10th to 16th, most frequently at 11th or 12th filament of inner demibranch. Mean value of this character 11.9±1.7 (n = 20). Brood pouch formed by four or five filaments. The number of larvae per pouch usually three to five, sometimes one or two.

Nephridia of same type, as in *P. casertanum* and *P. hallae*.

Variability. The lots from southern Victoria are distinguished by their small size (shell length not more than 3.2 mm), narrower umbones, thinner hinge plate, coarse striation (Fig. 41). Shells from northern Tasmania are also small, but with broader umbones and less pronounced sculpture (Fig. 42).

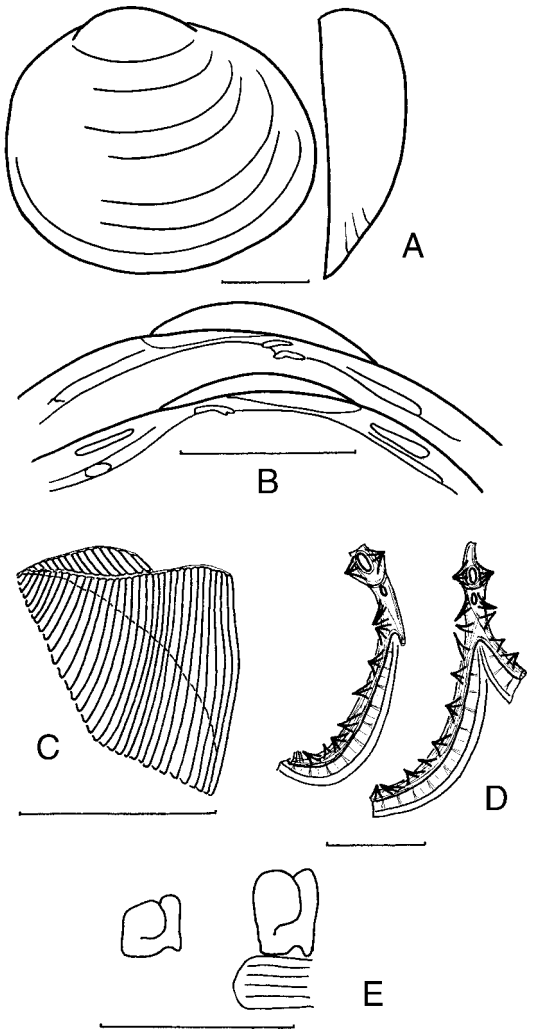

Figure 40. *Pisidium kosciusko*, shell and anatomy: A,B—holotype, Blue Lake, Mt Kosciusko, NSW (AM C100523), right valve and hinge; C–E—Lake Albino, Mt Kosciusko, NSW (AM C315739), C—gill, D—mantle edge, E—nephridia dorsally. Scale bars = 1 mm.

Southern Tasmanian lots (including the probable type lot) are relatively large (3.4–3.6 mm long), less convex, with broader umbones, more similar to *P. etheridgei* from this area (Fig. 43C,D,G). Some lots have intermediate characters (Fig. 43A,B,E,F).

Distribution. Southern Victoria and Tasmania (Fig. 57C).

Ecology. Creeks, occasionally in lakes (in Tasmania).

Remarks. The northern form of *P. tasmanicum* is readily distinguished from *P. etheridgei* by its smaller size, narrow and protruding umbones, narrow hinge plate, and cardinal teeth being thin and only weakly bent. However, some variation of all these characters takes place and reliable identification is only possible with a series of specimens. The situation in Tasmania, especially in its southern part, is more complicated. The local form of *P. tasmanicum* is larger and can be confused with *P. etheridgei* and *P. hallae*. In general, *P. tasmanicum* and *P. etheridgei* widely overlap in all shell indices and the differences in pooled data are not statistically significant. Anatomical distinction is also not reliable: concentrated mantle musculature, a characteristic feature of *P. tasmanicum*, does occur in *P. etheridgei*.

The differences between *P. tasmanicum* and *P. etheridgei* are much more pronounced when sympatric populations are compared. In all these cases it was possible to discriminate two species by shell size, convexity and length of the mantle suture. Unfortunately, there were insufficient specimens in the lots from sympatric populations for statistical treatment (usually only one species was abundant). When found together with *P. hallae*, *P. tasmanicum* can be distinguished by its circular, not elongate, shell (Figs. 37G, 43A,B). Thus, while consistently reliable characters separating *P. tasmanicum* and *P. etheridgei* are still lacking, in some sympatric localities the two species are readily separated. However, identification of some other local populations is rather difficult, and further investigation is required to resolve the relationships of these two taxa.

In the structure of the mantle musculature, *P. tasmanicum* is similar to the widely distributed Eurasian species *P. personatum* Malm, 1855 and *P. obtusale* (Lamarck, 1818). Some shell characters of these species are also similar (notably the rounded and swollen shell and thin hinge plate with straight cardinal teeth). However, the outer demibranch in *P. tasmanicum* is much more reduced than in *P. personatum* and *P. obtusale*.

Specimens from New South Wales identified by Kuiper (1983) as *P. tasmanicum* have another type of sculpture (regular ribs), which indicates their affinity to *P. carum*. These specimens are described below as the new species *Pisidium ponderi*.

Pisidium (Euglesa) fultoni Kuiper, 1983

Figs. 45, 46

Pisidium fultoni Kuiper, 1983: 34, fig. 74–77.

Type material: HOLOTYPE TMH E14436, East Lake (north), part of Arthurs Lake, Tas. PARATYPES TMH E14437*, AM C135460, NMV F31818*, BMNH*, SMF 192865, 20 specimens altogether, same data as holotype.

Other material examined: TASMANIA: Great Lake, Taffin coln., 2 June 1902, det. J. Kuiper as *S. lacusedes* (TMH E5194d); Lake Malbena, 41°57'S 146°16'E, coll. JW, 3 February 1988, with *P. etheridgei* (AMw); Lake Butters, 41°48'S 146°26'E, coll. JW, 5 February 1988, with *P. etheridgei* (AMw); Lake Olive, 41°56'S 146°20'E, coll. JW, 5 February 1988 (AMw); Lake Nugetena, near Lake Olive, 41°56'S 146°19'E, coll. JW, 2 February 1988 (AMw).

Diagnosis. Shell tetragonal or pentagonal, flat. Surface irregularly striated. Pores of moderate density. Hinge plate narrow. Cardinal teeth bent. Presiphonal mantle suture short or slightly elongated. Inner radial mantle muscles form five to six strong bundles. Outer demibranch small, strongly shifted posteriorly.

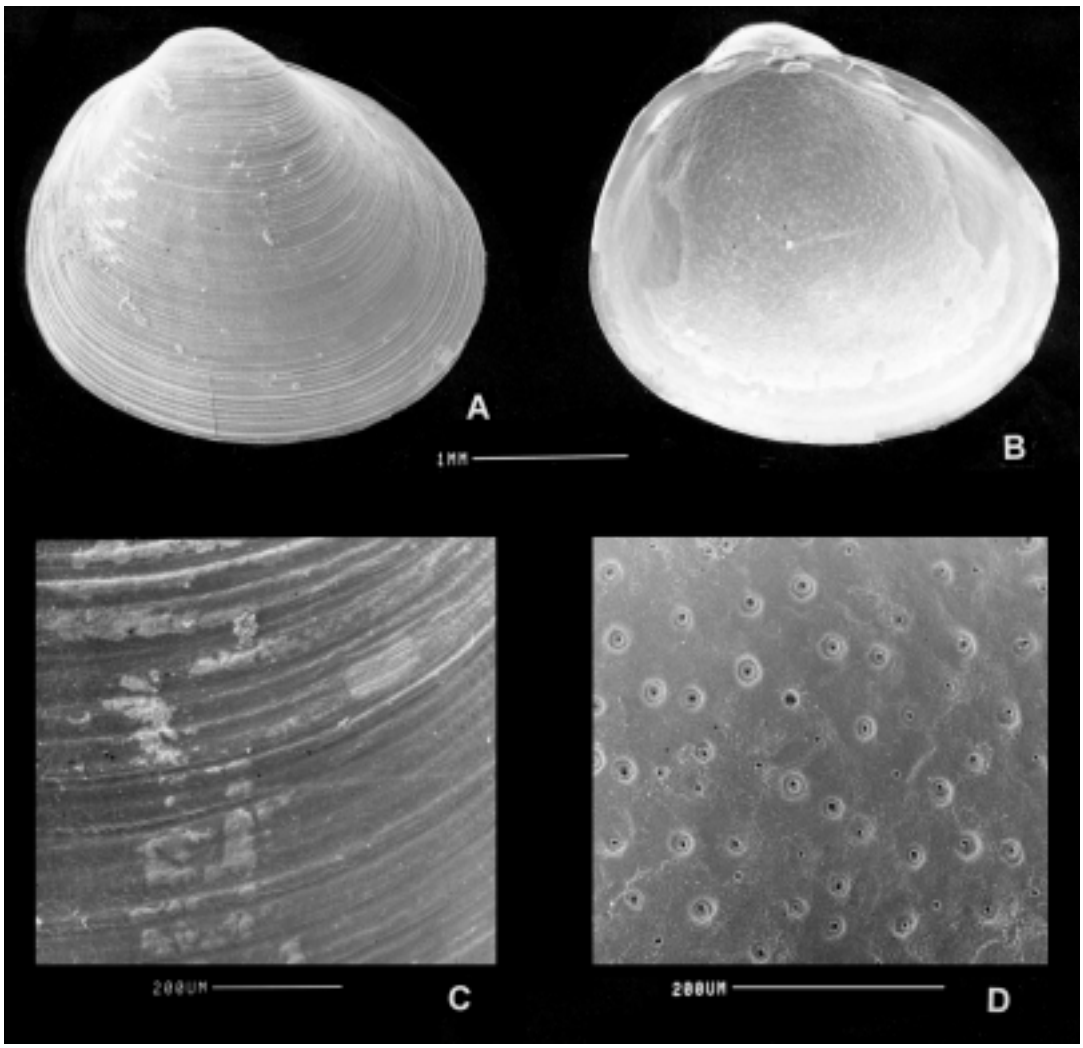

Figure 41. *Pisidium tasmanicum* (Tenison Woods), tributary of Morwell River, Vic. (AM, no number), shell: A—right valve from outside, B—left valve from inside, C—sculpture, D—internal pores.

Shell: rather small (largest specimen: L 4.6, H 4.0, W/2 1.2 mm), angulate (tetragonal or pentagonal), usually of somewhat irregular shape, thin, with characteristic yellow periostracum, flat. Upper edge straight, with clear angles at extremities, especially posteriorly. Hind edge straight, often oblique, sometimes with depressed outline. Front edge also straight, with most extending point below horizontal median plane. Hind edge often bent forward, almost parallel to front one. Umbones moderately shifted posteriorly, narrow in young specimens and relatively broad in large shells. Sculpture: weak irregular striations and growth lines. Internal pores rather numerous: mean density 457±210 per mm^2.

Hinge plate narrow. Cardinal teeth thin, c4 and c3 evidently bent, c3 cleft posteriorly. Lateral teeth thin, outer teeth in right valve shorter than inner, sometimes reduced.

Anatomy. Mantle edge broad. Presiphonal suture variable (from 1/7 to 1/4 length of pedal slit). Inner radial mantle muscles long and strong, more concentrated than in *P. etheridgei*, usually five to six bundles distinguishable.

Outer demibranch anterior edge placed at 10th to 13th filament of inner demibranch (mean value 10.8±1.0, n = 4). Gravid specimens with one or two free larvae in each demibranch, brood pouches not seen.

Nephridium of closed type, with rectangular dorsal lobe.

Variability. Variability of the shell outline in this species is remarkable, even amongst individuals inhabiting one lake. Quite often the shell outline is distorted, with angles or depressions, which may be caused by irregularities of growth or deformation (Fig. 46E,F). Variability in mantle and gill characters is also notable.

Distribution. Found only in central Tasmania (Fig. 57B).

Ecology. Found only in lakes, abundant in littoral samples, presence in deeper benthos not clear.

