The Nature and Origin of the New Zealand Freshwater Mussel Fauna

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Abstract

The recent freshwater mussels of New Zealand are briefly reviewed and related to those of Australia. With the selection of a lectotype, *Unio lutulentus* Gould is made a subjective synonym of *Unio menziesi* Gray. The hypothesis of a land bridge to account for the origin of the New Zealand freshwater mussels is reviewed and rejected. The fossil species are discussed and it is concluded that they are not good evidence for an evolutionary sequence which would account for the recent species As an alternative, it is suggested that the recent New Zealand mussels were derived by transfer of Australian stocks across the Tasman Sea by birds A relationship between the freshwater mussels of Australasia and those of South America is confirmed.

The freshwater mussel fauna of New Zealand has long been of interest to zoogeographers, because of certain similarities in anatomy and shell morphology which the species have with South American forms. This resemblance was first emphasised by von Ihering (1891) and later confirmed by Suter (1891) and Simpson (1897). This morphological resemblance was reflected taxonomically when the New Zealand species, along with the majority of the Australian forms, were assigned to the South American genus *Diplodon* Spix in Simpson's Synopsis (1900) and Catalogue (1914) of the Najades.

The Australian and New Zealand species were separated subgenerically under *Hyridella* Swainson, which was eventually given full generic rank. There has been considerable confusion as to the exact application of the name *Hyridella,* because the type species *Unio australis* Lamarck has been misidentified for many years. Recently it has been shown that *U. australis* is the species which has been known for many years as *U. nepeanensis* Conrad and that *Hyridella* Swainson must stand as the generic name for the group of species allied to *U nepeanensis* (= *australis*) which had previously been known as *Propehyridella* Cotton and Gabriel (McMichael, 1955).

Iredale (1934) first separated the Australian freshwater mussels into four groups, which he called subfamilies. The largest group is the Velesunioninae, which contains three of four genera characterised by the absence of beak sculpture. The second largest group is the Hyridellinae based on *Hyridella* Swainson, characterised by the possession of V-shaped beak sculpture but lacking nodular shell sculpture. The third subfamily Cucumerunioninae included only one monotypic genus *Cucumerunio* Iredale, which possesses an elongate shell, very strong hinge teeth, V-shaped beak sculpture and in addition, extensive shell sculpture consisting of lachrymose nodules spread out over the surface of the valves in a fairly definite pattern. The fourth subfamily, the Lortiellinae includes only one genus with aberrant, elongate shells resembling the burrowing mycetopodine mussels of Asia and South America.

The status of these groups as subfamilies remains in doubt, but still they probably represent distinct groups within the Australian fauna. Iredale's revision did not include the New Zealand species. Dell (1953) was the first worker to revise the

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taxonomy of the New Zealand species subsequent to Iredale's work. Dell recognises only two species from New Zealand, in contrast to the several species and many subspecies allowed by Suter (1913) and earlier workers. Dell realised that one species (*Unio menziesi* Gray) was very variable and included among its constituent populations most of the forms which had previously been given species or subspecies rank. Dell left this species in the genus *Hyridella* where it correctly belongs. The characteristic beak sculpture is present and some populations are quite similar in form to Australian species of *Hyridella*. Dell admitted two subspecies, the nominate race occurring over most of New Zealand, the other (*H. menziesi depauperatus* Hutton) found in two widely separated localities in the North Island. There seems good reason to regard *depauperatus* as an ecophenotypical variant only, the product of calcium deficient waters.

For the second species, Dell used the name *Hyridella aucklandica* Gray. As synonyms, he included *Unio lutulentus* Gould and *Unio websteri* Simpson. Study of the type material of all three nominal species suggests that two different species are included in Dell's concept of *H. aucklandica* and that *U. lutulentus* requires reconsideration.

The identity of *U. lutulentus* Gould has been a problem for some time, because the type series includes at least two different forms. A number of the paratypes are typical *H. menziesi* (a low-winged form), while others are elongate shells, with practically no winging and a sinuate ventral margin, clearly separable from the *menziesi* series, but still belonging with the genus *Hyridella*. The description of *U. lutulentus* was apparently taken from both forms, but the specimen figured by Gould, 1852, Pl. 37, Figs. 542, 542a and 542b (but not 542c) is the *menziesi* form. It is in the United States National Museum, No. 5927, and is here selected as lectotype, thus fixing *Unio lutulentus* as a subjective synonym of *Hyridella menziesi* Gray. Dell (1953) has suggested the Bay of Islands as the restricted type locality for *U. lutulentus*.

To return to "*H. aucklandica*" as recognised by Dell, the holotype of *U. aucklandicus* Gray, which Dell figured, is in the British Museum, and proves to be the same as the second series of paratypes of *U. lutulentus* Gould mentioned above, that is, a second species of *Hyridella*. While it is very close to some forms of *menziesi*, it differs consistently in a few minor characters, and is apparently much less common with a restricted distribution. This species is here recognised as a valid species under the name *Hyridella aucklandica* Gray.

