

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

Author

Walker, Keith F, Jones, Hugh A, Klunzinger, Michael W

Published

2014

Journal Title

Hydrobiologia

Version

Accepted Manuscript (AM)

DOI

[10.1007/s10750-013-1522-9](https://doi.org/10.1007/s10750-013-1522-9)

Rights statement

© 2014 Springer Netherlands. This is an electronic version of an article published in Hydrobiologia, 2014, 735 (1), pp. 61-79. Hydrobiologia is available online at: <http://link.springer.com/> with the open URL of your article.

Downloaded from

<http://hdl.handle.net/10072/416124>

Griffith Research Online

<https://research-repository.griffith.edu.au>

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

**Keith F. Walker · Hugh A. Jones · Michael W. Klunzinger**

K. F. Walker

School of Earth & Environmental Sciences, The University of Adelaide, SA 5005, Australia;

School of Veterinary & Life Sciences, Murdoch University, WA 6150, Australia.

Post: PO Box 331, Yankalilla, SA 5203, Australia; e-mail: keith.walker@adelaide.edu.au

H. A. Jones

NSW Office of Environment and Heritage, PO Box 3720, Parramatta, NSW 2124, Australia;

Department of Anatomy & Histology, University of Sydney, NSW 2006, Australia.

M. W. Klunzinger

School of Veterinary & Life Sciences, Murdoch University, Murdoch, WA 6150, Australia;

South East Regional Centre for Urban Landcare, Beckenham, WA 6107, Australia.

**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

38

## 39 **Introduction**

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

47 The freshwater mussels (Unionoida) of the Australasian Ecozone are in a taxonomic  
48 ‘bottleneck’. The ecozone, as defined by the World Wildlife Fund, includes Australia,  
49 New Zealand, the Solomon Islands and New Guinea (Papua New Guinea and Indonesian  
50 West Papua). The fauna includes more than 32 known species (30+ Hyriidae, 2  
51 Unionidae) but it has not been revised for 55 years (McMichael & Hiscock, 1958). In the  
52 interim there have been nomenclatural changes and descriptions of new species (Walker  
53 et al., 2001; Ponder & Bayer, 2004; Fenwick & Marshall, 2006; Graf & Cummings, 2006,  
54 2007). There have also been exploratory studies using molecular methods, including a  
55 comparison of species from Australia and New Zealand (Graf & Ó Foighil, 2000) that led  
56 to a reappraisal of New Zealand taxa (Fenwick & Marshall, 2006) and other research that  
57 exposed still un-named species in Australia (Baker et al., 2003, 2004). These studies  
58 demonstrate the hazards in over-reliance on morphological characters, and they  
59 underscore the need for a comprehensive revision of the Australasian fauna.

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

## 67 Systematics and phylogeny

### 68 Unionoida

69 Freshwater mussels are bivalves of the subclass Palaeoheterodonta, order Unionoida  
70 (variously ‘Unionacea’, ‘Unionida’, ‘Unioniformes’). There have been frequent name  
71 changes in the taxonomic literature, leaving many synonyms and re-assignments that are  
72 a significant impediment to research. Issues of supra-familial taxonomy are beyond the  
73 scope of this paper, and we have adopted the framework provided by Graf and Cummings  
74 (2006, 2007), although this is provisional and in some respects contentious (cf. Bogan,  
75 2008; Bogan & Roe, 2008; Hoeh et al., 2009; Bieler et al., 2010; Graf & Cummings,  
76 2010; Carter et al., 2011; Whelan et al. 2011). According to the ‘Mussel Project’ website  
77 maintained by Dan Graf and Kevin Cummings (<http://www.mussel-project.net>; March  
78 2013), the global tallies of valid unionoid species and genera in August 2007 were 858  
79 and 163, respectively.

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

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

---

<sup>1</sup> 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.

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

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

## 108 Hyriidae in Australasia

### 109 Subfamilies

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

114 Two subfamilies erected by Iredale (1934) have been synonymized. In the first case,  
115 McMichael and Hiscock (1958) retained 'Lortiellinae' for *Lortiella froggatti* and *L.*  
116 *rugata*, acknowledging their unusual, elongated shells, but they did not have access to  
117 whole specimens. Later reports noted anatomical similarities with Velesunioninae  
118 (Hiscock in McMichael, 1967), and glochidia typical of Velesunioninae (Walker et al.,  
119 2001; H. A. Jones, unpubl.), and examination of whole specimens led Ponder and Bayer  
120 (2004) to conclude that the subfamilies were synonymous. Ponder and Bayer (2004) also  
121 confirmed the morphological separation of *L. froggatti* and *L. rugata* and described a  
122 third species, *L. opertanea*, citing differences in shell shape but acknowledging the need  
123 for molecular data. *Lortiella* spp. thereby are confirmed as Velesunioninae, although there  
124 may be subtle anatomical differences (Klunzinger et al., 2013b). The three species occupy  
125 separate regions in the Timor Sea and Indian Ocean Drainage Divisions of Western  
126 Australia and the Northern Territory.

127 The second change was to synonymize ‘Cucumerunioninae’ with Hyriinae, based on  
128 molecular and morphological evidence (Graf & Cummings, 2006, 2007; cf. Carter et al.,  
129 2011). The former subfamily was established by Iredale (1934) for *Cucumerunio*  
130 *novaehollandiae*, and expanded by McMichael and Hiscock (1958) to include *C. websteri*  
131 from New Zealand and *Virgus beccarianus* from New Guinea. These species all have  
132 conspicuously elongated, sculptured shells and strong, serrated cardinal teeth, although  
133 these could be homoplastic traits. The shell sculpture appears as radial ridges in *V.*  
134 *beccarianus* and as lachrymose nodules in *Cucumerunio* spp., although variably so in *C.*  
135 *websteri* (Dell, 1953; McMichael & Hiscock, 1958).

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

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

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

160 Ponder & Bayer, 2004; Jones, 2013; Klunzinger et al., 2013a). The glochidia of  
 161 *Echyridella* are exceptional as they do possess a larval filament (Percival, 1931; Jones,  
 162 2013). The glochidia of *H. australis* and *C. novaehollandiae* are unusually small, with  
 163 modified teeth that are much reduced in the latter species (Jones et al., 1986). Thus,  
 164 glochidial morphology is diagnostic for families and subfamilies and, pending more  
 165 study, it may also differentiate genera and species (cf. Pimpão et al., 2012).

166 [TABLE 1 NEAR HERE](#)

167 [PLATES I–II NEAR HERE](#)

168 Species

169 The shells and glochidia of some species from Australia and New Guinea are shown in  
 170 [Plates I–II](#).

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

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

185 The number of described species of Hyriidae in Australasia presently is 30, and could  
 186 increase to 32 if known ‘cryptic’ species of *Velesunio* spp. in central Australia were  
 187 formally described (Baker et al. 2003, 2004; cf. Hughes et al., 2004). In the Lake Eyre  
 188 Basin, the genus *Velesunio* is represented by at least four species, including the  
 189 widespread *V. ambiguus* and three taxa morphologically similar to (and possibly  
 190 including) *V. wilsonii*. It is not clear whether *V. wilsonii* is among the three taxa, because

191 there are no genetic data for museum specimens of that species (Baker et al., 2003). The  
192 three un-named taxa are sympatric in some areas, yet form divergent mitochondrial DNA  
193 lineages and show corresponding fixed differences at allozyme loci, suggesting that they  
194 are separate species. Baker et al. (2004) showed also that *Alathyria jacksoni* is genetically  
195 distinct from *V. ambiguus* in the Murray-Darling Basin, where they are sympatric, but  
196 that it is allied to one of the cryptic *Velesunio* ‘species’ in the Lake Eyre Basin. They  
197 suggested that the genera *Alathyria* and *Velesunio* are in need of revision.