Remarks. As shown here, *P. fultoni* may have a much larger size than previously realised (Kuiper, 1983). The larger specimens are conspecific judging from young shells from

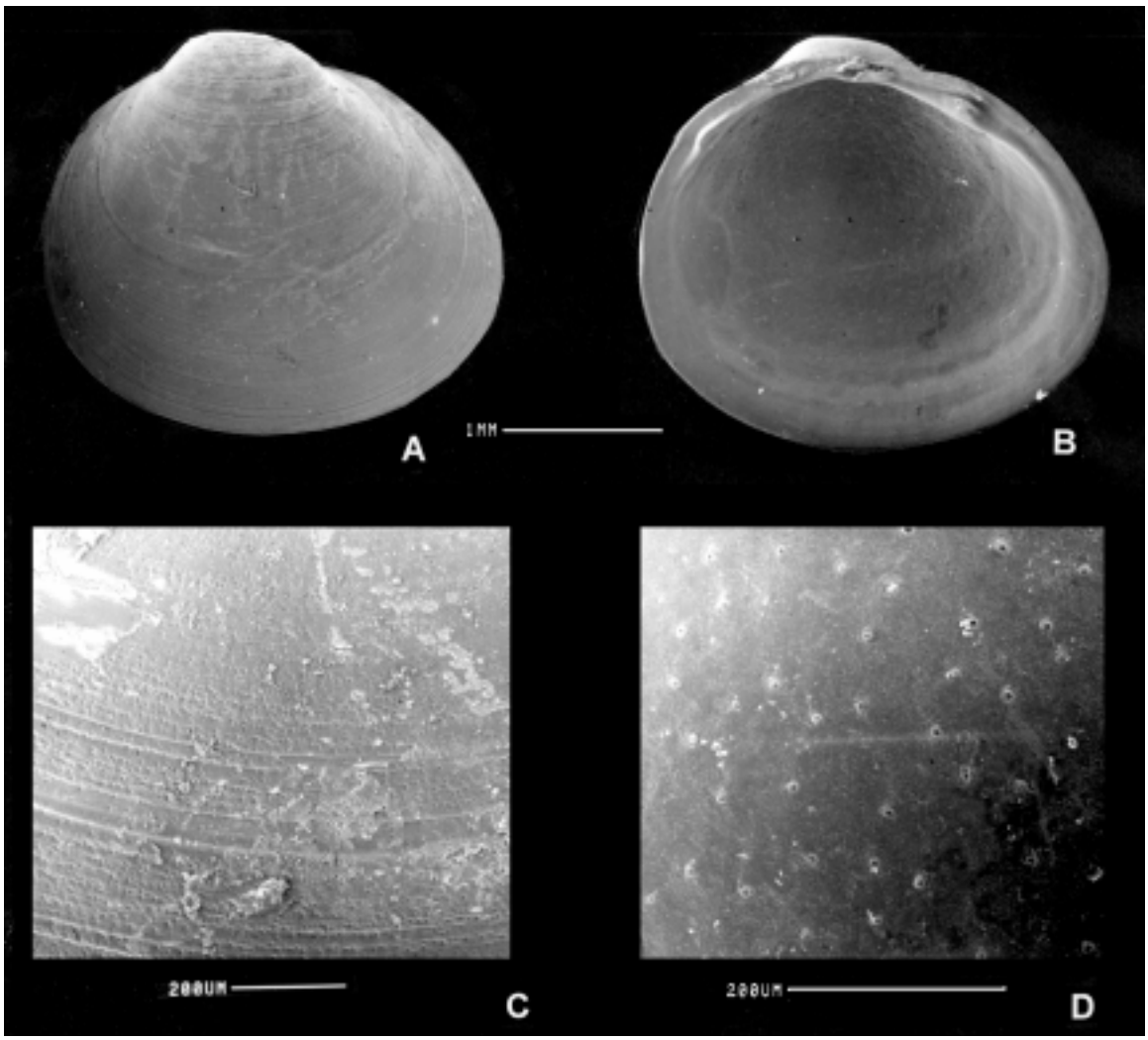

Figure 42. *Pisidium tasmanicum*, Wandle River, Tas. (AM C135192), shell: A—right valve from outside, B—left valve from inside, C—sculpture, D—internal pores.

the same localities that well agree with the original description.

This species can be distinguished from *Pisidium etheridgei* which inhabits the same lakes in the very characteristic yellow colour of the periostracum (notably another endemic species of Tasmanian lakes, *Musculium lacusedes*, has the same colour), and very flat shell with angulate, sometimes irregular (deformed) outline (see Figs. 31D,E, 45C,D). Differences in pores density, position of the outer demibranch, length of the presiphonal suture and number of muscle bundles can also separate the two species (for pores density of *P. etheridgei* and *P. fultoni* in Lake Butters $t = 3.85$, $p<0.01$.). However, *P. etheridgei* and *P. fultoni* are similar and occasional intermediate specimens combining the characters of the two species (i.e. yellow periostracum with elongate shell) have been found.

Thus, in large series, *P. fultoni* can be discriminated from *P. etheridgei* unequivocally, but identification of single specimens can be problematic.

In gill and mantle characters *P. fultoni* shows some similarity to *P. carum*. However, the peculiar sculpture of the latter has never been found in *P. fultoni*.

Pisidium (Euglesa) carum (Cotton, 1953)

Figs. 47–49

Australpera cara Cotton, 1953: 21, pl. 2, fig. 2; Cotton, 1961: 189, fig. 188.

Pisidium carum.–Kuiper, 1983: 28, figs. 55–57 (except Tasmanian localities).

Type material: LECTOTYPE SAM D14454, right valve, Brown Hill Ck, western slopes of Lofty Ranges, SA, Cotton coln. PARALECTOTYPE SAM D14454, 1 specimen, same data as holotype.

Other material examined: QUEENSLAND: 0.5 km SE of Crediton, tributary of Broken River, pool with weeds in fast flowing stream, coll. WFP, P. Colman & J.B. Burch, 29 April 1975 (AMd); tributary of Lace Ck, SW of Caboolture, 27°12'S 152°45'E, coll. WFP, WP & OG, 30 August 1982 (AM C135526w); peat bogs, Carnarvon Gorge NP, 24°50'S 147°11'E, coll. WFP & P. Colman, 29 September 1984 (AM C184152w). NEW SOUTH WALES: Molong Ck, SE of Molong, coll. WFP & AK, 15 September 1996 (AMw). VICTORIA: Loddon River at Newstead, 37°07'S 144°03'E, alt. 220

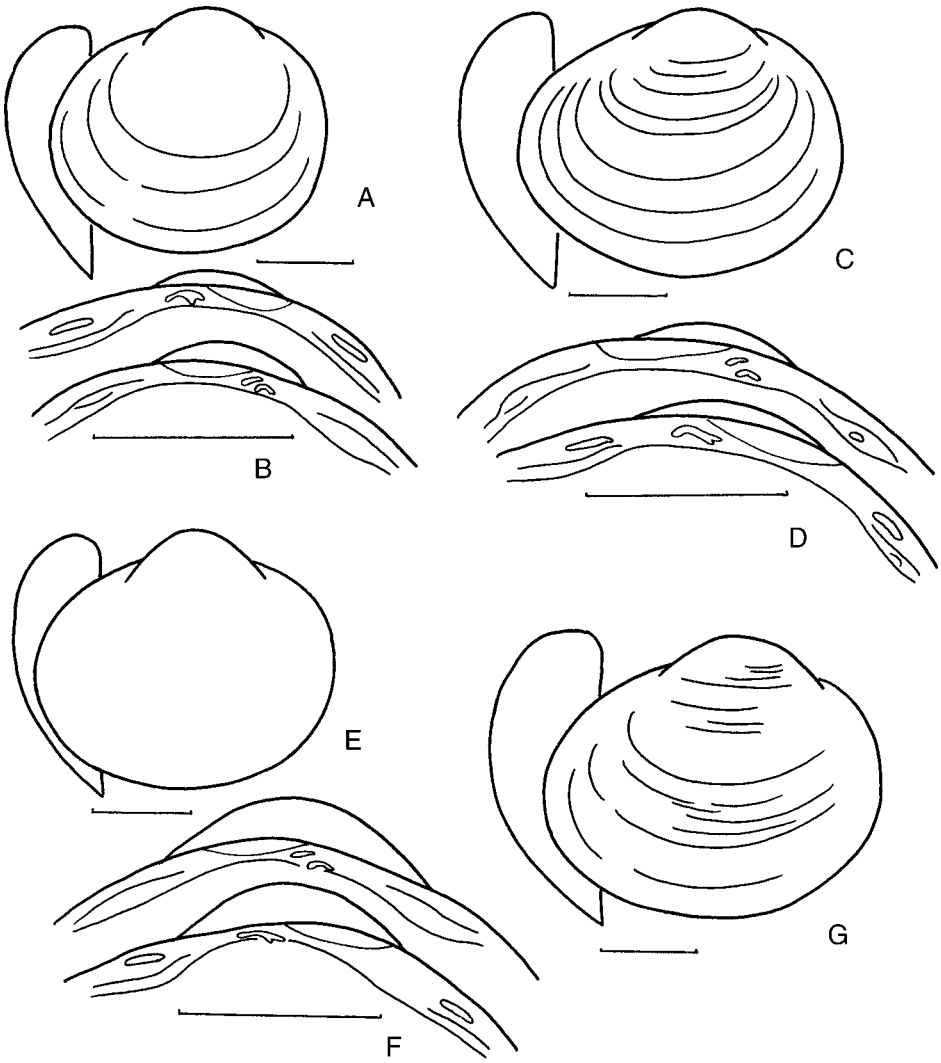

Figure 43. *Pisidium tasmanicum*, variation of shell form: A,B—Ben Lomond Rivulet, Tas. (AM, no number), left valve and hinge of the left valve; C,D—probable type lot, unlocated (TMH E112), left valve and hinge; E,F—Lake Dulverton, Tas. (SAM D19060), left valve and hinge; G—Nora River, Tas. (AM, no number), left valve. Scale bars = 1 mm.

m, coll. WFP & R. Hershler, 2 February 1984 (AM C315746w). SOUTH AUSTRALIA: Spring, Ororoo, 32°43'S 138°36'E, coll. WFP, WP & Jenkins, 7 May 1981 (AMw).

Diagnosis. Shell tetragonal or pentagonal, flat. Surface with fine regular ribs, more pronounced around umbo. Pores very dense. Hinge plate broad. Cardinal teeth strongly curved. Presiphonal mantle suture short. Inner radial mantle muscles form five to seven weak bundles. Outer demibranch relatively large, slightly shifted posteriorly.

Shell rather large (largest specimen: L 4.2, H 3.5, W/2 1.1 mm), tetragonal (trapezoid) or pentagonal, flat, thick and strong, not transparent, periostracum white or yellowish. Upper edge straight, with clear angles at extremities. Front and hind edges also straight, most extended points below horizontal median plane. Umbones relatively narrow, flat, not protruding, almost medially placed. Sculpture: clear regularly spaced ribs, more pronounced around umbones, delicate on periphery. Embryonic shell smooth. Pores abundant, their density very high (mean value 1015±462 pores per mm^2, n = 8, maximum value 1630 per mm^2).

Hinge plate broad, ligament pit short. C2 bent in smaller specimens and strongly curved in large shells, c4 hooked, placed behind c2, c3 curved, hind arm in large specimens definitely longer than front one, deeply cleft on posterior end and forming two diverging branches. Lateral teeth strong, swollen, outer lateral teeth (a3 and p3) much shorter than inner lateral teeth (a1 and p1), diverging from latter.

Anatomy (Fig. 49M–U). Mantle edge narrow. Presiphonal suture not elongate (usually 1/8 to 1/6 length of pedal slit). Inner radial muscles long, but weaker than in species observed above, forming five to seven bundles: three to four larger ones in anterior section of pedal slit and two or three smaller ones posteriorly, near presiphonal suture.

Outer demibranch relatively large, with anterior edge placed at 8th to 10th filament of inner one; mean value 9.5±0.70 (n = 10). Brood pouch formed by 5 to 8 filaments, including up to 6 embryos.

