MESOZOIC FRESHWATER AND ESTUARINE BIVALVES FROM AUSTRALIA

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Australian freshwater and estuarine bivalves are described from the Hyriidae, Glauconomidae and Sphaeriidae. The following taxa are now known from the Mesozoic of Australia: from the Triassic, Hyriidae, comprising *Prohyria eyrensis*, *Megalovirgus* gen. nov., *Megalovirgus clellandi*, *Megalovirgus jaenschi* and *Mesohyridella ipsvicensis*, Glauconomidae, *Unionella wianamattensis*, *Protovirgus dunstani and Protovirgus brookvalensis* sp. nov.; from the Jurassic, Hyriidae, *Hyridella (Protohyridella)* sp. *Prohyria skepticsi* sp. nov., ?Sphaeriidae, *Protosphaerium talbragarensis* gen. et sp. nov. and *Protosphaerium gianae* sp. nov.; and, from the Cretaceous, Hyriidae, *Megalovirgus wintonensis*, *Hyridella macmichaeli*, *Hyridella (Protohyridella) goondiwindiensis*, *Hyridella whitecliffsensis*, *Alytharia jaqueti*, *Alytharia coatsi* and *Palaeohyridella godthelpi* gen. et sp. nov. It is apparent that over the course of freshwater bivalve evolution in Australia there has been a distinct faunal dichotomy between large and small taxa. The large forms are exclusively hyriids and dominate lacustrine, riverine and lagoonal environments and the small forms, either glauconomids, sphaeriids and/or corbiculids dominate brackish and estuarine environments. This dichotomy is also present in the modern estuarine and freshwater taxa. The presence of glauconomids during the Triassic is the first and earliest record, providing good evidence for estuarine depositional environment of the Wianamatta Shales, Sydney Basin. This is also the earliest record of sphaeriids in Australia. Little is known of the evolutionary relationships within these groups due to their conservative morphology. ❐ *Megalovirgus gen. nov. Palaeohyridella godthelpi gen. et sp. nov. Prohyria skepticsi sp. nov., Protosphaerium talbragarensis gen. et sp. nov. Protosphaerium gainae sp. nov. Protovirgus brookvalensis sp. nov. Hyriidae, Sphaeriidae, Glauconomidae.*

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Australian fossil freshwater and estuarine molluscs are poorly known, with few publications on the higher taxonomy of present day and extinct taxa. A review is offered here for the Mesozoic freshwater bivalves comprising the families Hyriidae, Glauconomidae and Sphaeriidae, with redescription of previously described species and description of new forms. Detailed illustrations and measurements are provided so that further collection does not confuse issues of variation and taxonomic position.

Etheridge Jr (1888, 1892) described several forms from Australia assigning most to *Unio*, apart from the smaller forms to which he assigned *Unionella*. Newton (1915) described new Cretaceous unionoids from Lightning Ridge and White Cliffs, also allocating these to *Unio*. At this point the Unionoida comprised the Unionidae, Margretifidae and Mutelidae.

Later, McMichael (1956) revised Etheridge Jr's and Newton's material, presenting detailed descriptions of fossil nonmarine taxa from Australasia in an effort to alleviate some of the taxonomic confusion within these morphologically conservative groups. McMichael proposed that these fossil unionoids were from a Mutelidae lineage, and included the modern fauna within this family in a regional revision (McMichael & Hiscock, 1958). Most of McMichael's fossil descriptions were paraphrased from Etheridge Jr's and Newton's earlier work and little new material was incorporated into his study.

McMichael (1956) did, however, erect three mostly Mesozoic genera of mutelids: *Prohyria*, *Mesohyridella* and *Protovirgus*, neatly accomodating large and medium-sized bivalve taxa. Ludbrook (1961) described new taxa from the Triassic Leigh Creek Formation, South Australia, proposing that the genus *Unio* was valid for some Australian unionoids and that this confirmed the presence of Unionidae in Australia. I provide evidence to the contrary. Ludbrook also assigned one species to McMichael's *Protovirgus*, which is now placed within *Alathyria*.

Parodiz & Bonnetto (1963) provided evidence for a separate endemic Gondwanan lineage on the presence and morphology of the glochidial larval stage. They proposed that the Australian

radiation was distinct enough to allow familial uniquity and several taxa in South America were also assignable to this new group, Hyriidae, instead of the dominant Mutelidae. These conclusions suggest that the unionoids from Australia are mostly Gondwanan in origin with recent, presumably Pleistocene – Holocene, invasions from southeast Asia. This view is supported by the present study.

Since McMichaels' review, more material has come to light that has shed new and interesting information on the taxonomic validity and position of the fossil taxa. Shell characteristics that McMichael & Hiscock (1958) put forward for the subfamilies within the Hyriidae have also assisted herein in allocating the fossil taxa to these subfamilies.

Smaller Triassic bivalves (*Unionella*) described by Etheridge Jr (1888) and reviewed by McMichael (1956) from the Sydney Basin and Bowral posed problems for McMichael with his only suggestion that they were Triassic holdovers of the Permo-Carboniferous family Anthracosiidae. This family has a conspicuous presence in North America (Rogers, 1965), United Kingdom (Weir, 1960) and the former Soviet Union (Haas, 1969) during the Carboniferous and Permian. I place these small bivalves with the modern family Glauconomidae, but do not rule out distant phylogenetic links to the anthracosiids. There is a strong possibility that convergence has been acting on both these groups, indeed all freshwater and estuarine bivalves reported here. However, enough characteristics have been found that ally these small Triassic bivalves to the Glauconomidae.

Most recently, Hocknull (1994) described a new taxon from the Late Triassic of southeast Queensland allocating it to *Protovirgus*, here revised to *Megalovirgus* gen. nov. Hocknull (1997) described new taxa from the Cretaceous of Queensland placing all taxa within previously recognised genera. The understanding that there is considerable confusion over the taxonomy of the unionoids and the presence of unrecorded families of small freshwater faunas prompted the present review.

New material from the Talbragar Fossil Fish Beds, New South Wales, indicate the possible presence of Sphaeriidae in Australia. Hampered by the lack of well-preserved specimens the allocation of the small bivalves to Sphaeriidae is tentative.

As there is an apparent dichotomy between bivalve faunas, depositional environment, their sizes and phylogenetic history, it remains to be seen whether the assignment of different sized faunas should lie at the family level. Such possibilities are discussed later. Fossils are given the prefix SAMF (South Australian Museum), QMF (Queensland Museum), UQF (University of Queensland) and AMF (Australian Museum) and are deposited in their respective institutions.

AGE AND STRATIGRAPHY

Ten major sites, containing nonmarine bivalves, are recognised from Queensland (Qld), New South Wales (NSW) and South Australia (SA) (Fig. 1). The hyriids are restricted in the Triassic to the Ipswich Coal Measures, Qld and the Leigh Creek and Springfield Basins, SA. During the Jurassic they occur sporadically in the Walloon Coal Measures, Warwick, SE Qld and the Koonwarra Fossil Bed, South Gippsland, Victoria. In the Cretaceous the family is abundant throughout the entire Eromanga Basin, especially the Coreena, Griman Creek and Winton Fomations of northern NSW and Qld.

Small freshwater and estuarine bivalve fossil faunas (glauconomids and sphaeriids) are restricted in the Triassic to the Wianamatta Shales, Sydney Basin, and in the Jurassic to the outlying Talbragar Fossil Fish Bed derived from the Purlawaugh Formation. No small nonmarine bivalves are as yet known from the Australian Cretaceous.

There are three major stratigraphic units, in which Triassic freshwater bivalves are preserved. In SE Qld, the units containing hyriids are the Blackstone and Tingalpa Formations, both considered Late Triassic (Carnian) in age by de Jersey (1975) and de Jersey & Hamilton (1965), respectively. Both formations consist of fine grained to coarse-grained sandstones and siltstones/shales, with most of the bivalves being derived from the finer carbonaceous siltstones and shales. Preservation is good, with most individuals having both valves intact and fine ornamentation preserved. The valves are generally external moulds with little internal morphology preserved. The cavities have been replaced with ferrous sediment. The preservation of both valves suggests an in situ taphonomy.

Playford & Dettman (1965) ascribe the Leigh Creek Formation, SA, a Late Triassic age on the basis of similar palynological floras to those in Ipswich. Whilst other authors ascribe ages between Late Triassic (Rhaetic) to Early Jurassic

FIG. 1. Map illustrating Australian localities for Mesozoic freshwater and estuarine bivalve fossils.

(Liassic) on the basis of fish faunas (Wade, 1953), plant floras (Chapman & Cookson, 1926) and unionoids such as *Prohyria eyrensis* (Ludbrook, 1961). The Springfield Coal Basin, SA, is also attributable to the Late Triassic from diagnosis of equivalent sediments to the Leigh Creek Formation (Johnson, 1960) and, again, the presence of the distinctive *Dicroidium* and *Thinnfeldia* floras with the presence of the hyriid; *Prohyria eyrensis* (= *Unio springfieldensis* Ludbrook, 1961).

Like the Blackstone Formation, the bivalves are preserved as moulds with both valves intact. The deposit is interpreted as in situ.

The Brookvale Quarry and Bowral Quarry expose sections through the Wianamatta Shales, Sydney Basin, NSW. Small valved glauconomids occur at all sites and are attributable to the Late Triassic, being derived from the Hawkesbury Sandstone and Wianamatta Group (Lovering & Elroy, 1969). The shells are preserved as whole specimens or as singular valves. Mass accumulations suggest fast burial and aggregation of these taxa in the bottom sediment. Little is known of the aggregation behaviour/taphonomy of modern glauconomids, therefore, no interpretation of the depositional environment is given here.

There is one occurrence of small freshwater bivalves in the Jurassic of eastern Australia from the Talbragar Fossil Fish Beds, derived from the Purlawaugh Formation. The beds are an outlier group so an exact age is uncertain (Dulhunty & Eadie, 1969). They consist of 'chert containing Jurassic plant and fish fossils ... in soil derived by weathering from Jurassic Purlawaugh sediments ...' (Dulhunty & Eadie, 1969). The small bivalve fauna shows a mixture of depositional environments, preserving both isolated, singular valves and whole animals in aggregations. Modern sphaeriids and corbiculinids exhibit such mass aggregations after flooding (pers. obs.).

Fossil hyriids identified herein occurring in the Jurassic have an unknown position within the Waloon Coal Measures due to inaccuracies in locality data. They are badly preserved and are isolated throughout the measures. Both valves are usually found intact.

Three major units containing unionoids are derived from the Eromanga Basin; Winton, Griman Creek and Coreena Formations. The Griman Creek and Coreena Formation, derived from the Rolling Downs Group is considered Early Cretaceous (early-middle Albian) in age by Exon & Senior (1976) and Burger (1986, 1995) and consists of a brackish water unit with outcrops within the Surat Basin (Exon & Senior, 1976). This unit is comprised generally of lithic glauconitic sandstones, siltstones and mudstones. The younger Winton Formation, in central and southwestern Eromanga Basin, is of latest Albian to Cenomanian age (Senior et al., 1978), consisting for the most part of lacustrine and fluviatile siliciclastic sediments that produced labile sandstones, siltstones and mudstones.

