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Affinities, Generic Classification and Biogeography of the Australian and New Zealand Mudfishes (Salmoniformes: Galaxiidae)

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ABSTRACT. The Australian mudfish, *Galaxias cleaveri*, resembles the three New Zealand mudfishes (*Neochanna* spp.) in general external morphology. It is the least specialised of a transformation series that includes all four mudfishes, in which the body is elongated, eyes are small, anterior nostrils long, tubular and forward directed, dorsal and anal fins low and long, flanges on the caudal peduncle well developed, pectoral fins small, paddle-shaped, and high on sides behind head, and pelvic fins reduced or lost. Unique specialisations in the vomerine-ethmoid region of the cranium and in the form of the pectoral girdle support the view that these four species are a monophyletic group. The Australian species is therefore included in *Neochanna*. The presence of a marine larval and juvenile life stage in the Australian species (diadromy) probably explains the distribution of the genus, with New Zealand species together derived from the Australian one or their common ancestor by dispersal across the Tasman Sea in prevailing ocean currents. The biogeography of the Australian and New Zealand species is consistent with post-Oligocene geology, and in particular with events during and since the Pleistocene.

The genus *Neochanna* was established by Günther (1867) to contain a small, cigar-shaped fish found when drains were being dug in swamplands on the West Coast of the South Island of New Zealand; it was described as *N. apoda* (Fig. 1D). While apparently a galaxiid (Galaxiidae) from its posterior dorsal fin and lack of scales, it was distinguished from *Galaxias* species by lacking pelvic fins, having flattened incisor-like jaw teeth, no endopterygoid teeth, long-based and low dorsal and anal fins that are nearly confluent with a distinctly rounded caudal fin, elongated, tubular anterior nostrils that point forwards, and small eyes (McDowall, 1970). Known commonly as "brown mudfish", it became well-known as a fish often found, semi-torpid and aestivating, in damp locations from which water had dried up—beneath logs and stumps, down old root holes around the bases of forest trees, and in similar, damp places where water is ephemeral

(Fitzgerald, 1873; Reid, 1886; Eldon, 1968; McDowall, 1990). Stokell (1949) described a second species of *Neochanna* from the northern North Island of New Zealand—the "black mudfish", *N. diversus* (Fig. 1C)—which shares most of the distinctive features of *N. apoda*, except that its jaw teeth are the typical, recurved somewhat fang-like teeth of other galaxiids, and it occasionally has endopterygoid teeth-though when present they are few and small. It, too, has often been reported as aestivating in locations similar to those reported for *N. apoda* (McDowall, 1990). A third New Zealand species, the "Canterbury mudfish", was described as *Galaxias burrowsius* (Fig. 1B) by Phillipps (1926), and it closely resembles the other mudfishes in many characters. It was excluded from *Neochanna* by both Phillipps (1926) and Stokell (1949) because it possesses pelvic fins, though these are much smaller than in other New Zealand *Galaxias* (and have only 4–5 rays, compared with 7 in most species) and it also has a few, if very small, endopterygoid teeth. Like *N. diversus* it has conical, fang-like jaw teeth. McDowall (1970) included the Canterbury mudfish in *Neochanna* because of the several distinctive similarities between the three species. He considered that they formed a radiation within the New Zealand Galaxiidae, and preferred to group these species on the basis of relationship indicated by shared derived characters, even though doing so meant that absence of pelvic fins was no longer an explicit diagnostic character of the genus. All three species show a trend towards anguilliform characteristics, being least specialised in the Canterbury mudfish and most specialised in the brown mudfish.

Australia also has a species commonly known as "Tasmanian mudfish", originally described as several species from Tasmania (*G. cleaveri* Scott, 1934, *Saxilaga anguilliformis* Scott, 1936, and *G. upcheri* Scott, 1942), but these were treated as a single species, *G. cleaveri*, by McDowall & Frankenberg (1981) (Fig. 1A). This species has since been found also on Flinders Island, in Bass Strait (Green, 1984), and in southern, coastal Victoria (Jackson & Davies, 1982; Koehn & O'Connor, 1990; Koehn & Raadik, 1991); the Victorian populations are separated from Tasmanian populations by Bass Strait (see Fig. 10).

McDowall (1969, 1970, 1990) drew attention to obvious external similarities between the Australian *G. cleaveri* and New Zealand *Neochanna* species, and discussed the prospect that they are phylogenetically more closely related to each other than any of them is to other galaxiids. McDowall & Frankenberg (1981) commented only that *G. cleaveri* resembles New Zealand *Neochanna* and did not further discuss or investigate their relationships.

