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45 The distribution of freshwater mussels
(Mollusca: Pelecypoda) in the Australian
Zoogeographic Region

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1	Introduction	1233
2	Composition and relationships of the regional fauna	1233
3	Distribution in relation to fluvifaunular provinces	1237
3.1	Jardinian province	1238
3.2	Krefftian province	1238
3.3	Lessonian province	1240
3.4	Tobinian province	1241
3.5	Mitchellian province	1241
3.6	Sturtian province	1241
3.7	Vlaminghian province	1241
3.8	Greyian province	1242
3.9	Leichhardtian province	1242
3.10	Riechian province	1242
3.11	Gaimardian province	1243
4	Dispersal	1243
5	Phylogeny and distribution	1245
	Conclusion	1247
	References	1248



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45 The distribution of freshwater mussels (Mollusca: Pelecypoda) in the Australian Zoogeographic Region

1. Introduction

Freshwater mussels are a group of late Palaeozoic origin, and have virtually a world-wide distribution, being found on all continents other than Antarctica. Their possible zoogeographic significance has been recognized by many authors, although taxonomic confusion has been a persistent problem, less so in recent years (e.g. Parodiz & Bonetto, 1963).

For the Australian Region, including Australia, New Guinea and New Zealand, details of the distributions of freshwater mussel species are provided by McMichael & Hiscock (1958), as part of a taxonomic revision of the regional fauna. McMichael & Hiscock related the species distributions to a concept of *fluvifaunulae*, earlier introduced by Iredale & Whitley (1938). The term refers to assemblages of river animals. Iredale & Whitley defined for Australia and New Guinea ten fluvifaunular provinces, corresponding in a general way with the extent of the principal drainage divisions. The fluvifaunulae were assigned names that honour certain naturalists and explorers, and characteristic animal species were decided from consideration of the distributions of molluscs and fish, reflecting the authors' specialities. In later years the original scheme has been modified in various ways (Iredale, 1943; Whitley, 1947), the most significant change being McMichael & Hiscock's proposal that an additional fluvifaunula (the Riechian) be recognized. Figure 1 shows McMichael & Hiscock's interpretation of the fluvifaunular provinces, and for comparison the principal drainage divisions are shown in Fig. 2.

Several freshwater mussel species were cited by Iredale & Whitley in support of the fluvifaunula concept, and the supporting role was given further emphasis by McMichael & Hiscock. In each case, however, the authors apparently worked from the presumption that discrete fluvifaunulae in fact do occur, each assemblage having a geographic range more or less distinct from that of its neighbors. The selection of 'characteristic' species on this basis provides spurious support for the concept, as all members of the group must be considered. It is reasonable, therefore, to question whether the distribution of the regional freshwater mussel fauna does substantiate the fluvifaunula concept, as claimed. An examination of this question is a general theme for this chapter.

2. Composition and relationships of the regional fauna

There are about 1000 species of freshwater mussels, with representatives on each continent other than Antarctica. Following Parodiz & Bonetto (1963),

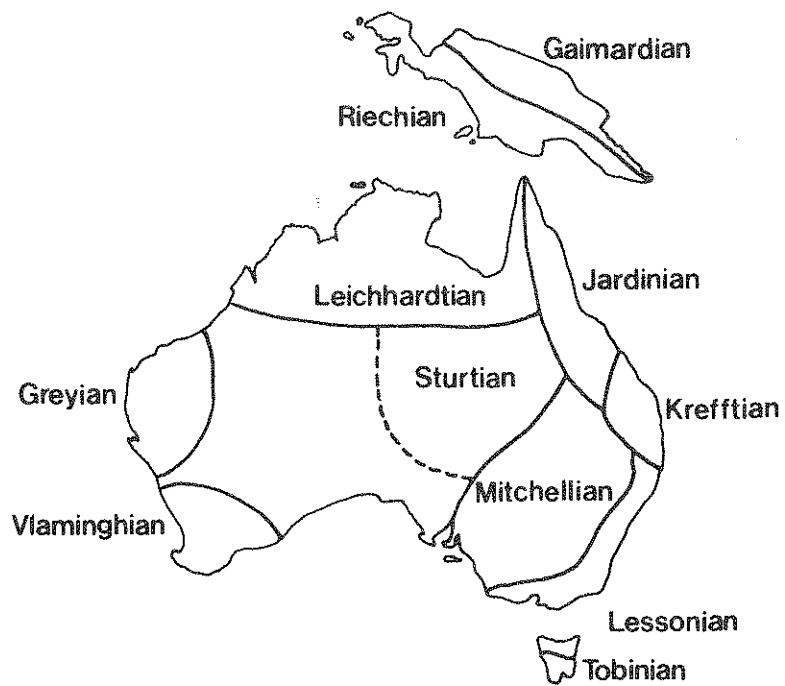


Fig. 1. Fluvifaunular provinces of Australia and New Guinea (McMichael & Hiscock 1958).