198 In general, the phylogenetic data obtained by Baker et al. (2003, 2004) did not match the  
199 shell characters. Indeed, the morphological differences between the taxa were subtle and  
200 may not be detected using the standard metrics employed by McMichael and Hiscock  
201 (1958). The Lake Eyre Basin fauna therefore awaits further study. Situations like this—  
202 where species are identified using genetic criteria but not formally described—should not  
203 be allowed to decouple progress in taxonomy and cladistics.

#### 204 Trans–Tasman relationships

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



223 curious, then, that the only extant hyriid species on both sides of the Tasman are Hyriinae  
224 (Hyridellini) and not Velesunioninae.

225 Fossil Hyriidae are recorded from throughout the Mesozoic Era in Australia, and the state  
226 of preservation in some cases is sufficient to reveal hinge dentition and shell sculpture,  
227 and to distinguish Velesunioninae from Hyridellini (e.g. Hocknull, 2000). There are  
228 records of fossil Hyridellini in New Zealand (e.g. Hayward, 1973; Pole et al., 2003),  
229 including *Megalovirgus flemingi* from the Cretaceous of New Zealand and Victoria  
230 (Thompson & Stilwell, 2010). There are also claims of fossil Velesunioninae from New  
231 Zealand (McMichael, 1957, 1958; McMichael and Hiscock, 1958), but the specimens are  
232 not well-preserved and confirmation is required. Clearly, there is a need for an updated  
233 checklist and revision of fossil taxa from Australia and New Zealand. Ideally, this would  
234 be extended to South America, although Mesozoic records there are scant (cf. Parodiz,  
235 1969; Wesselingh et al., 2006).

236 The genetic study by Graf and Ó Foighil (2000) indicated a clear separation between two  
237 subgenera, *Echyridella* and *Hyridella*, within the genus *Hyridella*. Fenwick and Marshall  
238 (2006) promoted *Echyridella* to genus, and the widespread New Zealand species *H. (E.)*  
239 *menziesi* (*sic*) became *E. menziesii*. They resurrected *Echyridella lucasi* from synonymy  
240 with *E. menziesii*, based on a shell dredged from Lake Manapouri on the South Island in  
241 1902 but not recorded subsequently. They also described a new species, *E. onekaka*, from  
242 the South Island.

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

## 253 Unionidae in Australasia

254 McMichael and Hiscock (1958) assigned the anomalous *Haasodonta fannyae* to the  
255 Rectidentinae, a subfamily of Unionidae that is widespread in south-east Asia. They had  
256 access to shell material only, and a single shell was judged sufficiently distinctive to  
257 warrant description of a second species, *Ha. vanheurni*. Both species are recorded only  
258 from the Merauke and Bian rivers in Indonesian West Papua, and apparently have not  
259 have been collected since about 1956 (McMichael & Hiscock, 1958: 483). The claim that  
260 *Haasodonta* spp. are members of the Unionidae must be viewed with some scepticism,  
261 but, if it proves correct, these are the only known unionids east of Lydekker's Line,  
262 separating New Guinea and the islands of 'Wallacea' (cf. Wallace's Line: Lohman et al.,  
263 2011). This issue is highly significant for taxonomy and phylogeography and new  
264 material, including whole specimens, is needed for resolution.

## 265 High-level phylogeny

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

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

285 (2013a), who showed that V-shaped sculpture is the ancestral state and that other types,  
286 including smooth umbos, are derived characters. Further, Zieritz et al. (2013b) described  
287 beak sculpture in two velesunionine species, evident as radiating lines of nodules in  
288 *Alathyria* cf. *pertexta* and as elaborate V-/W-shaped ridges in juvenile *Westralunio*  
289 *carteri*, and confirmed its absence in two other species (*Lortiella froggatti*, *Velesunio*  
290 *wilsonii*). These observations should now be extended to other species.

## 291 **Phylogeography**

### 292 Global diversity and distribution

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

300 The Hyriidae are relicts, isolated by the separation of South America from Gondwana  
301 (130–100 million years ago), and the separation of New Zealand from Antarctica (130–85  
302 million years) and Australia from Antarctica (80 million years). Hyriids in Australasia are  
303 represented by the Velesunioninae (16 known species) and the Hyriinae, shared with the  
304 Neotropical Ecozone (Central and South America, the Caribbean region). Following Graf  
305 and Cummings (2007), the Hyriinae (58 species) include four ‘tribes’, the Hyridellini in  
306 Australasia (14 species) and the Castaliini (12 species), Hyriini (4 species) and  
307 Rhipidodontini (28 species) in South America. The Neotropical fauna also includes  
308 species of Etheriidae<sup>2</sup>, Mycetopodidae and Unionidae, making a total of 208 species of  
309 Unionoida.

### 310 Australasian distribution

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

---

<sup>2</sup> As noted, there is doubt over inclusion of Etheriidae in the South American fauna.

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

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

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

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

342

FIGURE 1 NEAR HERE

### 343 Regional assemblages

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

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

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

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

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

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

## 393 TABLE 2 NEAR HERE

### 394 Conservation

#### 395 Threatened species

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

402 The IUCN *Red List of Threatened Species* (<http://iucnredlist.org>; March 2013) is an  
 403 international standard for biodiversity conservation, based on information about  
 404 population size, generation length, rate of decline, extent of occurrence and area of  
 405 occupancy. Nominations are formally assessed and qualifying taxa are assigned to a

406 category ('Data Deficient', 'Least Concern', 'Near Threatened', 'Vulnerable,  
407 'Endangered', 'Critically Endangered', 'Extinct in the Wild', 'Extinct'). Although  
408 governmental legislation in Australia does not accord fully with IUCN, the criteria and  
409 categories are not very different (e.g. <http://www.environment.gov.au/threatened>; March  
410 2013). There are processes underway to reconcile parts of the EPBC Act with IUCN  
411 criteria, and to align State and Federal listings.

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

422 *Hyridella glenelgensis* is a small species confined to the Glenelg River system of  
423 southwestern Victoria and southeastern South Australia. It was rarely reported from its  
424 discovery in 1898 until 1990, and again in 2000, when fewer than 1000 individuals were  
425 located in the lower reaches of a small tributary (Walker et al., 2001; Playford & Walker,  
426 2008). The restricted 'area of occupancy' (1 km<sup>2</sup>) and small numbers were significant  
427 factors in listing the species as 'Critically Endangered' under the EPBC Act. Local threats  
428 include flow diversions, land clearance, stock access to the stream channel and riparian  
429 areas (hence trampling, bank erosion), salinisation and the predatory common carp,  
430 *Cyprinus carpio*. Although drought is not a 'threatening process' under the EPBC Act,  
431 because it is seen as a stochastic rather than anthropogenic phenomenon, there was a  
432 severe drought in the decade before 2010 and many empty shells were cast up along the  
433 stream banks. A survey by the present authors in December 2012, after the drought had  
434 broken, showed that live mussels still remained, with evidence of new recruitment.

435 This species is closely allied to *H. narracanensis*, found in the same region and in  
436 northern Tasmania (Smith, 2005), and named on the Red List as a 'Data Deficient'  
437 species (Table 2). Although shell characters differ between the species, preliminary  
438 mitochondrial DNA analysis suggests little genetic divergence (Playford & Walker, 2008)

439 and they may prove to be ecophenotypes. The ecology and demography of *H.*  
440 *narracanensis* are little known, but it is rare and the few known populations are  
441 threatened by agriculture and urbanisation (Smith, 2005; H. A. Jones & M. W.  
442 Klunzinger, unpubl.).