This paper explicitly addresses that question and presents a cladogram that expresses an hypothesis of these relationships on the basis of common, distinctive, derived characters. It examines the biogeography of the mudfishes, in the context of the proposed phylogeny.

Methods and material examined

Study is based on unregistered material in the NIWA fish archive of galaxiid fishes, including both whole preserved specimens and cleared and alizarin-stained osteological specimens, listed in Appendix 1. The cladogram derived from the study, presented in Fig. 9, was produced using HENNIG86 (Farris, 1988) and CLADOS (Nixon, 1991). Alternative character states used in analysis are listed in Table 1 and a coding matrix for these is in Table 2.

Results

1. Identification of outgroup for determination of phylogenetic relationships: Fruitful examination of relationships depends in part on the appropriate choice of outgroups for determining the distinctiveness and polarity of morphological characters. The closest relatives of the mudfishes within the Galaxiidae are not obvious. The four species form a transformation series from least to more specialised (Fig. 1A-D) with the Australian species the least specialised and most *Galaxias*-like. They possess no identified characters that point to a relationship with any of the other, usually more specialised and distinctive, galaxiid genera such as *Brachygalaxias*, *Galaxiella* and *Nesogalaxias*. Amongst the distinctive features of the Australian mudfish is the presence of a diadromous (amphidromous) life cycle (McDowall, 1988, 1993) involving spawning in fresh water, a larval migration to sea, life there for several months, followed by a return migration of small juveniles to fresh water (Fulton, 1986). This is considered to be a primitive feature in the Galaxiidae (McDowall, 1993), and hence a common ancestry of the mudfishes and other amphidromous species seems likely within the family Galaxiidae; derivation from some non-diadromous species is less likely since a return to a diadromous life history is then required. Five other known diadromous *Galaxias*, viz. *G. truttaceus* Valenciennes (Australia), *G. brevipinnis* Günther (Australia, New Zealand), *G. fasciatus* Gray, *G. argenteus* (Gmelin) and *G. postvectis* Clarke (all New Zealand) share numerous apparently primitive characters in the genus. From amongst these, the Australian *G. truttaceus* was used for cladistic analysis as an outgroup for determining character polarities within the mudfishes. However, use of any of the above species, or all five of them together, would have produced an identical result.