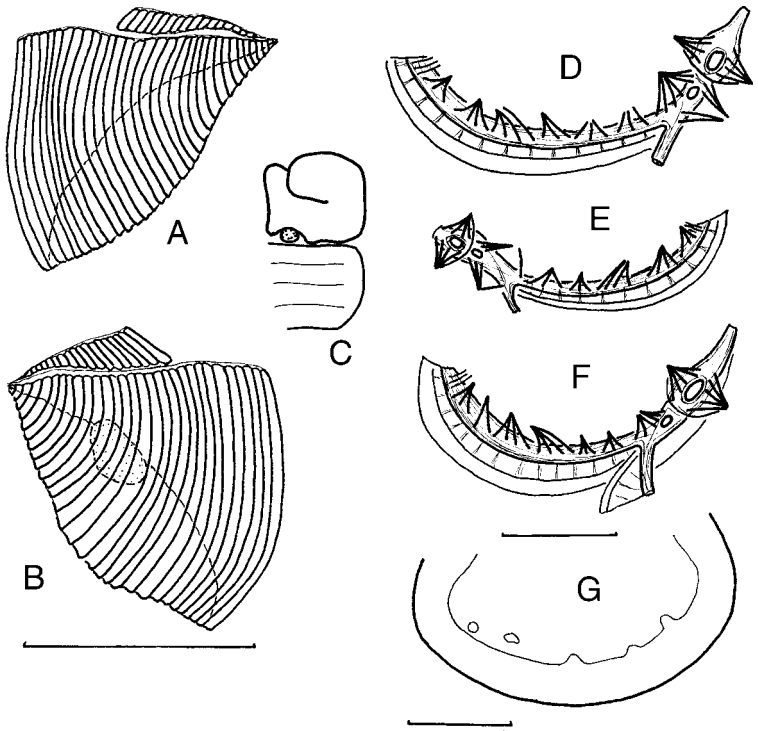

Figure 44. *Pisidium tasmanicum*, anatomy: A,B—Barwon River, Vic. (AM C317041), gills from outside; C—Wandle River, Tas. (AM C135192), nephridium dorsally; D,E—tributary of Morwell River, Vic. (AM, no number), mantle edge; F—Ben Lomond Rivulet, Tas. (AM, no number), mantle edge; G—Wandle River, Tas., mantle muscle scars. Scale bars = 1 mm.

Nephridium of closed type, with rectangular dorsal lobe.

Variability. This species is less variable than the other species in the genus. However, shells from the west slope of the Great Dividing Range in NSW have a broader hinge plate and denser pores (1420 pores per mm^2) (Fig. 48). In contrast, in Queensland specimens mean pore density was 606 per mm^2. Young specimens with relatively narrow hinge and somewhat elongate presiphonal suture, similar to *Pisidium centrale* n.sp. described below, were found in western Queensland (Carnarvon Gorge NP) (Fig. 49E,F).

Distribution (Fig. 57A). Queensland (including the northern part), western slope of the Great Dividing Range in NSW and Victoria, sporadically in South Australia; everywhere rather scarce.

Ecology. Inhabits larger streams or rivers, with a preference for sand and other hard sediments.

Remarks. Well distinguished from the other species by the shape of the shell, its solidness, peculiar sculpture and broad hinge plate. It differs from species of the *P. etheridgei* group, in having pore density, distinctive mantle characters and the position of the outer demibranch (Fig. 34). Despite some overlap in the shell morphology, differences in the quantified characters, when compared to the related taxa, are statistically significant ($p<0.05$).

Pisidium (Euglesa) ponderi n.sp.

Figs. 50–53

Pisidium tasmanicum.–Kuiper, 1983: 27 (part), figs. 59, 60.

Type material. HOLOTYPE C315642d, one valve gold coated for SEM, Norfolk Falls, Warung State Forest, 31°44'S 150°00'E, coll. IL & JW, 6 November 1985. PARATYPES C350019d&w, 3 valves gold coated for SEM & 13 complete specimens, same data as holotype.

Other material examined. NEW SOUTH WALES: Tia River above Tia Falls, Apsley Gorge NP, 31°10'S 151°51'E, coll. IL & JW, 10 November 1985 (AM C317038w); creek on SW side of Jamieson Park, Narrabeen Lagoon, Sydney, 33°43'S 151°16'E, coll. P. Colman & AK, August 1996 (IZK); Bindi Brook, NE of Braidwood, 35°07'S 150°05'E, coll. WFP& WP, 12 January 1981, det. J. Kuiper as *P. tasmanicum* (AM C126348w); Currambene Ck on Snowball Rd, 35°54'S 149°36'E, coll. WFP, 1981, det. by J. Kuiper as *P. tasmanicum* (AM 126716d); Bobundara Ck at road crossing, 29 km south of Cooma on Myalla Rd, 36°30'S 149°07'E, alt. 900 m, coll. GC, 4 November 1990, with *Pisidium etheridgei* (AM C315743w).

Diagnosis. Shell short oval or subtrigonal, convex. Surface with fine regular ribs, more pronounced around umbo. Pores very dense. Hinge plate relatively narrow. Cardinal teeth slightly bent. Presiphonal mantle suture short. Inner radial mantle muscles form five to seven weak bundles. Outer demibranch relatively large, slightly shifted posteriorly.

Table 5. Measurements (mm) of *Pisidium ponderi* n.sp.

	L	H	HH	LL	LH	LA	W/2
holotype	2.77	2.31	0.10	0.46	1.53	1.62	0.89
paratype	3.53	3.00	0.12	0.72	1.93	2.60	1.02
paratype	3.22	2.78	0.15	0.77	1.78	2.42	0.99
paratype	3.21	2.65	0.13	0.69	1.78	2.33	1.05
paratype	2.99	2.50	0.11	0.61	1.60	1.83	0.88
paratype	2.80	2.30	0.12	0.61	1.59	1.56	0.78
paratype	3.11	2.57	0.12	0.72	1.72	1.72	1.12
paratype	2.71	2.27	0.11	0.54	1.55	1.48	0.80
paratype	2.23	1.87	0.10	0.42	1.25	1.29	0.73
paratype	2.33	1.88	0.14	0.51	1.32	1.36	0.75

Shell small (Table 5, largest specimen 3.5 mm long), circular, short oval or subtrigonal, convex (some specimens inflated, almost spherical), rather solid, white or yellowish. Upper margin straight, usually with rounded angles at extremities. Back margin rounded or somewhat truncated. Front margin straight in upper section, then strongly curved, with most extended point below horizontal median plane. Umbones rather broad, protruding, almost median. Sculpture: thin regularly spaced ribs, higher and coarser around umbones. Prodissoconch smooth. Pores dense, on average 575±118 pores per mm^2 (n = 12).

Hinge plate narrow. Ligament pit rather long and narrow. Cardinal teeth: c2 bent or arched, c4 straight, placed above and behind c2, c3 curved or bent, posterior arm longer than anterior one and deeply cleft into two diverging branches. Lateral teeth rather thick and strong, but not swollen.

Anatomy. Mantle edge narrow. Presiphonal suture not elongate (usually about 1/7, in small animals 1/6–1/5 length of pedal slit). Mantle musculature of same pattern as in *P. carum*: inner radial mantle muscles long, moderately developed, forming five to seven bundles, four anterior bundles largest (Fig. 53C,D).

Anterior edge of outer demibranch placed at 8th to 10th filament of inner one (mean value 9.5±0.66, n = 12) (Fig. 53A,B). Brood pouch formed by five to six filaments, with four to six embryos.

Nephridia of closed type, dorsal lobe rectangular (Fig. 53E).

Variability. Shell size and convexity are apparently associated: smaller specimens being more convex, the smallest ones having a globose shell.

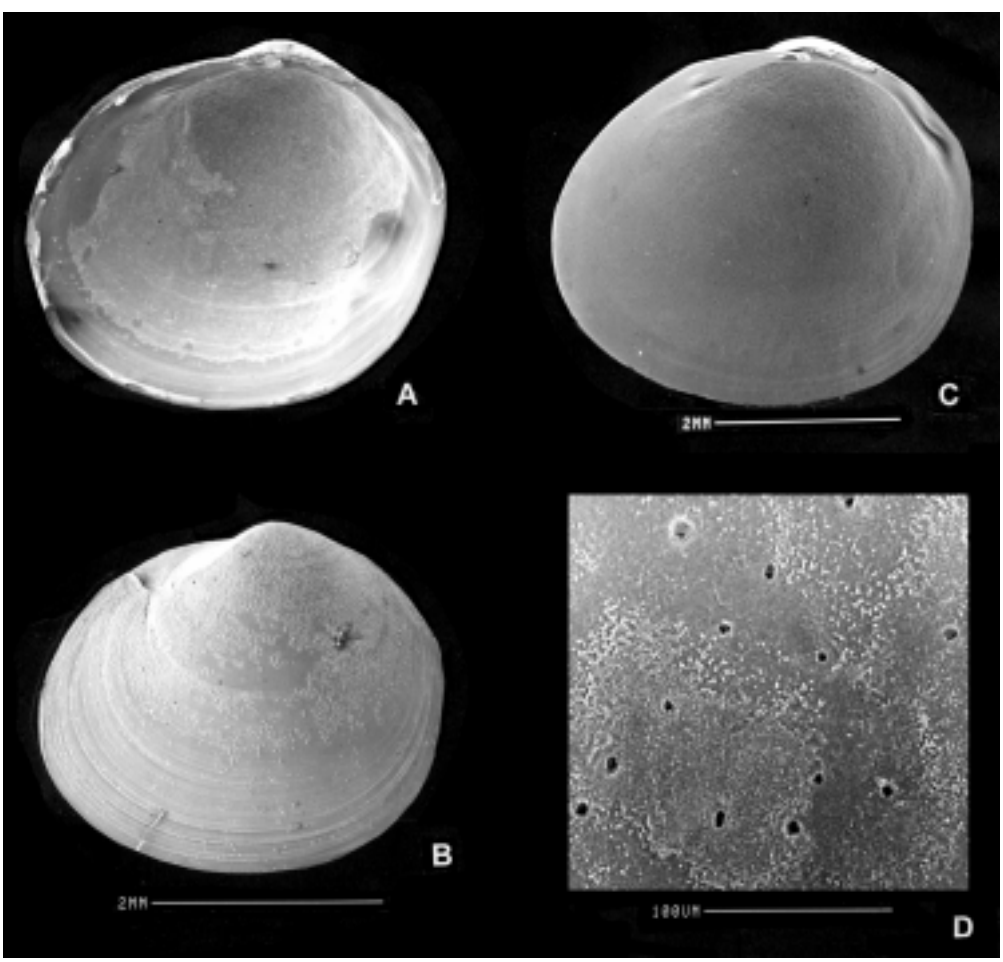

Figure 45. *Pisidium fultoni* Kuiper, shells: A,B—Lake Butters, Tas. (AM, no number), right valve from inside, left valve from outside; C,D—Lake Malbena, Tas. (AM, no number), C—right valve from inside, D—internal pores.