All three units contain mass aggregations of bivalves with whole animals preserved in situ. Mass aggregations of hyriids occurring today tend to be observed after flooding, hence the Griman Creek, Winton and Coreena Formations may be considered to be more fluviatile than brackish-marine. The presence of marine molluscs in two of the formations (Griman Creek & Coreena) may then be attributed to marine incursions onto the fluviatile systems. As there is very poor, if any, recorded stratigraphy the occurrence of the taxa in sympatry cannot be analysised. The relative abundance, however, may give clues to the placement of former drainage systems and in what direction they

flowed. For example, the Winton Formation has no record of marine taxa, whereas the Griman Creek and Coreena formations have. The Griman Creek formation specimens seem to be dominated by hyriids and the Coreena formation dominated by marine taxa. Examination of all the available species and their analogous environments need to be assessed in greater detail before such conclusions can be evaluated.

PALAEOECOLOGY

The families of freshwater bivalves present in the Mesozoic (Hyriidae, Glauconomidae and ?Sphaeriidae) illustrate analogous faunal assemblages to those occurring in modern Australia freshwater and estuarine systems. Regardless of climate dynamics, one large and several small bivalve groups have continually dominated the freshwater and estuarine bivalve faunas since the Triassic. The large bivalve fauna is comprised entirely of the hyriids, and the small bivalve faunas of either; glauconomids, sphaeriids or corbiculids. During the Mesozoic, there is an apparent faunal change occurring at the end of the Triassic, early Jurassic, and within the Jurassic toward the Cretaceous.

At the end of the Triassic there were two major faunal groups, the large *Prohyria* and *Megalovirgus* hyriids and the small *Unionella* and *Protovirgus* glauconomids. Both these faunas have been preserved separately in the fossil record and reveal no sign of overlap into either faunal system. It is, therefore, probable that the small glauconomids inhabited environments not suited for the larger unionoids and visa versa. Indeed, today glauconomids are only known from estuarine environments, and are therefore, quite distinct from the freshwater hyriids. This provides good evidence that the Wianamatta Shales were derived from such a system of deposition.

An analogous system is found today in the brackish to estuarine dwelling sphaeriids and corbiculids with the modern intercontinental riverine hyriid radiation. One can then speculate at the life habits of the Mesozoic taxa. The heavy shelled, large hyriids were presumably living in more lacustrine, fluviatile regions of Australia's Mesozoic, whereas the smaller valved glauconomids and ?sphaeriids would have been respectively confined to the brackish, estuarine and riverine regions of coastal Mesozoic Australia.

SYSTEMATIC PALAEONTOLOGY

HYRIIDAE Ortmann, 1911
VELESUNIONAE Iredale, 1934

Prohyria McMichael 1956

TYPE SPECIES. *Prohyria johnstoni* (Etheridge Jr, 1892); from the Oligocene, West Tamar River.

DIAGNOSIS. (After McMichael, 1956) 'Medium sized to large freshwater mussels of the subfamily Velesunionae, the anterior end moderately to markedly swollen, the posterior end drawn out into a bluntly rounded rostration, which is of maximum length at a position in the middle of the height of the shell; hinge well developed, with large cardinal teeth.' Rostration of the posterior end is distinct in all growth forms. Escutcheon broad, extending almost the entire length of the valves. Anterior adductor muscle scars deep, elongate, orientated antero-ventrally and relatively small. Umbones consistently eroded. Prominent hinge with one elongate lateral tooth and large cardinals.

REMARKS. The genus is placed within Velesunionae due to the absence of beak sculpturing. McMichael (1956) erected this genus for the placement of two species, *P. johnstoni*, from the Oligocene of Launceston Basin and *P. eryensis*, from the Late Triassic of Leigh Creek, SA and Ipswich Coal Measures, SE Qld, within the velesunionines. Ludbrook (1961) assigned another large unioid from the Late Triassic, *Unio springfieldensis*, considered as *Prohyria springfieldensis* here, from the Springfield Basin, SA. Recently, an additional form, *P. macmichaeli*, was described by Hocknull (1997) from the Cretaceous of Qld, however, new specimens attributable to this taxon from Lightning Ridge, NSW, suggests alliance with the hyridellines. All three taxa are distinct from any other velesunionine genus by their large size, thick ornamented shell, rostrate posterior profile and distinctly inflated umbones.

Prohyria eyrensis (Etheridge Jr, 1892) (Fig. 2K)

Unio eyrensis Ethridge Jr 1892: 389, pl. 28(1); 1941: 11, pl. 3(1-3).
Prohyria eyrensis (Etheridge Jr) McMichael 1957: 228, pl. 13(8, 11) (non 9, 10).
Unio springfieldensis Ludbrook, 1961: 145, pl. 2(1,2).

MATERIAL. AMF51624, 51651, 51642, 51647, 51644, 51648, 51649, 51625, 51626, 51638, 51640. SAM15473, 15474.

AGE AND DISTRIBUTION. Late Triassic from the Blaek Stone, Tingalpa, Bundamba formations, SE Qld. Leigh Creek Formation and Springfield Coal Basin, SA.

DIAGNOSIS. Large, elongate-oval, equivalved unioid with distinct rostration in the posterior end. Anterior end inflated and rounded. Hinge distinct with strong escutcheon produced along most of the dorsal margin. Lunule large and excavated. Beaks high and unsculptured, usually eroded. Commarginal ornamentation with coarse growth lines. Shell thick. From Ludbrook (1961); 'hinge with two triangular pseudo-cardinal and one long posterior lateral in the right valve, one triangular pseudo-cardinal and two long posterior laterals in left valve'. Anterior adductor muscles deep, elongate-oval and orientated antero-ventrally.

DESCRIPTION. Shell equivalved, inequilateral, umbones inflated and anteriorly placed 1/3 from anterior end. Beaks unsculptured but usually eroded. Shell thick with coarse growth lines producing ridged ornamentation. From Etheridge Jr (1892); 'Hinge line straight, ventral margin rounded , passing rather sharply upwards into the anterior and posterior margins. Anterior end small, somewhat acutely curved, posterior end narrow, obtusely pointed'. Anterior adductor muscle scars deeply set, behind beaks, elongate-ovoid and postero-ventrally orientated. Large cardinal teeth, with long bifurcating lateral tooth. Morphometrics given in Table 1.

REMARKS. *P. eyrensis* is one of the most common taxa found in the Ipswich and Leigh Creek deposits. It is a cosmopolitan taxon and is the largest in the Mesozoic. Attaining sizes over 12cm long it is comparable to modern species of *Velesunio* and *Alathyria*. These modern genera have been restricted to coastal river systems and lakes and may provide good analogues to the depositional environment of the Triassic coal deposits of SE Qld and SA.

P. eyrensis was reviewed by McMichael (1956) and placed within *Prohyria* when he erected the genus to fit one other taxon, *P. johnstoni*. Its placement within *Prohyria* is due to the large size, wedge-shaped profile, inflated beaks positioned anteriorly and the prominent hinge. *Prohyria eyrensis* differs from *Prohyria johnstoni* in its size, size proportions and amount of tapering. *Prohyria johnstoni* tapers more sharply to the posterior than *Prohyria eyrensis*. *Prohyria springfieldensis* is markedly similar to *Prohyria eyrensis* and is synonymised here; however, it differs having: finer comarginal ornamentation; more rostrate appearance in ocelusal view; straighter, more prominent hinge line. *P. eyrensis* differs from *Hyridella macmichaeli* formally placed within *Prohyria* by Hocknull (1997) by being much larger, with a more rostrate posterior profile. The beak sulcus is relatively less produced in *P. eyrensis*. Juvenile forms of *P. eyrensis* do not possess the characteristic V-shaped beak sculpture, as seen in *Hyridella macmichaeli*.

On inspection of the holotype and comparison to a series of specimens referrable to *P. eyrensis*, including the holotype, from the Leigh Creek Basin and Ipswich Coal Measures, there is little evidence for the separation of these specimens from what is obviously a cosmopolitan taxon, *P. eyrensis*.

Prohyria skepticsi sp. nov.
(Fig. 3)

TYPE SPECIES. *Prohyria johnstoni* (Etheridge, 1892).

ETYMOLOGY. For the Australian Skeptics.

MATERIAL. HOLOTYPE: UQF52158. PARATYPES: UQF52160, UQF29708A/B.

AGE AND DISTRIBUTION. Jurassic, Waloon Coal Measures, Warwick District, SE Qld.

DIAGNOSIS. Medium-sized, equivalved velesunioninc hyriid. Elongate-ovoid, thick shell with rugose comarginal ornamentation. Shell tapering to the posterior to produce a triangulate wedge-shaped posterior margin. Umbones placed anteriorly and orientated antero-laterally to the shells' anterior-posterior axis. Anterior adductor muscle scar small, rounded and placed high, underneath the beaks. Beaks not sculptured. Lateral teeth simple, comprising a single tooth and socket in at least the left valve. Hinge line long and robust.

TABLE 1. Morphometrics (in mm) for *Prohyria eyrensis* (Etheridge Jr).

	Length	Height	Width	Beak Length	Beak Height	Beak Width	Ligament Length
Mean	85.75	46.57	34.09	15.85	41.04	16.65	46.78
s.d.	18.11	10.41	7.53	4.02	9.28	3.69	7.75
Number	12	12	12	12	12	12	12