2. External morphology: The three New Zealand and one Australian mudfishes resemble each other and differ from most other galaxiids in the following combination of external, macroscopic characters (Fig. 1A-D):
- elongate, cigar-shaped form with dorsal and ventral body profiles near parallel from head to tail (other than sometimes a deepening of the belly in mature to ripe fish prior to spawning);
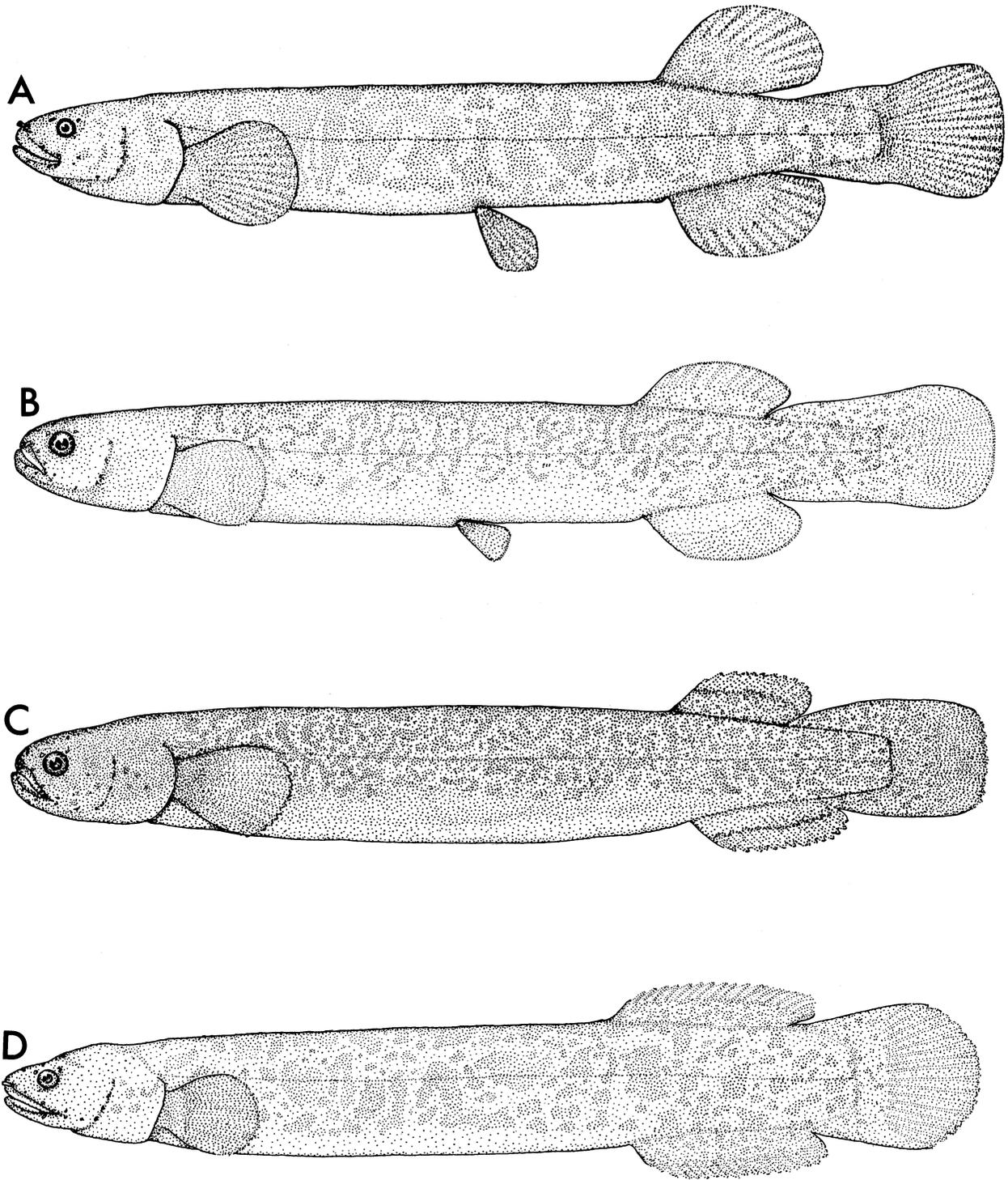
Fig. 1. The four galaxiid mudfishes: **A**, Australian mudfish—*Neochanna cleaveri*, Pieman River, Tasmania, 79 mm T.L.; **B**, Canterbury mudfish—*N. burrowsius*, Gawler Downs, Hinds River, N.Z., 108 mm T.L.; **C**, Black mudfish—*N. diversus*, swamp at Waiharara, 112 mm T.L.; **D**, Brown mudfish—*N. apoda*, tributary of Mangatarere Stream, Ruamahanga River, 110 mm T.L.
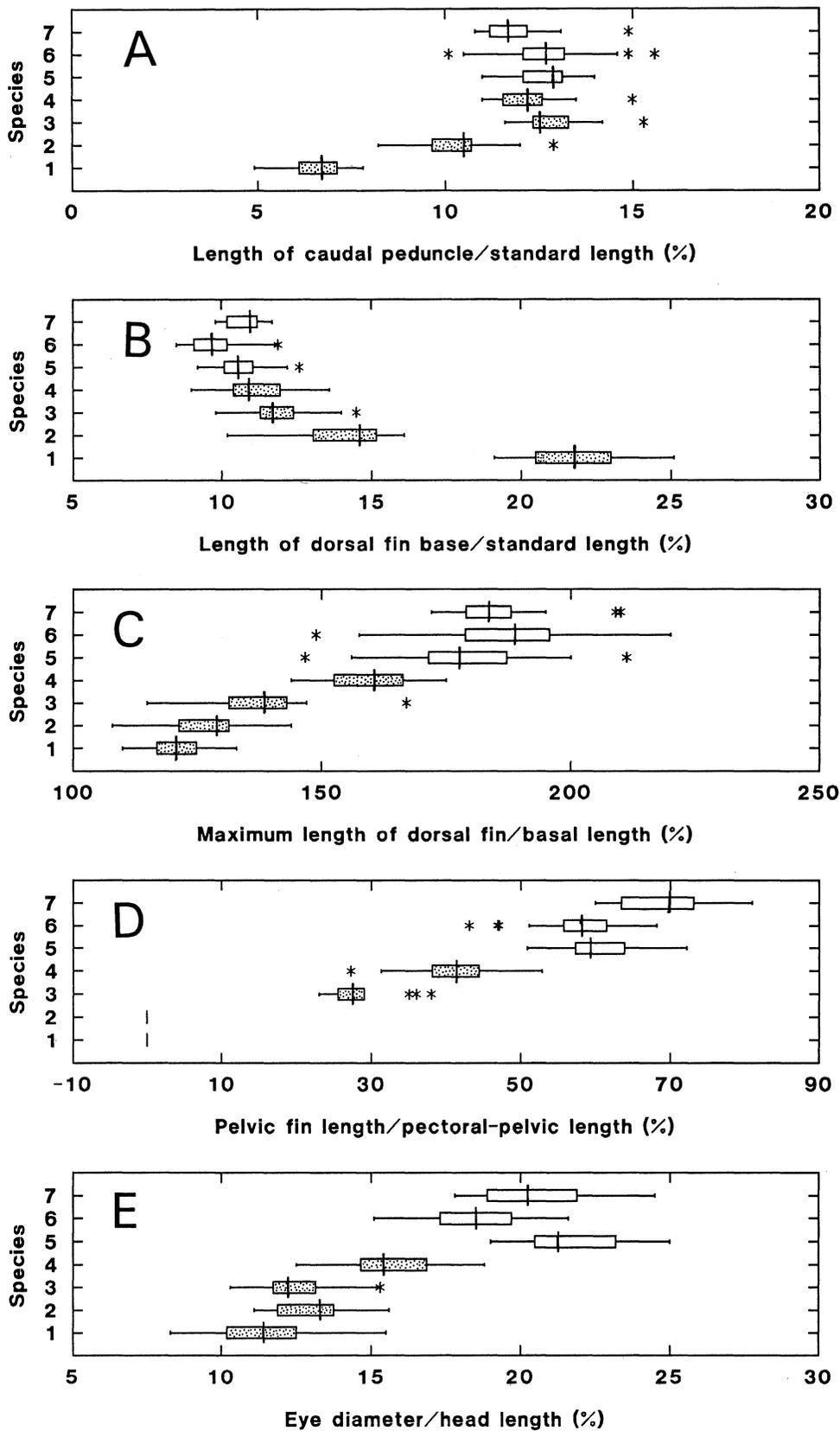
Fig. 2. Morphometric ratios in *Neochanna* species (stippled) and selected *Galaxias* species: **A**, length of caudal peduncle/ S.L. (%); **B**, length of dorsal fin base/S.L. (%); **C**, maximum length of dorsal fin/basal length of fin (%); **D**, pelvic fin length/pectoral-pelvic length (%); **E**, eye diameter/head length (%): 1 *Neochanna apoda*, 2 *N. diversus*, 3 *N. burrowsius*, 4 *N. cleaveri*, 5 *Galaxias truttaceus*, 6 *G. brevipinnis*, 7 *G. fasciatus*—data from McDowall (1970) and McDowall & Frankenberg (1981). Plots use the box-plot facility in SYSTAT (Wilkinson, 1990) and show median, interquartile range (box), and 1.5 times interquartile range; asterisks are outside values.