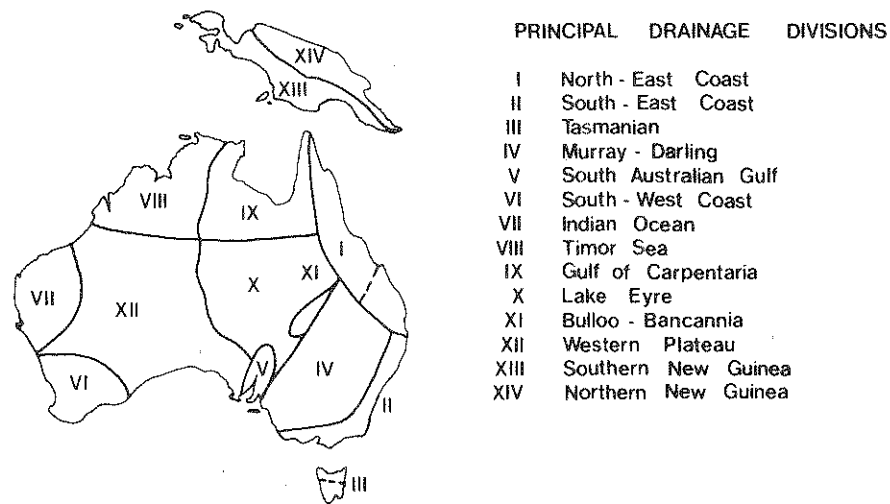
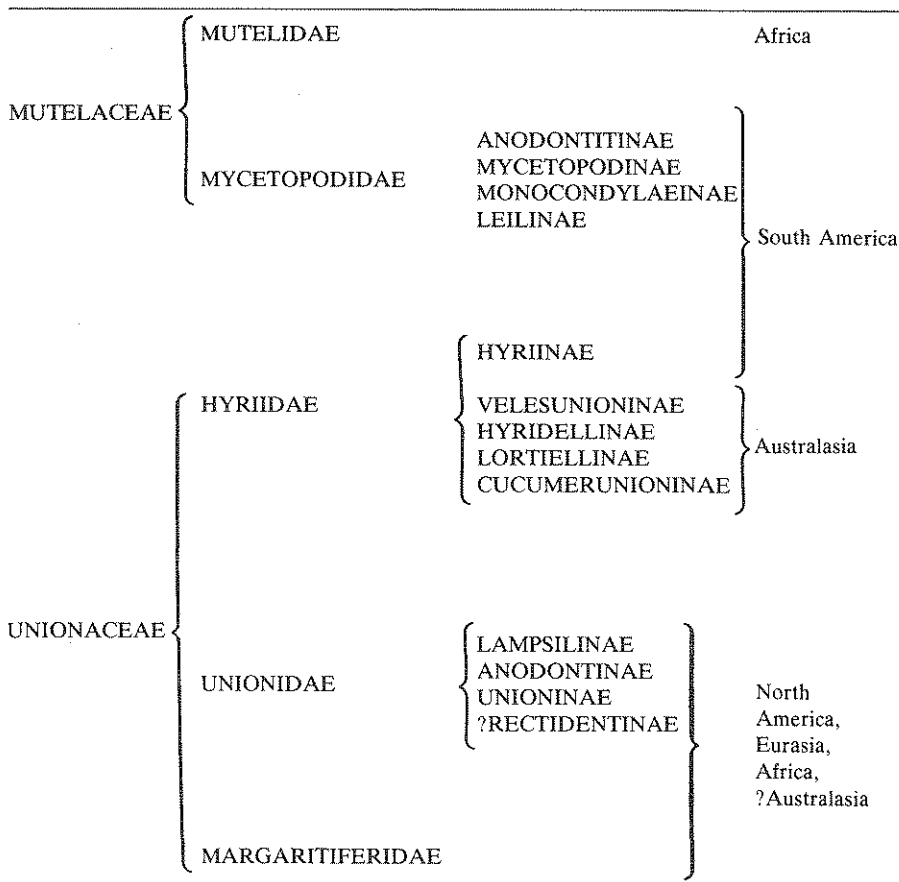


Fig. 2. Principal drainage divisions of Australia and New Guinea (based on Australian Water Resources Council 1975). The broken lines are artificial separations to aid comparison with fluvifaunular provinces.

the world fauna is divided into two superfamilies, the Mutelaceae and Unionaceae, according to larval characteristics (Table 1). Larval features again provide a basis for distinguishing the family Hyriidae, found only in Australasia and South America, from other Unionaceae. Aside from two genera (four species) of uncertain affinities (see below), the fauna of the Australian Region comprises seven genera (25 species) of Hyriidae.* The South American fauna consists of seven other hyriid genera plus representatives of the Mutelaceae, the latter indicating an affinity with the African fauna (Table 1).

Despite a history of taxonomic confusion, several zoogeographers have recognized that a close relationship exists between the mussel faunas of Africa, Australasia and South America, and that collectively these form a

Table 1. Synopsis of higher taxa in the world fauna of freshwater mussels (modified after Parodiz & Bonetto 1963)



* The glochidia of most Australian mussels are unknown; hence Parodiz & Bonetto's classification is not strictly adhered to. Further, because this is a recent classification, the unwary reader may meet with considerable confusion in earlier literature.

group clearly separable from northern hemisphere species (see McMichael & Hiscock, 1958; Parodiz & Bonetto, 1963). Speculation about the patterns of distribution variously have referred to northern hemisphere, Gondwanaland or Indo-Pacific origins, and to dispersal across Asian or Antarctic landbridges. Parodiz & Bonetto re-affirmed the similarities of the southern hemisphere faunas, but left open the questions of origins and dispersal, pointing out that existing ideas were either inconsistent with, or unsupported by, fossil evidence. They apparently were unaware of McMichael's (1957) review of Australasian fossil species, although this may not affect broad concepts.

A firmer basis for such discussions will emerge when the relationships of the anomalous genera *Haasodonta* and *Lortiella* from the Australian subregion are clarified. *Haasodonta* includes two species (*H. fannyae* and *H. vanheurni*) found near Merauke in southern New Guinea. McMichael & Hiscock (1958) tentatively placed these species with the unionid subfamily Rectidentinae, but as both are known only from shells this must remain tentative pending anatomic and larval studies. McMichael (1956) considered that the closest relative of *Haasodonta* may be *Physunio* among the south-east Asian Rectidentinae. The issue is clouded by McMichael & Hiscock's (1958) suggestion that *H. vanheurni* in particular may have some affinities with the Australian *Alathyria*.