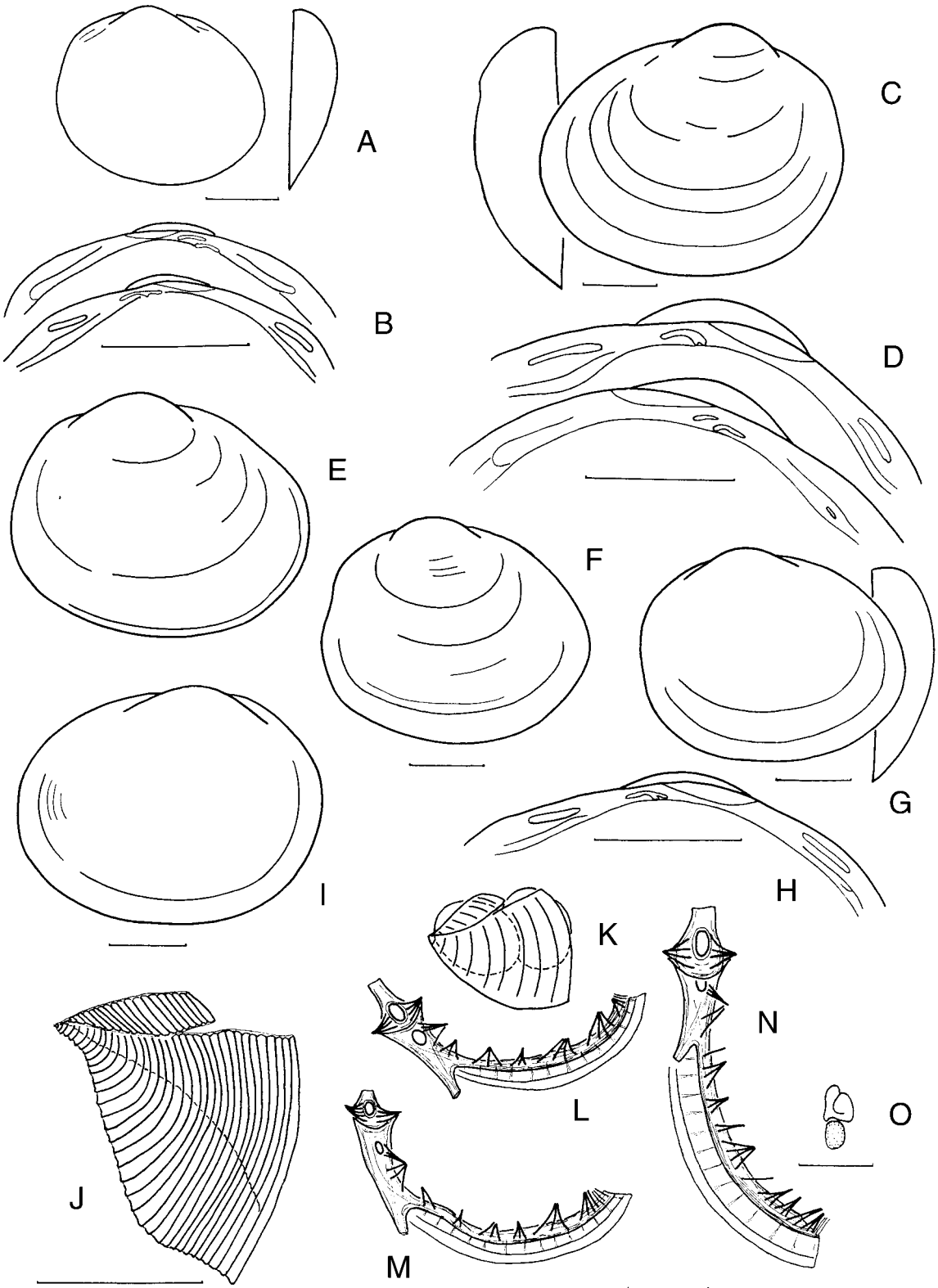

Figure 46. *Pisidium fultoni*, shells and anatomy: A,B—one of the paratypes (SMF 192865), right valve and hinge; C,D—Great Lake, Tas. (TMH E5194), large specimen, left valve and hinge; E,F—Lake Malbena, Tas. (AM, no number), variations of the shell form; G,H—Lake Olive, Tas. (AM, no number), right valve and hinge of the right valve; I—Lake Nugetena, Tas. (AM, no number), left valve; J—Lake Butters, Tas., gill from outside; K—gill with large larvae from the same locality; L,M—Lake Butters, Tas., mantle edge; N,O—Lake Malbena, Tas., N—mantle edge, O—nephrium dorsally. Scale bars = 1 mm.

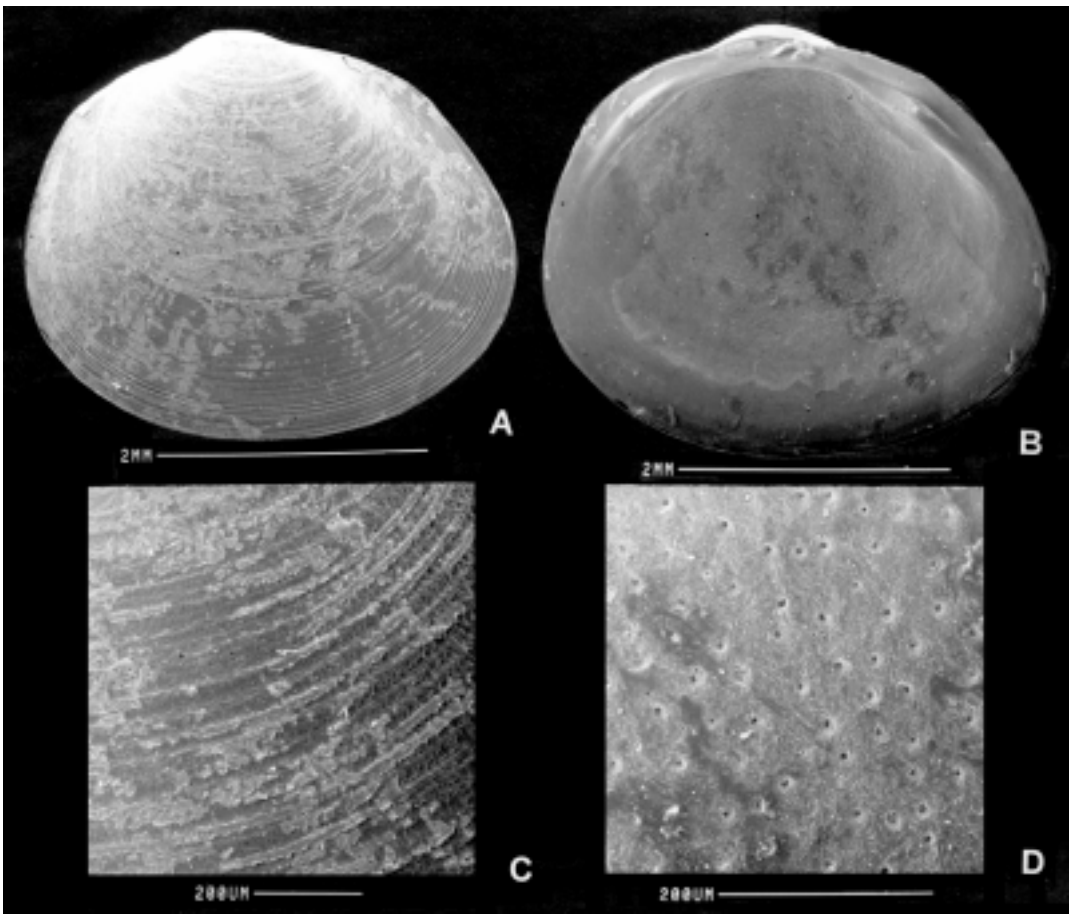

Figure 47. *Pisidium carum* (Cotton), near Caboolture, Qld (AM C135526), shell: A—right valve from outside, B—left valve from inside, C—sculpture, D—internal pores.

Distribution. The most southern part of Queensland, eastern New South Wales along the Great Dividing Range and at least one locality on the nearby coast (Fig. 57A).

Ecology. Small creeks and swamps; often associated with *P. etheridgei* or *P. hallae*.

Etymology. Named after Winston F. Ponder, Australian Museum, Sydney.

Remarks. Specimens of this species were identified by Kuiper (1983) as *Pisidium tasmanicum*. Indeed, shell outlines of these two species are rather similar. However, investigation by SEM shows that their sculpture is quite different. In the new species it is almost identical to that of *P. carum*. This affinity is also supported by the pore density, mantle musculature and the position of the outer demibranch. *Pisidium ponderi* may be distinguished from *P. carum*, by reference to its rounded, convex shell and narrower hinge plate.

Association of *P. ponderi* with *P. etheridgei* or *P. hallae* is one of the typical associations of *Pisidium* species in Australia. The most constant and reliable diagnostic character to distinguish these species is sculpture (see Figs. 55 and 115). Some other characters distinguishing *P. ponderi*, such as the rounded shell, dense porosity, short presiphonal suture and relatively large outer demibranch are also useful, but considerable individual variation should be taken into account.

Pisidium (Euglesa) centrale n.sp.

Figs. 54, 55

Type material. HOLOTYPE AM C138753d, gold coated for SEM, swamp in Stokes Ck Canyon, George Gill Range, NT, 24°22'S 131°45'E, 26 May 1983. PARATYPES AM C350021d&w, 2 valves and 16 complete specimens, same data as holotype.

Other material examined. NORTHERN TERRITORY: Reedy Ck on George Gill Range, coll. W. Horn, undated, det. by J. Kuiper as *Pisidium* sp. (AM C2148).

Diagnosis. Shell broad oval, flat. Surface with fine regular ribs, more pronounced around umbo. Pores of moderate density. Hinge plate relatively narrow. Cardinal teeth bent or arched. Presiphonal mantle suture slightly elongate. Inner radial mantle muscles form up to eight weak bundles. Outer demibranch relatively large, slightly shifted posteriorly.

Shell rather large (Table 6, maximum 4.4 mm long), broad oval, very flat, thin and fragile, subtransparent, with horn-

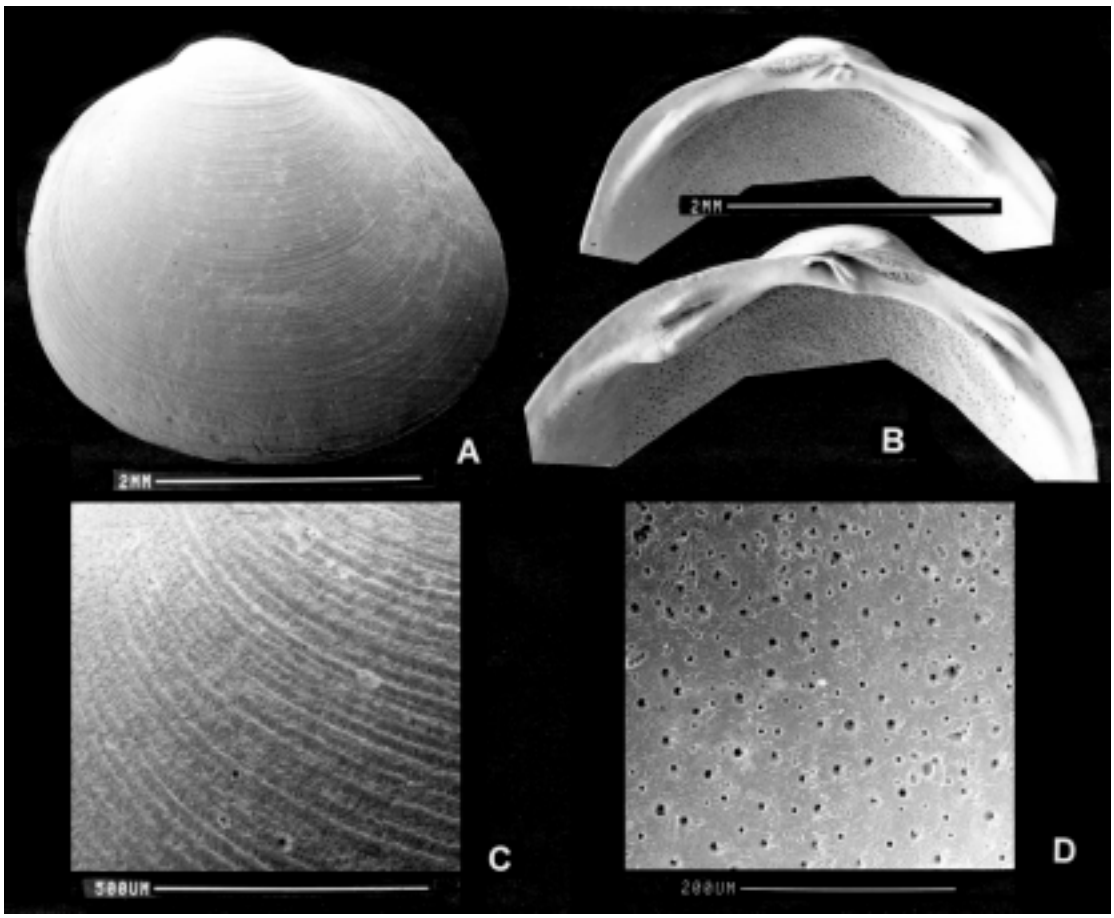

Figure 48. *Pisidium carum*, Molong Ck, NSW (AM, no number), shell: A—right valve from outside, B—left valve from inside, C—sculpture, D—internal pores.

coloured periostracum (old shells white). Upper margin long and straight, angles at its extremities rounded. Other margins evenly curved; ventral margin strongly curved. Most extended points of front and back margins are approximately at level of horizontal median plane. Umbones narrow, flat, not protruded, placed medially or slightly shifted posteriorly. Sculpture: regularly spaced concentric ribs of the same type as in *P. carum* and *P. ponderi*, several definitely higher ribs are noticeable around the umbo. Moderately porous, mean density 356±24 pores per mm^2.