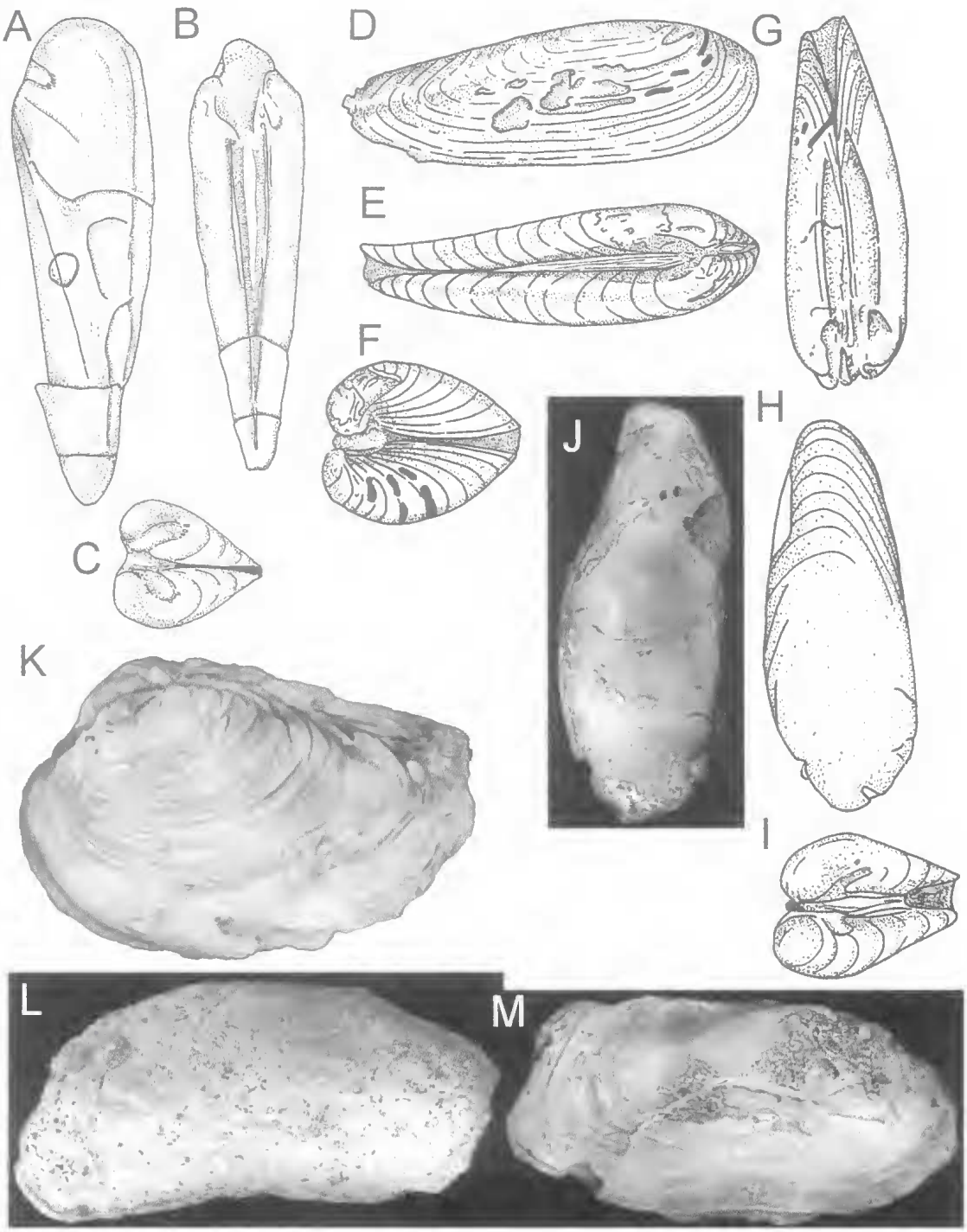

FIG. 2. A-C, *Megalovirgus clellandi* Holotype QMF29473; A, right valve ×0.5; B, dorsal view ×0.44; C, anterior view ×0.5. D-F, *Megalovirgus wintonensis* Holotype QMF34635; D, right valve ×0.7; E, dorsal view ×0.7; F, anterior view ×0.8. G-J, *Megalovirgus jaenschi* Holotype SAMF1547a; G, dorsal view ×0.46; H, right valve ×0.46; I, anterior view ×0.44; J, right valve ×0.56. K, *Prohyria eyrensis* Holotype SAMF15473, right valve ×0.7. L, *Alathyria coatsi* Holotype SAMF15477, right valve ×0.8. M, *Alathyria jaqueti*, QMF103903 right valve ×1.0.

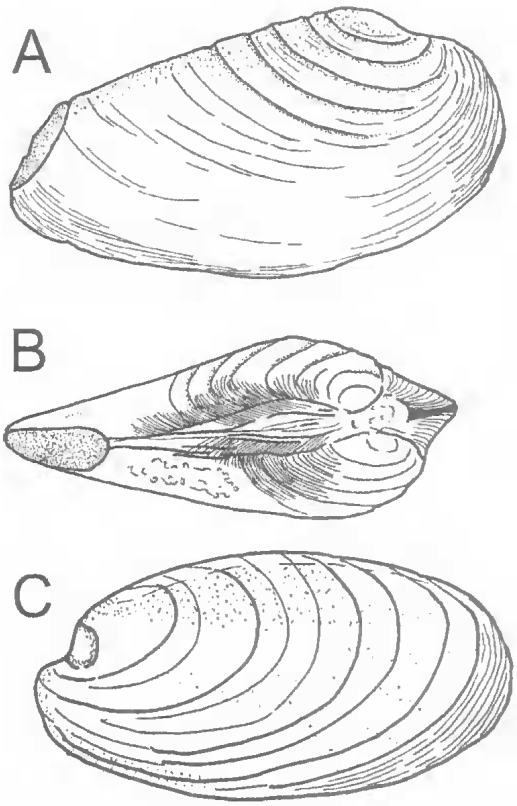

FIG. 3. *Prohyria skepticsi* sp. nov.; A, UQF52158 right valve ×1.2; B, UQF52158 dorsal view ×1.0; C, UQF29708 left valve ×1.5.

DESCRIPTION. Medium-sized, elongate-ovoid hyriid with rugose comarginal ornamentation. Shell thick with long thick ligament. Hinge broad near umbones and tapers gradually to posterior margin. Umbones placed anterior at about 1/5 of total length. Posterior margin rounded. Anterior margin rounded and begins slightly below beak. Beaks not sculptured but possess fine lines conspicuous around margin. Escutcheon inconspicuous. Anterior adductor muscles placed antero-ventrally to anterior edge of beak. Muscle scar small and ovoid. Dentition simple comprising single lateral tooth in the left valve and possibly two cardinal teeth. Rugose ornamentation interspersed by fine growth lines. Umbones orientated anteriorly to lateral axis of valves. The shell immediately posterior to umbones is inflated and produces a slight ridge that runs the length of the shell to the posterior margin. The ventral is straight and rounded to both ends.

REMARKS. The absence of sculpture and the elongate-ovoid shape places this hyriid within the velesunonines. It's placement within *Prohyria* is warranted due to the rugose and thick shell interspersed with fine growth lines, triangulate-ovoid outline of the posterior margin, small ovoid highset anterior adductor scar and anteriorly placed umbones with laterally orientated beaks. *Prohyria skepticsi* differs from *Prohyria eyrensis* and *Prohyria johnstoni*, by it's smaller size, more elongate outline, relatively smaller adductor muscle, and relatively broader hinge line. Morphometrics given in Table 2.

Alathyria Iredale, 1934

Alathyria jaqueti (Newton, 1916)
(Fig. 2M)

Unio jaqueti Newton, 1916: 230, pl. 6(2-6).
Velesunio jaqueti (Newton) McMichael, 1957.

MATERIAL. QMF10887, 15812, 103859, 103862, 103868, 103879, 103880, 103892, 103894, 103898, 103899, 103903.

AGE AND DISTRIBUTION. Uppermost Albian – Cenomanian Formations, Winton, Griman Creek and Coreena. Localities: QML229, QML379, QML570, Lightning Ridge and White Cliffs.

DIAGNOSIS. Large velesunionine hyriid, elongate-ovoid with distinct winged dorsal posterior rim. Ventral margin of valves in lateral aspect show distinct concave form. Beaks posterior, relatively inflated. Anterior margin tapers sharply from umbonal region. Umbonal region always eroded in large individuals. Long indistinct lateral tooth with small indistinct cardinals of unknown number.

DESCRIPTION. Shell large, elongate, medium sized, equivalved. Shell width narrow in young individuals, inflating as the shell becomes larger. Anterior margin tapers away sharply from beak, to a rounded profile. Dorsal edge subparallel with ventral margin with a truncated posterior producing a 'winged' profile. Beaks relatively anterior placed 1/3 from the anterior end. Pronounced inflation just postero-ventral of umbones carrying down to the postero-ventral edge. Umbones characteristically eroded with some being broken off post-deposition. Beaks unsculptured. Anterior adductor muscle scars inconspicuous, being small and just anterior to the cardinal teeth. Hinge relatively strong and short. Ventral margin concave toward the mid region. The concavity is more pronounced in larger individuals. Posterior adductor muscle

TABLE 2. Morphometrics (in mm) for *Prohyria skepticsi* sp. nov.

UQF No.	Length	Height	Width	Beak Length	Beak Height	Beak Width	Hinge Length
UQF52158	52.41	30.14	23.84	13.35	28.67	10.35	32.32
UQF52160	43.65	25.64	?	6.04	18.23	?	?
UQF29708A	48.59	29.75	15.90	11.13	26.72	10.09	27.64

scars indistinct. Cardinal teeth typically unionid. Lateral teeth obscured. Escutcheon narrow and encompasses most of the hinge area. Ligament is prominent within this area. Morphometrics given in Table 3. Shell allometry is illustrated in Figure 8. Note that the specimens allied to this taxon are distinct from *Megalovirgus wintonensis* on the basis of height to length ratios.

REMARKS. Newton (1915) placed this taxon within *Unio*, as with most other unionoids at that time. McMichael's reinterpretation of the material lead him to place the taxon within Velesunionae, as *Velesunio jaqueti*. The present review agrees with McMichael's placement within the velesunionines, based on the absence of any distinct umbonal sculpturing in small individuals. The shells are also less quadrate than those seen most prevalently in the hyridellines. The large size, winged posterior and tapering anterior margin show close similarities to *Alathyria*. The current study has examined many more specimens and the overall size shows that the taxon shares more similarities to *Alathyria* than *Velesunio*. *A. jaqueti* differs from it's sympatric taxa by possessing a unique height to length ratio (only similar to *H. macmichaeli*). It differs from *H. macmichaeli* because it is winged posteriorly and does not possess juvenile beak sculpture.

Alathyria coatsi (Ludbrook, 1961)
(Fig. 2L)

Protovirgus coatsi Ludbrook 1961: 146, pl. 2(6).

MATERIAL. SAM15477.

AGE AND DISTRIBUTION. Early Cretaceous (Neocomian), Blythesdale Group. Localities: as in Ludbrook (1961).

DIAGNOSIS. Medium-sized, equivalved, inequilateral hyriid with fine comarginal ornamentation. Umbones relatively deflated. Dorsal margin convex, with ventral margin highly concave in lateral profile.

DESCRIPTION. From Ludbrook (1961); 'Shell of medium size, compressed, elongate ... dorsal and ventral margins slopes approximately parallel; dorsal margin gently convex and elevated posterior to beaks then curving more sharply downwards to the posterior margin ... Posterior ridge fairly well marked and gently arcuate. Beaks flattened, apparently unsculptured, not prominent; ligament moderately prominent, no lunule visible'.

REMARKS. Ludbrook placed this taxon within *Protovirgus* with no direct characteristic defining it's position within the genus. Inspection of the holotype allowed the present study to place *P. coatsi* within the extant genus *Alaythria*. This placement is on the basis of the following characters present in *P. coatsi* and *Alaytharia*: convex dorsal and concave ventral margins; flattened beaks in most members of the group; and marked postero-dorsal wing. The specimen differs from other species of *Alaytharia* by it's smaller size, more pronounced convexo-concavo lateral profile and less prominent winged postero-dorsal face.

HYRIDELLINAE Iredale, 1934

Megalovirgus gen. nov.

TYPE SPECIES. *Megalovirgus jaenschi* (Ludbrook), from the Upper Triassic, Leigh Creek Formation, SA.

ETYMOLOGY. *Megalos*, Greek, pertaining to the taxons large size; *–virgus* for the genus *Virgus* which it resembles closely.

DIAGNOSIS. Shells medium to large, elongate, knife-like, with umbones inflated and positioned extremely anterior. Anterior adductor muscle scar set on platform, oblong, ventro-laterally orientated. Shell thin with little or no ornamentation. V-shaped sculpturing in the umbones with sculpture proceeding down a postero-dorsal ridge in smaller individuals. Ornamentation lost in most adult valves. Posterior musculature unknown. Escutcheon long and broad with distinct ligament.

DESCRIPTION. Shells that are distinctly hyridelline in juvenile morphology, losing this in the larger individuals. Medium to large shells, equivalved, inequilateral, elongate with beaks placed extremely anterior. Posterior margin tapering moderately to sharply, all knife-like.

TABLE 3. Morphometrics (in mm) for *Alathyria jaqueti* (Newton).

	Length	Height	Width	Beak Length	Beak Height	Beak Width	Ligament Length
Mean	61.82	34.2	23.57	17.09	34.28	11.12	27.44
s.d.	12.49	7.73	5.67	4.96	7.73	3.40	6.72
Number	12	12	12	9	12	7	3

Anterior margin truncated and rounded, with indistinct lunule, producing weak beak sulcus. Fine comarginal growth lines, with smooth ornamentation. Anterior adductor muscle elongate and placed high in the shell, in front of beaks; orientated postero-ventrally or just ventrally. Raised on small platform. Dorsal and ventral margins run subparallel producing elongate tear-shaped outline to valves. Escutcheon broad, housing distinct hinge with prominent ligament. Teeth comprise of one large lateral tooth, weakly preserved and two weak cardinal teeth. Typical unionid teeth. Valves produced laterally to provide distinct height.