The genus *Lortiella* accommodates two species (*L. froggatti* and *L. rugata*) from separate localities in north-western Australia. Each was described from limited collections of shells only, and with further study may prove to be ecophenotypic variants of the one species. McMichael & Hiscock (1958) allowed *Lortiella*, within the Lortiellinae, to remain tentatively as part of the 'Mutelidae' (now Hyriidae). McMichael & Iredale (1959) emphasized the possibility that, in view of its similarities with the south-east Asian *Solenaia*, *Lortiella* may belong with the Unionidae. More recently, however, Hiscock (*vide* McMichael, 1967) reported that, after examining new preserved material, the gross anatomy of *Lortiella* resembles that of Velesunioninae. Again, a confident decision awaits more detailed studies.

Information about the genera and species of the Australian Region is summarized in Table 2. The following points arise:

a. The New Zealand subregion has a mussel fauna that clearly is of Australian origin (McMichael, 1958). The three New Zealand species (*Cucumerunio websteri*, *Hydridella aucklandica* and *H. menziesi*) have congeners in coastal eastern Australia. The fossil evidence is inconsistent with the notion of dispersal via land-bridges, but good arguments have been advanced for adventitious transport by waterfowl (McMichael, 1957; 1958).

b. With the probable exception of *Haasodonta* spp., the New Guinean fauna also is thought to be a derivative from mainland Australia (McMichael, 1956; McMichael & Hiscock, 1958). New Guinea has a total 11 species in seven genera; four genera are shared with Australia, but at the specific level only *Alathyria pertexta* and *Velesunio wilsonii* are shared. In the area of the Sahul Shelf land-bridge dispersal could have occurred as recently as the Pleistocene. An incidental point is that a subspecies of

Table 2. Genera and numbers of species of freshwater mussels in the Australian Region (cA, continental Australia; tA, Tasmania; NG, New Guinea; NZ, New Zealand)

genus	species	species in			
		cA	tA	NG	NZ
Alathyria	4	4		1	
Cucumerunio	2	1			1
Hyridella	9	5	1	2	2
Microdontia	1			1	
Velesunio	5	3	1	2	
Virgus	1			1	
Westralunio	3	1		2	
Haasodonta	2			2	
Lortiella	2	2			
totals	29	16	2	11	3

Hyridella guppyi occurs in certain islands of the Solomon group, some 700 km distant from New Guinea.

c. In Australia (including Tasmania) there are 17 mussel species in six genera. At the generic level only *Lortiella* is peculiar to Australia, but 13 of the remaining 15 species are Australian endemics.

3. Distribution in relation to fluvifaunular provinces

This section is concerned with identifying those species present in each of the presumed fluvifaunular provinces (cf. Fig. 1). No reference is made to New Zealand species, as these are not considered in the original concept. New Zealand is in fact a separate subregion, although the distinction is less obvious for the freshwater mussels than for most other animal groups. As pointed out above, the New Zealand mussel fauna is derived from that of Australia and New Guinea.

The numbers of species in each fluvifaunular province, and the numbers shared with other provinces, are shown in Table 3. These data might easily be used to calculate various indices of 'faunal resemblance' (e.g. Simpson, 1960), but indices are not dealt with here for two reasons: in this case they offer little information not already apparent from a simple tabulation, and they become unreliable where low numbers of species are involved.

Table 3 alone might be used to draw certain conclusions regarding the integrity or otherwise of individual fluvifaunulae, but this would place an unrealistic emphasis on the boundaries between provinces. Several species occupy only marginal areas of provinces, yet must still be accounted for as resident species, if not as members of the respective fluvifaunulae. Before attempting conclusions, it is necessary to consider the mussel species resident in each of the eleven provinces. Figure 3 shows the approximate distributions of the species concerned.

Table 3. A cross-tabulation showing the numbers of freshwater mussel species in each fluvifaunular province (indicated by the first three letters in each name; see Fig. 1). Bold-type numbers forming the outermost diagonal show the number of species in each province. The right-hand column (R) indicates the number of species in each province not shared with other provinces

JAR	KRE	LES	TOB	MIT	STU	VLA	GRE	LEI	RIE	GAI		R
3	3	1	0	1	3	0	1	2	2	0	JAR	0
	7	5	0	1	3	0	1	2	2	0	KRE	0
		10	0	2	1	0	0	0	0	0	LES	4
			0	0	0	0	0	0	0	0	TOB	0
				3	1	0	0	0	0	0	MIT	1
					3	0	1	2	2	0	STU	0
						1	0	0	0	0	VLA	1
							2	2	1	0	GRE	0
								5	2	0	LEI	2
									10	1	RIE	7
										2	GAI	4

3.1 Jardinian province

Resident species: *Alathyria pertexta*, *Velesunio ambiguus* and *V. wilsonii*. The Jardinian province occupies the greater part of the North-East Coast Drainage Division, with boundaries corresponding in all but the southernmost area (cf. Fig. 1, 2). None of the three resident species is confined to the Jardinian province (Fig. 3, Table 3); all three occur in the Krefftian and Sturtian provinces, and two in the Leichhardtian and Riechian provinces. Although both *V. ambiguus* and *V. wilsonii* are widespread in the province, they are regarded by McMichael & Hiscock as predominantly inland species. *A. pertexta* (strictly, *A. p. pertexta*) occurs in the Fitzroy system and part of the Burdekin system.

Although Iredale & Whitley (1938) suggested that *Rugoshyria aquilonalis* Iredale was typical of the Jardinian fluvifaunula, this species was considered by McMichael & Hiscock to be of doubtful validity. It was, in any case, described from a single specimen from the Bloomfield River, north Queensland.