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

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

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



## 472 Threatened ecological communities

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

## 482 Threatening processes

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

502

[TABLE 3 NEAR HERE](#)

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

#### 516 Prospectus

517 The worldwide decline of freshwater mussels parallels declines among other fauna, and  
518 progress in biodiversity research and conservation is not keeping pace (Strayer, 2006;  
519 Downing et al., 2010; Vaughn, 2010). We may warn of the consequences and argue for  
520 redress on ethical, philosophical, cultural, economic and ecological grounds, even for  
521 species without commercial value, and we may point to a lack of investment and  
522 commitment by governments, grant agencies and research institutions. We can show that  
523 freshwater mussels are threatened by a multitude of stressors, mainly of human origin,  
524 and that managing these will have some effect. These are valued contributions, but they  
525 may achieve no more than incremental progress because they depend, ultimately, on the  
526 values of everyday people. Until more members of the public become actively interested  
527 in less familiar species, like freshwater mussels, and more engaged in monitoring and  
528 conservation, progress will be slow. The process is facilitated by scientists, teachers and  
529 others able to communicate their enthusiasm and knowledge, and there are relevant  
530 reports, fact sheets and blogs on the Internet portals of community groups, not-for-profit  
531 organizations, online media, government departments, museums and universities  
532 throughout Australia and New Zealand (e.g. <http://www.musselwatchwa.com>;  
533 [www.arkive.org/carters-freshwater-mussel/westralunio-carteri/](http://www.arkive.org/carters-freshwater-mussel/westralunio-carteri/);  
534 [www.environment.nsw.gov.au/animals/mussels.htm](http://www.environment.nsw.gov.au/animals/mussels.htm); [collections.tepapa.govt.nz](http://collections.tepapa.govt.nz); March  
535 2013). Greater involvement of ‘citizen scientists’ (e.g. Bell et al., 2008) could catalyse

536 new empathy for mussels and other little-known species, and entrain support from  
537 institutions. It is axiomatic, however, that to conserve these species we need to recognize  
538 and understand them, hence the need for a revised taxonomic framework.

### 539 **Conclusion**

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

548 The paramount need is for a comprehensive, systematic revision of the regional fauna,  
549 rather than a ‘cherry-picking’ approach. As only limited genetic material is available in  
550 existing museum collections, a revision will require intact topotypes, where possible, so  
551 that synonymies can be determined and documented. For rare or threatened species, tissue  
552 samples and dead shells should be substituted to avoid adverse impacts on local  
553 populations. Once the nature and relationships of species are clarified, it will become  
554 easier to argue for listing freshwater mussels as threatened species, where appropriate.  
555 There is abundant evidence of declines of freshwater mussels in other ecozones (e.g.  
556 Downing et al., 2010), and Palaeartic taxa are well-represented on the IUCN Red List,  
557 but for most Australasian species there are too few data to sustain more than listing as  
558 ‘Data Deficient’ (cf. IUCN Standards & Petitions Subcommittee, 2011). Under IUCN  
559 criteria, data-deficient species are known from only a few specimens or localities, with  
560 scant population data, or are of uncertain taxonomic status. The category is not a ‘catch  
561 all’, as little-known taxa can be assigned to a threat category on the basis of habitat  
562 degradation or other factors, and that may be the best interim course of action. Mere  
563 listing by IUCN or government does not secure the survival of species, of course, but it  
564 may help to rescue some from obscurity. For Hyriidae, the consequences of inaction are  
565 clear; indeed, we may have already incurred a significant ‘extinction debt’ (cf. Haag,  
566 2010). Freshwater mussels are founding members of the Gondwana fauna; they outlived  
567 the dinosaurs, but will they survive the challenges of the modern era?

568 **Acknowledgements**

569 We are grateful for support from Professor Maria Byrne, University of Sydney, post-  
570 graduate supervisor to HAJ, and Associate Professor Alan Lymbery, Dr Stephen Beatty  
571 and Dr David Morgan, Murdoch University, supervisors to MWK. Our thanks also to Dr  
572 Bruce Marshall, Museum of New Zealand Te Papa Tongarewa, and Mr Mark Fenwick,  
573 National Institute of Water and Atmospheric Research, Wellington, New Zealand, for  
574 advice about *Echyridella*, to Dr Manuel Lopes Lima, Universidade do Porto, Portugal, for  
575 inviting us to contribute to the symposium *in absentia*, and to two reviewers for helpful  
576 advice.

577

578 **References**

- 579 Abell, R., M. L. Thieme, C. Revenga, M. Bryer, M. Kottelat, N. Bogutskaya, B. Coad, N.  
580 Mandrak, S. Contreras Balderas, W. Bussing, M. L. J. Stiassny, P. Skelton, G. R. Allen, P.  
581 Unmack, A. Naseka, R. Ng, N. Sindorf, J. Robertson, E. Armijo, J. V. Higgins, T. J. Heibel, E.  
582 Wikramanayake, D. Olson, H. L. López, R. E. Reis, J. G. Lundberg, M. H. Sabaj Pérez & P.  
583 Petry, 2008. Freshwater ecoregions of the world: A new map of biogeographic units for  
584 freshwater biodiversity conservation. *BioScience* 58: 403–414.
- 585 Baker, A. M., C. Bartlett, S. E. Bunn, K. Goudkamp, F. Sheldon & J. M. Hughes, 2003. Cryptic  
586 species and morphological plasticity in long-lived bivalves (Unionoida: Hyriidae) from inland  
587 Australia. *Molecular Ecology* 12: 2707–2717.
- 588 Baker, A. M., F. Sheldon, J. Somerville, K. F. Walker & J. M. Hughes, 2004. Mitochondrial DNA  
589 phylogenetic structuring suggests similarity between two morphologically plastic genera of  
590 Australian freshwater mussels (Unionoida: Hyriidae). *Molecular Phylogenetics and Evolution* 32:  
591 902–912.
- 592 Balla, S. A. & K. F. Walker, 1991. Shape variation in the Australian freshwater mussel *Alathyria*  
593 *jacksoni* Iredale (Bivalvia, Hyriidae). *Hydrobiologia* 220: 89–98.
- 594 Barrios-Garcia, M. N. & S. A. Ballari, 2012. Impact of wild boar (*Sus scrofa*) in its introduced  
595 and native range: a review. *Biological Invasions* 14: 2283–2300.
- 596 Bauer, G. & K. Wächtler (eds), 2001. *Ecology and Evolution of the Freshwater Mussels*  
597 *Unionoida*. Springer, Berlin. 394 p.
- 598 Beatty S. J., D. L. Morgan, F. J. McAleer & A. Ramsay, 2010. Groundwater contribution to  
599 baseflow maintains habitat connectivity for *Tandanus bostocki* (Teleostei: Plotosidae) in a south-  
600 western Australian river. *Ecology of Freshwater Fish* 19: 595–608.
- 601 Bell, S., M. Marzano, J. Cent, H. Kobierska, D. Podjed, D. Vandzinskaite, H. Reinert, A.  
602 Armaitiene, M. Grodińska-Jurczak & R. Muršič, 2008. What counts? Volunteers and their  
603 organisations in the recording and monitoring of biodiversity. *Biodiversity Conservation* 17:  
604 3443–3454.
- 605 Bieler, R., J. G. Carter & E. V. Coan, 2010. Nomenclator of bivalve families with a classification  
606 of bivalve families, Part 2: Classification of bivalve families. *Malacologia* 52: 113–153.
- 607 Bishop, P., 1995. Drainage rearrangement by river capture, beheading and diversion. *Progress in*  
608 *Physical Geography* 19: 449–473.
- 609 Bogan, A. E., 2008. Global diversity of freshwater mussels (Mollusca, Bivalvia) in freshwater.  
610 *Hydrobiologia* 595: 139–147.