Table 6. Measurements (mm) of *Pisidium centrale* n.sp.

	L	H	HH	LL	LH	LA	W/2
holotype	4.24	3.44	0.16	0.80	2.45	2.15	1.01
paratype	4.38	3.61	0.28	0.83	2.44	2.27	1.05
paratype	3.95	3.25	0.15	0.78	2.22	2.10	0.96
paratype	3.76	3.06	0.20	0.84	2.27	1.91	0.89
paratype	2.98	2.40	0.16	0.57	1.69	1.57	0.72
paratype	3.25	2.62	0.13	0.54	1.85	1.72	0.74
paratype	3.00	2.49	0.08	0.61	1.77	1.53	0.64
paratype	3.33	2.64	0.17	0.62	1.93	1.67	0.65

Hinge plate relatively narrow. Ligament pit rather long and narrow. Cardinal teeth: c2 bent or arched, c4 straight or slightly arched, c3 bent at its middle point forming an obtuse angle, its posterior arm deeply cleft, with widely diverging branches. Lateral teeth long, straight, narrow but with swollen cusps. Outer lateral teeth of right valve smaller (shorter and thinner) than inner ones.

Anatomy (Fig. 55C–E). Mantle edge narrow. Presiphonal suture slightly elongate (1/5 length of pedal slit). Inner radial muscle bundles long, anterior bundles (four to five) rather strong, posterior bundles (two to four) weakened, total number of bundles seven to eight.

Outer demibranch beginning at 10th or 11th filaments of inner one. Brood pouches of up to eight filaments and up to seven embryos.

Nephridium of closed type, with rectangular dorsal lobe.

Distribution and ecology. Known only from two creeks in the George Gill Range, Northern Territory, central Australia (Fig. 57A).

Etymology. The name refers to the central Australian distribution.

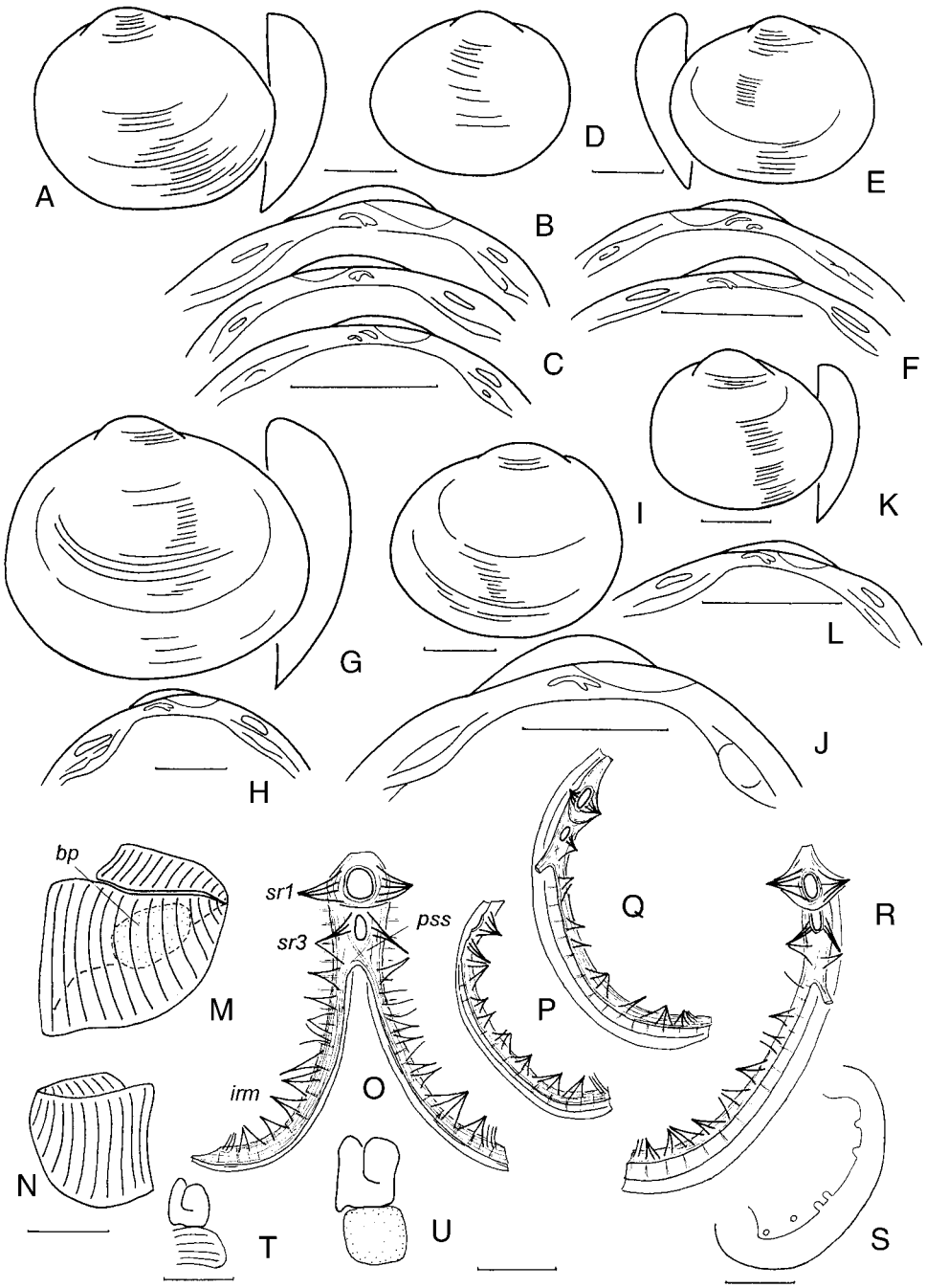

Figure 49. *Pisidium carum*, shells and anatomy: A–D—near Crediton, northern Qld (AM, no number), A—right valve, B—hinge of this valve, C—hinge with inverted cardinal and anterior lateral teeth, D—another specimen, left valve; E,F—Carnarvon Gorge NP, young specimen (AM C184152), left valve and hinge; G,H—Loddon River, Vic. (AM C315746), right valve and hinge of this valve; I,J—lectotype, Western slopes of Lofty Ranges, SA (SAM D14454), left valve and hinge of the right valve; K,L—Ororoo, SA, young specimen (AM, no number), right valve and hinge of the right valve; M,N—gills from outside, M—Loddon River, Vic., N—Caboolture, Qld (AM C135526); O–R—mantle edge, O,P—Molong Ck, NSW (AM, no number), Q,R—Loddon River, Vic.; S—muscle scars of a specimen from Caboolture, Qld; T,U—the same lot, nephridia dorsally. Scale bars = 1 mm.

Remarks. The new species is evidently related to *P. carum*, sharing with the latter a peculiar type of sculpture and pattern of mantle musculature. It is distinguished by the very flat shell (low value of convexity index notable), ovate shell outline, and the long and almost straight hinge. Differences in pore density and outer demibranch position should be confirmed on more material. In the elongate presiphonal suture of mantle the new species is similar to *P. etheridgei*.

Key to Australian sphaeriid species

Young shells of *Musculium (Sphaerinova)* species have more posteriorly placed umbones than adults and are sometimes very similar to *Pisidium* species. To distinguish the genera, study of gills and siphons is recommended. Anatomical characters also help to distinguish P. carum and *P. ponderi* from *P. etheridgei* and *P. hallae*.

1 Umbones median or slightly posterior. Adult shell more than 6.5 mm long. Both siphons with tubular extensions. Outer demibranch overlaps inner one ..... *Musculium* 2

—— Umbones placed posteriorly. Adult shell smaller (up to 5.5 mm long). Only upper siphon tubular. Outer demibranch does not overlap inner one; sometimes absent ..... *Pisidium* 8

2 Umbones very narrow, strongly protruding, prodissoconch separated by sulcus, forms a cap. Siphonal retractors strong, with their scars separated from those of adductor muscles ..... *M.* cf. *lacustre*

—— Umbones broad, prodissoconch not separated or marked by a growth break line, never forms a cap. Siphonal retractors weak, with their scars merged with those of adductor muscles 3

3 Right valve with one pair of lateral teeth (outer lateral teeth reduced) ..... *M. lacusedes*

—— Right valve with 2 pairs of lateral teeth (outer lateral teeth normally developed) 4

4 Shell rather thick and strong, not transparent (except young specimens), hinge plate relatively broad, cardinal teeth placed within hinge plate 5

—— Shell very thin and fragile, transparent. Hinge plate very narrow, cardinal teeth protrude beyond hinge plate 7

5 Shell elongate-oval, convex, umbones protruding ..... *M. quirindi*

—— Shell circular or short oval, compressed, umbones not protruding 6

6 Upper margin slightly arched, with rounded angles at extremities. Hinge plate long (cusps of lateral teeth nearer to front and back margins of shell than to umbo) ..... *M. kendricki*

—— Upper margin evenly curved, without angles. Hinge plate short, cusps of lateral teeth nearer to umbo ..... *M. tatiarae*

7 Umbones nearly median ..... *M. tasmanicum tasmanicum*

—— Umbones considerably posterior ..... *M. tasmanicum queenslandicum*

8 Ligament of enclosed type. Outer demibranch and branchial opening present ..... subgenus *Euglesa* 9

—— Ligament of other type. Outer demibranch and branchial opening absent 16

9 Shell with distinct sculpture of regularly spaced concentric ribs 10

—— Shell surface smooth or irregularly striated 12

10 Shell solid. Upper margin of shell with angles; hinge plate broad ..... *P. carum*

—— Shell fragile. Upper margin without angles. Hinge plate not broadened 11

11 Shell flat (convexity index less than 0,60), oval ..... *P. centrale*

—— Shell convex (convexity index 0.60 or more), circular ..... *P. ponderi*

12 Upper margin oblique, with definite angles, especially the posterior one. Periostracum yellow ..... *P. fultoni*

—— Upper margin parallel to the ventral one, angles rounded or not distinguished. Periostracum white, gray or brownish 13

13 Shell elongate (height/length index less than 0.78) ..... *P. hallae*

—— Shell shorter (height/length index more than 0.81) 14

14 Shell small (up to 3.5 mm), convex, umbones relatively narrow and protruding. Presiphonal suture only slightly elongate ..... *P. tasmanicum*

—— Shell larger, umbones broad, not protruding. Presiphonal suture considerably elongate 15

15 Hinge plate very narrow, cardinal teeth straight ..... *P. kosciusko*

—— Hinge plate moderately broad, cardinal teeth strongly bent or arched ..... *P. etheridgei*

16 Ligament exterior. Shell elongate, moderately convex. Sculpture—fine dense striation ..... subgenus *Afropisidium, P. aslini*

—— Ligament introverted. Shell circular, flat. Sculpture—delicate widely spaced ribs ..... subgenus *Odhneripisidium, P. australiense*

Affinities of Australian sphaeriids

A set of anatomical characters described here provides a basis for testing different phylogenetic hypotheses. However, each of the currently recognised large generic and subgeneric groups of sphaeriids represented in Australia includes non-Australian taxa or has related taxa outside Australia. Because sphaeriids from tropical regions, particularly from Southeast Asia, are poorly studied, a comprehensive phylogenetic analysis of Australian taxa is not possible. However, some preliminary suggestions on the affinities of the Australian sphaeriids are provided. The polarity of characters can be defined on the basis of phylogenetic investigations published by Dreher-Mansur & Meier-Brook (1992) and Korniushin (1998a).

A phylogenetic tree for the genera of Sphaeriidae was constructed by Dreher-Mansur & Meier-Brook (1992). According to this paper, *Musculium* and *Pisidium* are sister taxa; in turn, these two genera together form a sister taxon of *Sphaerium*. As shown above, Australian species of the genus *Musculium* included in the subgenus *Sphaerinova* (except one poorly known species identified here as *M.* cf. *lacustre*) are characterised by the considerable reduction of siphons and siphonal muscles, particularly the upper retractors of the inhalant siphon, and by the externally visible ligament. The state of the first character differs from that in the nominate subgenus of *Musculium*, and in the genus *Sphaerium*, being closer to the situation seen in the genus *Pisidium*. Thus, its apomorphic status is suggested. This suggestion is concordant with the view that reduction of siphons and some other organs is one of the principal trends in the evolution of sphaeriids (Dreher-Mansur & Meier-Brook, 1992). Phylogenetic status of the externally visible ligament is not clear, but nevertheless close relationship of the Australian species of *Musculium* seems to be well supported.

