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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

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 America¹), 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).

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.

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 Unionoidea 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 Etheriidae², 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

² 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 km²) 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⁻¹. 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/;
534 www.environment.nsw.gov.au/animals/mussels.htm; 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?

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577

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- 884
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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) ^a	NZ
<i>Hyridella aucklandica</i> (Gray, 1843) ^a	NZ
<i>Echyridella menziesii</i> (Gray, 1843) ^b	NZ
<i>Echyridella lucasi</i> (Suter, 1905) ^b	NZ

Velesunioninae^c

<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) ^d	A, NG ^d
<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 ^a Likely to be synonymized as *Echyridella aucklandica* (see text)

889 ^b Likely to be synonymized as *Echyridella menziesii* (see text)

890 ^c “*Velesunio ovata*” is omitted (see text)

891 ^d 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*^a 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> ^b	...	Data Deficient ^b	Hitchmough et al., 2007
<i>Cucumerunio websteri websteri</i> ^b	...	Data Deficient ^b	Hitchmough et al., 2007
<i>Echydella menziesii</i> ^b	...	Gradual Decline ^b	Butterworth, 2008; Rainforth, 2008
<i>Hyridella glenelgensis</i>	...	Critically Endangered ^{c, d}	Playford & Walker, 2008; DSE, 2009; DSEWPac, 2012
<i>Hyridella narracanensis</i>	Data Deficient	...	Van Damme, 2011
<i>Westralunio carteri</i>	Least Concern	Priority 4 ^e	Köhler, 2011; DEC, 2012

896 ^a *Red List of Threatened Species*, v. 9.0 (September 2011)

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

898 ^c Commonwealth of Australia: *Environment Protection & Biodiversity Conservation Act 1999*

899 ^d Victoria: *Flora & Fauna Guarantee Act 1988*

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

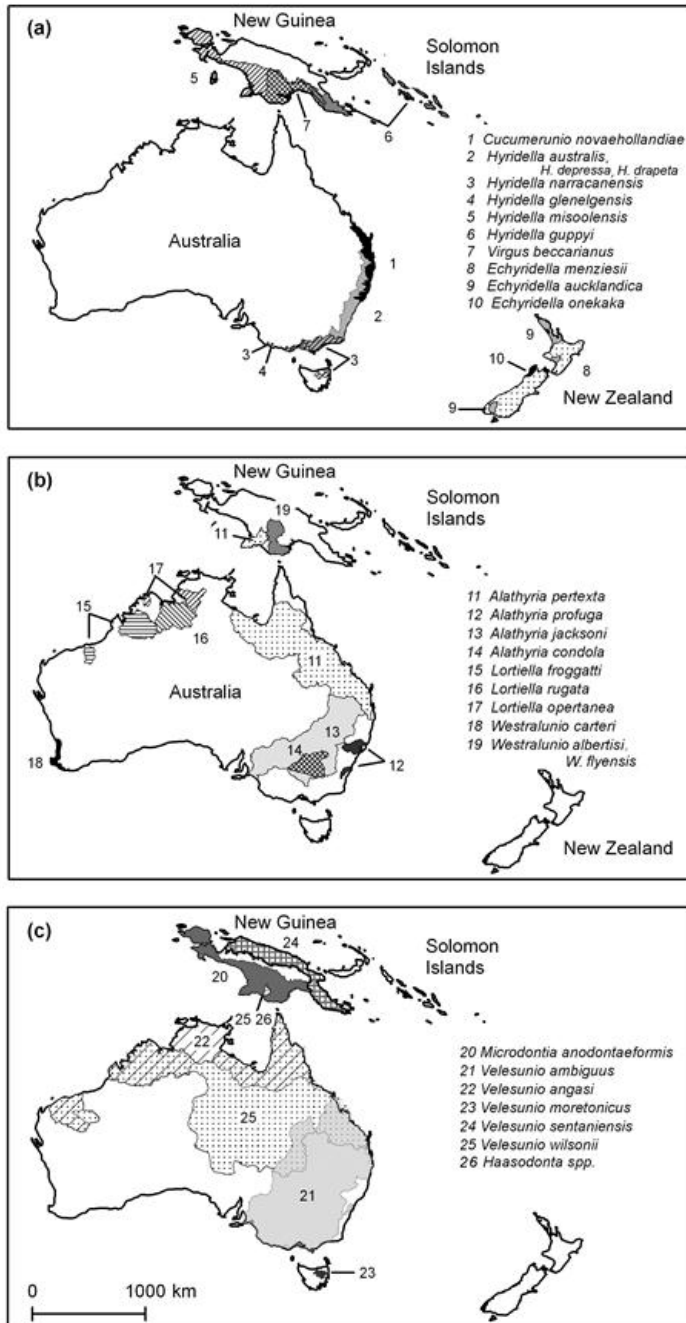
902

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

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	
	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	