- 611 Bogan, A. E. & W. R. Hoeh, 2000. On becoming cemented: evolutionary relationships among the  
612 genera in the freshwater bivalve family Etheriidae (Bivalvia: Unionoida). In E. M. Harper, J. D.  
613 Taylor & J. A. Crame (eds), *The Evolutionary Biology of the Bivalvia*. Geological Society,  
614 London: Special Publications: 159–168.
- 615 Bogan, A. E. & K. J. Roe, 2008. Freshwater bivalve (Unioniformes) diversity, systematics, and  
616 evolution: status and future directions. *Journal of the North American Benthological Society* 27:  
617 349–369.
- 618 Bortolus, A., 2008. Error cascades in the biological sciences: the unwanted consequences of using  
619 bad taxonomy in ecology. *Ambio* 37: 114–118.
- 620 Brainwood, M., S. Burgin & M. Byrne, 2006. Is the decline of freshwater mussel populations in a  
621 regulated coastal river in south-eastern Australia linked with human modification of  
622 habitat? *Aquatic Conservation: Marine and Freshwater Ecosystems* 16: 501–516.
- 623 Brainwood, M., S. Burgin & M. Byrne, 2008a. The role of geomorphology in substratum patch  
624 selection by freshwater mussels in the Hawkesbury–Nepean River (New South Wales), Australia.  
625 *Aquatic Conservation: Marine and Freshwater Ecosystems* 18: 1285–1301.
- 626 Brainwood, M., S. Burgin & M. Byrne, 2008b. The impact of small and large impoundments on  
627 freshwater mussel distribution in the Hawkesbury–Nepean River, southeastern Australia. *River*  
628 *Research and Applications* 24: 1325–1342.
- 629 Brierley, G. J., T. C. Cohen, K. A. Fryirs & A. P. Brooks, 1999. Post-European changes to the  
630 fluvial geomorphology of Bega Catchment, Australia: implications for river ecology. *Freshwater*  
631 *Biology* 41: 839–848.
- 632 Butterworth, J., 2008. Lake Rotokakahi: The kakahi (*Hyridella menziesi*) in a general framework  
633 of lake health. MSc (Biological Science) thesis, The University of Waikato, New Zealand.
- 634 Byrne, M., 1998. Reproduction of river and lake populations of *Hyridella depressa* (Unionacea:  
635 Hyriidae) in New South Wales: implications for their conservation. *Hydrobiologia* 389: 29–43.
- 636 Byrne, M., 2000. Calcium concretions in the interstitial tissues of the Australian freshwater  
637 mussel *Hyridella depressa* (Hyriidae). In E. M. Harper, J. D. Taylor & J. A. Crame (eds), *The*  
638 *Evolutionary Biology of the Bivalvia*. Geological Society, London; Special Publications: 29–43.
- 639 Cardoso, P., T. L. Erwin, P. A. V. Borges & T. R. New, 2011. The seven impediments in  
640 invertebrate conservation and how to overcome them. *Biological Conservation* 144: 2647–2655.
- 641 Carter, J. G., C. R. Altaba, L. C. Anderson, R. Araujo, A. S. Biakov, A. E. Bogan, D. C.  
642 Campbell, M. Campbell, Chen J-h., J. C. W. Cope, G. Delvene, H. H. Dijkstra, Fang Z-j., R. N.  
643 Gardner, V. A. Gavrilova, I. A. Goncharova, P. J. Harries, J. H. Hartman, M. Hautmann, W. R.

- 644 Hoeh, J. Hylleberg, Jiang B-y., P. Johnston, L. Kirkendale, K. Kleemann, J. Koppka, J. Kříž, D.  
645 Machado, N. Malchus, A. Márquez-Aliaga, J-P. Masse, C. A. McRoberts, P. U. Middelfart, S.  
646 Mitchell, L. A. Nevešskaja, S. Özer, J. Pojeta Jr, I. V. Polubotko, J. Maria Pons, S. Popov, T.  
647 Sánchez, A. F. Sartori, R. W. Scott, I. I. Sey, J. H. Signorelli, V. V. Silantiev, P. W. Skelton, T.  
648 Steuber, J. B. Waterhouse, G. L. Wingard & T. Yancey, 2011. A synoptical classification of the  
649 Bivalvia (Mollusca). Kansas University Paleontological Institute, Paleontological Contributions 4.  
650 47 p.
- 651 Clearwater, S. J., S. A. Wood, N. R. Phillips, S. M. Parkyn, R. Van Ginkel & K. J. Thompson,  
652 2012. Toxicity thresholds for juvenile freshwater mussels *Echyridella menziesii* and  
653 crayfish *Paranephrops planifrons*, after acute or chronic exposure to *Microcystis* sp.  
654 Environmental Toxicology, DOI: 10.1002/tox.21774
- 655 Colville A. E. & R. P. Lim, 2003. Microscopic structure of the mantle and palps in the freshwater  
656 mussels *Velesunio ambiguus* and *Hyridella depressa* (Bivalvia: Hyriidae). Molluscan Research  
657 23: 1–20.
- 658 Cummings, K. & D. Van Damme, 2011. *Cucumerunio novaehollandiae*. In IUCN *Red List of*  
659 *Threatened Species*, v. 2012.1. At <http://www.iucnredlist.org/details/189415/0> (March 2013).
- 660 DEC, 2012. Current List of Threatened and Priority Fauna Rankings, Department of Environment  
661 and Conservation, Western Australia. At: <http://www.dec.wa.gov.au> (March 2013).
- 662 Dell, R. K., 1953. The freshwater Mollusca of New Zealand, Part I: The genus *Hyridella*.  
663 Transactions of the Royal Society of New Zealand 81: 221–237.
- 664 Downing, J. A., P. van Meter & D. A. Woolnough, 2010. Suspects and evidence: a review of the  
665 causes of extirpation and decline in freshwater mussels. Animal Biodiversity and Conservation  
666 33: 151–185.
- 667 DPIPWE, 2009. Status of fish communities and observations on South Esk freshwater mussel  
668 (*Velesunio moretonicus*) populations in the Macquarie River catchment upstream of Lake River.  
669 Water Assessment Aquatic Ecology Report Series, Report WA 09/02. Department of Primary  
670 Industries, Parks, Water and Environment, Tasmania. 78 p.
- 671 DSE, 2009. Advisory list of threatened invertebrate fauna in Victoria. Department of  
672 Sustainability and Environment, Victoria. At: <http://www.dse.vic.gov.au> (March 2013).
- 673 DSEWPaC, 2012. *Hyridella glenelgensis*. In: Species Profile and Threats Database, Department  
674 of Sustainability, Environment, Water, Population and Communities, Canberra. At:  
675 <http://www.environment.gov.au/sprat> (March 2013).

