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FRESHWATER BIVALVES **Review Paper**

Bivalves in a bottleneck: taxonomy, phylogeography and conservation of freshwater mussels (Bivalvia: Unionoida) in Australasia

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Abstract The conservation biology of Australasian freshwater mussels is hindered by lack of a taxonomic framework that employs molecular data as a complement to shell characters, larval forms and internal anatomy. The fauna includes more than 32 known species (30+ Hyriidae, 2 Unionidae), but has not been revised for 55 years, despite minor amendments. The hyriids are relics of Gondwana, represented in Australia and New Guinea by the ancestral Velesunioninae and in Australia and New Zealand by the Hyriinae (Tribe Hyridellini). Many taxonomic and phylogeographic issues await resolution, including the relationships between Australasian and South American species, and between Australian and New Zealand species, and the status of species in New Guinea (including uncertain reports of Unionidae) and the Solomon Islands. Once these are clarified, it will be easier to identify threatened species and evaluate the conservation status of the fauna. At present, only seven taxa are named in the IUCN *Red List* or under national/state legislation, and these are not representative. Threatening processes include altered flow regimes, catchment disturbances, salinisation, pollution and invasive species. While the need for a taxonomic revision is paramount, progress in conservation may depend also upon involving the wider community.

Key words Unionoida · Hyriidae · Unionidae · Australia · Papua New Guinea · West Papua · New Zealand · Solomon Islands · Sahul · taxonomy · biogeography · phylogeny · conservation · threatened species · IUCN Red List · EPBC Act · citizen science

Introduction

Invertebrates are much neglected in biodiversity conservation, in favour of vertebrates with aesthetic, commercial or other human associations (e.g. Cardoso et al., 2011). Yet they account for 95 percent or more of all animal species and are keystones in most ecological systems. Freshwater invertebrates especially are among the most imperilled fauna (Strayer, 2006). Although some conservation policies target ecological communities rather than species (e.g. Nicholson et al., 2009), there remains a fundamental need to understand the identities, origins and relationships of species.

The freshwater mussels (Unionoida) of the Australasian Ecozone are in a taxonomic ‘bottleneck’. The ecozone, as defined by the World Wildlife Fund, includes Australia, New Zealand, the Solomon Islands and New Guinea (Papua New Guinea and Indonesian West Papua). The fauna includes more than 32 known species (30+ Hyriidae, 2 Unionidae) but it has not been revised for 55 years (McMichael & Hiscock, 1958). In the interim there have been nomenclatural changes and descriptions of new species (Walker et al., 2001; Ponder & Bayer, 2004; Fenwick & Marshall, 2006; Graf & Cummings, 2006, 2007). There have also been exploratory studies using molecular methods, including a comparison of species from Australia and New Zealand (Graf & Ó Foighil, 2000) that led to a reappraisal of New Zealand taxa (Fenwick & Marshall, 2006) and other research that exposed still un-named species in Australia (Baker et al., 2003, 2004). These studies demonstrate the hazards in over-reliance on morphological characters, and they underscore the need for a comprehensive revision of the Australasian fauna.

In the absence of a revision, progress in conservation, phylogeography, biology and ecology of the Australasian freshwater mussels has been desultory. In this paper, we summarise current knowledge and highlight problems awaiting resolution, stressing the need for a robust taxonomic framework and warning of the dangers of ‘cherry-picking’ rather than a systematic analysis. We begin with an overview of the current taxonomic framework for Australasian species, and progress to discussions of phylogeography and conservation.

Systematics and phylogeny

Unionoida

Freshwater mussels are bivalves of the subclass Palaeoheterodonta, order Unionoida (variously ‘Unionacea’, ‘Unionida’, ‘Unioniformes’). There have been frequent name changes in the taxonomic literature, leaving many synonyms and re-assignments that are a significant impediment to research. Issues of supra-familial taxonomy are beyond the scope of this paper, and we have adopted the framework provided by Graf and Cummings (2006, 2007), although this is provisional and in some respects contentious (cf. Bogan, 2008; Bogan & Roe, 2008; Hoeh et al., 2009; Bieler et al., 2010; Graf & Cummings, 2010; Carter et al., 2011; Whelan et al. 2011). According to the ‘Mussel Project’ website maintained by Dan Graf and Kevin Cummings (http://www.mussel-project.net; March 2013), the global tallies of valid unionoid species and genera in August 2007 were 858 and 163, respectively.

The Unionoida includes two superfamilies, the Etherioidea and Unionoidea, each with three families. The Etherioidea includes the Etheriidae (Africa, India, Madagascar, South America[1]), Iridinidae (Africa) and Mycetopodidae (Central and South America), and the Unionoidea includes the Hyriidae (Australasia, South America), Margaritiferidae (Africa, Eurasia, North America) and Unionidae (North and Central America, Eurasia, Africa, New Guinea). The distinctions between families emphasize anatomical features, although these may not be synapomorphic and thereby not useful in cladistic analyses. Thus, families are characterized by the number and arrangement of marsupial demibranchs, the form of water tubes and brood chambers in the demibranchs, the presence or absence of a supra-anal aperture and mantle fusion relative to the incurrent and excurrent apertures, and by larval forms (e.g. Heard & Guckert, 1970; Bauer & Wächtler, 2001).

Following Parodiz and Bonetto (1963), the superfamilies have been distinguished by *lasidia* larvae (Etherioidea) or *glochidia* larvae (Unionoidea). Cladistic analyses do not support this division, but there is no consensus (Whelan et al., 2011). Thus, hyriids share some anatomical features with Etherioidea but not with other Unionoidea (Graf, 2000).

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[1] Graf and Cummings (2006, 2007) consider the South American *Acostaea rivolii* as an etheriid, whereas Bogan and colleagues (Bogan & Hoeh, 2000; Bogan & Roe, 2008; Hoeh et al., 2009) regard it as a mycetopodid. This point determines whether or not Etherioidea can be said to occur in South America.

The shared features include fusion of the inner demibranchs to the visceral mass, fusion of the anterior margin of the inner demibranchs to the visceral mass, adjoining the labial palps, mantle fusion between the incurrent and excurrent apertures and larval brooding in the two innermost demibranchs. Unionids (and margaritiferids) brood glochidia, either in the outer demibranchs or in both inner and outer demibranchs; the water tubes may be perforated or not; the mantle is not fused between the incurrent and excurrent apertures and there is a supra-anal aperture.

Inter-familial relationships have been investigated by molecular methods based on COI (cytochrome oxidase subunit I) mitochondrial DNA and 28S nuclear ribosomal DNA sequences (e.g. Hoeh et al., 2002; Graf & Cummings, 2006). The position of Hyriidae within the Unionoida is uncertain (Hoeh et al., 2009; Graf & Cummings, 2010), but there is an emerging consensus that they may belong to the Etherioidea rather than the Unionoidea (Bogan & Roe, 2008).