Reduction of siphonal retractors similar to that in *Musculium tasmanicum* was observed in several South American species, especially in *Musculium forbesi* (Philippi, 1869) (Korniushin, 1998b). In the African *Musculium incomitatum* (Kuiper, 1966) it is even more marked and combined with diminution of the outer demibranch and a peculiarity of the nephridium (a larger excretory sac) (Korniushin, 1995, 1998b). Some other species similar in shell characters to *Sphaerinova* are known from New Zealand (Kuiper, 1966) and India (Subba Rao, 1989), but their anatomy is unknown. Until revision of the entire genus *Musculium* is completed, it is not clear whether these similarities indicate common ancestry or convergence.

Alimov & Starobogatov (1968) assumed close relationship between *Sphaerium macgillivrayi, S. transversum* from North

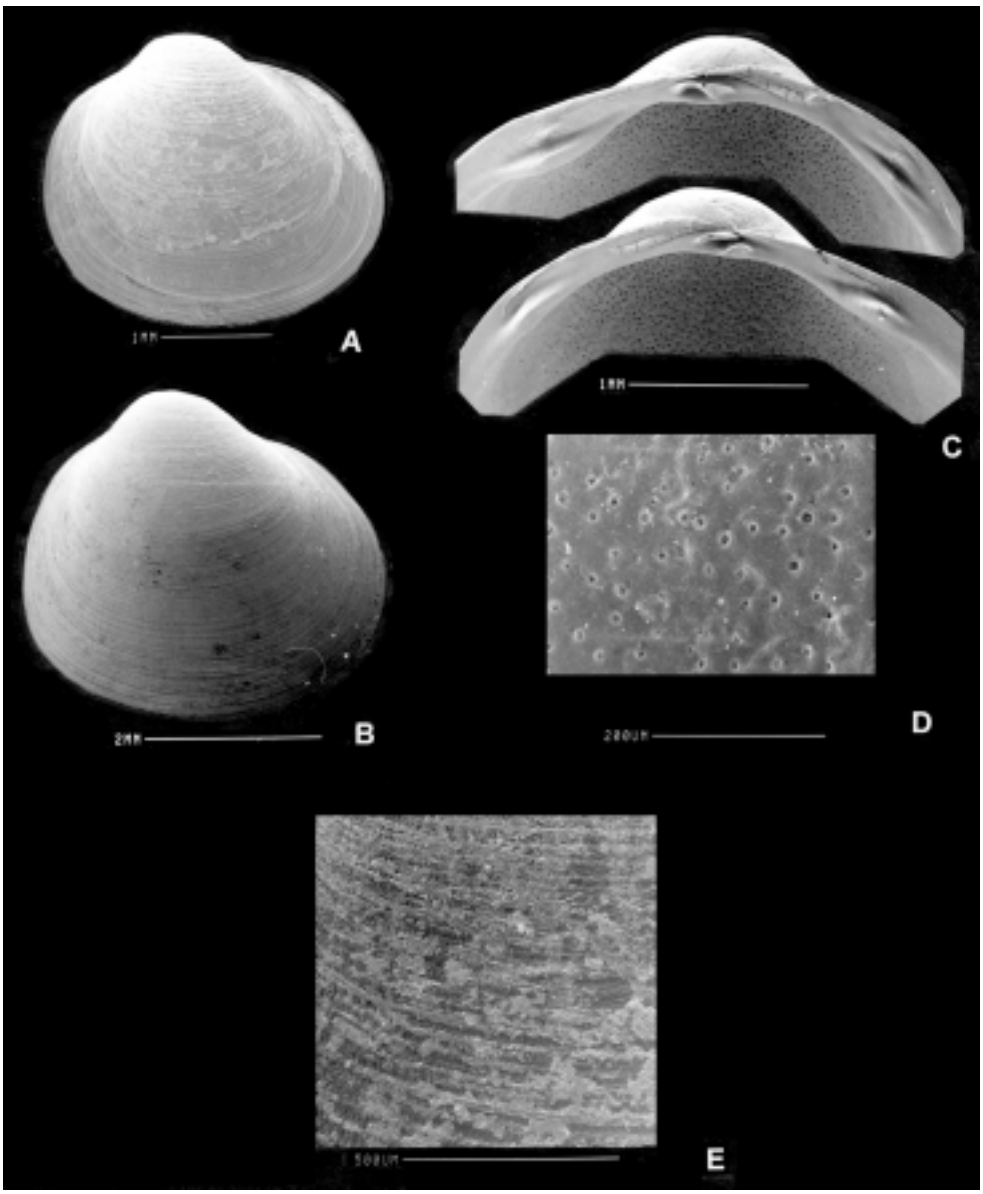

Figure 50. *Pisidium ponderi* n.sp., shells of the type specimens: A—right valve of the holotype (AM C315642) from outside, B—hinge of the paratype (AM C350019), C—right valve of the paratype, D—and pores of the paratype, E—sculpture of the paratype.

America, some African and Siberian species of *Sphaerium*. All of them were included in Iredale's (1943a) genus *Sphaerinova* and Alimov & Starobogatov attributed strong siphonal muscles and separated scars to the whole group. These views are clearly incorrect in the light of the new data on siphonal musculature of the Australian taxa.

Pisidium (Afropisidium) aslini is the most distinct Australian endemic. It differs from other consubgenors distributed in south Asia, Africa and South America in its very small size and the number of important anatomical characters (particularly in the arrangement of mantle muscles and in the shape of the nephridium). It is difficult to derive *Pisidium aslini* from any of the Asian species (for example, *P. javanum*) because of these differences and the wide geographic gap (the Australian species is distributed only in the southern part of the continent and in Tasmania). Another very peculiar species attributed to *Afropisidium* is known from New Zealand (Kuiper, 1966). Gondwanan distribution of the whole subgenus (Kuiper, 1983), and the distinct position of *P. aslini* in it, may suggest a rather ancient origin of the latter species.

In contrast, the only species of the subgenus *Odhneripisidium* found in Australia is similar to the numerous species distributed in Southeast Asia. Kuiper (1983) noted the presence of this group in Papua New Guinea, thus there is a more or less continuous distribution from the Russian Far East (Korniushin, 1996b) and Japan (Kuiper, 1983) in the north to northern Queensland in the south. The considerable species diversity of *Odhneripisidium* in east Asia suggests that Australian species may have originated from there.

Euglesa is the subgenus of *Pisidium* represented in the Australian fauna by eight species. Two major species groups are distinguished in this subgenus. The first one includes

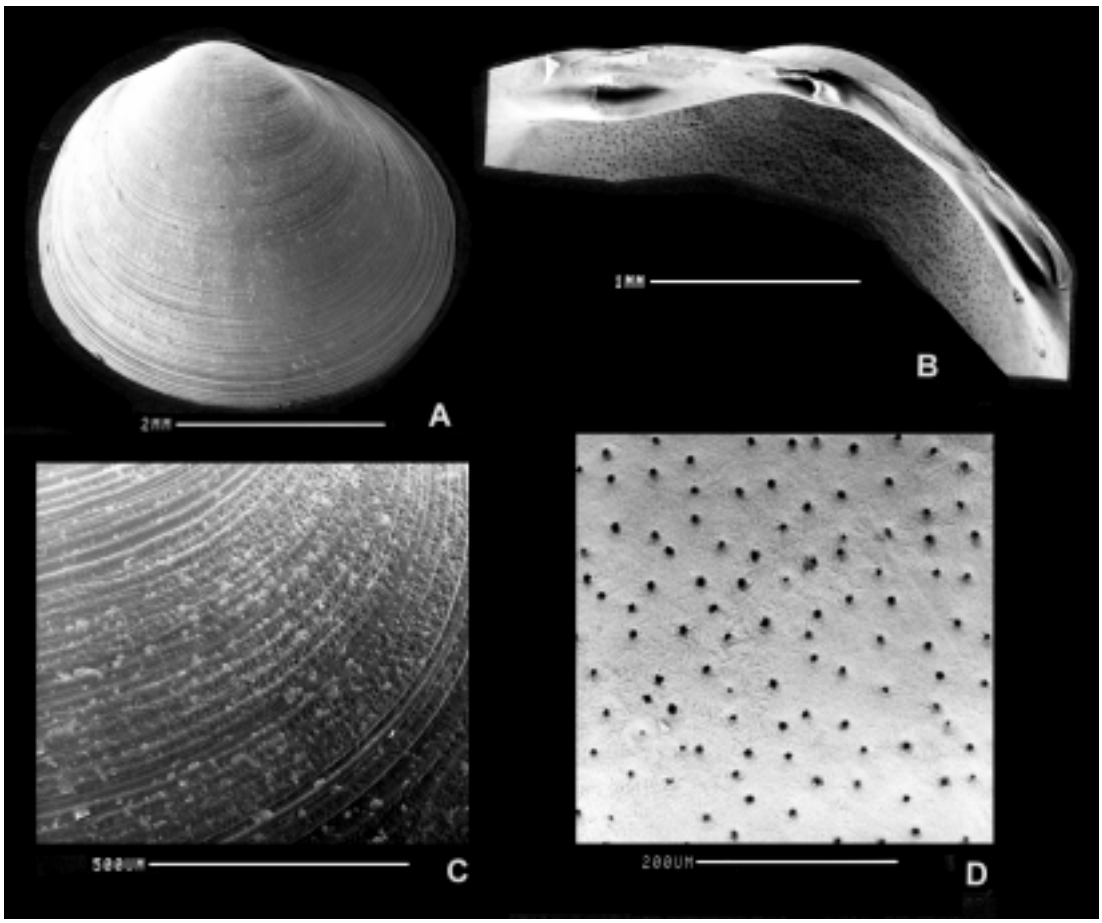

Figure 51. *Pisidium ponderi* from Bobundara Ck, NSW (AM C315743), shell: A—right valve from outside, B—hinge of this valve, C—sculpture, D—pores.

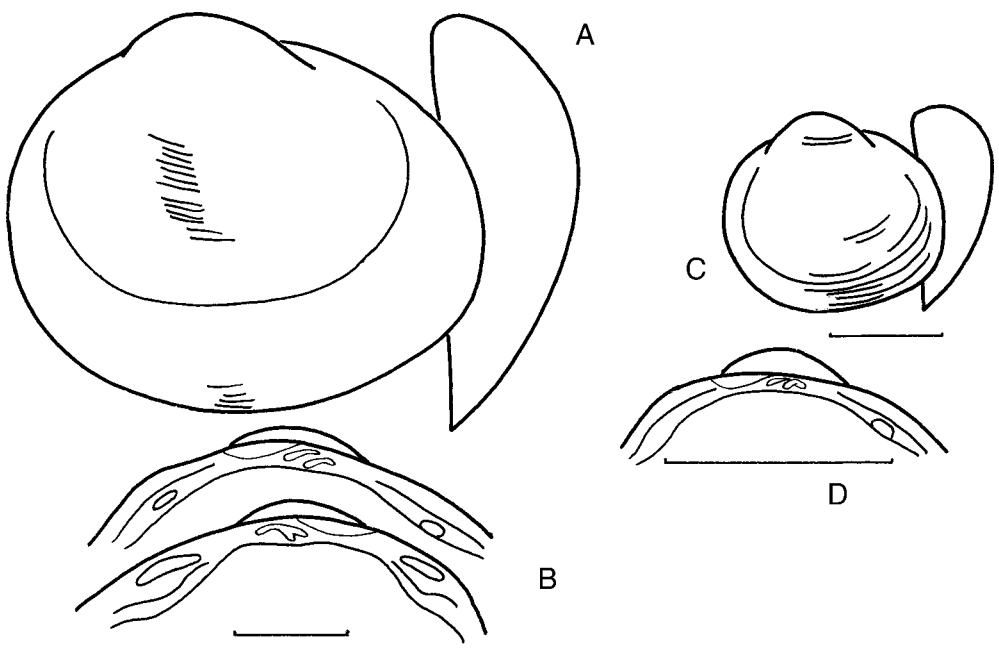

Figure 52. *Pisidium ponderi*, variability of shell form: A,B—Braidwood, NSW (AM C126348), right valve and hinge; C,D—Currambene Ck, NSW (AM C126716), right valve and hinge of the left valve. Scale bars = 1 mm.