3.2 Krefftian province

Resident species: *Alathyria pertexta*, *Cucumerunio novaehollandiae*, *Hyridella australis*, *H. depressa*, *H. drapeta*, *Velesunio ambiguus*, and *V. wilsonii*.

The Krefftian province occupies the southernmost portion of the North-East Coast Drainage Division, but the correspondence is not clear-cut. By its original definition the Krefftian province extends from the Burnett River in Queensland to include the Richmond and Clarence Rivers in New South Wales. Although the Australian Water Resources Council (1975) draws the divisional boundary at the State border, the North-East Division might

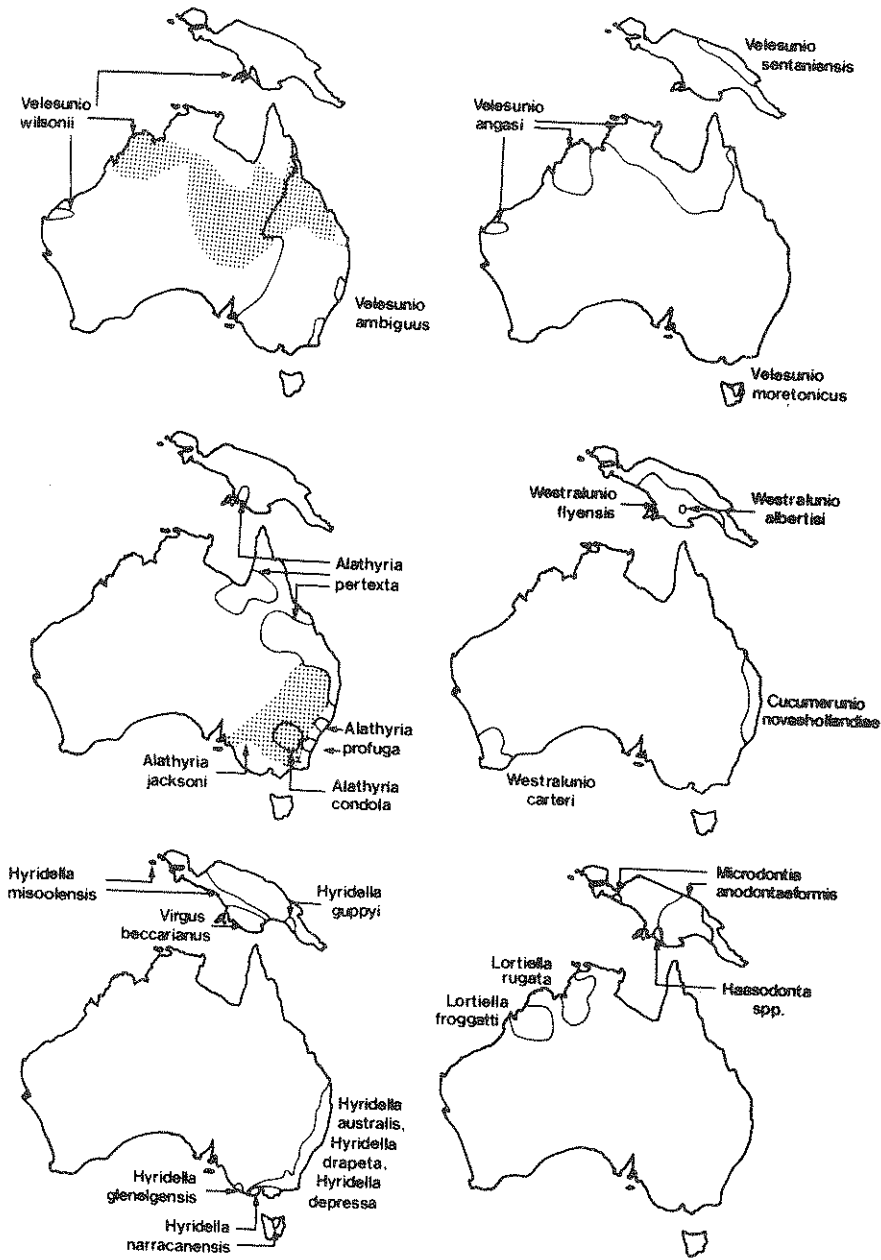


Fig. 3. Approximate distributions of freshwater mussel species in Australia and New Guinea. Based largely on McMichael & Hiscock (1958), with minor amendments after Walker (unpublished) and Williams (1979).

reasonably be taken to encompass the entire Krefftian province. Ultimately this would best be decided once analyses for other groups are available.

The distribution of *C. novaehollandiae* extends slightly beyond the Krefftian boundary into the Lessonian province; this however has not prejudiced its admission as a 'characteristic' species. Although McMichael & Hiscock identified *A. Pertexta* (*A. p. pertexta*) as another characteristic form, its distribution does encroach significantly on adjacent provinces. Further, it is arguable whether a subspecies is a valid consideration in this context; as a species, *A. pertexta* does not conform to any one fluvifaunular province.

As before, the widespread presence of *V. ambiguus* and three species of *Hyridella* might be interpreted as outward extensions of species associated mainly with other provinces. Concessions such as this, however, seem to make the definition of fluvifaunular provinces increasingly arbitrary. *V. wilsonii* is reported only from the Mary River within the province.

Of the seven members of the Krefftian fluvifaunula, five are shared with the Lessonian, three with both the Jardinian and the Sturtian, and two with both the Leichhardtian and the Riechian. Apart perhaps from the presence of *C. novaehollandiae* (and to an even lesser extent *A. p. pertexta*) there seemingly are slight grounds for recognizing a distinct province.

3.3 Lessonian province

Resident species: *Alathyria jacksoni*, *A. profuga*, *Cucumerunio novaehollandiae*, *Hyridella australis*, *H. depressa*, *H. drapeta*, *H. glenelgensis*, *H. narracanensis*, *Velesunio ambiguus* and *V. moretonicus*.