Hyriidae in Australasia

Subfamilies

Within the Australasian Hyriidae there are two lineages: the Velesunioninae with 16 described species and the Hyriinae (Tribe Hyridellini) with 14 species. This arrangement will remain tentative, however, until the relationships of *Cucumerunio*, *Echyridella* and *Hyridella* in Australia and New Zealand are clarified (see *Trans-Tasman relationships*).

Two subfamilies erected by Iredale (1934) have been synonymized. In the first case, McMichael and Hiscock (1958) retained ‘Lortiellinae’ for *Lortiella froggatti* and *L. rugata*, acknowledging their unusual, elongated shells, but they did not have access to whole specimens. Later reports noted anatomical similarities with Velesunioninae (Hiscock in McMichael, 1967), and glochidia typical of Velesunioninae (Walker et al., 2001; H. A. Jones, unpubl.), and examination of whole specimens led Ponder and Bayer (2004) to conclude that the subfamilies were synonymous. Ponder and Bayer (2004) also confirmed the morphological separation of *L. froggatti* and *L. rugata* and described a third species, *L. opertanea*, citing differences in shell shape but acknowledging the need for molecular data. *Lortiella* spp. thereby are confirmed as Velesunioninae, although there may be subtle anatomical differences (Klunzinger et al., 2013b). The three species occupy separate regions in the Timor Sea and Indian Ocean Drainage Divisions of Western Australia and the Northern Territory.

The second change was to synonymize ‘Cucumerunioninae’ with Hyriinae, based on molecular and morphological evidence (Graf & Cummings, 2006, 2007; cf. Carter et al., 2011). The former subfamily was established by Iredale (1934) for *Cucumerunio novaehollandiae*, and expanded by McMichael and Hiscock (1958) to include *C. websteri* from New Zealand and *Virgus beccarianus* from New Guinea. These species all have conspicuously elongated, sculptured shells and strong, serrated cardinal teeth, although these could be homoplastic traits. The shell sculpture appears as radial ridges in *V. beccarianus* and as lachrymose nodules in *Cucumerunio* spp., although variably so in *C. websteri* (Dell, 1953; McMichael & Hiscock, 1958).

The Australasian Hyriidae therefore include two subfamilies, the Hyriinae and Velesunioninae, differing in shell characters and glochidial morphology. There may be anatomical differences relating to the presence or absence of a perforate gill diaphragm, but this requires clarification (see *High–level phylogeny*). There may also be taxonomic significance in the abundance and distribution of calcified extracellular granules in the mantle tissues, as in *Hyridella depressa* (Hyriinae) and *Velesunio ambiguus* (Velesunioninae) (Byrne, 2000; Colville & Lim, 2003).

Beak and shell sculpture occur in Hyriinae and were presumed absent in Velesunioninae, but this was disproved recently (see *High–level phylogeny*). In Velesunioninae, the hinge teeth typically are ‘lamellar’ (two short cardinals, two long lateral teeth in the left valve, a single cardinal and lateral in the right; e.g. *Velesunio* spp.), but in some species (e.g. *Alathyria* spp.) the cardinals are stronger and grooved and the hinge teeth are of the ‘unionid’ type (McMichael & Hiscock, 1958). In Hyriinae, the hinge dentition typically is ‘unionid’. In Velesunioninae the anterior retractor and adductor muscle scars are fused, whereas in Hyriinae the anterior scars are deeply impressed and separated from the corresponding adductor scar, forming a pit beneath the cardinal teeth. Otherwise, differences in shell morphology are likely to reflect differences in habitats. For example, *Velesunio* spp. often occur in lentic habitats and tend to have comparatively light, inflated shells, whereas most *Alathyria* spp. occur in lotic habitats and have heavier, sometimes dorsally-arched shells (e.g. Walker, 1981a; Balla and Walker, 1991).

The glochidia of about half of the Australasian hyriid species are known, and there appear to be consistent differences between those of Velesunioninae, with an S-shaped tooth on each valve and a larval filament, and Hyridellini, with bifurcate teeth and usually without a filament (Walker, 1981a; Jones et al., 1986; Jupiter & Byrne, 1997; Walker et al., 2001;

Ponder & Bayer, 2004; Jones, 2013; Klunzinger et al., 2013a). The glochidia of *Echyridella* are exceptional as they do possess a larval filament (Percival, 1931; Jones, 2013). The glochidia of *H. australis* and *C. novaehollandiae* are unusually small, with modified teeth that are much reduced in the latter species (Jones et al., 1986). Thus, glochidial morphology is diagnostic for families and subfamilies and, pending more study, it may also differentiate genera and species (cf. Pimpão et al., 2012).

TABLE 1 NEAR HERE

PLATES I–II NEAR HERE

Species

The shells and glochidia of some species from Australia and New Guinea are shown in Plates I–II.

Known species of Australasian Hyriidae are listed in Table 1. The list owes a strong debt to McMichael and Hiscock (1958), and it is consistent with the framework of Graf and Cummings (2006, 2007) except for changes to *Echyridella* (see *Hyriidae in New Zealand*) and the omission of “*Velesunio ovata* (Haas, 1910)”, recognized by some authors (e.g. Graf & Cummings, 2007) but regarded by McMichael (1956: 40) and McMichael and Hiscock (1958: 481) as a species ‘of doubtful validity’, ostensibly from New Guinea.

The 1958 revision has been remarkably robust, as its concepts of species and other taxa were not clearly articulated by modern standards and it pre-dated modern ideas of cladistic analysis (and continental drift). Its longevity partly reflects a continued failure to integrate molecular and morphological systematics. The revision acknowledged that anatomical features are conservative within families, and it relied heavily on adult shell morphology to characterize genera, species and subspecies. Given the propensity of shell shapes to vary with local environments, diagnoses for lower taxa must be regarded cautiously; subspecies in particular are not considered here.

The number of described species of Hyriidae in Australasia presently is 30, and could increase to 32 if known ‘cryptic’ species of *Velesunio* spp. in central Australia were formally described (Baker et al. 2003, 2004; cf. Hughes et al., 2004). In the Lake Eyre Basin, the genus *Velesunio* is represented by at least four species, including the widespread *V. ambiguus* and three taxa morphologically similar to (and possibly including) *V. wilsonii*. It is not clear whether *V. wilsonii* is among the three taxa, because there are no genetic data for museum specimens of that species (Baker et al., 2003). The three un-named taxa are sympatric in some areas, yet form divergent mitochondrial DNA lineages and show corresponding fixed differences at allozyme loci, suggesting that they are separate species. Baker et al. (2004) showed also that *Alathyria jacksoni* is genetically distinct from *V. ambiguus* in the Murray-Darling Basin, where they are sympatric, but that it is allied to one of the cryptic *Velesunio* 'species' in the Lake Eyre Basin. They suggested that the genera *Alathyria* and *Velesunio* are in need of revision.