REMARKS. This genus is erected to house species that have been confused with another family (the glauconomids) of freshwater bivalves inhabiting other areas at similar times. The Glauconomidae, presented later, has an unusual presence within Australia and has evolved to fill an ecology not used by unionoids. The species formally placed within *Protovirgus* by McMichael (1956) are now placed within *Megalovirgus* except for the type species, *P. dunstani*. This is because all of the other taxa are believed to be hyriids, whereas, *P. dunstani*, is thought to be a glauconomid. The reasons for this will be presented under *P. dunstani*.

Megalovirgus differs from all other hyriid genera on the basis of the following differences: elongate profile with indistinct beak sculpture (cf. Cucumerunionae); indistinct lunule and weak sulcus; fine growth lines with no ornamentation; and distinct anterior adductor muscle, raised on platform, just in front of beaks. The new genus is now used for *M. jaenschi*, *M. femingi*, *M. clellandi* and *M. wintonensis*. *Protovirgus coatsi* Ludbrook, 1961, is redescribed above as, *Alathyria coatsi*.

Megalovirgus jaenschi (Ludbrook, 1961)
(Fig. 2G-J)

Protovirgus jaenschi Ludbrook, 1961: 145 pl. 2(3-4).

MATERIAL. HOLOTYPE: SAM1547a and PARATYPE 1547b. AMF51627, 51639, 51645, 51650, 51635, 51664.

AGE AND DISTRIBUTION. Late Triassic, formations: Leigh Creek, Springfield Coal Basin. Localities: Leigh Creek Coal Fields, Leigh Creek Golf Course, Springfield Coal Fields, SA.

DIAGNOSIS. Large elongate, inflated hyridelline with fine comarginal ornamentation. Shell thin and valves deep. Posterior edge tapering to a relatively pointed end. Anterior rim rounded and short. Beaks placed at 1/10 the length from the anterior end.

DESCRIPTION. See Ludbrook (1961), Morphometrics given in Table 4.

REMARKS. *M. jaenschi* is distinct from the other species within this genus due to the placement of the beaks, narrow form, overall size and orientation of the anterior adductor muscle scars. *M. jaenschi* is longer than *M. wintonensis* with beaks placed more anteriorly. The anterior adductor muscle scar is set more ventrally in *M. jaenschi* than in *M. wintonensis*. The valves are relatively narrower than in *M. wintonensis*. When compared to *M. clellandi*, *M. jaenschi* is shorter, wider with less height. The anterior adductor muscles are placed higher in *M. clellandi*. *M. femingi* is smaller, narrower with thicker ornamentation. Beaks are placed more posteriorly than in *M. jaenschi*.

Megalovirgus clellandi (Hocknull, 1994)
(Fig. 2A-C)

Protovirgus clellandi Hocknull, 1994: 146 (fig. 1A-D).

MATERIAL. HOLOTYPE: QMF29473; 29475.

AGE AND DISTRIBUTION. Late Trassic, formations: Black Stone, Tingalpa, SE Qld. Localities: Ebbw Vale and Tingalpa, SE Qld.

DIAGNOSIS. Large, equivalved, elongate hyriid with inflated umbonal area and fine comarginal ornamentation. Hinge straight and long with escutcheon broad and distinct. Tapering posterior to a very pointed posterior margin. Anterior adductor muscle scars raised on platform just anterior to beaks and lunule.

DESCRIPTION. See Hocknull (1994).

REMARKS. *M. clellandi* differs from *M. jaenchi* in it's larger size, higher placed adductor scars, more tapering posterior and more anterior

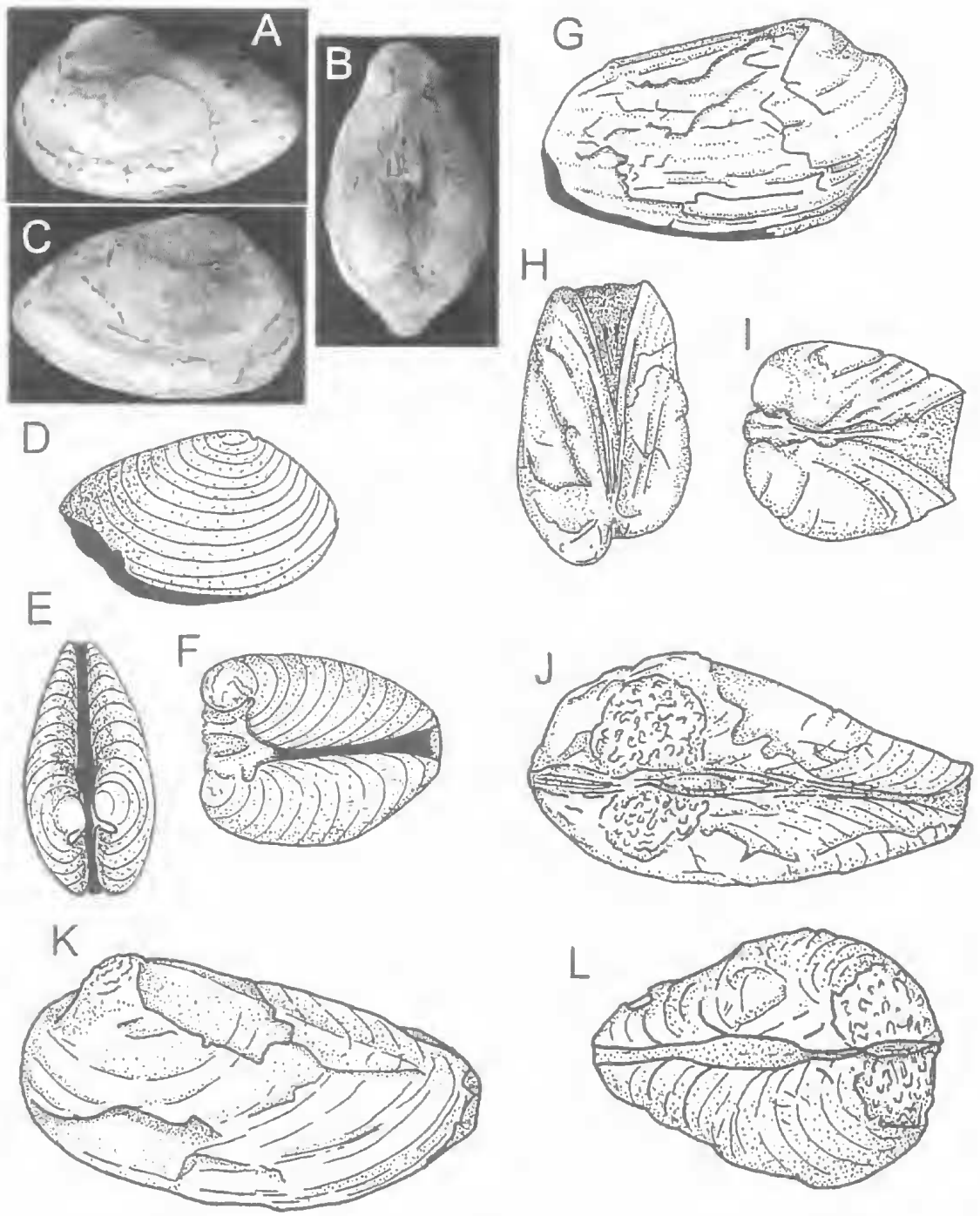

FIG. 4. A-F, *Hyridella (Protohyridella) goondiwindiensis*; A-C, AMF103849, A, left valve × 1.3, B, dorsal view × 1.4, C, right valve × 1.3; D-F, Holotype QMF5684, D, left valve × 1.4, E, anterior view × 2.0, F, dorsal view × 1.4. G-L, *Hyridella (Hyridella) macmichaeli* Paratype QMF34637, G, right valve × 1.3, H, dorsal view × 0.9, I, anterior view × 1.5, Holotype QMF34636, J, dorsal view × 1.5, K, left valve × 1.5, L, anterior view × 1.75.

TABLE 4. Morphometrics (in mm) for *Megalovirgus jaenschi* (Ludbrook).

	Length	Height	Width	Beak Height	Beak Length	Beak Width	Ligament Length
Mean	85.93	30.51	34.89	27.21	9.53	13.9	44.49
s.d.	9.51	7.91	1.75	5.78	2.61	2.04	8.03
Number	10	10	10	10	10	10	10

umbonal-beak region. *P. jaenschi* also has a greater height to length ratio. *M. clellandi* is longer, narrower, tapers more sharply, has a more anteriorly placed beak and has a larger height to length ratio than *M. wintonensis*. *M. flemingi* is much smaller and the umbones are placed more posteriorly than in *M. clellandi*.

Megalovirgus wintonensis (Hocknull, 1997)
(Fig. 2D-F)

Protovirgus wintonensis Hocknull, 1997: 223 (fig. 1A-E).

MATERIAL. HOLOTYPE: QMF34635. PARATYPES: QMF5681-5682, 34645, 34646, 34634, 34644, 34647, 34648. AMF15815, 47175, 68358, 103838, 103841, 103843, 103844, 103847, 104848, 103850, 103852, 103857, 103867, 103873, 103893, 103897, 103901, 103911.

AGE AND DISTRIBUTION. Latest Albian – Cenomanian, formations: Winton, Griman Creek, Coreena Formation. Localities: QML229, L379, L570, Lightning Ridge, White Cliffs, NSW.

DIAGNOSIS. Medium-sized hyriid, equivalved, inequilateral, slightly inflated umbones and fine comarginal ornamentation. Hinge straight; anterior adductor muscle raised on platform. Tapering strongly to the posterior with short well rounded anterior end. Umbones 1/15 length of shell from anterior end.

DESCRIPTION. Medium to large hyriid with produced posterior end. Elongate with umbones inflated. Umbones 1/15 length from the anterior end. Anterior margin rounded. Hinge straight, ligament long and thick. Dorsal margin long and straight tapering to a knife-like posterior profile. Ventral margin gracile, tapering sharply to meet posterior edge of dorsal margin. Fine growth lines producing fine comarginal ornamentation. Hinge teeth long and thin, cardinals short and indistinct, distinctly unionid. Beaks usually eroded or small, closely set. Escutcheon long and narrow. Lunule short and broad. Anterior muscle scars elongate and orientated antero-ventrally. Posterior muscle scar unknown, presumably small and indistinct. Juveniles possess V-shaped rugae on their beaks, being eroded later in life. Rugae also occur along the margins of the escutcheon. Shell relatively thin. Juveniles start out being triangular in profile and becoming more elongate produced shell. Morphometrics given in Table 5. Allometry given in Figure 8.

REMARKS. *M. wintonensis* differs from *M. clellandi* in having a smaller profile, wider and thicker shell, less anterior umbones, narrower escutcheon and less tapering at the posterior end. *M. jaenschi* is larger, has a less developed anterior adductor muscle scar which is placed lower in the valve than in *M. wintonensis*. *M. femingi* is smaller, with the umbones less anterior than in *M. wintonensis*.

Hyridella (Hyridella) Swainson, 1840

Hyridella (Hyridella) macmichaeli
(Hocknull, 1997)
(Fig. 4G-L)

Prohyria macmichaeli Hocknull, 1997: 224 (fig. 2A-C), (non fig. 1F-H).