Most of the specimens figured by Dell as "*H. aucklandica*" however, are the form which has been known for many years as *Unio websteri* Simpson. This species, typically, differs from both the *Hyridella* species in having shell sculpture of lachrymose nodules. The hinge teeth are strongly developed, and in shape the shell tapers towards the posterior. In some populations, the sculpture tends to disappear, but the peculiar shape and strong hinge teeth are retained. It was these sculptureless populations which led Dell to consider *H. websteri* a synonym of *H. aucklandica*. It is true that the two forms are at times difficult to separate. However, I believe they can be separated by their shape, *H. aucklandica* having a slightly sinuate ventral margin and a more robust shell, while the sculptureless *websteri* never has a sinuate ventral margin and the shell is relatively thin, especially at the posterior end. The final determination of the validity of these two species must be made by local New Zealand students.

The generic position of *websteri* requires consideration. While the sculptureless forms would normally be classified in *Hyridella*, the pattern of sculpture in typical *websteri* is basically similar to that of *Cucumerunio novaehollandiae*, while the strong serrated cardinal teeth and the general appearance of the shell recall the latter species. I therefore regard the species as *Cucumerunio websteri* Simpson. The sculptureless populations of this species may represent a geographical race as Dell (1953) suggested.

Speculation as to the origin of the New Zealand freshwater mussel fauna has so far been confined to suggestions of a southern origin via a land bridge from South America. This suggestion was based on the widespread belief that freshwater mussels require freshwater connections, and consequently land connections, for dispersal. An alternative hypothesis might suppose a northern land bridge, as has been suggested for other groups, though such a suggestion has never been put forward in regard to freshwater mussels.

There is, however, much evidence to suggest that there has been no direct land connection between Australia and New Zealand since the end of the Cretaceous. The prime supporting fact is that while the floras of Australia and New Zealand were very similar during Cretaceous time, they have been steadily diverging ever since, implying continued isolation. There is no good geological evidence to suggest that New Zealand was connected with Australia during the Tertiary, either directly or by way of the island archipelagoes to the North. Although there is a submarine ridge connecting New Zealand with the islands to the North, it is unlikely that this ever formed a continuous land connection. Further evidence against this northern origin for the New Zealand mussels is the fact that no species are known from New Caledonia, while those from the Solomon Islands and eastern New Guinea are quite distinct generically from the New Zealand species. The absence of mammals, most reptiles and amphibia, and primary and secondary freshwater fishes (Myers, 1953) from New Zealand also implies that it has had no continuous land connections with any continental area for a very long time.

To return to the theory of a southern origin, if this be accepted, then there should be some evidence of a fossil ancestry for the recent species extending back to the Cretaceous. We should also expect to find that considerable differences between the Australian and New Zealand species have developed during the long period of isolation since the end of the Cretaceous (assuming that normal evolutionary rates apply to freshwater mussels). This, however, is not the case. The recent New Zealand species appear to be rather closely related to species living today in the south-east coastal drainage of Australia.

A study of the fossil freshwater mussels of Australia and New Zealand has recently been made (McMichael, 1957) and the results are significant here. The earliest Australian species occur in the Triassic and seem to have little or no relationship with the recent species. The ancestry of some of the recent Australian groups (including *Hyridella*) possibly goes back to the Upper Cretaceous, though the remainder appear only in the Tertiary or else have no known fossil history. One pecular species occurs in the Upper Triassic Wianamatta Group of shales and has been named *Protovirgus dunstani* (Etheridge). The New Zealand fossils include a Cretaceous species which appears to be congeneric and has been named *Protovirgus flemingi* McMichael. While these forms suggest a possible Mesozoic connection between Australia and New Zealand, they also seem quite unrelated to the recent species. A second New Zealand fossil species may belong with the recent Australian genus *Velesunio* (*V. huttoni* McMichael = *U. inflata* Hutton preoccupied), though its exact affinities are doubtful. It occurs in basal Oligocene coal measures in the South Island.

Impressions of freshwater mussels appear in the Miocene shales of the Taranaki Series, and these may represent the two recent species of *Hyridella*. There is at least one other undescribed Cretaceous species which could be a *Hyridella*, but as only a single impression is available, it cannot be assigned with accuracy. While the fossil record is far from complete, the evidence for an evolutionary sequence from the Cretaceous through to recent forms is not good. *Cucumerunio websteri* has no known fossil history, while the species of *Hyridella* may have had their origins as late as the middle Tertiary.

It remains, therefore, to consider alternative means by which the New Zealand mussel fauna may have arisen. The fact that the three recent species are all apparently closely related to present day Australian species suggests a fairly recent origin from Australian stocks. In view of these facts it seems a more reasonable hypothesis to derive the recent New Zealand species directly from Australian ancestors, by direct transfer across the Tasman Sea.