The Lessonian province encompasses the South-East Coast Drainage Division and extends to the northern half of Tasmania. The occurrences of *A. jacksoni* and *C. novaehollandiae* basically are outliers of distributions centred elsewhere. *V. ambiguus* again is widely distributed through this province. Three species of *Hyridella* (*H. australis*, *H. depressa* and *H. drapeta*) occur nearly throughout the province and, if their presence in the Krefftian is considered unimportant, might be taken as characteristic. The two other *Hyridella* species and *V. moretonicus* occur in isolated pockets within the province; *H. narracanensis* is noteworthy for its presence in both Victoria and Tasmania. Dispersal might have occurred by waterfowl or across a Pleistocene land-bridge. This argues for the retention of provinces defined by species distributions rather than drainage divisions.

A point of interest is that the Tasmanian fossil mussel fauna includes *Alathyria tamarensis*, from Eocene(?) deposits, and a probable member of the early Velesunioninae, *Prohyria johnstoni*, from Oligocene sediments (McMichael, 1957). Both fossils, like the modern Tasmanian fauna, are from the Tamar River system.

The Lessonian province shares with the Riechian the distinction of having the largest number of species (10), although there are relatively few species restricted to the province (4 cf. 7 respectively). Five Lessonian species occur in the Krefftian province, and two in the Mitchellian province.

3.4 Tobinian province

Resident species: nil

The division of Tasmania into northern and southern halves has no apparent physiographic or climatic basis. Iredale & Whitley (1938) characterized the Tobinian fluvifaunula in terms of certain fish and gastropod species, and an absence of freshwater mussels. In view of the liberal interpretations given to the limits of other provinces, it appears unrealistic to separate the Tobinian from the Lessonian province.

3.5 Mitchellian province

Resident species: *Alathyria condola*, *A. jacksoni* and *Velesunio ambiguus*.

The Mitchellian province includes the Murray-Darling Drainage Division and the subsidiary Bulloo-Bancannia and South Australian Gulf Drainage Divisions. Two species, *A. jacksoni* and *V. ambiguus*, predominate and the latter extends well beyond the province. *A. jacksoni* is characteristic in the sense that it is widespread in the province, and virtually restricted to it. *A. condola* apparently is confined to the Murrumbidgee and Lachlan Rivers, and may be derived from *A. profuga* of coastal New South Wales (McMichael & Hiscock, 1958).

3.6 Sturtian province

Resident species: *Alathyria pertexta*, *Velesunio ambiguus* and *V. wilsonii*.

The Sturtian province coincides with the Lake Eyre Drainage Division. The Western Plateau Division is not considered, as it contains neither rivers or mussels. It is arguable whether, as McMichael & Hiscock claim, *V. wilsonii* is characteristic of this province, because although it is widespread there are important extensions to its range in other provinces. *A. pertexta* (*A. p. pertexta*) and *V. ambiguus* occur only in the upper reaches of the Diamantina River system.

The Sturtian fluvifaunula is poorly defined in that the three resident mussel species are present also in the Jardinian and Krefftian provinces, and two in both the Leichhardtian and Riechian provinces.

3.7 Vlaminghian province

Resident species: *Westralunio carteri*.

The genus *Westralunio* is known only from the south-western corner of Western Australia (the South-West Coast Drainage Division) and from southern New Guinea. McMichael & Hiscock suggested that this anomalous distribution may reflect morphological convergence or the remnants or a formerly widespread genus. Transport by waterfowl also is a possible explanation. In any case, *W. carteri* clearly is separable from other Australian species and justifiably considered characteristic of the Vlaminghian province.

3.8 Greyian province

Resident species: *Velesunio angasi* and *V. wilsonii*.

The Greyian province coincides with the Indian Ocean Drainage Division. Given that Iredale & Whitley's claim that *Lortiella* is present is erroneous (McMichael & Hiscock, 1958), it has generally been thought that freshwater mussels were absent. However, specimens of *V. wilsonii* and also *V. angasi* have recently been collected from pools in the bed of the Fortescue River (Walker, unpublished). The very limited zoogeographic knowledge that exists for this area suggests that its affinities are with the Timor Sea Drainage rather than the Lake Eyre Division (although *V. wilsonii* is common to all three divisions). There are now unpublished records of both species from the Fortescue and Ashburton Rivers.

3.9 Leichhardtian province

Resident species: *Alathyria pertexta*, *Lortiella froggatti*, *L. rugata*, *Velesunio angasi* and *V. wilsonii*.

The Leichhardtian province encompasses the Gulf of Carpentaria and Timor Sea Drainage Divisions. The former division contains three species, and the latter four, with two species common to both. Ignoring the doubts concerning *Lortiella*, the province does appear to have sufficient integrity to warrant the 'merging' of two drainage divisions. The physiographic boundary is in fact only poorly defined (Australian Water Resources Council, 1975).

V. angasi is shared only with the Greyian province. *V. wilsonii* is widespread; its presence, together with *A. pertexta wardi*, suggests dispersal by river capture (Fig. 3). *Lortiella* occurs only in the western part of the province. Two species, *A. pertexta* and *V. wilsonii*, occur also in the Jardinian, Krefftian, Sturtian and Riechian provinces.

3.10 Riechian province

Resident species: *Alathyria pertexta*, *Haasodonta fannyae*, *H. vanheurni*, *Hyridella guppyi*, *H. misoolensis*, *Microdontia anodontaeformis*, *Velesunio wilsonii*, *Virgus beccarianus*, *Westralunio albertisi* and *W. flyensis*.