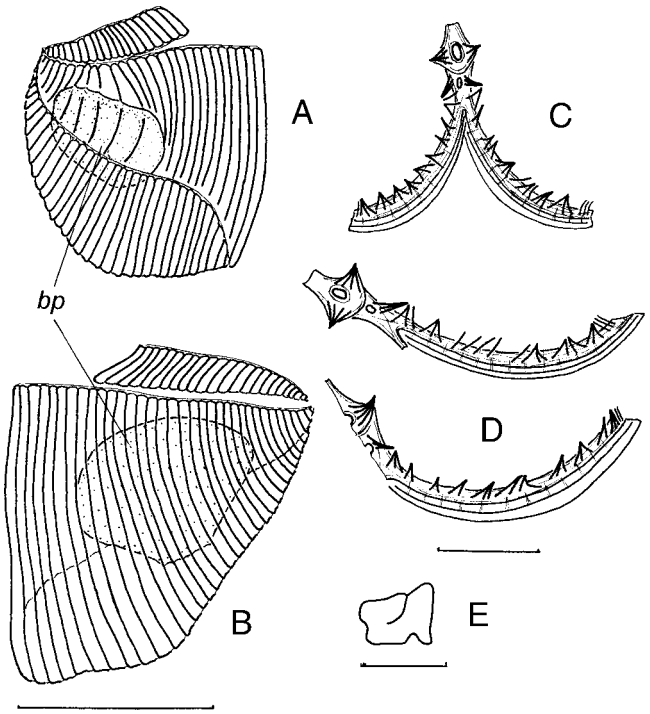

Figure 53. *Pisidium ponderi*, anatomy: A,B—gills, A—paratype (AM C350019), B—Bobundara Ck, NSW (AM C315743); C,D—mantle edge, C—paratypes, D—Braidwood, NSW (AM C126348); E—nephridium dorsally, paratype. Scale bars = 1 mm.

four species: *P. etheridgei, P. hallae, P. kosciusko* and *P. fultoni*; it is distinguished first of all in its elongate presiphonal suture which is considered an apomorphy within the genus (Korniushin, 1998a). Position of the umbo (moderately shifted posteriorly) and peculiarities of the hinge teeth (rather short lateral teeth stretched parallel to the dorsal edge of the hinge plate) are also tentative synapomorphies. Among non-Australian species, these characters are shared by *P. floresianum* found in Papua New Guinea and adjacent islands and *P. khurbaense* from the Amur River (Russian Far East). While affinities of these species to the Australian taxa are probable, this remains to be tested. The African species *P. viridarium* Kuiper, 1956 is similar to *P. etheridgei* in the shape of the shell and the arrangement of mantle muscles (Piechocki & Korniushin, 1994), but its presiphonal suture is not as elongate.

Among the species of the group discussed here *P. etheridgei, P. hallae* and *P. kosciusko* are the most similar. They are almost identical in anatomy and differ only in shell outlines and indices. *Pisidium fultoni* differs in some anatomical characters as well as in shell shape. However, ranges of variation in shell and anatomical characters in the species pairs *P. etheridgei–P. hallae, P. etheridgei–P. kosciusko*, and *P. etheridgei–P. fultoni* overlap. Species of each pair are separated geographically or by habitat (as in *P. fultoni*) and the areas of contact appear to be relatively narrow. Such a situation suggests close relationship between these species and recent speciation in the group.

Another group includes *P. carum, P. ponderi* and *P. centrale*. The close affinity of these species is supported by such tentative synapomorphies as dense pores and some reduction of mantle muscles, especially in the middle part of the mantle. The regular concentric sculpture is the other similarity between these species, but the status of this character is not clear. These patterns of sculpture and mantle musculature are shared by the South African *P. langleyanum* Melville & Ponsonby, 1891, but that species differs in its elongate presiphonal suture (Korniushin, 1995).

The relationships of *Pisidium tasmanicum* are disputable. Its affinity to the *P. carum* group is indicated by similar shell characters, but convergent development of these characters is probable. The relationship of *P. tasmanicum* with *P. etheridgei* seems to be more supportable. The short presiphonal suture found in the first species may be explained by its small size and rather short (circular) outline, and in some sympatric populations the two species are difficult to separate.

Zoogeographic regions

A summary of the distribution data (Figs. 56, 57; Table 7) makes it possible to outline several regions characterised by distinct sphaeriid faunas (Fig. 58).

A poor, but rather peculiar fauna is found in northern Queensland (one species and one subspecies are endemic for this area). The only Australian species of *Odhneripisidium* with its evident Asian affinities is the most characteristic for this area. Only one lot of sphaeriids from the coastal area in the Northern Territory is known and is considered to be consubspecific to the northern Queensland form of *M. tasmanicum*. However, sphaeriids of this area are still poorly known and the future discovery of undescribed species seems probable.

On the contrary, the fauna of the mountainous area stretching from southern Queensland to Victoria is one of the best represented in sphaeriid collections. The most characteristic species for this area are *Pisidium hallae* and *P. ponderi* (the first is scarcely represented in Victoria and Tasmania, the second is endemic). Two species, namely *Musculium quirindi* and *Pisidium kosciusko* are restricted to limited areas: an area around Tamworth and alpine lakes in the Snowy Mountains, respectively (Fig. 58). Three widely distributed species (*Musculium tasmanicum, Pisidium carum, P. etheridgei*) have mountain populations with some peculiar characters. The eastern and western slopes of the Great Divide have different faunas of sphaeriids, but the barrier is not absolute. For example, most of the localities of *P. carum* in NSW are from the western slopes, but in southern Queensland the species is represented on the eastern slopes as well. All localities of *Musculium quirindi* are from the western slopes, but *M. tasmanicum* is present on both slopes. At least three closely related species live sympatrically in the Snowy Mountains: *Pisidium etheridgei, P. hallae* and *P. kosciusko*.

The east coast has a poor sphaeriid fauna with no endemics; all the taxa recorded (three species) also being distributed along the Great Dividing Range as well.

In the vast area of the Murray-Darling basin (western plains), sphaeriids seem to be scarce, as they are poorly represented in collections. Two widely distributed species, M. tasmanicum and *P. carum*, are found in this area. There are no endemic species, but a peculiar form of *M. tasmanicum*, possibly an unnamed subspecies, is restricted

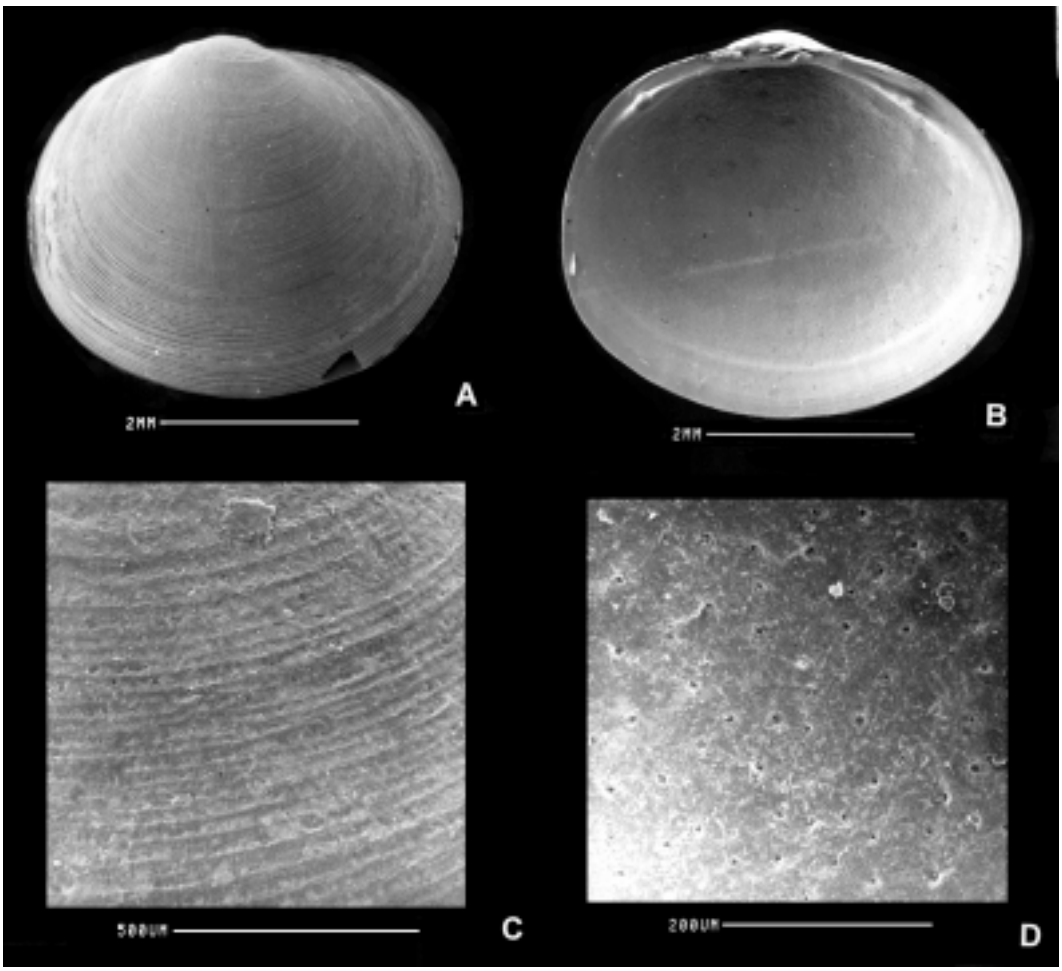

Figure 54. *Pisidium centrale* n.sp., holotype (AM C138753): A—right valve from outside, B—left valve from inside, C—sculpture, D—pores.

Table 7. Summary of the distribution data for the Australian sphaerids; 8 present, 6 absent. CA, central Australia; GD, Great Dividing Range and eastern coast; NQ, northern Queensland; NT, Northern Territory (coastal areas); SE, southeastern Australia; SW, southwestern Australia; TS, Tasmania; WP, western plains.

species	NT	NQ	GD	WP	CA	SE	TS	SW
Musculium tasmanicum s.str.	6	6	8	8	6	8	8	6
Musculium t. queenslandicum	8	8	6	6	6	6	6	6
Musculium tatiarae	6	6	6	6	6	8	8	6
Musculium lacusedes	6	6	6	6	6	6	8	6
Musculium kendicki	6	6	6	6	6	6	6	8
Musculium quirindi	6	6	8	6	6	6	6	6
Musculium cf. *lacustre*	6	6	6	6	6	8	6	6
Pisidium aslini	6	6	6	6	6	8	8	6
Pisidium australiense	6	8	6	6	6	6	6	6
Pisidium etheridgei	6	6	8	?8	6	8	8	6
Pisidium hallae	6	6	8	6	6	6	8	6
Pisidium kosciusko	6	6	8	6	6	6	6	6
Pisidium fultoni	6	6	6	6	6	6	8	6
Pisidium tasmanicum	6	6	6	6	6	8	8	6
Pisidium carum	6	8	8	8	6	8	6	6
Pisidium ponderi	6	6	8	6	6	6	6	6
Pisidium centrale	6	6	6	6	8	6	6	6

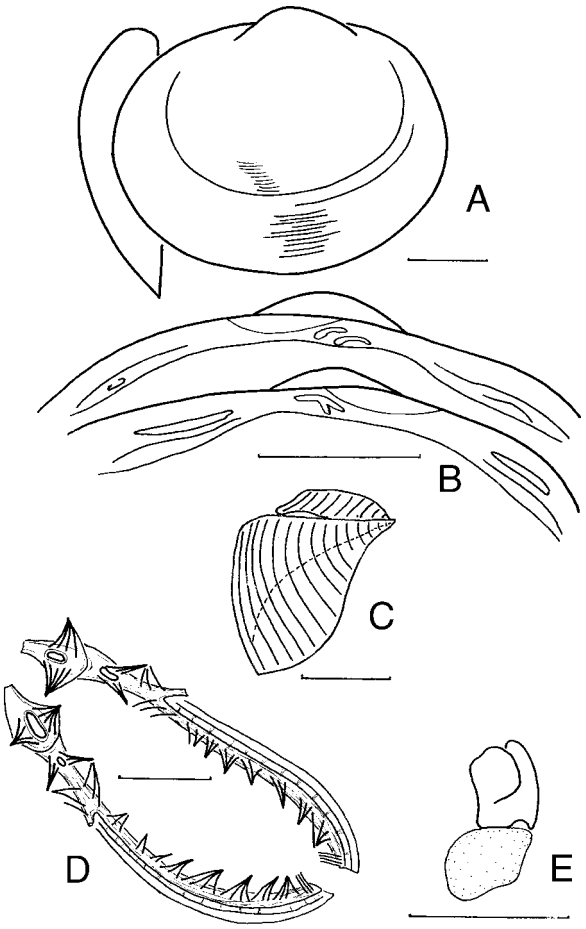

Figure 55. *Pisidium centrale*, shell and anatomy: A,B—Reedy Ck, NT (AM C2148), left valve and hinge; C–E—paratypes (AM C350021), C—gill from outside, D—mantle edge, E—nephridium dorsally. Scale bars = 1 mm.

to this region. The occurrence of another species (*Musculium tatiarae*) needs to be confirmed, and one species described from the Murray River (*M. problematicum*) is dubious. *Pisidium etheridgei* is recorded in the literature (Gabriel, 1939; B.J. Smith, 1978), but no specimens attributable to this species were seen during this study.