- 676 Erskine, W. D., 1985. Downstream geomorphic impacts of large dams: the case study of  
677 Glenbawn Dam, NSW. *Applied Geography* 5: 195–210.
- 678 Fenwick, M. C., 2006. The molecular phylogenetics of the New Zealand freshwater mussels. MSc  
679 thesis, Victoria University of Wellington, New Zealand. 113 p.
- 680 Fenwick, M. C. & B. A. Marshall, 2006. A new species of *Echyridella* from New Zealand, and  
681 recognition of *Echyridella lucasi* (Suter, 1905) (Mollusca: Bivalvia: Hyriidae). *Molluscan*  
682 *Research* 26: 69–76.
- 683 Flannery, T., 1998. *Throwim Way Leg: An Adventure*. Text Publishing, Melbourne. 326 p.
- 684 Gehrke, P. C. & J. H. Harris, 2001. Regional-scale effects of flow regulation on lowland riverine  
685 fish communities in New South Wales, Australia. *Regulated Rivers: Research and Management*  
686 17: 369–391
- 687 Graf, D. L., 2000. The Etherioidea revisited: a phylogenetic analysis of hyriid relationships  
688 (Mollusca: Bivalvia: Paleoheterodonta: Unionoida). *Occasional Papers of the University of*  
689 *Michigan Museum of Zoology* 729: 1–21.
- 690 Graf, D. L. & D. Ó Foighil, 2000. Molecular phylogenetic analysis of 28S rDNA supports a  
691 Gondwanan origin for Australasian Hyriidae (Mollusca: Bivalvia: Unionoida). *Vie et Milieu* 50:  
692 245–254.
- 693 Graf, D. L. & K. S. Cummings, 2006. Palaeoheterodont diversity (Mollusca: Trigonioidea:  
694 Unionoida): what we know and what we wish we knew about freshwater mussel evolution.  
695 *Zoological Journal of the Linnean Society* 148: 343–394.
- 696 Graf, D. L. & K. S. Cummings, 2007. Review of the systematics and global diversity of  
697 freshwater mussel species (Bivalvia: Unionoida). *Journal of Molluscan Studies* 73: 291–314.
- 698 Graf, D. L. & K. S. Cummings, 2010. Comments on the value of COI for family-level freshwater  
699 mussel systematics: a reply to Hoeh, Bogan, Heard & Chapman. *Malacologia* 52: 191–197.
- 700 Haag, W., 2010. Past and future patterns of freshwater mussel extinctions in North America  
701 during the Holocene. In S. T. Turvey (ed.), *Holocene Extinctions*. Oxford University Press: 107–  
702 128.
- 703 Hayward, B. A., 1973. Upper Tertiary freshwater mussel fossils from the Coromandel Volcanic  
704 sequence. *Journal of the Royal Society of New Zealand* 3: 61.
- 705 Heard, W. H. & R. H. Guckert, 1971. A re-evaluation of the recent Unionacea (Pelecypoda) of  
706 North America. *Malacologia* 10: 333–355.
- 707 Hickey, C. W., S. J. Buckland, D. J. Hannah, D. S. Roper & K. Stuben, 1997. Polychlorinated  
708 biphenyls and organochlorine pesticides in the freshwater mussel *Hyridella menziesi* from the



- 709 Waikato River, New Zealand. *Bulletin of Environmental Contamination and Toxicology* 59: 106–  
710 112.
- 711 Hettler, J., G. Irion & B. Lehmann, 1997. Environmental impact of mining waste disposal on a  
712 tropical lowland river system: a case study on the Ok Tedi Mine, Papua New Guinea. *Mineral*  
713 *Deposita* 32: 280–291.
- 714 Hitchmough, R., L. Bull & P. Cromarty, 2007. New Zealand Threat Classification System Lists,  
715 2005. Department of Conservation, Wellington. 194 p.
- 716 Hobday, A.J. & J. M. Lough, 2011. Projected climate change in Australian marine and freshwater  
717 environments. *Marine and Freshwater Research* 62: 1000–1014.
- 718 Hocknull, S. A., 2000. Mesozoic freshwater and estuarine bivalves from Australia. *Memoirs of*  
719 *the Queensland Museum* 45: 405–426.
- 720 Hoeh, W. R., A. E. Bogan, K. S. Cummings & S. I. Guttman, 2002. Evolutionary relationships  
721 among the higher taxa of freshwater mussels (Bivalvia: Unionoida): inferences on phylogeny and  
722 character evolution from analyses of DNA sequence data. *Malacological Review* 31/32: 123–141.
- 723 Hoeh, W. R., A. E. Bogan, W. H. Heard & E. G. Chapman, 2009. Palaeoheterodont phylogeny,  
724 character evolution, diversity and phylogenetic analysis. *Malacologia* 51: 307–317.
- 725 Hughes, J. M., A. M. Baker, C. Bartlett, S. E. Bunn, K. Goudkamp & J. Somerville, 2004. Past  
726 and present patterns of connectivity among populations of four cryptic species of freshwater  
727 mussels *Velesunio* spp. in central Australia. *Molecular Ecology* 13: 3197–3212.
- 728 Humphrey, C. L., 1995. Reproduction in the freshwater mussel *Velesunio angasi* in response to  
729 the release of water from Ranger Uranium Mine to Magela Creek. Technical Memorandum 49,  
730 Supervising Scientist for the Alligator Rivers Region, Canberra.
- 731 Iredale, T., 1934. The freshwater mussels of Australia. *Australian Zoologist* 8: 57–78.
- 732 Iredale, T. & G. Whitley, 1938. The fluvifaunulae of Australia. *South Australian Naturalist* 18:  
733 64–68.
- 734 IUCN Standards & Petitions Subcommittee, 2011. Guidelines for using the IUCN Red List  
735 categories and criteria, v. 9.0. At: <http://www.iucnredlist.org/documents/RedListGuidelines.pdf>  
736 (March 2013).
- 737 Jones, H. A., 2007. The influence of hydrology on freshwater mussel (Bivalvia: Hyriidae)  
738 distributions in a semi-arid river system, the Barwon-Darling River and intersecting streams. In C.  
739 R. Dickman, S. Burgin & D. Lunney (eds), *Animals of Arid Australia: Out on their Own*. Royal  
740 Zoological Society, Sydney, New South Wales: 132–142.

- 741 Jones, H. A., 2013. Landscape scale impacts on freshwater mussel (Unionoida: Hyriidae)  
742 distribution and status in southeastern Australia. PhD thesis, University of Sydney, New South  
743 Wales. In preparation.
- 744 Jones, H. A., R. D. Simpson & C. L. Humphrey, 1986. The reproductive cycles and glochidia of  
745 freshwater mussels (Bivalvia: Hyriidae) of the Macleay River, northern New South Wales,  
746 Australia. *Malacologia* 27: 185–202.
- 747 Jones, H. A. & M. Byrne, 2010. The impact of catastrophic channel change on freshwater mussels  
748 in the Hunter River system, Australia: a conservation assessment. *Aquatic Conservation: Marine  
749 and Freshwater Ecosystems* 20: 18–30.
- 750 Jones, H. A. & M. Byrne, 2013. Detecting changes in the distribution of freshwater mussels  
751 (Unionoida: Hyriidae) in coastal southeastern Australia and implications for conservation status.  
752 *Aquatic Conservation: Marine and Freshwater Ecosystems*. In press..
- 753 Jupiter, S. D. & M. Byrne, 1997. Light and scanning electron microscopy of the embryos and  
754 glochidia larvae of the Australian freshwater bivalve *Hyridella depressa* (Hyriidae). *Invertebrate  
755 Reproduction and Development* 32: 177–186.
- 756 Kendrick, G. W., 1976. The Avon: faunal and other notes on a dying river in south-western  
757 Australia. *The Western Australian Naturalist* 13: 97–114.
- 758 Kingsford, R. T, K. F. Walker, R. E. Lester, W. J. Young, P. G. Fairweather, J. Sammut & M. C.  
759 Geddes, 2011. A Ramsar wetland in crisis—the Coorong, Lower Lakes and Murray Mouth,  
760 Australia. *Marine and Freshwater Research* 62: 255–265.
- 761 Klunzinger, M. W., 2012. Ecology, life history and conservation status of *Westralunio carteri*  
762 Iredale, 1934, an endemic freshwater mussel of south-western Australia. PhD thesis, Murdoch  
763 University, Western Australia.
- 764 Klunzinger, M. W., S. J. Beatty, D. L. Morgan, G. J. Thompson & A. J. Lymbery, 2012a.  
765 Glochidia ecology in wild fish populations and laboratory determination of competent host fishes  
766 for an endemic freshwater mussel of south-western Australia. *Australian Journal of Zoology* 60:  
767 26–36.
- 768 Klunzinger, M. W., S. J. Beatty, D. L. Morgan, A. J. Lymbery, A. M. Pinder & D. J. Cale, 2012b.  
769 Distribution of *Westralunio carteri* Iredale, 1934 (Bivalvia: Unionoida: Hyriidae) on the south