The island of New Guinea is longitudinally bisected by a central mountainous region that effectively defines two main drainage divisions, one flowing northward to the Solomon and Bismarck Seas, and the other southward to the Coral and Arafura Seas. The southern division corresponds to the Riechian province, and the northern division to the Gaimardian province.

The widespread *W. flyensis* and the slightly more restricted *H. misoolensis* may be regarded as characteristic species. Species found only in isolated pockets are *W. albertisi*, *Haasodonta* spp. and *V. beccarianus*. *H. guppyi* occurs as one subspecies in the St. Joseph's River, eastern New Guinea, and as another in some of the Solomon Islands. *A. pertexta* (*A. p. magnifica*) and *V. wilsonii* are each known from only one locality, and both records

require confirmation. As the records stand, these are the only two species shared between New Guinea and Australia.

3.11 Gaimardian province

Resident species: *Microdontia anodontaeformis* and *Velesunio sentaniensis*.

V. sentaniensis occurs in several places along the north coast of New Guinea, and is a characteristic species. The one northern record of *M. anodontaeformis*, from the Sepik River, is queried by McMichael & Hiscock (1958), presumably because the single specimen was a juvenile. Whether or not the northern extension of *M. anodontaeformis* proves valid, it is clear that the Gaimardian province is distinguished by a remarkable paucity of mussel species compared to the neighboring Riechian province.

4. Dispersal

Freshwater mussels generally are regarded as animals having relatively limited powers of dispersal; this is of obvious importance in a zoogeographic context. Important factors are river capture and transport by waterfowl and fish. In North America, Van Der Schalie (1939, 1963) has shown that former stream confluences have been a significant factor in mussel distribution, and that present day distributions are indicative of paleodrainage systems. In Australia, a possible example of dispersal by river capture, mentioned earlier, is the presence of *Velesunio wilsonii* in part of the Gulf of Carpentaria Drainage Division. Other possible examples exist, but they are no more than circumstantial evidence. More information about ancient drainage systems would be helpful. Such information for Western Australia (Mulcahy & Bettenay, 1972) and South Australia (Howchin, 1931; 1933) shows that the now dry Western Plateau formerly was traversed by extensive networks of streams. Former drainage channels in south-eastern Australia are reasonably well-known (e.g. Gregory, 1903; Hills, 1959), and the occurrence of similar aquatic animals in Tasmania and mainland Australia (e.g. Walker, 1969) is evidence for contiguous streams at the time of the Pleistocene land-bridge. It is clear that opportunities have existed in the relatively recent past for widespread dispersal *via* confluent streams. The fact that some of the principal drainage divisions have boundaries that are, in physiographic terms, poorly defined suggests these may have merged during the pluvial periods of the Pleistocene, subsequently offering only a relatively short time for faunal divergences to occur. This lack of sustained physiographic integrity may mitigate against distinctive fluvifaunal assemblages.

In the world literature there are numerous reports of waterfowl bearing adult mussels, one being Cotton's (1934, 1961) record of a specimen of *Velesunio ambiguus* attached to the foot of a black duck shot in South Australia (Fig. 4). Waterfowl transport may have been responsible for two isolates of the Murray-Darling species *Alathyria jacksoni* in coastal Victoria (Maribyrnong and Mitchell Rivers; McMichael & Hiscock, 1958), and