In general, the phylogenetic data obtained by Baker et al. (2003, 2004) did not match the shell characters. Indeed, the morphological differences between the taxa were subtle and may not be detected using the standard metrics employed by McMichael and Hiscock (1958). The Lake Eyre Basin fauna therefore awaits further study. Situations like this—where species are identified using genetic criteria but not formally described—should not be allowed to decouple progress in taxonomy and cladistics.

Trans–Tasman relationships

Graf and Ó Foighil (2000) examined nucleotide sequences in hyriids from either side of the Tasman Sea, a 2000-km barrier between Australia and New Zealand. They compared selected Velesunioninae ('Velesunionini') from Australia, Hyridellini from Australia and New Zealand and other Hyriinae from South America with Margaritiferidae and Unionidae as out-groups. Their analysis indicated that evolution of the Hyriidae pre-dated the break-up of Gondwana, 80+ million years ago, and that New Zealand species are relicts rather than colonizers, contrary to popular belief. Hoeh et al. (2002) also suggested that the Unionoida are of Gondwanan origin, and that the Hyriidae are the most primitive of extant taxa. The latter study has been criticised for its dependence on COI, a homoplastic sequence at this phylogenetic level, and the issue is not fully resolved (cf. Hoeh et al., 2009; Graf & Cummings, 2006, 2010). Within the constraints of these analyses, the evidence points to the Hyriidae as a monophyletic clade more closely related to Etherioidea rather than Unionoidea. Under this arrangement, the Etherioidea and Hyriidae share a number of anatomical synapomorphies (Graf & Cummings, 2006). The Hyriidae have glochidia rather than lasidia as in Etherioidea, but these have distinctive sub-triangular valves and S-shaped hooks without microstylets, unlike the glochidia of other Unionoidea. Within the Hyriidae, the basal lineage appears to be the Velesunioninae of Australia and New Guinea, as suggested by McMichael and Hiscock (1958). It is curious, then, that the only extant hyriid species on both sides of the Tasman are Hyriinae (Hyridellini) and not Velesunioninae.

Fossil Hyriidae are recorded from throughout the Mesozoic Era in Australia, and the state of preservation in some cases is sufficient to reveal hinge dentition and shell sculpture, and to distinguish Velesunioninae from Hyridellini (e.g. Hocknull, 2000). There are records of fossil Hyridellini in New Zealand (e.g. Hayward, 1973; Pole et al., 2003), including *Megalovirgus flemingi* from the Cretaceous of New Zealand and Victoria (Thompson & Stilwell, 2010). There are also claims of fossil Velesunioninae from New Zealand (McMichael, 1957, 1958; McMichael and Hiscock, 1958), but the specimens are not well-preserved and confirmation is required. Clearly, there is a need for an updated checklist and revision of fossil taxa from Australia and New Zealand. Ideally, this would be extended to South America, although Mesozoic records there are scant (cf. Parodiz, 1969; Wesselingh et al., 2006).

The genetic study by Graf and Ó Foighil (2000) indicated a clear separation between two subgenera, *Echyridella* and *Hyridella,* within the genus *Hyridella*. Fenwick and Marshall (2006) promoted *Echyridella* to genus, and the widespread New Zealand species *H.* (*E.*) *menziesi* (*sic*) became *E. menziesii*. They resurrected *Echyridella lucasi* from synonymy with *E. menziesii*, based on a shell dredged from Lake Manapouri on the South Island in 1902 but not recorded subsequently. They also described a new species, *E. onekaka*, from the South Island.

According to the published record, therefore, *Echyridella* includes three species, and there are two other species, namely *Cucumerunio websteri*, from the North Island, and *Hyridella aucklandica*, from both North and South Islands. This may change soon, however, following a reappraisal of the New Zealand fauna (B. A. Marshall, Museum of New Zealand Te Papa Tongarewa, pers. comm.), utilising morphological (B. A. Marshall, unpubl.) and molecular (COI) data (Fenwick, 2006). The status of *E. onekaka* is not in doubt, but the revision is likely to show that *E. lucasi* should be synonymized with *E. menziesii* and that *C. websteri* should be synonymized with *H. aucklandica* as *E. aucklandica*. If these proposals are supported, the New Zealand fauna would consist of three species in a single endemic genus, *Echyridella*.

Unionidae in Australasia

McMichael and Hiscock (1958) assigned the anomalous *Haasodonta fannyae* to the Rectidentinae, a subfamily of Unionidae that is widespread in south-east Asia. They had access to shell material only, and a single shell was judged sufficiently distinctive to warrant description of a second species, *Ha. vanheurni*. Both species are recorded only from the Merauke and Bian rivers in Indonesian West Papua, and apparently have not have been collected since about 1956 (McMichael & Hiscock, 1958: 483). The claim that *Haasodonta* spp. are members of the Unionidae must be viewed with some scepticism, but, if it proves correct, these are the only known unionids east of Lydekker's Line, separating New Guinea and the islands of 'Wallacea' (cf. Wallace's Line: Lohman et al., 2011). This issue is highly significant for taxonomy and phylogeography and new material, including whole specimens, is needed for resolution.

High–level phylogeny

In the current phylogenetic view, the Velesunioninae are ancestral (or nearest to the ancestral lineage), and distinguished from Hyriinae by molecular characters (Graf & Ó Foighil, 2000) and the absence of radial beak sculpture (Graf & Cummings, 2006). This perspective needs to be reviewed in light of recent studies. First, evidence is accumulating to show that glochidial morphology is another feature to distinguish Hyriinae and Velesunioninae (e.g. Jones, 2013). Second, the significance of a perforate gill diaphragm needs to be clarified. This is cited as a common character in Hyriinae and Velesunioninae (Graf & Cummings, 2006), but it is absent in *Echyridella menziesii* (McMichael & Hiscock, 1958: 463) and *E. aucklandica* (Jones, 2013), and its presence in *Cucumerunio* and *Hyridella* needs confirmation (McMichael & Hiscock (1958) refer to it as 'minutely perforate'). If it proves to be absent in Hyriinae that would be another synapomorphy for Velesunioninae.

A third point is that the significance of beak (umbo) sculpture needs to be reconsidered. While many Unionoida do show beak sculpture, it has been assumed absent in Velesunioninae (and some other taxa). It is an unreliable feature in taxonomy because it is prone to abrasion through burrowing in sediment, and juvenile shells are most likely to show a true picture. Following Graf and Cummings (2006), smooth umbos are seen as a plesiomorphic character to distinguish Velesunioninae from Hyriinae, which have V-shaped sculpture. This assumption has been overturned by Zieritz (2010) and Zieritz et al.