MATERIAL. HOLOTYPE: QMF34636. PARATYPES: 5677, 34637, 34638. Additional Material. AMF68346, 103864, 103866, 103869, 103870, 103871, 103874, 103878, 103882, 103884, 103886, 103889, 103890, 103910.

AGE AND DISTRIBUTION. Cenomanian, formations: Winton Formation (type) and Griman Creek. Localities: QML379, QML570, QML229 and Lightning Ridge.

DIAGNOSIS. 'Medium-sized, equivalved unioid, ovate, rugose ornamentation, umbones anterior and inflated, beak slightly sculptured, shell thick' Hocknull (1997). Juveniles with V-shaped ornamentation. Anterior muscle scar

TABLE 5. Morphometrics (in mm) for *Megalovirgus wintonensis* (Hocknull).

	Length	Height	Width	Beak Length	Beak Height	Beak Width	Ligament Length
Mean	51.83	22.7	16.42	11.63	20.76	7.10	20.34
s.d.	20.98	9.71	9.19	5.7	9.10	3.72	8.5
Number	20	20	20	18	19	17	14

set below beak and raised slightly on platform. Simple unionid teeth, with two peg-like cardinals and one long lateral tooth.

DESCRIPTION. Medium-sized, elongate-ovoid unionid. Equivalved with slightly inflated umbones. Hinge line distinct and convex, tapering to the posterior to produce a pointed posterior profile. Beaks 1/5 from the anterior end, usually eroded. Fine growth lines produce ridged commarginal ornamentation. Thick shell. Escutcheon broad and ligament short and distinct. Juveniles have V-shaped rugae on the beaks, absent in the adults as the beak is eroded. Anterior adductor muscle scars small and set below the beaks, raised on platforms. Unionid teeth with a long lateral tooth and small indistinct cardinals. Morphometrics given in Table 6. Allometry shown in Figure 8.

REMARKS. The presence of V-shaped rugae as beak sculpturing in smaller individuals places this taxon within the hyridellines and more specifically *Hyridella*. The anteriorly placed, inflated and thick shelled umbones coupled with tapering elongate-ovoid profile ally *P. macmichaeli* to *Prohyria*. The taxon is smaller than the other members of this small but cosmopolitan genus. The type species, *P. johnstoni* (Etheridge Jr, 1892) of McMichael (1956) is longer, wider and the dorsal margin produces a sharper, tapering edge. *P. eyrensis* is also longer, wider with the umbones placed further anterior. *Unio springfieldensis* has similar attributes as *P. eryensis*, being longer, wider with anteriorly placed umbones. This taxon also tapers more, as in *P. johstoni*. It seems that *Hyridella* shares many similarities with *Prohyria*; however, this is apparently due to convergence and not homology.

Hyridella (Protohyridella) Cotton & Gabriel, 1932

Hyridella (Protohyridella) goondiwindiensis (Hocknull, 1997) (Fig. 4A-F)

Velesunio goondiwindiensis Hocknull, 1997: 225 (fig. 2D-J)

MATERIAL. HOLOTYPE: QMF5684, 5683. PARATYPES: 5685, 5686, 34639-36341 AMF68342, 103849, 103853, 103858, 103865, 103881, 103883, 103895, 103896, 103900, 103902, 103904, 103906, 103907.

AGE AND DISTRIBUTION. Latest Albian – Cenomanian, formations: Griman Creek Formation (type) and Coreena Formation. Localities: Goondiwindi (type), Lightning Ridge and White Cliffs.

DIAGNOSIS. Small, unioid with fine comarginal ornamentation. Quadrate-angulate with strong posterior ridge. Umbones relatively inflated and positioned anteriorly. Beaks sculpturing, V-shaped in juveniles, eroded in adult forms. Teeth simple and unionoid. Anterior adductor muscle small placed just in front of beaks. Shell expanded posteriorly, forming a slight winged appearance in adult forms.

DESCRIPTION. Small, equivalved quadrate-angulate hyriid. Fine growth lines form ridges producing distinct commarginal ornamentation. Beaks distinct and usually eroded laterally. Umbones anterior, situated 1/3 from the anterior margin. Ligament short and distinct producing a strong hinge. Hinge line tapers smoothly to a rounded posterior margin. Antero-ventral margin distinctly convex. Shell relatively thick. Juveniles with distinct V-shaped rugae on the beak, lost in the adult. Juveniles are more ovoid without the pronounced posterior ventral margin of adults. Lunule small and indistinct. Escutcheon broad with the borders smooth and tapering to the posterior. Anterior adductor muscle scars small, oval and just beneath the beak. Teeth simple unionid. Morphometrics given in Table 7. Valve growth pattern is illustrated in Figure 8.

REMARKS. Initially, Hocknull (1997) placed *H. goodiwindiensis* within *Velesunio* due to it's overall similarities in morphology. However, *Hyridella* (*Protohyridella*) *goodiwindiensis* is distinctly hyridelline because of the presence of distinct V-shaped beak sculpture in the juvenile forms (McMichael & Hiscock, 1958), now known from additional specimens. Placement in *Hyridella* is somewhat tentative, due to the marked difference in maximum sizes and relative sizes, when compared to modern taxa of the same genus. However, the overall variation within

TABLE 6. Morphometrics (in mm) for *Hyridella (Hyridella) macmichaeli* (Hocknull).

	Length	Height	Width	Beak Length	Beak Height	Beak Width	Ligament Length
Mean	43.15	26.04	19.52	11.79	23.64	8.21	14.80
s.d.	15.74	9.80	7.28	4.94	8.75	3.34	6.74
Number	14	14	13	14	14	12	11

TABLE 7. Morphometrics (in mm) for *Hyridella (Protohyridella) goondiwindiensis* (Hocknull).

	Length	Height	Width	Beak Length	Beak Height	Beak Width	Ligament Length
Mean	28.6	18.68	14.36	8.55	18.61	6.55	10.39
s.d.	4.48	3.87	2.23	1.79	3.82	1.46	3.31
Number	14	14	14	14	14	14	14

Hyridella supports a conservative approach to higher taxonomy in this group (McMichael & Hiscock, 1958) and therefore placement within *Hyridella* is warranted. When compared to modern *Hyridella* species it is evident that this taxon is much smaller with finer growth and thinner shell and is, therefore, distinct from them. It does, however, bear striking similarities to the type species of the monotypic subgenus *Protohyridella*. The small size, quadrate-angulate form with posterior ridge prominent is characteristic of *Hyridella (Protohyridella) glenelgensis* (Dennant). Extinct *Hyridella* species are also a lot larger than this taxon, with the exception of *Palaeohyridella godthelpi* gen. et sp. nov., suggesting that this species is a dwarf representative of the hyridellines leading towards *Protohyridella*. Whether this provides evidence for separation of *Protohyridella* as a distinct genus is controversial when dealing with unioid species concepts (McMichael & Hiscock, 1958). When comparing the allometry seen in *H. (P.) goondiwindiensis* with that of *Palaeohyridella godthelpi* gen. et sp. nov. it can be shown that, even though they develop similarily sized adults, the growth pattern to this end is quite different, being positive allometry in *H. (P.) goondiwindiensis* and negative allometry in *Palaeohyridella godthelpi* gen. et sp. nov.

Hyridella whitecliffsensis (Newton, 1916)

Unio whitecliffsensis Newton, 1916: 231 pl. 6 (7-8).
Hyridella whitecliffsensis (Newton), McMichael, 1957: 240.

AGE AND DISTRIBUTION. Early Cretaceous, formations: Coreena. Localities: White Cliffs NSW.

DIAGNOSIS. Shell small, equivalve, ovoid hyriid of hyridelline affinity. Moderately inflated valves with V-shaped beak sculpturing. 'Periodic growth divisions, and numerous, close-set, microscopical concentric striations ... posterior ridge become angulate' (Newton, 1916).

DESCRIPTION. See Newton (1916).

REMARKS. The holotype of this taxon was unavailable for study during this review, however, it is possible to diagnose this taxon from other members of *Hyridella*. The most apparent distinguishing features being the angulate posterior margin and concentric growth striae. It differs from *H. (Protohyridella) goondiwindiensis* by it's smaller size and more angulated posterior profile. It differs from *Palaeohyridella godthelpi* gen. et sp. nov. by it's smaller size, less pronounced posterior ridge, closer growth ornamentation, more ovoid profile and narrower shell.

Hyridella (Protohyridella) sp.
(Fig. 5A-C, D-E)

MATERIAL. UQF52157, UQF52159, UQF52161, UQF44278, UQF44276, UQF44277.

AGE AND DISTRIBUTION. Jurassic, Waloon Coal Measures, Warwick District and Rathdowney area, SE Qld.

DESCRIPTION. Medium-sized, equivalved, ovoid hyriid with the comarginal ornamentation. Beaks eroded. Posterior margin tapers abruptly at the posterior 2/5 of valve, producing a triangulate-ovoid posterior margin. Small anterior adductor muscle scar placed antero-laterally to umbone. The escutcheon is shallow. The anterior margin begins 2/3 of the beak height and produces a small rounded margin about 8.19mm to the anterior. The dorsal margin is inflated distal to the anterior and is inflated past the umbones, tapering to the posterior. This produces a wedge-shaped hinge jutting out of the general line of the shell. The umbones are placed anteriorly to the general line of the valves. The ventral margin is rounded to both ends. Ligament short. UQF52157 & 52161 are both medium-sized inequivalved, ovoid inflated hyriids. The inflation and inequilateral morphology is interpreted as an abnormal growth form for the shells. The general morphology follows that described above. Morphometrics given in Table 8.

REMARKS. The material is placed within *Hyridella (Protohyridella)* based on the following characteristics: 1, beak sculptured and eroded; 2, inflation posterior to beak and producing a flanged ventral margin; 3, shell thin with fine comarginal ornamentation. Due to the paucity of specimens and closeness in morphology to