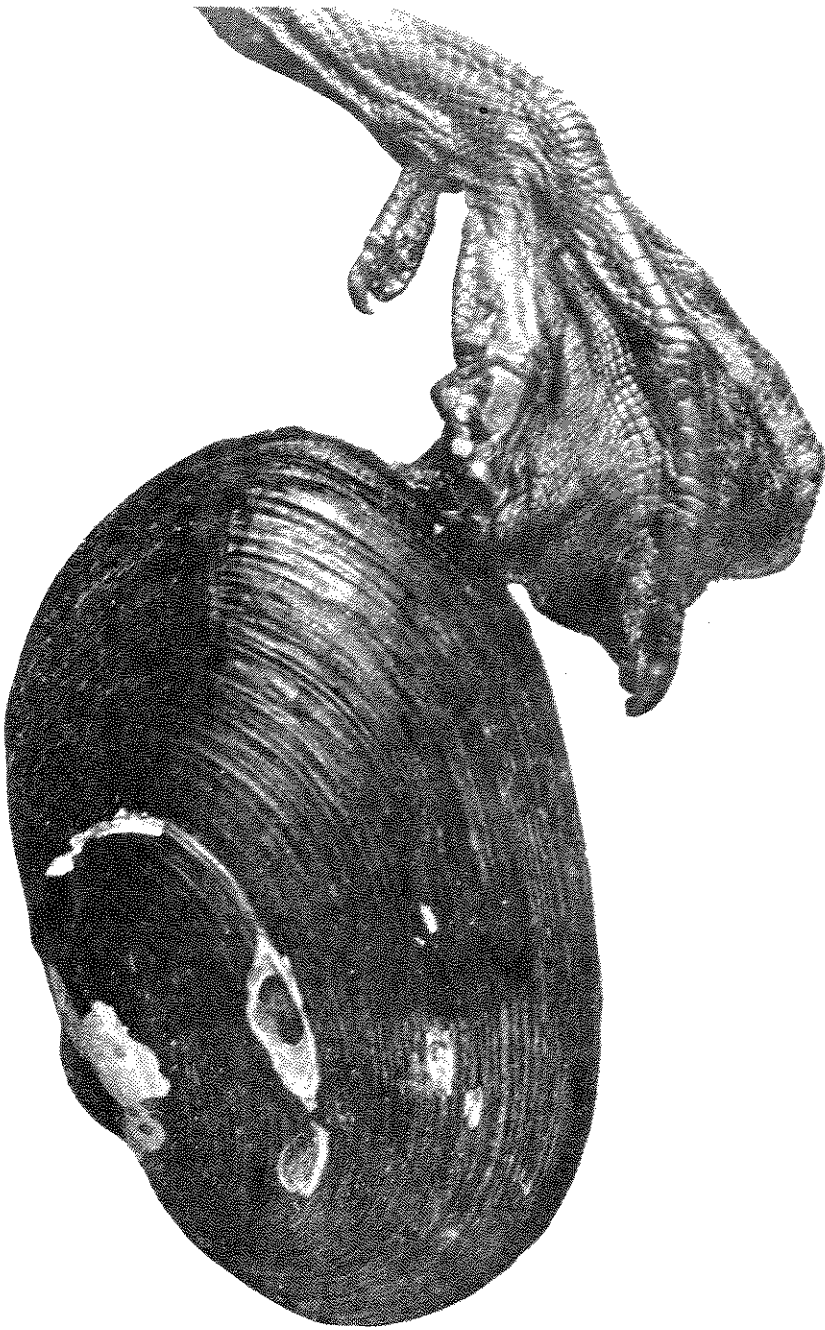


Fig. 4. *Velesunio ambiguus* attached to the foot of a black duck (*Anas superciliosa* Gmelin) shot in flight at Naracoorte, South Australia. Reproduced from Cotton (1961) with permission of the Flora and Fauna of South Australia Handbooks Committee.

notably for the origin of the New Zealand mussel fauna (McMichael, 1958). Two further instances may be the presence of *Alathyria pertexta* and *Velesunio wilsonii* on the island of New Guinea. Van Der Schalie (1939) argued against a significant role for waterfowl, partly because no conclusive evidence existed for the actual transport of mussels from one stream to another. This is a tenuous objection, and one that might also be applied with some success to the case for dispersal by river capture. In Australia at least, the case rests on observations (some unpublished) of mussels attached to birds in flight, and on the knowledge that the flight pathways of some waterfowl species are sufficiently wide-ranging and often-traversed for numerous opportunities for adventitious transport to have arisen (e.g. Frith, 1967).

The remaining factor, dispersal on fish, has received surprisingly little attention, probably because the fish host preferences of individual mussel species are little known. The parasitic glochidium, however, is the primary dispersive phase in the life history of mussels. During the few weeks of parasitic life the glochidium metamorphoses to become a juvenile mussel, and its subsequent fate depends to a large extent on the habitat preferences and migratory inclinations of its host. Some native fish, for example the callop, *Macquaria ambigua* (Richardson), undertake extensive migrations (Anon., 1977), particularly during rising floods. Some, perhaps many, mussel species would be limited in distribution by their dependence on particular fish hosts; this point was raised by Van Der Schalie (1939) in arguing against the likelihood of long-range dispersal by waterfowl. Not all mussel species, however, are strongly selective of fish hosts. *Velesunio ambiguus* will readily complete its larval metamorphosis on at least 11 of the fish species occurring in the Murray-Darling river system (Hiscock, 1951; Walker, unpublished) and, remarkably, also on tadpoles of the common froglet *Ranidella signifera* (Girard) (Walker, unpublished). In addition, there is an unconfirmed report (Hiscock *vide* Dean, 1968) of a population of *V. ambiguus* in which the parasitic stage was suppressed, the juvenile mussels having metamorphosed while retained by the females. It is therefore not surprising that *V. ambiguus* ranks with the most widely distributed Australian species. In general, although the distributions of Australian freshwater fish are well-documented (Lake, 1971), information is needed about the host preferences of other mussel species before conclusions can be drawn about the role of fish in their dispersal.

5. Phylogeny and distribution

Phylogenetic aspects of the regional mussel fauna are discussed by McMichael & Hiscock (1958), although the scarcity of fossil material precluded firm conclusions. Among the modern fauna, the genus *Velesunio* is considered least remote from the primitive northern stock that invaded Australia during the Triassic. The oldest known velesunionid (?) is the Triassic *Prohyria eyrensis*; other fossils, some perhaps of greater antiquity, are reported, but their affinities are uncertain (McMichael, 1975). *Alathyria*,

Microdontia and *Westralunio* are thought, with varying certainty, to be derivatives of *Velesunio*. *Lortiella* also may be an ancient offshoot of *Velesunio*. The Hyridellinae are believed to be a derivative of the Velesunioninae in late Mesozoic time, although this may need modification in view of Parodiz & Bonetto's (1963) suggestion that the South American *Diplodon* is an evolutionary precursor of *Hyridella* (fossil *Diplodon* are known from the Triassic of North America). In Australia the hyridelline stock may have given rise to *Cucumerunio*, and *Cucumerunio* to *Virgus*. Finally, *Haasodonta*, if a member of the Rectidentinae (Unionidae), apparently is of comparatively recent south-east Asian origin.

These speculations (McMichael & Hiscock, 1958) followed partly from fossil evidence and partly from present relationships. Although there are several uncertainties, it appears that it is the most primitive members of the Australian fauna—the Velesunioninae—that are most widely distributed. The most primitive of the extant genera, *Velesunio*, occurs in all principal drainage divisions apart from the South-West Coast, although with only a meagre claim to representation in southern New Guinea. Another primitive genus, *Alathyria*, is distributed over most of eastern Australia, and occurs also as an isolate in southern New Guinea. Representatives of *Westralunio* inhabit south-western Australia, where *W. carteri* evidently has been isolated since the Miocene (McMichael & Hiscock, 1958), and southern New Guinea. Finally, the monotypic *Microdontia*, unlike other Velesunioninae, virtually is restricted to one drainage division (Southern New Guinea), giving due regard to the uncertain record from the Sepik River in northern New Guinea.