(2013a), who showed that V-shaped sculpture is the ancestral state and that other types, including smooth umbos, are derived characters. Further, Zieritz et al. (2013b) described beak sculpture in two velesunionine species, evident as radiating lines of nodules in *Alathyria* cf. *pertexta* and as elaborate V-/W-shaped ridges in juvenile *Westralunio carteri*, and confirmed its absence in two other species (*Lortiella froggatti*, *Velesunio wilsonii*). These observations should now be extended to other species.

Phylogeography

Global diversity and distribution

While this paper is focused on the Australasian hyriid fauna and issues awaiting resolution in that context, a complete phylogeographic understanding will require new linkages in knowledge of the faunas of Australasia and South America. Notwithstanding important initiatives by North American colleagues, cited above, austral researchers have tended to work independently. There are exciting opportunities for international collaborations to elucidate the unionoid legacies of Gondwana; indeed, a shared taxonomic framework is a prerequisite for robust revisions of regional faunas.

The Hyriidae are relicts, isolated by the separation of South America from Gondwana (130–100 million years ago), and the separation of New Zealand from Antarctica (130–85 million years) and Australia from Antarctica (80 million years). Hyriids in Australasia are represented by the Velesunioninae (16 known species) and the Hyriinae, shared with the Neotropical Ecozone (Central and South America, the Caribbean region). Following Graf and Cummings (2007), the Hyriinae (58 species) include four ‘tribes’, the Hyridellini in Australasia (14 species) and the Castaliini (12 species), Hyriini (4 species) and Rhipidodontini (28 species) in South America. The Neotropical fauna also includes species of Etheriidae[2], Mycetopodidae and Unionidae, making a total of 208 species of Unionoida.

Australasian distribution

Although Australia and New Zealand have been separated geologically for more than 80 million years, mainland Australia has been separated from Tasmania and New Guinea for a mere 10–12,000 years. New Caledonia also may be considered part of Australasia, but

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[2] As noted, there is doubt over inclusion of Etheriidae in the South American fauna.

freshwater mussels do not occur there. From a biogeographic perspective, mainland Australia, Tasmania, New Guinea (including Aru Islands, Raja Ampat Islands) and the Solomon Islands are parts of one ecozone often referred to as 'Sahul' (e.g. Whittaker & Fernández-Palacios, 2007).

Species of Velesunioninae in New Guinea are confined to the main island, and are absent from the Solomon Islands, but they occur throughout Australia. The most widespread velesunionine species is *Velesunio wilsonii*, found across the northern half of Australia and apparently in New Guinea (where a single specimen is recorded: McMichael, 1956; McMichael & Hiscock, 1958). Its range is rivalled by *V. angasi* in northern Australia and by *V. ambiguus* in eastern Australia. The apparent disjunct distribution of *Westralunio*, including two species in New Guinea and another in remote southwestern Western Australia, is an intriguing puzzle for biogeographers (e.g. Klunzinger, 2012a).

Species of Hyriinae (Hyridellini) occur from the island of Misool (Raja Ampat Islands) in the west across New Guinea to the Solomon Islands in the east. The spread of *Hyridella guppyi* between southern New Guinea and islands in the Solomons group presumably was facilitated by land bridges, or dispersal by humans or host fish. There are no extant species on the Aru Islands, but 9750-year old shells of *H. misoolensis* are known from an archaeological site at Liang Nabulei Lisa, a limestone cave on one of the islands, Pulau Kobroor (O'Connor et al., 2006). Otherwise, Hyridellini occur in coastal eastern Australia, including northern Tasmania, and New Zealand. They are conspicuously absent from inland Australia and the western half of the continent.

The hyriid fauna of New Guinea (and the Solomon Islands) is very poorly known. It includes several old, unconfirmed records of shells rather than whole animals, but the apparent diversity of species rivals that of southeastern Australia. Until further material becomes available, the taxonomic 'bottleneck' for Hyriidae will remain. Claims of Unionidae (*Haasodonta* spp.) there are also intriguing. The challenge for adventurous malacologists in New Guinea is akin to that described by mammalogist Tim Flannery in *Throwim Way Leg* (Flannery, 1998).

FIGURE 1 NEAR HERE

Regional assemblages

The distributions of species in Australasia are shown in Figure 1. These correspond broadly to major climatic zones, with anomalies due perhaps to past vicariant events. Patterns may be obscured, of course, by errors in taxonomy. The Velesunioninae are widespread in Sahul, and the Hyridellini occur from New Guinea to coastal eastern Australia and in an arc from the Solomon Islands to New Zealand. New Guinea and eastern Australia therefore are a zone of overlap for the two lineages.

The ‘fluvifaunula’ concept identified 11 subregions in Sahul (Iredale & Whitley, 1938), following drainage divides and characterised by mussels and other freshwater fauna. A later review suggested that freshwater mussels provide only limited support for this idea (Walker, 1981b), and it has not been further developed. The concept of ‘freshwater ecoregions’ defined by the distributions of fish (Abell et al., 2008) might be applied to mussels. Another regionalization is ventured by the ‘Mussel Project’ (http://www.mussel-project.uwsp.edu), suggesting separate subregions for New Guinea and New Zealand, and for eastern and western Australia. In this case the east–west divide is somewhat arbitrary and probably not significant for biogeography (compare, for example, the distributions of *V. angasi* and *V. wilsonii*: Fig. 1).

In Australia, some drainage basin boundaries are topographically ill-defined and would not have been significant barriers to dispersal of freshwater fish or mussels. Most basins support no more than 2–3 mussel species, usually species with more extensive geographic ranges. Half of all Australian species, mainly members of the Hyridellini, occur in the mesic crescent of the southeastern coast. *Lortiella* species are restricted to the northwest. An assemblage led by *V. angasi* extends across the northern monsoonal zone. The northeastern coastal region shares species with the southeast, and with the inland Lake Eyre and Murray-Darling basins.

McMichael and Hiscock (1958) suggested that the geographic ranges of *Hyridella australis*, *H. depressa* and *H. drapeta* were similar, even sympatric, but later records show that *H. drapeta* occurs mainly east of the Otway Ranges, Victoria, whereas the other congeners extend from the Mitchell River, eastern Victoria, to southeastern Queensland (Jones & Byrne, 2013). *Hyridella depressa* and *H. drapeta* tend not to cohabit; for example, *H. depressa* is abundant in the Hawkesbury-Nepean river (New South Wales), but virtually absent from the neighbouring Shoalhaven and Hunter rivers.

Part of the explanation may be that *H. australis*, *H. drapeta* and *H. depressa*, respectively, are associated with habitats of increasing current velocity (Jones & Byrne, 2013). The exclusion of these species, indeed all Hyridellini, from the inland Murray-Darling Basin might be due to intolerance of salinity and erratic river flows (Walker, 1981a).