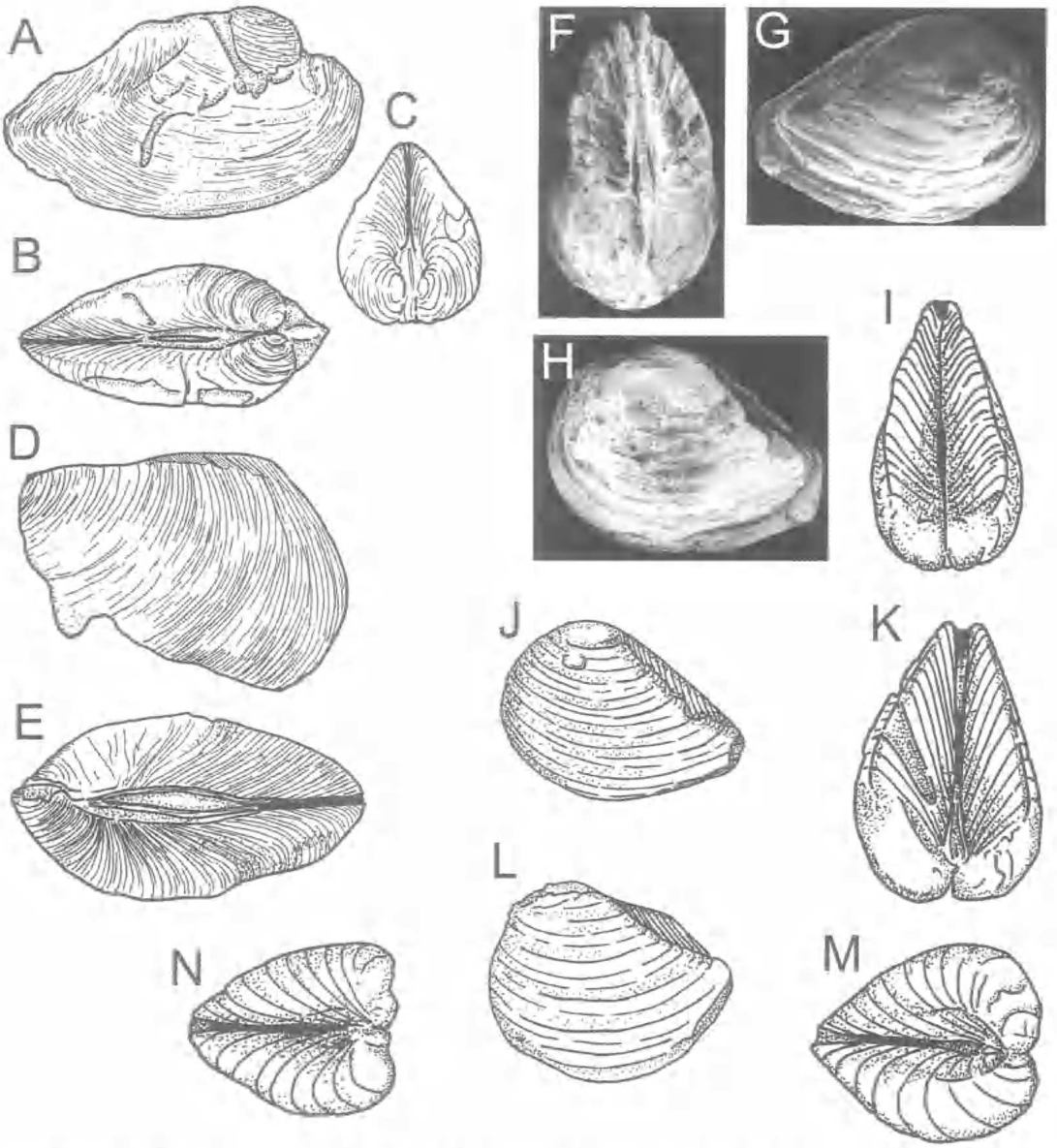

FIG. 5. A-C, *Hyridella (Protohyridella)* sp. UQF52159; A, right valve ×0.8; B, dorsal view ×1.0; C, anterior view ×0.7. D-E, deformed individual of *Hyridella (Protohyridella)* sp. UQF52161; D, left valve ×0.8; E, dorsal view ×0.8. F-N, *Palaeohyridella godthelpi* gen. et sp. nov.; F-I, M, Holotype AMF103912; F, dorsal view ×2.0; G, right valve ×2.0; H, left valve ×1.4; I, dorsal view ×1.4; J, left valve × 1.4; L, anterior view ×1.6. K-L, N, Paratype AMF103913; K, left valve ×1.4; L, dorsal view ×1.4; N, anterior view ×1.6.

Hyridella (Protohyridella) goondiwindiensis specific assignment is not warranted until more specimens are available.

Mesohyridella McMichael, 1956

TYPE SPECIES. *M. ipsviciensis* (Etheridge Jr,1892) from the Upper Triassic, Ipswich Coal Measures.

DIAGNOSIS. Small hyridelline unioid with elongate-oval, equivalved, inequilateral valves. Beaks anteriorly placed with small anterior adductor muscle scar, ovoid and set anteriorly to beaks. Both posterior and anterior margins produced, widely concave. Moderately inflated.

TABLE 8. Morphometrics (in mm) for *Hyridella (Protohyridella)* sp.

UQF No.	Length	Height	Width	Beak Length	Beak Height	Beak Width	Hinge Length
UQF52157	37.76	28.95	?	?	27.54	?	?
UQF52159	45.46	31.24	23.65	8.17	28.79	10.83	27.36
UQF52161	50.73	35.26	?	?	31.90	15.03	28.34

REMARKS. McMichael (1956) erected this genus to place one species of small ?hyridelline, *M. ipsviciensis*. It's affinities with modern subfamilies is thought to be hyridelline, however, this is superficial. Unfortunately, no more material has shed any light on its relations within the hyriids.

Mesohyridella ipsviciensis (Etheridge Jr, 1892)

Unio ipsviciensis Etheridge Jr, 1892: 388 pl. 42(2-3).
Mesohyridella ipsviciensis (Etheridge Jr) McMichael, 1957: 238 pl. 8(5).

AGE AND DISTRIBUTION. Late Triassic, formations: Black Stone, Tingalpa, Bundamba, SE Qld; Springfield Coal Basin. Localities: Ebbw Vale, Bundamba, Tingalpa, Bundamba, SE Qld, Springfield Coal Fields.

DIAGNOSIS. Shell small, elongate-oval with little winged posterior. Shell thick with strong ornamentation.

DESCRIPTION. From McMichael (1956); 'Small freshwater mussels of uncertain affinity, but possibly belonging to the subfamily Hyridellinae. Shells elongate-oval, not winged, moderately swollen. Dorsal margin behind the beaks more or less straight, then curving rather sharply downwards, and descending obliquely to form a rather blunt posterior end with the ventral margin. Beaks not elevated or swollen, heavy corroded, sculptural characters unknown. Shell surface marked with fairly strong growth lines. Hinge characters and muscle scars unknown'.

REMARKS. Etheridge Jr (1892) described *M. ipsvicensis* within *Unio*. McMichael (1956) proposed a genus for the species, in the absence of the holotype, and called it *Mesohyridella*. The present study has not located the holotype either, however, on inspection of many more unionoids recovered from the Ipswich Coal Measures (the type locality is within this formation) other specimens are allocated for this species. The hyriids that resemble the descriptions of Etheridge Jr and McMichael have strong ornamentation, relatively uninflated umbones and beaks placed more central than *P. eyrensis*, the other large ovoid hyriid present in the fauna. This morphologically distinct group of bivalves are present in the Blackstone formation, Tingalpa formation of the Ipswich Coal Measures, SE Qld and the Springfield Basin, SA.

Palaeohyridella gen. nov.

TYPE SPECIES. *Palaeohyridella godthelpi* gen. et sp. nov. from uppermost Albian – Cenomanian Griman Creek Formation, Lightning Ridge.

ETYMOLOGY. *Palaeos*, Greek, representing the ancient aspects of the taxon and *–hyridella* for the affinity to the freshwater bivalve genus *Hyridella*.

DIAGNOSIS. Small hyriid unioid of the hyridelline subfamily. Umbones inflated and placed extremely anterior, 1/13 of total length from anterior end. Posterior margin quadrate-angulate with prominent umbones to posterior ridge. Ridge preserving prominent ridging, developing into V-shaped sculpturing toward the beaks. Escutcheon broad, relative to length. Ornamentation coarse with fine comarginal growth lines. Anterior profile truncated and rounded, producing weak beak characteristics.

DESCRIPTION. Small, equivalved, inequilateral, hyriid with inflated umbones. Umbones greatly anterior being less than 1/13 the length from the anterior. Anterior profile truncated and rounded. Posterior end produced, producing a tear drop valve shape. Shell thick, growth lines fine, producing ridged comarginal ornamentation. Ventral margin gracile and convex. Hinge line straight with short thick ligament. Escutcheon broad and distinct with ornamentation producing a postero-dorsal ridge extending down both valves to the posterior end. V-shaped rugae on beaks and along postero-dorsal ridge on juveniles and adults. The rugae being present on the ridges in adults only. Beaks distinct and close-set. Lunule very short but relatively broad. Muscle scars unknown.

REMARKS. This genus is erected due to the presence of a taxon unlike any hyriid described previously. The V-shaped beak sculpturing in the juvenile and adult allies the new genus to the hyridelline lineage (McMichael & Hiscock 1958). When compared to *Hyridella (Hyridella)*

spp. and *Hyridella (Protohyridella)* spp. there are marked differences; these are 1, umbones more anteriorly situated; 2, broad, distinct escutcheon; 3, posteriorly rostrate profile; and 4, truncated, convex anterior margin.

Palaeohyridella godthelpi gen. et sp. nov. (Fig. 5F-N)

ETYMOLOGY. For Henk Godthelp, a good friend who brought some of the specimens to my attention.

MATERIAL. HOLOTYPE: AMF103912; 26 Paratypes.

AGE AND DISTRIBUTION. Uppermost Albian – Cenomanian, formations: Griman Creek Formation. Locality: Lightning Ridge.

DIAGNOSIS. As for genus.

DESCRIPTION. As for genus. Morphometrics given in Table 9. Allometry given in Figure 8.

GLAUCONOMIDAE Gray, 1853

Glauconomids are a group of estuarine to brackish water bivalves from the east coast of Australia, inhabiting mangrove systems, mudflats and sands. There are four extant species recognised from Lamprell & Healy (1998); *Glauconome plankta, G. virens, G. rugosa* and *G. cerea.*

Unionella Etheridge, 1879

TYPE SPECIES. *Unionella wianamattensis* Etheridge Jr, 1888 from Late Triassic, Gibraltar Tunnel.

DIAGNOSIS. Small, elongate-oval glauconomid. Beaks anterior and close-set. Umbonal region slightly inflated devoid of sculpturing. Posterior margin slightly winged in larger individuals. A series of characteristically elongate beak muscle scars is present just below the beak commissure. Hinge short and indistinct. Anterior adductor muscle scars deep, elongate and usually placed anteriorly to umbones. Muscle scar triangular in lateral profile. Two to three cardinal teeth present, median and posterior most distinct.

REMARKS. The small size, ovoid shape, deep adductor muscle scar and winged posterior along with the 'clumping' nature of the taxa suggest that this genus has evolutionary affinities to the modern Glauconomidae, and certain morphological features similar in Anthracosiidae. Anthracosiids have a well known presence in the Carboniferous and Permian of Eurasia. McMichael (1956) in his review of these forms suggested such an affinity of *Unionella* with the anthracosiids. When comparing these shells to the modern *Glauconome* spp. there are marked similarities: valves are closely set with the beak not well produced; a series of small beak muscle scars occur under the lip of each beak; shell is produced anteriorly, directly in front of the beaks, compared to on the midline as seen in the anthracosiids; two to three small cardinal teeth, increasing in size from the anterior end. The median and posterior cardinals are largest and are close-set.

This genus was described for three apparently distinct forms, *Unionella bowralensis*, *U. wianamattensis* and *U. carnei.* Comparing the overall morphological diversity in species from anthracosiids and glauconomids it is apparent that Etheridge Jr (1882) did not take into account the possible phenotypic plasticity. I have clumped the three forms into one species, as I believe there is not enough consistent variation to propose different species. The taxon available for this is *U. wianamattensis.*

Unionella wianamattensis Etheridge Jr 1888 (Fig. 6K)

Unionella bowralensis Etheridge Jr, 1888: 13, pl. 1 & 2, figs 8-14; McMichael, 1956: 236, pl. 13, fig 6.
Unionella carnei Etheridge 1888: 14, pl. 2, figs 5-7; McMichael, 1956: 237, pl. 13, fig. 7.