Mayr (1940, 1953) has emphasised the fact that recent studies of speciation have shown that the dispersal facilities of most animals and plants are much greater than previously thought. The reason why species are not more widely distributed lies not so much in the problem of dispersal beyond the normal range, but in the problem of survival and successful establishment in a new locality. It seems possible that this is also true of freshwater mussels.

While most authors have accepted the fact that freshwater mussels require land connections for dispersal, there has been for many years a controversy regarding the possibility of birds acting as passive agents in the dispersal of these animals. The argument in favour of birds as agents of dispersal has been detailed by Johnson (1939, 1941, 1942) and the case against bird transfer, by Van der Schalie (1939, 1945).

There are a number of points which should be mentioned here in connection with this controversy Evidence that birds can and do, on occasions, carry mussels from place to place was given by Cotton (1934) who recorded a living specimen of *Velesunio ambiguus* (Philippi) clinging to the foot of the Black Duck, *Anas superciliosa,* which was shot in flight at Narcoota, South Australia. Cotton estimated that the mussel had been out of water for several days.

One of the key arguments used against birds as effective agents in dispersal has been the claim that most freshwater mussels require a specific fish host for the glochidial stage. Van der Schalie suggests that even if a mussel were transferred to a new locality outside its normal range, it would not survive unless the appropriate fish host were present. While it may be true that some species of mussels are quite specific in their host requirement, this does not seem to be true for Australian and New Zealand species. At least two species of Australian mussels have been found to parasitise the introduced South American fish *Gambusia affinis* B. & G. while the New Zealand *H. menziesi* is reported to parasitise trout in the South Island. It seems likely that many mussels are quite adaptable in this regard, and many would probably be able to parasitise species which were closely related to their normal host.

One of the most telling arguments against birds as dispersal agents is the fact that most species of mussels have characteristic distribution patterns which would presumably be broken down if mussels were haphazardly carried about from stream to stream. While it is true that the distribution of a particular species of mussel is normally fairly discrete, often confined to a particular river system, there are occasional exceptions. These exceptions would be difficult to explain by stream confluence. As an example, *Velesunio ambiguus* (Philippi) occurs throughout the Murray-Darling River system of New South Wales, Queensland and Victoria. It is normally not found in the coastal rivers of New South Wales, but populations do occur in four coastal rivers, the Nepean, the Hunter, the Clarence and the Richmond. There is no good evidence that there has been any river capture between these streams and the Murray-Darling system, at least since early Miocene time. In each case, however, the headwaters of the coastal streams approach closely the headwaters of the inland rivers, so that it would require only a short flight from one side of the watershed to the other to effect the transfer. A possible explanation for the absence of *V. ambiguus* from most of the coastal streams is the preference of the species for a muddy environment. While most of the coastal streams are fast flowing and clear, the four streams in question have long muddy stretches in their lower reaches. It is also significant that flocks of inland water birds which periodically visit the coastal regions of New South Wales usually congregate on these same four coastal rivers.

It seems clear, therefore, that a good case can be made in support of the theory of birds acting as dispersal agents, and the suggestion is here put forward that birds could have been responsible for the introduction of colonising stocks of Australian mussels into New Zealand.

Strong objections might well be raised to the suggestion that birds could complete such a long flight carrying a large mussel clinging to one foot, or alternatively that the mussel could survive. It is quite possible, however, that minute mussels could be carried across in mud attached to the feet of wading birds. It is known that certain of the Australian species of mussels can survive long periods out of water when adult, and this is obviously an adaptation to the severe drought conditions which occur regularly in Australia. It is quite likely that the very young mussels can also withstand a fair amount of desiccation, at least sufficient to survive the journey from Australia to New Zealand.

It is well known that Australian birds are regular visitors to New Zealand (Falla, 1953). Several species of water birds, including the White-faced Heron, the Royal Spoonbill and the Eastern Swamp Hen have become established as breeding species in New Zealand during historic time, through migration across the Tasman Sea, and there are a number of other species of Australian water birds which have been reported from New Zealand at irregular intervals. The bird species recorded as visitors to New Zealand are all Australian species, none being from New Guinea or areas further East. It is also significant that where the birds are racially distinguishable, the migrants all belong to south-east Australian races.

Only two or three successful introductions would be necessary to account for the recent New Zealand species Even though the chances of a population of young mussels surviving the journey and becoming established are probably very low, none the less, during the vast expanse of geological time the few necessary introductions could have been effected successfully.

Whatever the origin of the New Zealand freshwater mussels, there can be no doubt that they are closely related to the Australian species and that this Australasian fauna is in turn related to the mussels of South America, rather than to those of the northern continents. A clear cut anatomical distinction exists between the northern hemisphere families (Unionidae and Margaritiferidae) and the family found in South America and Australasia and probably South Africa (Mutelidae). As such the freshwater mussels still stand as good evidence of some past connection between the southern continents. Bird dispersal certainly cannot be used to account for the pre-Tertiary distribution of freshwater mussels, for it is unlikely that birds were either abundant or highly specialised even in late Mesozoic time.

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