- 770 coast of south-western Australia, including new records of the species. Journal of the Royal  
771 Society of Western Australia 95: 77–81.
- 772 Klunzinger, M. W., S. J. Beatty, D. L. Morgan, G. J. Thomson & A. J. Lymbery, 2013a.  
773 Morphological and morphometrical description of the glochidia of *Westralunio carteri* Iredale,  
774 1934 (Bivalvia: Unionoida: Hyriidae). Molluscan Research. In press.
- 775 Klunzinger, M. W., H. A. Jones, J. Keleher & D. L. Morgan, 2013b. A new record of *Lortiella*  
776 *froggatti* Iredale, 1934 (Bivalvia: Unionoida: Hyriidae) from the Pilbara region, Western  
777 Australia, with notes on anatomy and geographic range. Records of the Western Australian  
778 Museum. In press.
- 779 Koehn, J. D. 2004. Carp (*Cyprinus carpio*) as a powerful invader in Australian waterways.  
780 Freshwater Biology 49: 882–894.
- 781 Köhler, F., 2011. *Westralunio carteri*. In IUCN Red List of Threatened Species, v. 2012.1. At  
782 <http://www.iucnredlist.org/details/23073/0> (March 2013).
- 783 Lohman, D. J., M. de Bruyn, T. Page, K. von Rintelen, R. Hall, P. K. L. Ng, H-T Shih, G. R.  
784 Carvalho & T. von Rintelen, 2011. Biogeography of the Indo-Australian Archipelago. Annual  
785 Review of Ecology, Evolution and Systematics 42: 205–226.
- 786 Markich, S. J., P. L. Brown & R. A. Jeffree, 2001. Divalent metal accumulation in freshwater  
787 bivalves: an inverse relationship with metal phosphate solubility. Science of the Total  
788 Environment 275: 27–41.
- 789 Martin, P. & B. Ryan, 2004. Natural-series radionucleotides in traditional Aboriginal foods in  
790 tropical northern Australia: A review. The Scientific World Journal 4: 77–95.
- 791 McMichael, D. F., 1956. Notes on the freshwater mussels of New Guinea. Nautilus 70: 38–48.
- 792 McMichael, D. F., 1957. A review of the fossil freshwater mussels (Mollusca, Pelecypoda) of  
793 Australasia. Proceedings of the Linnean Society of New South Wales 81: 222–244.
- 794 McMichael, D. F., 1958. The nature and origin of the New Zealand freshwater mussel fauna.  
795 Transactions of the Royal Society of New Zealand 85: 427–432.
- 796 McMichael, D. F., 1967. Australian freshwater Mollusca and their probable evolutionary relation-  
797 ships: a summary of present knowledge. In A. H. Weatherley (ed.), Australian Inland Waters and  
798 their Fauna: Eleven Studies. ANU Press, Canberra: 123–149.
- 799 McMichael, D. F. & I. D. Hiscock, 1958. A monograph of the freshwater mussels (Mollusca:  
800 Pelecypoda) of the Australian region. Australian Journal of Marine and Freshwater Research 9:  
801 372–508.

- 802 Morrongiello, J. R., S. J. Beatty, J. C. Bennett, D. A. Crook, D. N. E. N. Ikedife, M. J. Kennard,  
803 A. Kerezesy, M. Lintermans, D. G. McNeil, B. J. Pusey & T. Rayner, 2011. Climate change and its  
804 implications for Australia's freshwater fish. *Marine and Freshwater Research* 62: 1082–1098.
- 805 Nicholson, E., D. A. Keith & D. S. Wilcove, 2009. Assessing the threat status of ecological  
806 communities. *Conservation Biology* 23: 259–274.
- 807 Nobles, T. & Y. Zhang, 2011. Biodiversity loss in freshwater mussels: importance, threats, and  
808 solutions. In O. Grillo & G. Verona (eds), *Biodiversity Loss in a Changing Planet*. INTECH:  
809 Rijeka: 19–48.
- 810 O'Connor, S., K. Aplin, J. Pasveer & G. Hope, 2006. Liang Nabulei Lisa: A Late Pleistocene and  
811 Holocene sequence from the Aru Islands. In S. O'Connor, P. M. Veth & M. Spriggs (eds), *The*  
812 *Archaeology of the Aru Islands, Eastern Indonesia*, ANU E Press, Canberra: 125–161.
- 813 Ogilvie, S. C. & S. F. Mitchell, 1995. A model of mussel filtration in a shallow New Zealand  
814 lake, with reference to eutrophication control. *Archiv für Hydrobiologie* 133: 471–482.
- 815 Parodiz, J. J., 1969. The Tertiary non-marine Mollusca of South America. *Annals of the Carnegie*  
816 *Museum* 40: 1–242.
- 817 Parodiz, J. J. & A. A. Bonetto, 1963. Taxonomy and zoogeographic relationships of the South  
818 American naiades (Pelecypoda: Unionacea and Mutelacea). *Malacologia* 1: 179–214.
- 819 Percival, E., 1931. A note on the life history of *Diplodon lutulentus* Gould. *Transactions and*  
820 *Proceedings of the New Zealand Institute* 62: 86–91.
- 821 Pimpão, D. M., M. C. Dreher Mansur, P. E. Aydos Bergonci & C. R. Beasley, 2012. Comparative  
822 morphometry and morphology of glochidial shells of Amazonian Hyriidae (Mollusca: Bivalvia:  
823 Unionida). *American Malacological Bulletin* 30: 73–84.
- 824 Playford, T. J. & K. F. Walker, 2008. Status of the endangered Glenelg River Mussel *Hyridella*  
825 *glenelgensis* (Unionoida: Hyriidae) in Australia. *Aquatic Conservation: Marine and Freshwater*  
826 *Ecosystems* 18: 679–691.
- 827 Pole, M., B. Douglas & G. Mason, 2003. The terrestrial Miocene biota of southern New Zealand.  
828 *Journal of the Royal Society of New Zealand* 33: 415–426.
- 829 Polhemus, D. A. & G. R. Allen, 2007. Inland water ecosystems in Papua: classification, biota and  
830 threats. In A. J. Marshall & B. M. Beehler (eds), *The Ecology of Papua, Part 2. The Ecology of*  
831 *Indonesia Series*. Periplus Editions (HK), Singapore: 858–900.
- 832 Ponder, W. F. & M. Bayer, 2004. A new species of *Lortiella* (Mollusca: Bivalvia: Unionoidea:  
833 Hyriidae) from northern Australia. *Molluscan Research* 24: 89–102.