The southeast part of the Australian mainland is the area with the most diverse sphaeriid fauna. Its affinity to the fauna of northern Tasmania is supported by presence of *Musculium tatiarae, Pisidium aslini* and *P. tasmanicum* (the first two species are endemics to both these areas). It allows the treatment of these areas as one zoogeographic region (Fig. 58). *Pisidium aslini* is the most characteristic and possibly the most ancient element in the Australian fauna; it is presently known only from several isolated localities in Victoria and northern Tasmania. Two widely distributed species (*M. tasmanicum tasmanicum* and *P. etheridgei*) also reach Tasmania, *P. carum* is known only from the mainland. The presence of *P. hallae* in southern Victoria and Tasmania needs confirmation.

The fauna of southern part of Tasmania is poorer than that of the northern part, and most of the species are widely distributed. However, an area of endemism is located in the centre of Tasmania with two endemic species.

Only one species, the endemic *Musculium kendricki*, is known from Western Australia. Morphological study of this rather peculiar species suggests its long isolation, although some affinity to *M. tatiarae* from the southeastern Australia and Tasmania is also probable.

The other peculiar species, *P. centrale*, is known from two records in Central Australia. This extremely arid region is still poorly studied, therefore it is not clear if the mentioned species is restricted to the limited area (Fig. 58) from which it is currently known, or whether it has a wider distribution. Of interest is the lot from southwest Queensland identified as *P. carum* has some similarity to *P. centrale*.

Conclusions

The data presented here show connections of Australian sphaeriids not only to the taxa from Southeast Asia, but also to those from South Africa and South America. Among the other Australian molluscs, such distribution ranges are known for hyriid mussels (McMichael, 1967) and the heterobranch gastropod *Glacidorbis* (Meier-Brook & B.J. Smith, 1976). Such connections suggest an ancient origin of some Australian endemic taxa (*Sphaerinova, P. aslini, P. carum* and *P. etheridgei* groups) consistent in general with the point of view of Kuiper (1983). The Asian roots are evident only for the *Odhneripisidium* species found in northern Queensland; distribution of this subgenus being similar to that of the nominate subgenus of the gastropod *Gyraulus* (Planorbidae) (Meier-Brook, 1983).

Notably, Australian species form only a few anatomically distinct groups: *Sphaerinova, Afropisidium, Odhneripisidium* and two groups in *Euglesa*. The European and North American faunas are much more diverse anatomically, the former with about 20 distinct species groups (Korniushin, 1996b). At the same time, the total number of species and subspecies in Australia is rather high, with closely related species distinguished in each group. Allopatric distribution of these species and evident geographic trends in intraspecific variation suggest geographic speciation. However, this speciation was not so intensive as in small freshwater caenogastropods of the family Hydrobiidae (Ponder *et al*., 1994). In comparison with hydrobiids, Australian sphaeriids have wider distribution ranges and less distinct morphological gaps.

The picture of the Australian sphaeriid fauna is still not complete; some regions, particularly northern Queensland and the Northern Territory, Murray Basin and Western Australia are not sufficiently well represented in collections. In addition, delimitation of some widely distributed species is not clear. Areas known to be centres of speciation—along the Great Dividing Range, as well as the central Tasmanian plateau—also need closer attention.

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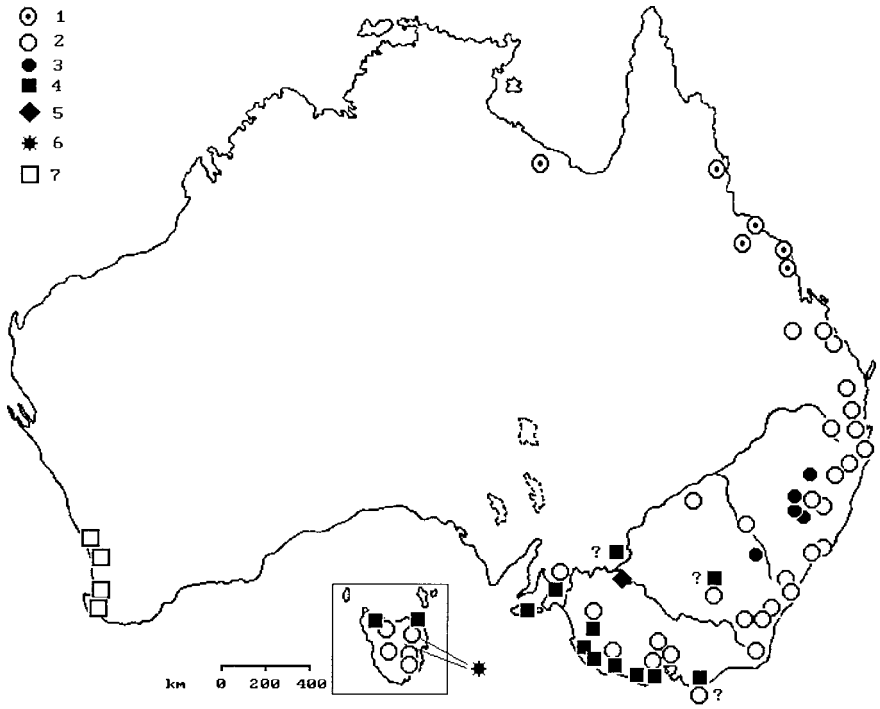

Figure 56. Distribution of *Musculium* species: 1—*Musculium tasmanicum queenslandicum*, 2—*M. t. tasmanicum*, 3—*M. quirindi*, 4—*M. tatiarae*, 5—*M. ?problematicum*, 6—*M. lacusedes*, 7—*M. kendricki*.

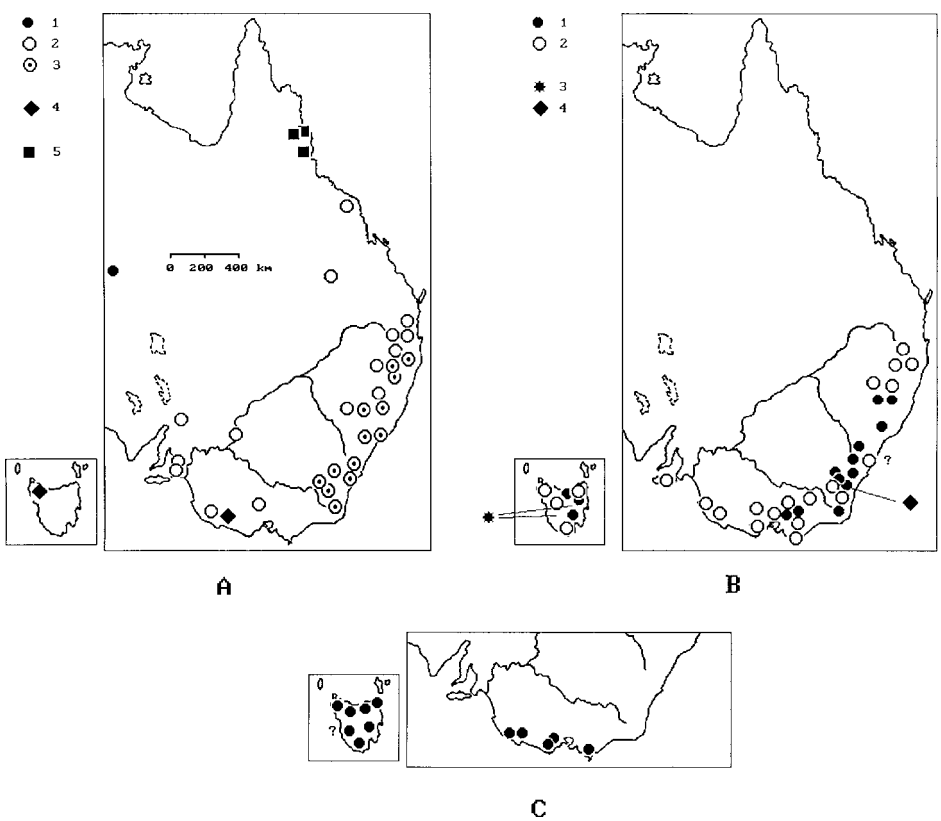

Figure 57. Distribution of *Pisidium* species: A—*P. (Euglesa) carum* (1), *P. (E.) ponderi* (2), *P. (E.) centrale* (3), *P. (Afropisidium) aslini* (4) and *P. (Odhneripisidium) queenslandicum* (5); B—species of the *P. (E.) etheridgei* group (1—*P. hallae*, 2—*P. etheridgei*, 3—*P. fultoni*, 4—*P. kosciusko*); C—*P. (E.) tasmanicum*.

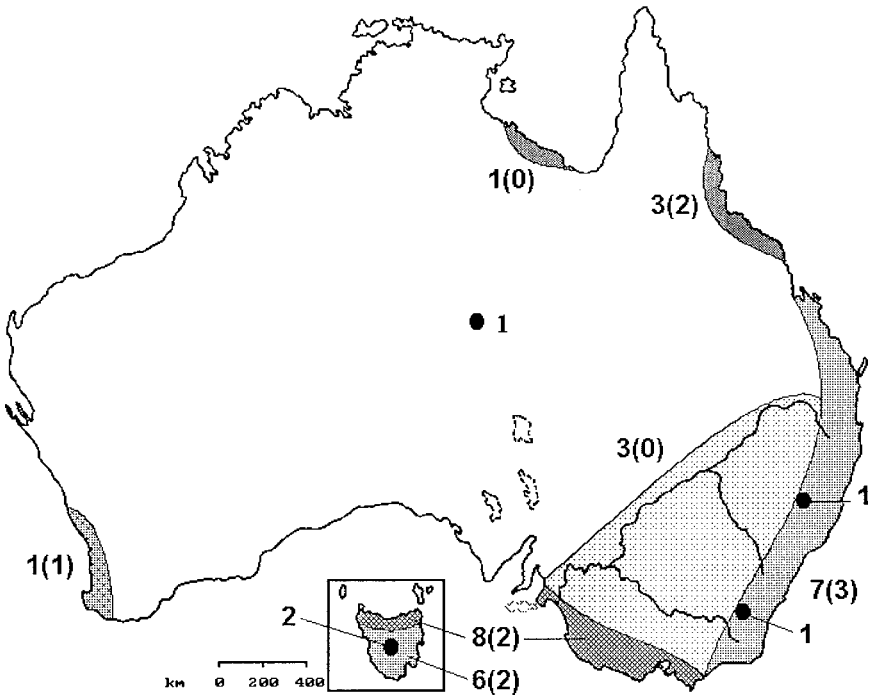

Figure 58. The regions characterised by distinct sphaeriid faunas. The total number of species and the number of endemic species (in brackets) are provided for each region. Black circles indicate the areas of local endemism, respective number of endemic species provided.

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