Velesunio ambiguus, typically an inland species, is distributed patchily in eastern coastal rivers (Fig. 1). It is one of the most widespread Australian species, with broad tolerances including a capacity to endure drought (Walker, 1981a). Its presence on either side of the continental divide invites questions about the roles of vicariance and dispersal in its distribution, but molecular data are needed to validate (and possibly answer) these hypotheses. Tectonism and river capture may be invoked, but there is little evidence in support (e.g. Bishop, 1995), and the same applies to speculations about dispersal by fish. In general, the apparent lack of strict host preferences suggests that there are not close associations between the distributions of particular mussel and fish species. For example, the distribution of Australian bass (*Percalates novemaculeata*), a host for *Cucumerunio novaehollandiae*, extends 800 km southward of the limit for that species. Similarly, flathead gudgeon (*Philypnodon grandiceps*) and Australian smelt (*Retropinna semoni*) are much more widely-distributed, respectively, than the associated *H. drapeta* and *Alathyria profuga*.

TABLE 2 NEAR HERE

Conservation

Threatened species

Seven Australasian freshwater mussel taxa are listed as ‘threatened species’ by the International Union for the Conservation of Nature (IUCN), or under national legislation (Australia: *Environment Protection & Biodiversity Conservation Act 1999* (EPBC Act); New Zealand: *Wildlife Act 1953*, *Conservation Act 1987*) or under Australian State legislation or policy (Table 2). Information for Indonesia, Papua New Guinea and the Solomon Islands is less accessible or non-existent, and is not considered here.

The IUCN *Red List of Threatened Species* (http://iucnredlist.org; March 2013) is an international standard for biodiversity conservation, based on information about population size, generation length, rate of decline, extent of occurrence and area of occupancy. Nominations are formally assessed and qualifying taxa are assigned to a category ('Data Deficient', 'Least Concern', 'Near Threatened', 'Vulnerable, 'Endangered', 'Critically Endangered', 'Extinct in the Wild', 'Extinct'). Although governmental legislation in Australia does not accord fully with IUCN, the criteria and categories are not very different (e.g. http://www.environment.gov.au/threatened; March 2013). There are processes underway to reconcile parts of the EPBC Act with IUCN criteria, and to align State and Federal listings.

Four Australian taxa are on the Red List: three are 'Data Deficient' and the other (*Westralunio carteri*) is 'Least Concern' (Table 2). *Hyridella glenelgensis* is not included, but it is 'Critically Endangered' under Federal legislation and 'Endangered' under State legislation. There are no New Zealand species on the Red List, and although three taxa are nationally listed they are likely to be synonymized (see *Trans-Tasman relationships*; cf. Tables 1-2). The current Red List therefore is not fully representative of the conservation status of the regional freshwater mussel fauna. Several species, particularly those from New Guinea, could be admitted as 'Data Deficient', and others, including *H. glenelgensis* and *W. carteri*, warrant a higher rank. The status of these two species is outlined below, to illustrate the data needed to further prosecute arguments for listing.

Hyridella glenelgensis is a small species confined to the Glenelg River system of southwestern Victoria and southeastern South Australia. It was rarely reported from its discovery in 1898 until 1990, and again in 2000, when fewer than 1000 individuals were located in the lower reaches of a small tributary (Walker et al., 2001; Playford & Walker, 2008). The restricted 'area of occupancy' (1 km^2) and small numbers were significant factors in listing the species as 'Critically Endangered' under the EPBC Act. Local threats include flow diversions, land clearance, stock access to the stream channel and riparian areas (hence trampling, bank erosion), salinisation and the predatory common carp, *Cyprinus carpio*. Although drought is not a 'threatening process' under the EPBC Act, because it is seen as a stochastic rather than anthropogenic phenomenon, there was a severe drought in the decade before 2010 and many empty shells were cast up along the stream banks. A survey by the present authors in December 2012, after the drought had broken, showed that live mussels still remained, with evidence of new recruitment.

This species is closely allied to *H. narracanensis*, found in the same region and in northern Tasmania (Smith, 2005), and named on the Red List as a 'Data Deficient' species (Table 2). Although shell characters differ between the species, preliminary mitochondrial DNA analysis suggests little genetic divergence (Playford & Walker, 2008) and they may prove to be ecophenotypes. The ecology and demography of *H. narracanensis* are little known, but it is rare and the few known populations are threatened by agriculture and urbanisation (Smith, 2005; H. A. Jones & M. W. Klunzinger, unpubl.).

Westralunio carteri is the sole species of freshwater mussel in southwestern Western Australia. It is presently not listed under the EPBC Act, but is a Priority 4 species (‘Rare, near threatened and other taxa in need of monitoring’) under State policy (Table 2). It was assessed as ‘Vulnerable’ on the Red List in 1996, but later relegated to ‘Least Concern’. The rationale was that the species is ‘…widespread in Western Australia, is a habitat generalist, and is resistant to organic pollution’, although it ‘…is highly sensitive to salinization and both its populations and habitats should be monitored to ensure future declines … are spotted early’ (Köhler, 2011).

This view was challenged by Klunzinger (2012), citing new evidence that *W. carteri* has disappeared from half of the sites where it formerly did occur, and that it has undergone nearly a 65 percent reduction in ‘extent of occurrence’ in 50 years. The species typically occurs in the freshwater reaches of perennial rivers, but there is widespread salinisation of soil and water owing to vegetation clearance and a long-term decline in rainfall (e.g. State of the Environment Committee, 2011). Tolerance trials show that the adult mussels succumb to drying (aerial exposure) within 5–10 days, confirming their need for permanent water, and that they do not tolerate salinities above 3–4 g L^{-1}. Given these data, and evidence of a continuing decline, Klunzinger (2012) claimed that there is a case to argue for ‘Endangered’ status on the Red List and to reconsider the State listing. The species recently has been nominated for assessment under the EPBC Act (M. W. Klunzinger, unpubl.).

At first encounter, the documentation needed to support an EPBC or IUCN nomination seems daunting, but while additional information may expedite assessment, the processes address only a small number of explicit criteria. Under the EPBC Act, for example, nominations are assessed against five criteria, and species are categorized according to the highest-ranking criterion that is met. The EPBC criteria, like those for the Red List, refer to population size, geographic range and area of occupancy of species, to the rates of decline in populations and the environment and to the likelihood of extinction (http://www.environment.gov.au/threatened). A nomination that meets even one criterion is sufficient for listing.

Threatened ecological communities

Under the EPBC Act, an ecological community in Australia may be listed as threatened (‘Vulnerable’, ‘Endangered’, ‘Critically Endangered’) if it meets one or more of six criteria (http://www.environment.gov.au/threatened). These refer to the extent and rate of decline in the geographic distribution of the community (or its environment, or a key species) and the likelihood that the community (or its environment, or a key species) could be lost due to a threatening process. An ecological community nomination embraces all resident native flora and fauna, and thereby sidesteps problems associated with unfamiliar species and uncertain taxonomy. Some nominations now being assessed include significant freshwater mussel populations.