- 834 Prosser, I. P., I. D. Rutherford, J. M. Olley, W. J. Young, P. J. Wallbrink & C. J. Moran, 2001.  
835 Large-scale patterns of erosion and sediment transport in river networks, with examples from  
836 Australia. *Marine and Freshwater Research* 52: 81–99.
- 837 Rainforth, H. J., 2008. *Tiakina Kia Ora – Protecting our freshwater mussels*. MSc thesis, Victoria  
838 University of Wellington, New Zealand.
- 839 Sheldon, F. & K. F. Walker, 1989. Effects of hypoxia on oxygen consumption by two species of  
840 freshwater mussel (Unionacea : Hyriidae) from the River Murray. *Australian Journal of Marine  
841 and Freshwater Research* 40: 491–499.
- 842 Smith, B. J., 2005. Significant range extension for the freshwater mussel *Hyridella (Hyridella)*  
843 *narracanensis* in Tasmania. *The Tasmanian Naturalist* 127: 49–53.
- 844 State of the Environment Committee, 2011. Australia: State of the Environment 2011.  
845 Independent Report to the Minister for Sustainability, Environment, Water, Population and  
846 Communities. DSEWPaC, Canberra. 932 p.
- 847 Strayer, D. L., 2006. Challenges for freshwater invertebrate conservation. *Journal of the North  
848 American Benthological Society* 25: 271–287.
- 849 Thompson, D. L. & J. D. Stilwell, 2010. Early Aptian (Early Cretaceous) freshwater bivalves  
850 from the Australian-Antarctic rift, southeast Victoria. *Alcheringa* 34: 345–357.
- 851 Van Damme, D., 2011. *Hyridella narracanensis*, In IUCN Red List of Threatened Species,  
852 v. 2012.1. At <http://www.iucnredlist.org/details/189387/0> (March 2013).
- 853 Vaughn, C. C., 2010. Biodiversity losses and ecosystem function in freshwaters: emerging  
854 conclusions and research directions. *BioScience* 60: 25–35.
- 855 Vaughn, C. C. & C. M. Taylor, 1999. Impoundments and the decline of freshwater mussels: a  
856 case study of an extinction gradient. *Conservation Biology* 13: 912–920.
- 857 Walker, K. F., 1981a. Ecology of freshwater mussels in the River Murray. Australian Water  
858 Resources Council Technical Paper 63, Canberra. 119 p.
- 859 Walker, K. F., 1981b. The distribution of freshwater mussels (Mollusca, Pelecypoda) in the  
860 Australian Zoogeographic Region. In A. Keast (ed.), *Ecological Biogeography of Australia*.  
861 Dr W. Junk, The Hague: 1233–1249.
- 862 Walker, K. F., 2006. Serial weirs, cumulative effects: the Lower River Murray, Australia.  
863 In R. Kingsford (ed.), *The Ecology of Desert Rivers*. Cambridge University Press: 248–279.
- 864 Walker, K. F., T. J. Hillman & W. D. Williams, 1978. The effects of impoundments on rivers:  
865 an Australian case study. *Verhandlungen der Internationalen Vereinigung für Theoretische und  
866 Angewandte Limnologie* 20: 1695–1701.

- 867 Walker, K. F., M. Byrne, C. W. Hickey & D. S. Roper, 2001. Freshwater mussels (Hyriidae) of  
868 Australasia. In G. Bauer & K. Wächtler (eds), *Ecology and Evolution of the Freshwater Mussels*  
869 *Unionoida*. Springer, Berlin: 5–31.
- 870 Wesselingh, F. P., A. Ranzi & M. E. Räsänen, 2006. Miocene freshwater Mollusca from western  
871 Brazilian Amazonia. *Scripta Geologica* 133: 419–437.
- 872 Whelan, N. V., A. J. Geneva & D. L. Graf, 2011. Molecular phylogenetic analysis of tropical  
873 freshwater mussels (Mollusca: Bivalvia: Unionoida) resolves the position of *Coelatura* and  
874 supports a monophyletic Unionidae. *Molecular Phylogenetics and Evolution* 61: 504–514.
- 875 Whittaker, R. J. & J. M. Fernández-Palacios, 2007. *Island Biogeography: Ecology, Evolution and*  
876 *Conservation*. Oxford University Press. 416 p.
- 877 Zieritz, A., 2010. Variability, function and phylogenetic significance of unionoid shell characters.  
878 PhD thesis, University of Cambridge, United Kingdom. 173 p.
- 879 Zieritz, A., A. E. Bogan & D. C. Aldridge, 2013a. Reconstructing the evolution of umbonal  
880 sculptures in the Unionoida. *Journal of Zoological Systematics and Evolutionary Research*.  
881 In press.
- 882 Zieritz, A, A. F. Sartori & M. W. Klunzinger, 2013b. Umbonal sculpture in some Velesunioninae:  
883 invalidation of previous assumptions. *Journal of Molluscan Studies*. In press.
- 884
- 885

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

---

**Hyriinae: Hyridellini**

<i>Cucumerunio novaehollandiae</i> (Gray, 1834)	A
<i>Hyridella australis</i> (Lamarck, 1819)	A
<i>Hyridella depressa</i> (Lamarck, 1819)	A
<i>Hyridella drapeta</i> (Iredale, 1934)	A
<i>Hyridella glenelgensis</i> (Dennant, 1898)	A
<i>Hyridella narracanensis</i> (Cotton & Gabriel, 1932)	A
<i>Hyridella misoolensis</i> (Schepman, 1897)	NG
<i>Hyridella guppyi</i> (E. A. Smith, 1885)	NG, SI
<i>Virgus beccarianus</i> (Tapparone Canefri, 1883)	NG
<i>Echyridella onekaka</i> Fenwick & Marshall, 2006	NZ
<i>Cucumerunio websteri</i> (Simpson, 1902) <sup>a</sup>	NZ
<i>Hyridella aucklandica</i> (Gray, 1843) <sup>a</sup>	NZ
<i>Echyridella menziesii</i> (Gray, 1843) <sup>b</sup>	NZ
<i>Echyridella lucasi</i> (Suter, 1905) <sup>b</sup>	NZ

**Velesunioninae<sup>c</sup>**

<i>Alathyria condola</i> Iredale, 1943	A
<i>Alathyria jacksoni</i> Iredale, 1934	A
<i>Alathyria profuga</i> (Gould, 1851)	A
<i>Lortiella froggatti</i> Iredale, 1934	A
<i>Lortiella opertanea</i> Ponder & Bayer, 2004	A
<i>Lortiella rugata</i> (G. B. Sowerby II, 1868)	A
<i>Velesunio ambiguus</i> (Philippi, 1847)	A
<i>Velesunio angasi</i> (G. B. Sowerby II, 1867)	A
<i>Velesunio moretonicus</i> (Reeve, 1865)	A
<i>Westralunio carteri</i> Iredale, 1934	A
<i>Alathyria pertexta</i> Iredale, 1934	A, NG
<i>Velesunio wilsonii</i> (Lea, 1859) <sup>d</sup>	A, NG <sup>d</sup>
<i>Microdontia anodontaeformis</i> (Tapparone Canefri, 1883)	NG
<i>Velesunio sentaniensis</i> (Haas, 1924)	NG
<i>Westralunio albertisi</i> (Clench, 1957)	NG
<i>Westralunio flyensis</i> (Tapparone Canefri, 1883)	NG

**Unionidae: Rectidentinae**

<i>Haasodonta fannyae</i> (Johnson, 1948)	NG
<i>Haasodonta vanheurni</i> McMichael & Hiscock, 1958	NG

---

888 <sup>a</sup> Likely to be synonymized as *Echyridella aucklandica* (see text)

889 <sup>b</sup> Likely to be synonymized as *Echyridella menziesii* (see text)

890 <sup>c</sup> “*Velesunio ovata*” is omitted (see text)

891 <sup>d</sup> Includes cryptic species in central Australia (Baker et al., 2003, 2004; Hughes et al., 2004).  
892 One specimen only is recorded from NG (McMichael & Hiscock, 1958: 399)

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

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

896 <sup>a</sup> *Red List of Threatened Species*, v. 9.0 (September 2011)

897 <sup>b</sup> New Zealand: *Wildlife Act 1953*; *Conservation Act 1987* (note pending synonymies: [Table 1](#))

898 <sup>c</sup> Commonwealth of Australia: *Environment Protection & Biodiversity Conservation Act 1999*

899 <sup>d</sup> Victoria: *Flora & Fauna Guarantee Act 1988*

900 <sup>e</sup> Western Australia: Department of Environment & Conservation, Current list of threatened and  
 901 priority fauna rankings (February 2012)