MATERIAL. LECTOTYPE: AMF35775; 20183, 21085, 35769, 35771, 3987, 20184, 35766, 35764, 35778, 35773A, 3577B,

AGE AND DISTRIBUTION. Late Triassic, Formations: 'transition beds between the Hawesbury Sandstone and the Wianamatta Group' (McMichael, 1956). Localities: Gibraltar Tunnel, Bowral, Smith's Brick Quarry at Crown Street, Waterloo and Surrey Hills, NSW.

DIAGNOSIS. Shell small, equivalved, elongate-ovate, with fine comarginal ornamentation. Valves inflated mid-laterally, however, umbones relatively flattened. Shell slightly winged posteriorly. Anterior adductor muscle scar deep,

TABLE 9. Morphometrics (in mm) for *Palaeohyridella godthelpi* gen. et sp. nov.

	Length	Height	Width	Beak Length	Beak Height	Beak Width	Ligament Length
Mean	21.88	15.5	12.47	3.65	14.39	4.12	9.21
s.d.	2.59	1.99	2.56	0.62	2.5	0.79	1.42
Number	15	15	15	15	15	15	15

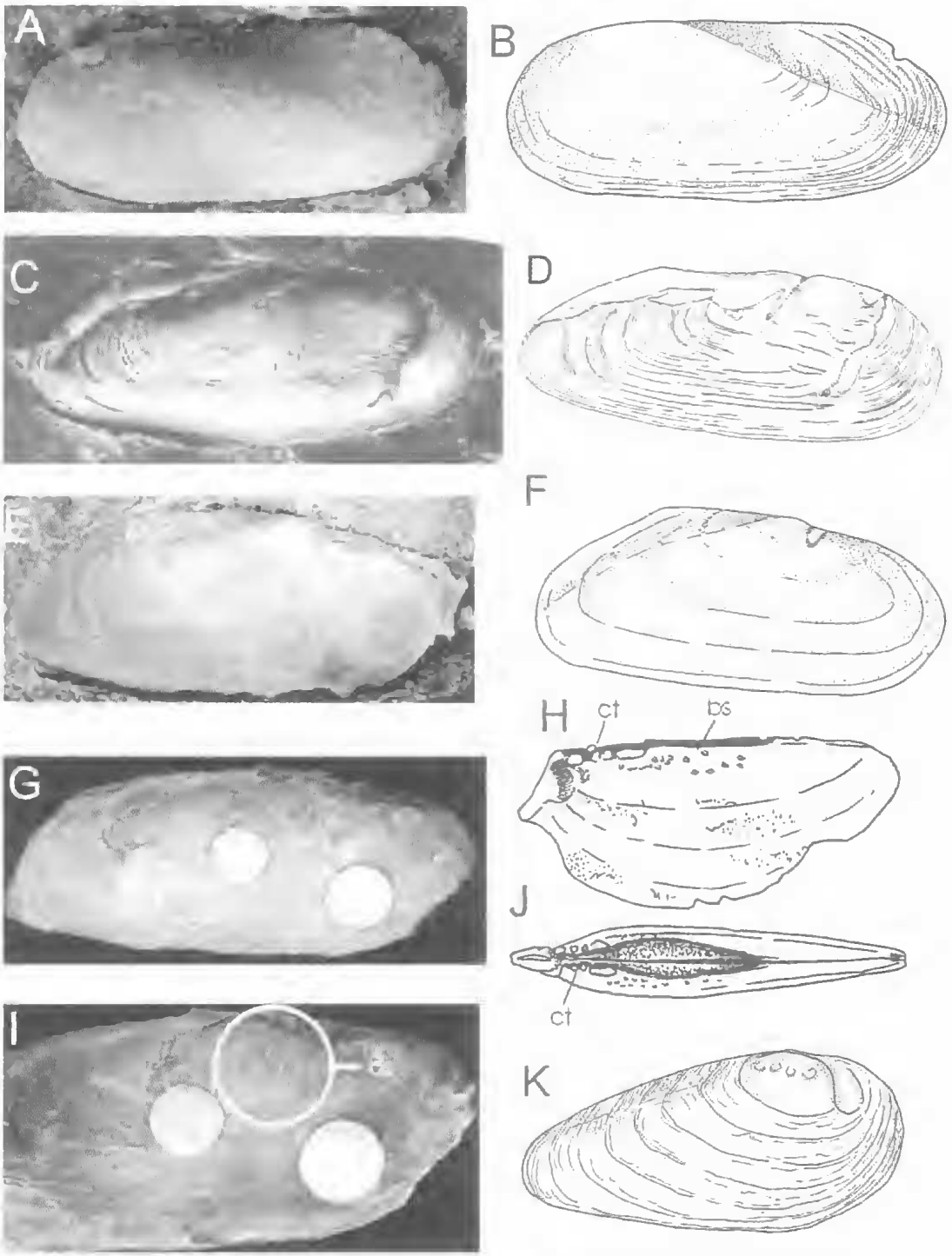

FIG. 6. A-F, *Protovirgus brookvalensis* sp. nov.; A-B, Paratype AMF41440, right valve ×3.0, C-D, Paratype AMF41442, left valve ×3.0. E-F, Holotype AMF19773, left valve ×3.0. G-J, *Protovirgus dunstani*; G, AMF35693, right valve ×2.0, H, AMF35776, left valve showing beak sculpture (bs) and cardinal teeth (ct) ×1.6, I, AMF35693, right valve showing beak sculpture ×2.25, J, AMF35776,dorsal view showing cardinal teeth ×1.7. K, *Unionella wianamattensis* AMF35775, right valve ×3.0.

elongate and postero-ventrally orientated. A series of beak muscle scars extend just postero-dorsally of the anterior adductor scar.

DESCRIPTION. From Etheridge (1888): 'Shell ovate-obliquely oblong, laterally compressed, thin. Dorsal margin or hinge line straight posteriorly, angulated at the anterior end, but in its entire length not as long as the shell; ligament small, and projecting but little above the dorsal margin. Ventral margin nearly straight, with a slight sinus at the middle. Anterior end small, very much compressed, and with the margin rounded; posterior end compressed, the diagonal ridge well marked. Although not strong; the flanks of the valves decrease rapidly in convexity from this ridge to the ventral margin, but an almost imperceptible sinus traverses them upwards from the ventral marginal inflections'. Forms initially described as *Unionella bowralensis* and *Unionella carnei* the shell shows more inflation in the valves. When height to length was measured for the specimens described by Etheridge Jr (1888) a consistent allometry is illustrated.

Morphometrics are presented for *Unionella bowralensis*, *Unionella carnei* and *Unionella wianamattensis* in Table 10.

TABLE 10. Morphometrics (in mm) for *Unionella wianamattensis (=Unionella bowralensis)* (Etheridge Jr), *Unionella wianamattensis (=Unionella carnei)* (Etheridge Jr), *Unionella wianamattensis* (Etheridge Jr).

AMF No.	Length	Height	Width	Beak Length
Unionella wianamattensis (=Unionella bowralensis)				
20183	21.7	8.75	5.15	6.7
20185	12.4	7.7	5.6	3.05
35769	12.15	6.7	5.4	3.15
35771	9.2	5.7	4.15	2.15
Mean	13.86	7.212	5.075	3.78
Unionella wianamattensis (=Unionella carnei)				
3987	12.45	6.7	4.05	3.75
20184	12.55	7.7	5.9	3.1
35764	18.35	8.6	7.5	15.91
35766	18	8.6	7.7	5.1
35778	16.7	8.55	6.05	4.7
Mean	15.01	8.23	8.23	4.51
Unionella wianamattensis				
35773a	15.4	8.7	5.65	4.9
35773b	12.15	8.75	5.9	3.55
35775	14.8	8.8	4.5	3.85
Mean	14.11	8.75	5.183	4.1

REMARKS. The three species initially decribed within *Unionella* are here synonymised as one species on the basis of the following similar but variable characteristics: elongate-ovoid shells that have similar growth allometries; slight winged postero-dorsal margin; and sympatric occurrence in the same horizon. As alluded to in McMichael (1956)'s review of *Unionella,* the overall shell variation in anthracosiid taxonomy is well documented and provides evidence that these three taxa are one. Glauconomids are also highly variable.

Protovirgus McMichael, 1956

TYPE SPECIES. *Protovirgus dunstani* (Etheridge Jr) from the Upper Triassic Wianammatta Shale, Sydney Basin.

DIAGNOSIS. Small, elongate, equivalved, inequilateral glauconomid with long tapering posterior profile. Umbones flattened and placed extremely anterior. Deep, long, posteroventrally orientated anterior adductor muscle scars. A series of beak muscle scars placed just below the beak commissure. Three cardinal teeth, median and posterior cardinal largest and closely spaced. Reduced or no lateral tooth.

REMARKS. This genus is related to *Unionella* in the possession of beak muscle pits, deep, elongate anterior adductor muscle pits and slightly wider postero-dorsal margin and three small cardinal teeth. The genus was described by McMichael (1956) to accommodate two species, *P. dunstani* and *P. flemingi*, from the Late Triassic of Sydney and Cretaceous of New Zealand, respectively. Unfortunately, *P. flemingi* was not examined during this study and will not be considered here.

Protovirgus dunstani (Etheridge Jr, 1888) (Fig. 6G-J)

Unionella dunstani Etheridge Jr 1888: 11 pl. 1(11-19).
Protovirgus dunstani (Etheridge Jr) McMichael, 1957: 232 pl. 14(8).

MATERIAL. LECTOTYPE: AMF35693; 35776, 35777, 35870.

AGE AND DISTRIBUTION. Late Triassic, formations; 'transition beds between the Hawesbury Sandstone and the Wianamatta Group' (McMichael, 1956). Localities: Gibraltar Tunnel, Bowral, Smith's Brick Quarry at Crown St, Waterloo, and Surrey Hills, NSW.

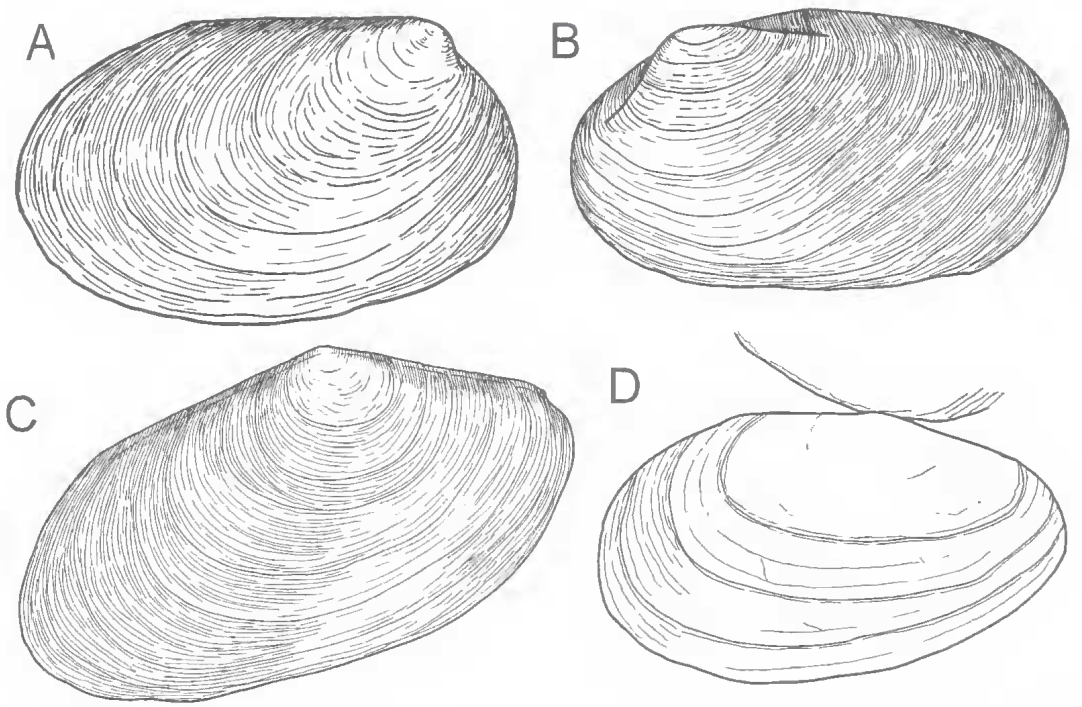

FIG. 7. A-B, *Protosphaerium gianae* sp. nov.; A, AMF38165 Holotype, right valve ×4.0, B, AMF103934b Paratype, left valve ×5.0. C-D, *Protosphaerium talbragarensis* gen. et sp. nov.; C, AMF103934a Holotype, right valve ×4.0, D, AMF103929 Paratype right valve ×5.4.