Threatening processes

The global decline in freshwater mussel biodiversity has been attributed to the combined effects of over-harvesting, invasive species and water pollution, altered flow regimes and other forms of habitat degradation (e.g. Vaughn & Taylor, 1999; Downing et al., 2010; Nobles & Zhang, 2011); all are likely to intensify in the future, especially with the advance of global warming. In Australasia, harvesting for button manufacture or pearl nuclei has never been significant as mussel populations are sparse and patchily distributed, the shells vary in thickness and often are discoloured by mineral inclusions. There is some evidence of impacts from dams and weirs (e.g. Walker et al., 2001, 2006; Brainwood et al. 2008b; DPIPWE, 2009), but not on the scale reported from North America (e.g. Vaughn et al., 1999). In Australia, invasive bivalves like the zebra mussel (*Dreissena polymorpha*) and Asian clam (*Corbicula fluminea*) do not occur, but in the Murray-Darling Basin the alien common carp (*Cyprinus carpio*) is a predator on benthic invertebrates (Koehn, 2004), including juvenile mussels, and there is some evidence that carp (and goldfish, *Carassius auratus*) may not be hosts for glochidia (Walker et al. 2001; Klunzinger et al., 2012a). Pollution is significant in localised, urban areas, but the effects of altered flow regimes and habitat degradation and fragmentation are more widespread (e.g. State of the Environment Committee, 2011). Table 3 provides a summary guide to factors affecting freshwater mussel populations in Australasia, and a challenge for ecologists: which of these factors potentially are ‘Key Threatening Processes’?

TABLE 3 NEAR HERE

In Australia, a Key Threatening Process under the EPBC Act is one that could prejudice the survival, abundance or evolutionary development of a native species or ecological community. In effect, it could cause a species or community to become eligible for listing as threatened, or it could advance the category of one already listed. The evidence supporting a nomination needs to demonstrate cause and effect, ideally with quantitative measurements at appropriate scales of space and time, depending on the nature of the process and the species or community. Recognition of a Key Threatening Process is a first step toward managing the impact; it may lead, for example, to a Threat Abatement Plan (http://www.environment.gov.au/threatened). Most of the processes that affect freshwater mussel populations (and other inland aquatic fauna) are understood in general terms, but surprisingly few are listed under the EPBC Act. Ecological science and resource management may have different agendas, but this is one area of convergence and ecologists need to provide more substantive data.

Prospectus

The worldwide decline of freshwater mussels parallels declines among other fauna, and progress in biodiversity research and conservation is not keeping pace (Strayer, 2006; Downing et al., 2010; Vaughn, 2010). We may warn of the consequences and argue for redress on ethical, philosophical, cultural, economic and ecological grounds, even for species without commercial value, and we may point to a lack of investment and commitment by governments, grant agencies and research institutions. We can show that freshwater mussels are threatened by a multitude of stressors, mainly of human origin, and that managing these will have some effect. These are valued contributions, but they may achieve no more than incremental progress because they depend, ultimately, on the values of everyday people. Until more members of the public become actively interested in less familiar species, like freshwater mussels, and more engaged in monitoring and conservation, progress will be slow. The process is facilitated by scientists, teachers and others able to communicate their enthusiasm and knowledge, and there are relevant reports, fact sheets and blogs on the Internet portals of community groups, not-for-profit organizations, online media, government departments, museums and universities throughout Australia and New Zealand (e.g. http://www.musselwatchwa.com; www.arkive.org/carters-freshwater-mussel/westralunio-carteri/; www.environment.nsw.gov.au/animals/mussels.htm; collections.tepapa.govt.nz; March 2013). Greater involvement of ‘citizen scientists’ (e.g. Bell et al., 2008) could catalyse new empathy for mussels and other little-known species, and entrain support from institutions. It is axiomatic, however, that to conserve these species we need to recognize and understand them, hence the need for a revised taxonomic framework.

Conclusion

This paper began with the premise that the ecology and conservation of Australasian freshwater mussels are hindered by lack of a modern taxonomic framework, particularly one using molecular data as a complement to shell characters, larval forms and anatomy. The ‘bottleneck’ is emphasized by the scarcity of material for rare taxa and regions that, like New Guinea, are *Terra Incognita* for freshwater malacology. Yet taxonomic ‘errors’, from misinformation or lack of data, can have cascading effects to confound research in ecology and other dependent disciplines (e.g. Bortolus, 2008). Progress will be hindered until the taxonomic impediment is removed.

The paramount need is for a comprehensive, systematic revision of the regional fauna, rather than a ‘cherry-picking’ approach. As only limited genetic material is available in existing museum collections, a revision will require intact topotypes, where possible, so that synonymies can be determined and documented. For rare or threatened species, tissue samples and dead shells should be substituted to avoid adverse impacts on local populations. Once the nature and relationships of species are clarified, it will become easier to argue for listing freshwater mussels as threatened species, where appropriate. There is abundant evidence of declines of freshwater mussels in other ecozones (e.g. Downing et al., 2010), and Palaearctic taxa are well-represented on the IUCN Red List, but for most Australasian species there are too few data to sustain more than listing as ‘Data Deficient’ (cf. IUCN Standards & Petitions Subcommittee, 2011). Under IUCN criteria, data-deficient species are known from only a few specimens or localities, with scant population data, or are of uncertain taxonomic status. The category is not a ‘catch all’, as little-known taxa can be assigned to a threat category on the basis of habitat degradation or other factors, and that may be the best interim course of action. Mere listing by IUCN or government does not secure the survival of species, of course, but it may help to rescue some from obscurity. For Hyriidae, the consequences of inaction are clear; indeed, we may have already incurred a significant ‘extinction debt’ (cf. Haag, 2010). Freshwater mussels are founding members of the Gondwana fauna; they outlived the dinosaurs, but will they survive the challenges of the modern era?