In contrast, members of the derived subfamilies Hyridellinae and Cucumerunioninae have more restricted distributions. The same applies to the Lortiellinae if, as seems likely, they are legitimate members of the Hyriidae. *Hyridella*, the sole genus of Hyridellinae, occurs in coastal south-eastern Australia (including Tasmania), in New Guinea (and the Solomon Islands) and in New Zealand. A broadly similar pattern is shown collectively by the Cucumerunioninae, consisting of *Cucumerunio* and *Virgus*. In each case, McMichael & Hiscock (1958) favoured the view that Australia has been the locus of differentiation, with representatives of the Hyridellinae and Cucumerunioninae having been transported by waterfowl to other areas. It seems certain that similar opportunities would have arisen for dispersal to inland and northern Australia. The fact that the Hyridellinae and Cucumerunioninae do not presently occupy these areas may be for reasons of ecological or physiological exclusion (see below). It is noteworthy that the Cretaceous fossil *Hyridella whitecliffsensis* was found far inland, in north-western New South Wales (McMichael, 1957). The present concentration of *Hyridella* species in south-eastern coastal areas therefore may be a relict of a more widespread ancient distribution, although this is unsubstantiated by other fossil finds.

Thus the principal subfamilies of Hyriidae are distributed either widely (the primitive Velesunioninae), or concentrated primarily in south-eastern coastal areas, with secondary dispersal elsewhere (the derived Hyridellinae

and Cucumerunioninae). In addition, the Lortiellinae are restricted to parts of north-western Australia. The distributions of genera, superimposed on those of the subfamilies, are in most cases broad, and there seems little support for the possibility that individual drainage divisions as they presently exist have been important centres of isolation and subsequent divergence. Rather, the present distribution suggests contractions of formerly more extensive ranges, as a result of post-Pleistocene aridity, modified perhaps by dispersal on waterfowl. However, assuming that mussels are readily transported by waterfowl, it seems that they have been more conservative in extending their ranges than the waterfowl (*cf.* Frith, 1967). Van Der Schalie & Van Der Schalie (1963) made a similar comment in relation to the comparative distributions of mussel species and their fish hosts. Hence it is pertinent to consider what ecological or physiological factors (other than availability of fish hosts) may operate to exclude mussel species from areas within their possible range of dispersal.

The distribution of *Hyridella* provides an example. Although five *Hyridella* species occur in south-eastern coastal Australia, there are no representatives in the adjacent Murray–Darling river system (Fig. 3). The Eastern Dividing Range, separating the respective drainage divisions, is not a major barrier to the migration of black duck and certain other waterfowl species (Frith, 1967), and therefore is unlikely to have been a long-term barrier to dispersal of mussels. Although the possibility of specific host fish requirements cannot be discounted, there is some evidence that the absence of *Hyridella* in the Murray–Darling system is a consequence of relatively high stream salinities (coupled perhaps with higher temperatures and more variable flows). Thus Dean (1968) showed that the distribution of *H. drapeta* in Victoria is limited to streams with salinities less than about 300 parts per million. An analogous situation may exist in South America, where the distribution of Hyriidae is correlated broadly with stream salinities (Parodiz & Bonetto, 1963).

Salinity tolerance does not however provide a general explanation for the limited distribution of *Hyridella*. In particular, it does not explain its absence in coastal north Queensland, where stream salinities are not obviously different from those in the south (Australian Water Resources Council, 1975). Although further speculations might be advanced, considering such possible factors as temperature, flow rate, substrate preference and water chemistry, these are best deferred pending the necessary ecological studies.

Conclusion

The earlier literature, stemming from Iredale & Whitley (1938), has considered faunal distributions only with a preconception of distinctive fluvifaunulae. Little regard has been shown for the overall patterns of distribution of faunal groups; rather, the method has been to select genera, species and subspecies 'representative' of the various fluvifaunulae. The criteria for deciding upon 'representative' forms have been vague and hence open to liberal interpretation. From this chapter it will be clear that among

the freshwater mussels there are species (notably *Velesunio ambiguus*, *V. wilsonii* and *Alathyria pertexta*) that do not conform closely with the boundaries of any fluvifaunal province. The most meaningful generalizations, in a zoogeographic context, may be those referring to the distributions of the subfamilies. Thus the primitive Velesunioninae are widely distributed in Australia and New Guinea, but curiously absent from New Zealand. The derived Hyridellinae and Cucumerunioninae are concentrated in coastal south-eastern Australia, but with outliers in New Guinea and New Zealand. There presently is no fully satisfactory explanation for this disjunct pattern, and it remains an intriguing problem for further research.

There is *some* correspondence between the ranges of mussel species and the geographic boundaries of the fluvifaunal provinces. The Lessonian and Krefftian provinces taken together correspond with the primary concentrations of Hyridellinae and Cucumerunioninae. The Vlaminghian province constitutes the entire range of *Westralunio carteri*, and the ranges of *Alathyria jacksoni* and *Velesunio angasi* nearly coincide with the Mitchelian and Leichhardtian provinces respectively. The Riechian province harbours seven species not found elsewhere, including two, perhaps three endemic genera. In general, however, the degree of overlap appears too great to warrant recognition of separate zoogeographic provinces. In particular, there appears little basis for distinguishing the mussel faunas of the Jardinian, Tobinian, Sturtian and Greyian provinces from those of neighbouring areas. The freshwater mussels do not provide effective support for the fluvifauna concept.

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Addendum

In an important paper, Ludbrook (1961) reaffirmed the presence of unionid mussels in the Australian Triassic, with obvious implications for McMichael & Hiscock's phylogenetic speculations.

Ludbrook, N. H. 1961. Mesozoic non-marine Mollusca (Pelecypoda: Unionidae) from the north of South Australia. Trans. R. S. Aust. 84: 139-147.

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