DIAGNOSIS. Small, equivalved, glauconomid. Elongate shell, tapering to posterior end. Beaks anterior, with flattened umbonal region. Beaks insignificant and closely set. Postero-dorsal margin slightly winged. Three cardinal teeth; large median and posterior cardinal and small anterior cardinal, no lateral tooth.

DESCRIPTION. From Etheridge (1879), 'Shell narrow, very transversely elongate, thin and compressed throughout its length ... cardinal margin very long and slightly arched ... anterior end very much compressed, the margin rounded, posterior end thin, attenuate ... umbones placed close to the anterior end, small, and laterally flattened ... anterior adductor impression fan-shaped, situated very high up under the anterior cardinal margin; umbonal scars very strongly marked, two immediately behind adductor scars in a line ...'.

Morphometrics given in Table 11.

REMARKS. *P. dunstani* is unique within it's fauna, differing from other members of *Unionella* by the extremely elongate nature of the valves. The presence of beak scars illustrates genetic relation to *Unionella*, however, it differs so markedly from them that separation at the generic level is relevant. *P. dunstani* differs from *P. flemingi* by it's smaller size and less tapering profile. The only other species of this genus is *Protovirgus brookvalensis* sp. nov. which differs in being smaller and more rounded posteriorly. The anterior adductor muscle in *P. brookvalensis* sp. nov. is much longer and situated higher than *P. dunstani*. The umbones are more flattened in *P. dunstani* than in *P. brookvalensis* sp. nov.

Protovirgus brookvalensis sp. nov.
(Fig. 6A-F)

ETYMOLOGY. For the type locality, Brookvale quarry.

AGE AND DISTRIBUTION. Late Triassic, formations: Wianamatta Shale. Localities: Brookvale Quarry, NSW.

MATERIAL. HOLOTYPE: AMF19773. PARATYPES: 19805, 43401, 41438, 41442, 41440, 41439, 49805.

DIAGNOSIS. Small, equivalved glauconomid with umbones anteriorly placed. Elongate valve shape with tapering posterior edge. Winged dorsal margin produced by ridge emanating from the umbonal area and terminating toward the

TABLE 11. Morphometrics (in mm) for *Protovirgus dunstani* (Etheridge Jr).

AMF No.	Length	Height	Width	Beak Length
35693	34.7	11.9	?	8.85
35776	37.2	12.2	6.05	8.65
35777	25.8	11.8	4.8	5
35870	40	16.6	8.75	9.05
Mean	34.42	13.12	6.53	7.88

posterior end. Umbonal region anterior with beaks closely set.

DESCRIPTION. Holotype FI9773, is a small equivalved, inequilateral, elongate-ovoid anthracosiid. Umbones anteriorly placed at 1/5 from the anterior end. Beaks weak with no sculpturing. Hinge line straight and long producing a straight dorsal profile. Rounded posteriorly. Anterior end rounded. Muscle scar unknown. Teeth unknown. Subumbonal ridge runs posteroventrally away from the umbo. Fine comarginal growth lines with weak ornamentation.

Morphometries presented in Table 12.

REMARKS. The elongate nature of the valves, anteriorly placed umbones and tapered posterior end place this taxon firmly within *Protovirgus*. Morphological features that differentiate *P. brookvalensis* from *P. dunstani*, the only other member of this genus, are it's smaller size, weakly defined umbones, more rounded posterior end, weaker anterior muscle scars.

?SPHAERIIDAE Jefferys, 1862

Protosphaerium gen. nov.

TYPE SPECIES. *Protosphaerium talbragarensis* gen. et sp. nov. Jurassic, Talbragar Fossil Fish Beds.

ETYMOLOGY. *Proto*, pertaining to this being the first of it's kind. *–sphaerium*, for the genus *Sphaerium*.

DIAGNOSIS. Small, equivalved, ovoid bivalve with beaks subcentral. Fine comarginal growth lines with rugose comarginal ornamentation. Hinge short and convex in lateral profile. Ventral margin rounded to form distinct 'pea shell' like shape.

DESCRIPTION. Small, equivalved, equilateral with fine growth lines. Little or no ornamentation. Shell very thin with umbones just slightly inflated. Ovoid with beak 1/3 length from anterior end. Posterior profile rounded continuous with convex hinge outline. Anterior profile also rounded with a small insignificant lunule. Escutcheon narrow and also insignificant. Hinge short with hinge ligament relatively thick.

TABLE 12. Morphometrics (in mm) for *Protovirgus brookvalensis* sp. nov.

AMF No.	Length	Height	Width	Beak Length
43401	22.5	9.85	?	9.85
41438	23.15	9.95	?	10.7
19773	25	10.5	?	12.1
41442	23.8	8.75	?	11.6
41440	22.4	8.7	?	4.45
41439	21.5	9.2	?	10.55
19805	20.7	9.1	?	8.6
Mean	22.72	9.43		9.69

Muscle scars unknown, presumed weak. Teeth unknown or insignificant.

REMARKS. The pea-shell shaped valves, subcentral beaks, small size and clumping deposition post death, are all characteristics of members of the Sphaeriidae (Kuiper, 1983) and Corbiculidae. As this genus is smaller than those normally found within the corbiculids it is concievable that this taxon belong within the sphaeriid lineage. As the tooth morphology of the type species is unknown it is with some degree of uncertainty that this placement within the Sphaeriidae is given.

Protosphaerium talbragarensis gen. et sp. nov. (Fig. 7C-D)

ETYMOLOGY. For the type locality of Talbragar.

MATERIAL. HOLOTYPE: AMF103934A. PARATYPES: AMF103929, 103935(b), 59823.

AGE AND DISTRIBUTION. Jurassic, formations: Talbragar Fossil Fish Beds. Localities: Talbragar.

DIAGNOSIS. As for genus.

DESCRIPTION. As for genus. Morphometries given in Table 13.

REMARKS. This taxon bears marked affinities to the small freshwater bivalves from the family Sphaeriidae. Uncertainty surrounds the decision to place *Protosphaerium talbragarensis* within the Sphaeriidae, however, it seems plausible that this group has a Jurassic presence in Australia and has remained here since then. Since it fits in no other family and the erection of a new family seems unwarranted, it is here placed within the sphaeriids.

Protosphaerium gianae sp. nov. (Fig. 7A-B)

ETYMOLOGY. For Gian Holmes.

TABLE 13. Morphometrics (in mm) for *Protosphaerium talbragarensis* gen. et sp. nov.

AMF No.	Length	Height	Width	Beak Length
103929	6.9	4.3	?	2.9
103934	11.5	6.8	?	4.25
103935b	10.75	6.25	?	4.2
59823	10.45	6.15	?	4.15
Mean	9.9	5.87	0	4.93

TABLE 14. Morphometrics (in mm) for *Protosphaerium gianae* sp. nov.

AMF No.	Length	Height	Width	Beak Length
38165	9	6.25	?	3.7
103931	5.7	4.1	?	2.5
103934B	6.55	9	?	3.1
103932	7.65	4.5	?	4.1
Mean	7.22	4.71	0	3.1

MATERIAL. HOLOTYPE: AMF38165. PARATYPES: AMF103931, 103932, 103934B.

AGE AND DISTRIBUTION. Jurassic, formations: Talbragar Fossil Fish Beds. Localities: Talbragar.

DIAGNOSIS. Small, equivalved, inequilateral freshwater bivalve of possible corbiculid affinity. Fine conmarginal growth lines and weak ornamentation placed periodically along the valves. Characteristically winged toward the posterior, producing a quadrate lateral profile to the valves. Beaks closely set and anteriorly placed. Hinge long with one thin, indistinct lateral tooth. Cardinals and anterior laterals unknown.

DESCRIPTION. Small, equivalved, inequilateral with fine growth lines. Subtriangular. Some periodic ornamentation produced by thickenings in the shell. Winged posterior produced from ridge originating from the umbonal region. Posterior end produced and somewhat rostrate. Anterior profile rounded. Beaks weak, closely set and placed anteriorly. Hinge weak with one thin indistinct lateral tooth. Cardinals and anterior laterals unknown. Muscle scars unknown, presumed weak. Morphometrics given in Table 14.

REMARKS. Placed tentatively within *Protosphaerium*, this species shares some characters with *Protosphaerium talbragarensis*. Until more material presents itself, this genus provides an adequate position. In some respects, *Protosphaerium talbragarensis* sp. nov. is similar to *Batissa (Batissa) violacea* (Lamark) within the corbiculids. While similar in morphology this is not considered as having close genetic affinity. *Proto. gianae* is much smaller and with reduced hinge length.

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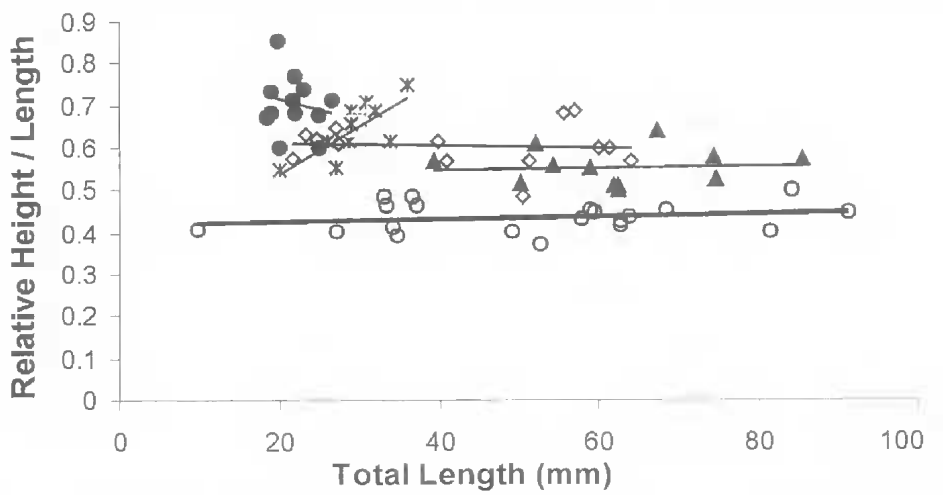

FIG. 8. Bivarate plot of relative height/length, plotted against length for hyriids from the Cretaceous. ● = *Palaeohyridella godthelpi* gen. et sp. nov., ◇ = *Hyridella (Hyridella) macmichaeli*, ✶ = *Hyridella (Protohyridella) goondiwindiensis*, ○ = *Protovirgus wintonensis*, ▲ = *Alaytharia jaqueti*.

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