902

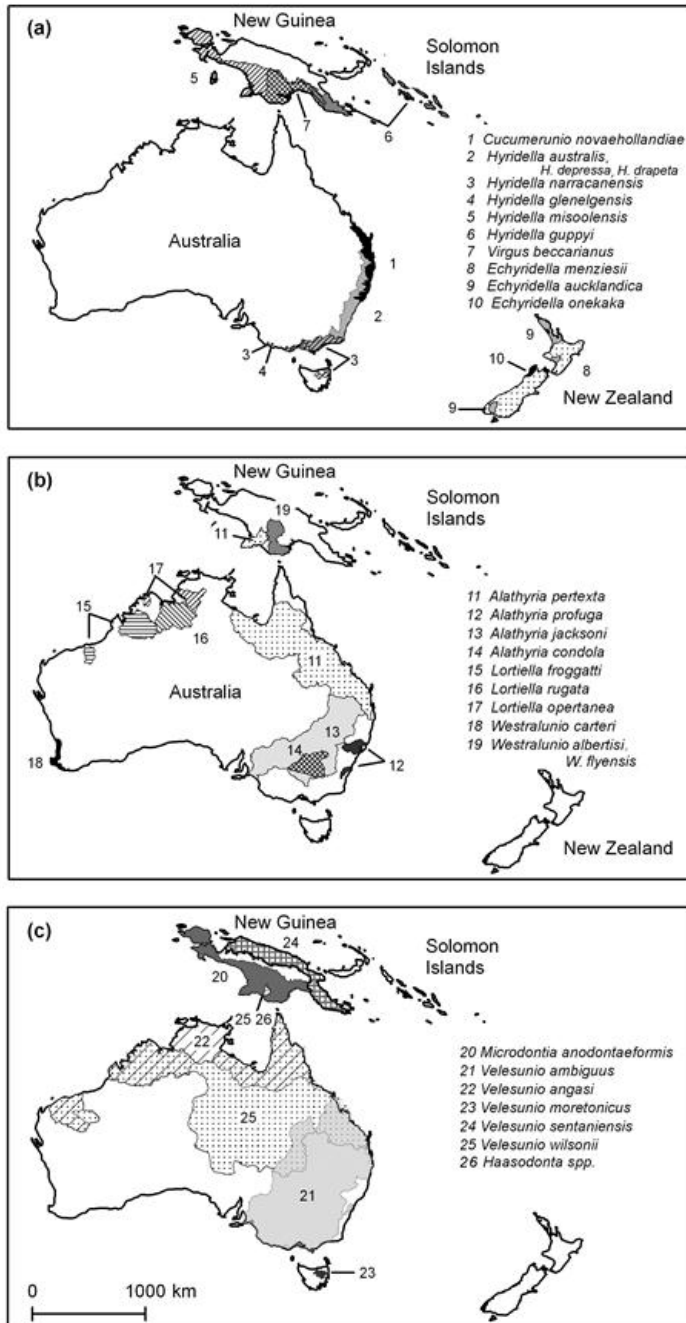


**Table 3** Processes that threaten freshwater mussel (and host fish) populations in Australasia, with selected references

<b>Causes</b>	<b>Consequences</b>	<b>References</b>	
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	
	Rainfall	Less average rainfall, hence runoff; more frequent extremes, hence drought/flood	Hobday & Lough, 2011; Morrongiello et al., 2011
	Ecological communities	Loss of biodiversity; spread of alien species	

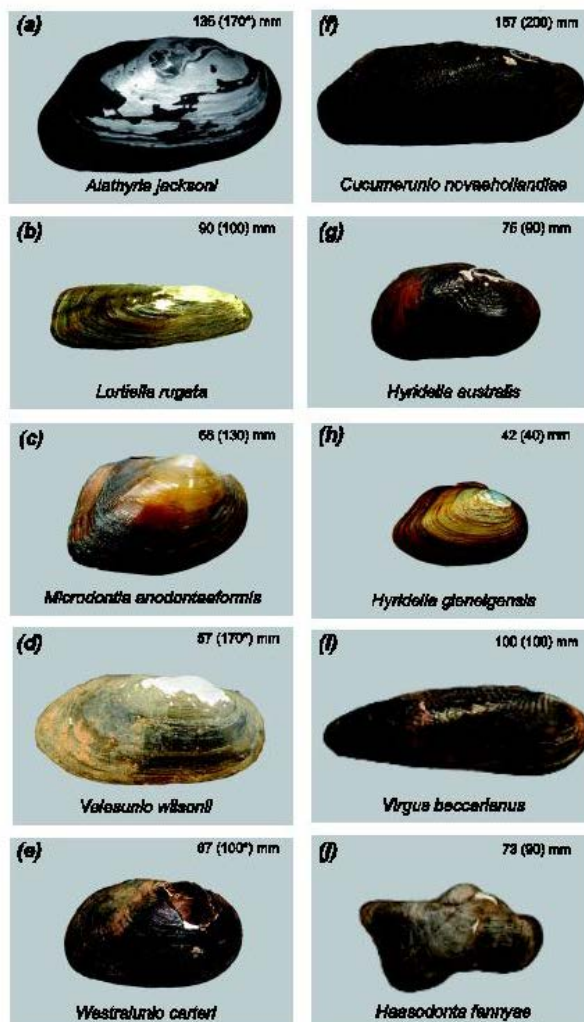
**Figure 1.** Geographic ranges of Hyriidae (Hyridellini, Velesunioninae) and Unionidae (Rectidentinae) in Australasia, from museum records and survey data: (a) Hyridellini, (b) Velesunioninae (*Alathyria*, *Lortiella*, *Westralunio*) and (c) Velesunioninae (*Microdontia*, *Velesunio*) and Rectidentinae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



DRAFT COPY ONLY:  
SEE ATTACHED TIFF IMAGE

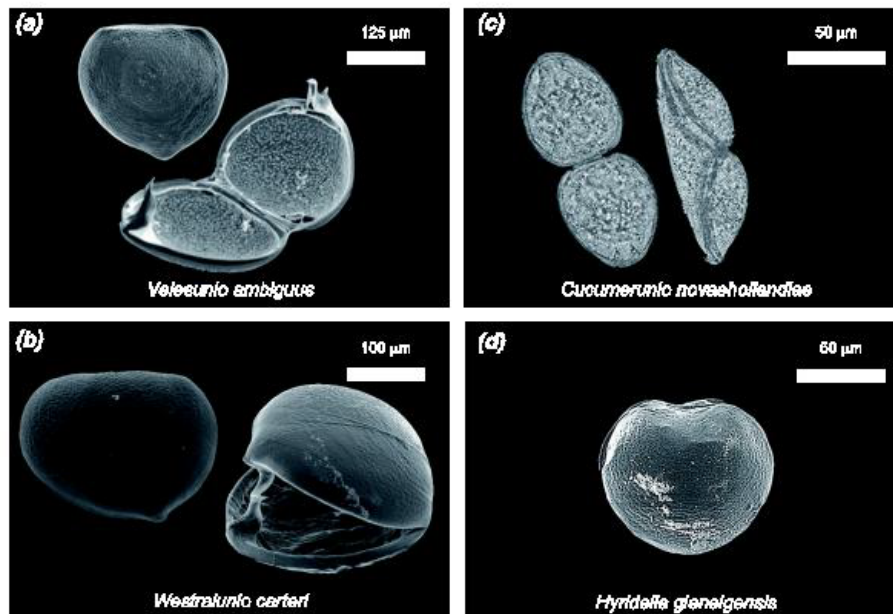
**Plate I.** Shells of Hyriidae (*a–e*: Velesunioninae; *f–i*: Hyridellini) and Unionidae (*j*: Rectidentinae) from Australia and New Guinea. Lengths of specimens are shown alongside maximum lengths recorded by McMichael & Hiscock (1958) or (\*) observed by the present authors. AMS = Australian Museum,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



DRAFT COPY ONLY:  
SEE ATTACHED EPS IMAGE

**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)



DRAFT COPY ONLY:  
SEE ATTACHED EPS IMAGE