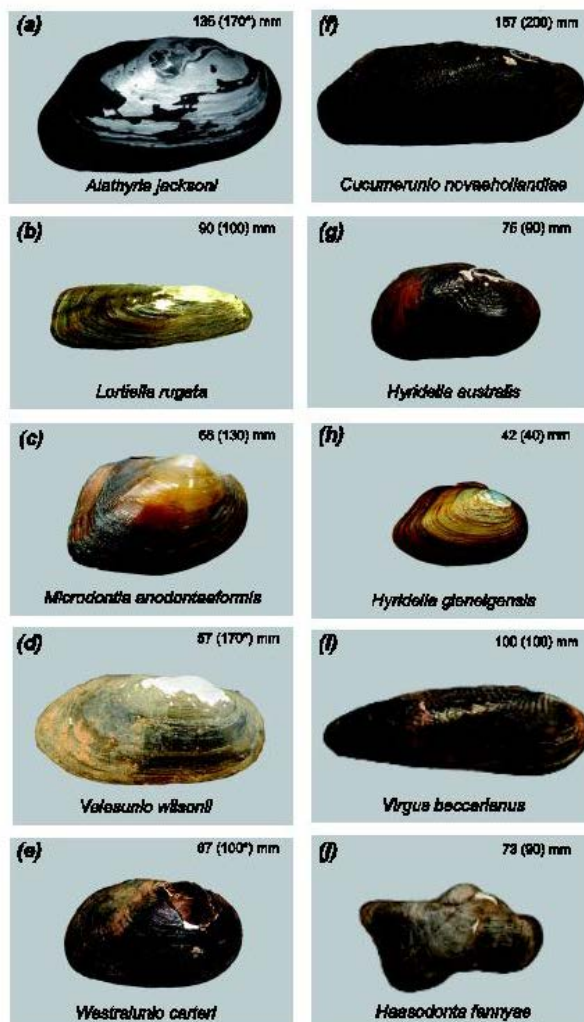
Figure 1. Geographic ranges of Hyriidae (Hyridellini, Velesunioninae) and Unionidae (Rectidentinae) in Australasia, from museum records and survey data: (a) Hyridellini, (b) Velesunioninae (*Alathyria*, *Lortiella*, *Westralunio*) and (c) Velesunioninae (*Microdontia*, *Velesunio*) and Rectidentinae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



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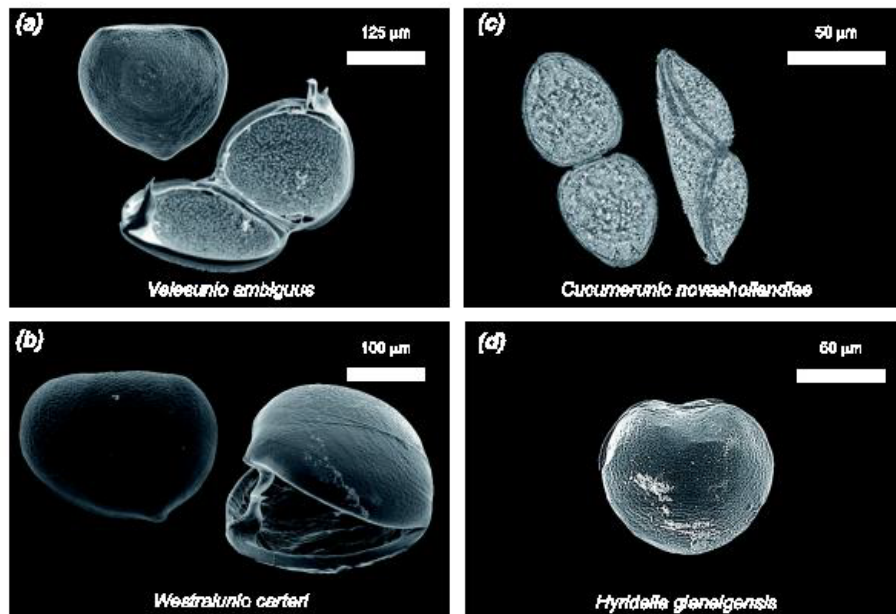
Plate I. Shells of Hyriidae (*a–e*: Velesunioninae; *f–i*: Hyridellini) and Unionidae (*j*: Rectidentinae) from Australia and New Guinea. Lengths of specimens are shown alongside maximum lengths recorded by McMichael & Hiscock (1958) or (*) observed by the present authors. AMS = Australian Museum, Sydney.

(*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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