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Table 1 Freshwater mussels (Hyriidae) of Australasia (A: Australia; NG: New Guinea (Papua New Guinea, Indonesian West Papua), SI: Solomon Islands; NZ: New Zealand)

Hyriinae: Hyridellini	
Cucumerunio novaehollandiae (Gray, 1834)	A
Hyridella australis (Lamarck, 1819)	A
Hyridella depressa (Lamarck, 1819)	A
Hyridella drapeta (Iredale, 1934)	A
Hyridella glenelgensis (Dennant, 1898)	A
Hyridella narracanensis (Cotton & Gabriel, 1932)	A
Hyridella misoolensis (Schepman, 1897)	NG
Hyridella guppyi (E. A. Smith, 1885)	NG, SI
Virgus beccarianus (Tapparone Canefri, 1883)	NG
Echyridella onekaka Fenwick & Marshall, 2006	NZ
Cucumerunio websteri (Simpson, 1902)[a]	NZ
Hyridella aucklandica (Gray, 1843)[a]	NZ
Echyridella menziesii (Gray, 1843)[b]	NZ
Echyridella lucasi (Suter, 1905)[b]	NZ
Velesunioninae[c]	
Alathyria condola Iredale, 1943	A
Alathyria jacksoni Iredale, 1934	A
Alathyria profuga (Gould, 1851)	A
Lortiella froggatti Iredale, 1934	A
Lortiella opertanea Ponder & Bayer, 2004	A
Lortiella rugata (G. B. Sowerby II, 1868)	A
Velesunio ambiguus (Philippi, 1847)	A
Velesunio angasi (G. B. Sowerby II, 1867)	A
Velesunio moretonicus (Reeve, 1865)	A
Westralunio carteri Iredale, 1934	A
Alathyria pertexta Iredale, 1934	A, NG
Velesunio wilsonii (Lea, 1859)[d]	A, NG[d]
Microdontia anodontaeformis (Tapparone Canefri, 1883)	NG
Velesunio sentaniensis (Haas, 1924)	NG
Westralunio albertisi (Clench, 1957)	NG
Westralunio flyensis (Tapparone Canefri, 1883)	NG
Unionidae: Rectidentinae	
Haasodonta fannyae (Johnson, 1948)	NG
Haasodonta vanheurni McMichael & Hiscock, 1958	NG

[a] Likely to be synonymized as *Echyridella aucklandica* (see text)

[b] Likely to be synonymized as *Echyridella menziesii* (see text)

[c] "*Velesunio ovata*" is omitted (see text)

[d] Includes cryptic species in central Australia (Baker et al., 2003, 2004; Hughes et al., 2004). One specimen only is recorded from NG (McMichael & Hiscock, 1958: 399)

Table 2 Status of Australasian Hyriidae on the IUCN *Red List*[a] and in national/State legislation. No species are listed for New Guinea or the Solomon Islands

Species	**IUCN**	**National/ State legislation**	**Reference**
Alathyria jacksoni	Data Deficient	…	Köhler, 2011
Cucumerunio novaehollandiae	Data Deficient	…	Cummings & Van Damme, 2011
Cucumerunio websteri delli[b]	…	Data Deficient[b]	Hitchmough et al., 2007
Cucumerunio websteri websteri[b]	…	Data Deficient[b]	Hitchmough et al., 2007
Echyridella menziesii[b]	…	Gradual Decline[b]	Butterworth, 2008; Rainforth, 2008
Hyridella glenelgensis	…	Critically Endangered[c, d]	Playford & Walker, 2008; DSE, 2009; DSEWPaC, 2012
Hyridella narracanensis	Data Deficient	…	Van Damme, 2011
Westralunio carteri	Least Concern	Priority 4[e]	Köhler, 2011; DEC, 2012

[a] *Red List of Threatened Species*, v. 9.0 (September 2011)

[b] New Zealand: *Wildlife Act 1953*; *Conservation Act 1987* (note pending synonymies: Table 1)

[c] Commonwealth of Australia: *Environment Protection & Biodiversity Conservation Act 1999*

[d] Victoria: *Flora & Fauna Guarantee Act 1988*

[e] Western Australia: Department of Environment & Conservation, Current list of threatened and priority fauna rankings (February 2012)

Table 3 Processes that threaten freshwater mussel (and host fish) populations in Australasia, with selected references

Causes		Consequences	References
River regulation	Diversions	Less connectivity	Hughes et al., 2004
	Water levels	Drawdown (‘de-watering’), stranding	Jones, 2007; DPIPWE, 2009; Klunzinger, 2012
	Flow regime	Changed hydrology in space/time	Gehrke & Harris, 2001; Walker et al., 2001; Jones, 2007; Brainwood et al., 2008a,b; DPIPWE, 2009
	Dam discharge	Cold water; shorter growing season	Walker et al., 1978, 2001, 2006
	Barriers	Less connectivity; less mobility for host fish; changed flow/water levels	Hughes et al., 2004; Klunzinger et al., 2012b
	Sediment	Erosion, siltation	Erskine, 1985; Brierley et al., 1999; Brainwood et al., 2008a,b
	Woody debris	Scouring; exposure to currents	Playford & Walker, 2008
Pollution	Pesticides	Accumulation; sub-lethal toxicity	Hickey et al., 1997
	Eutrophication	Nutrient enrichment; ammonia; low oxygen, algal toxins	Ogilvie & Mitchell, 1995; Byrne, 1998; Butterworth, 2008; Clearwater et al., 2012; Klunzinger, 2012
	Mining waste	Heavy metal accumulation; acidity (calcium metabolism); uranium (reproduction)	Humphrey, 1995; Hettler et al., 1997; Markich et al., 2001; Polhemus & Allen, 2007
	Blackwater	Low oxygen	Sheldon & Walker, 1989
	Oil	Spills, mining operations	Polhemus & Allen, 2007
Catchment disturbance	Sediment transport	Unstable sediments: erosion, siltation (agriculture, logging, mining, gravel extraction)	Brierley et al., 1999; Prosser et al., 2001; Polhemus & Allen, 2007; Brainwood et al., 2008a,b; Jones & Byrne, 2010, 2013; Klunzinger et al., 2012b
	Land use	Loss of riparian vegetation	Brainwood et al., 2006

Acid sulfate soils		Acidity (calcium metabolism)	Kingsford et al., 2010
Livestock	Erosion, nutrients	Unstable sediments, scouring, burial, pugging, trampling, organic pollution, eutrophication	Erskine, 1985; Smith, 2005
	Riparian vegetation	Destruction of plants; loss of shade, instream debris	Polhemus & Allen, 2007; Jones & Byrne, 2010
Salinisation	Secondary salinisation	Toxicity; loss of biodiversity	Kendrick, 1976; Klunzinger, 2012
	Salt incursions	Upstream penetration of saline water	Klunzinger, 2012
	Groundwater extraction	Less freshwater discharge to salinised channels	Beatty et al., 2010; Klunzinger, 2012
Alien species	Common carp, goldfish	Invasive ‘ecosystem engineers’, predators on juveniles, may not be glochidial hosts	Walker et al., 2001; Klunzinger et al., 2012a
	Salvinia	Low oxygen	Jones & Byrne, 2010
	Feral pig	Predation	Barrios-Garcia & Ballari, 2012
Climate change	Temperature	Higher seasonal temperatures	Hobday & Lough, 2011; Morrongiello et al., 2011
	Rainfall	Less average rainfall, hence runoff; more frequent extremes, hence drought/flood	
	Ecological communities	Loss of biodiversity; spread of alien species	

Figure 1. Geographic ranges of Hyriidae (Hyridellini, Velesunioninae) and Unionidae (Rectidentinae) in Australasia, from museum records and survey data: (a) Hyridellini, (b) Velesunioninae (*Alathyria*, *Lortiella*, *Westralunio*) and (c) Velesunioninae (*Microdontia*, *Velesunio*) and Rectidentinae (*Haasodonta*)

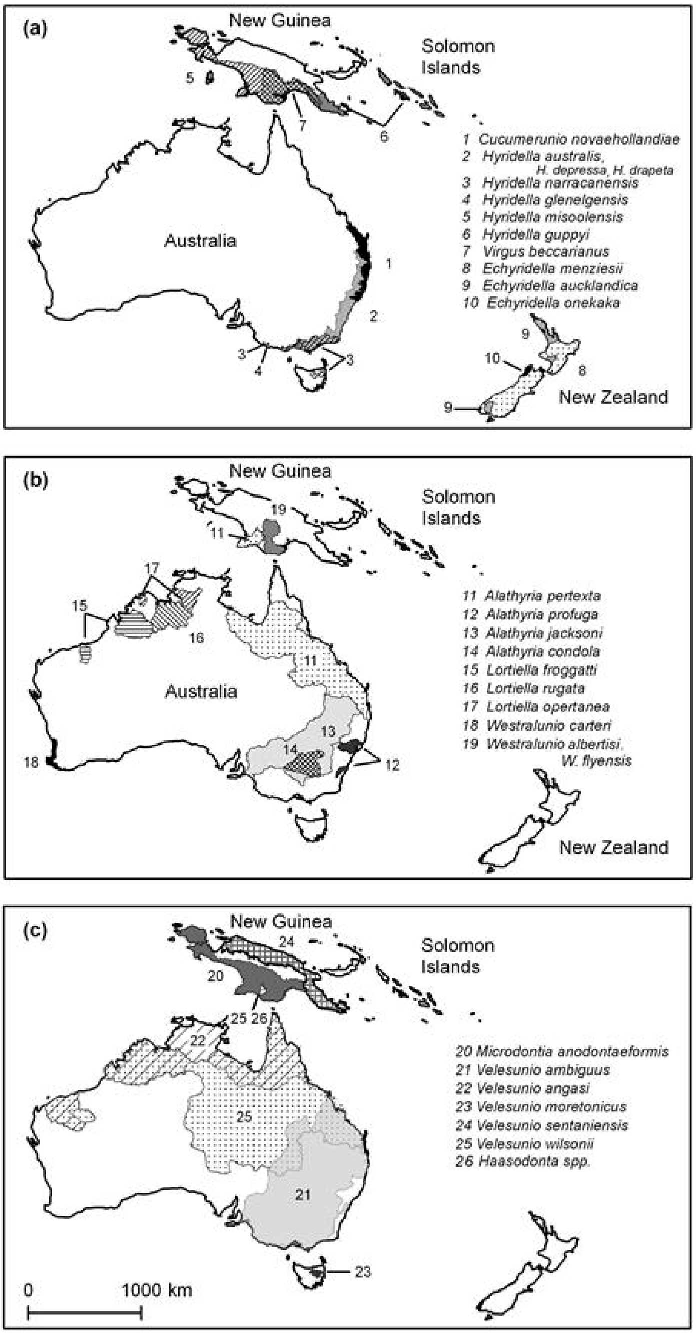

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Plate I. Shells of Hyriidae (*a*–*e*: Velesunioninae; *f*–*i*: Hyridellini) and Unionidae (*j*: Rectidentinae) from Australia and New Guinea. Lengths of specimens are shown alongside maximum lengths recorded by McMichael & Hiscock (1958) or (*) observed by the present authors. AMS = Australian Museum, Sydney.

(*a*) River Murray, South Australia (K. F. Walker coll.); *(b)* Victoria River, Northern Territory (AMS_c.313605); *(c)* Fly River, Papua New Guinea (A. W. Storey coll.); *(d)* Neales River, South Australia (J. & H. Snowball, J. & A. Robert coll.); *(e)* Canning River, Western Australia (M. W. Klunzinger coll.); *(f)* Williams River, New South Wales (AMS_c.126221); *(g)* Richmond River at Booyong, New South Wales (AMS_c.069184); *(h)* Crawford River, Victoria (K. F. Walker coll.); *(i)* Brown River, Papua New Guinea (AMS_c.126465); *(j)* Bian River, Boepoel, Indonesian West Papua (AMS_c.126214)

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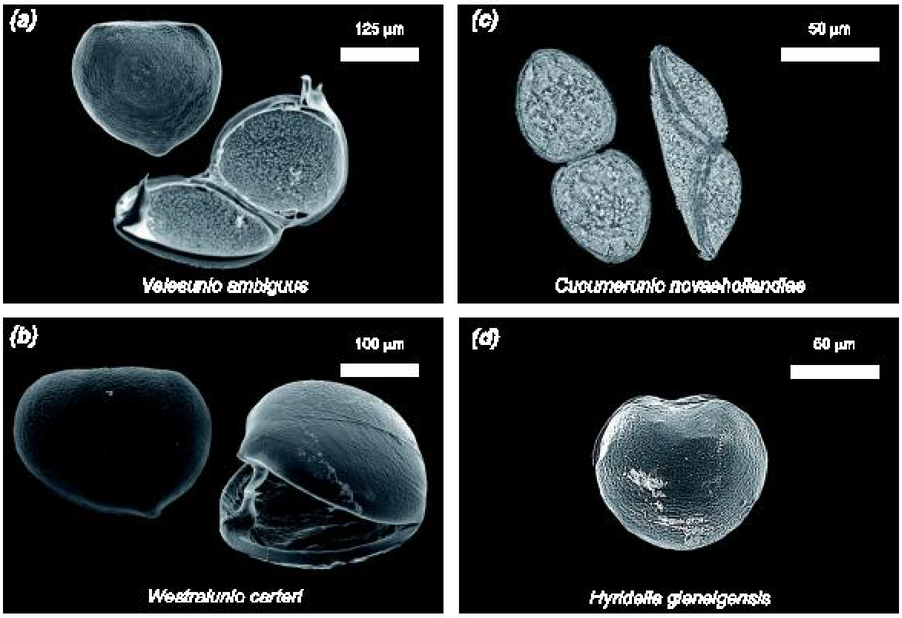
Plate II. Glochidia of Hyriidae (a–b: Velesunioninae; c–d: Hyridellini) from Australia. (a) River Murray, South Australia (after Walker, 1981a); (b) Bennett Brook, Western Australia (M. W. Klunzinger & G. J. Thomson, unpubl.); (c) Williams River, New South Wales (H. A. Jones, unpubl.); (d) Crawford River, Victoria (after Playford & Walker, 2008)



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