- small eyes (Fig. 2E) set well below the dorsal head profile;
- elongate, tubular, anterior nostrils that project forward over the upper lip;
- pectoral fins small and rounded, distinctly lateral in position and behind the opercular openings, fin base broad, upper edge of fin towards lateral line and the first ray forming the upper edge of the fin (in most *Galaxias* these fins are low on the sides, almost below the rear of the opercular openings, and they face downwards in almost shark-like fashion (Fig. 3); the first pectoral ray, which articulates with the scapula, rotates forward to form the leading edge of the fin);
- caudal fin rounded.

There is also a series of distinctive character trends among the four species:

- strongly developed flanges may occur along the dorsal and ventral edges of the caudal peduncle, as a result of which the dorsal, caudal and anal fins tend to be confluent, or nearly so; this character is least developed in the Australian mudfish, but is increasingly evident in Canterbury, black and brown mudfishes (Fig. 1A-D);
- dorsal and anal fins are rather long (Fig. 2B) and low with the same trend of increasing development of this character in the four species; the distal fin margins are distinctly rounded and middle rays the longest (and thus most *Galaxias*-like) in the Australian species, but fins are progressively longer, lower, and flatter, with the distal edge tending to be parallel with body profile and all fin rays of similar length in the Canterbury, black and brown mudfishes (Figs 1A-D, 2C);
- pelvic fins are reduced in size in the Australian species, sometimes have 6, but usually have 7 rays as in most *Galaxias*; the Canterbury mudfish has even more reduced pelvic fins that have 4 or more usually 5 rays; brown and black mudfishes have no pelvic fins or girdle at all (Fig. 2D);
- endopterygoid teeth are reduced but present in the Tasmanian species, and similarly in the Canterbury mudfish, usually absent in the black mudfish and few and small when present, but always absent in the brown mudfish.
- the brown mudfish differs from all others in having flattened, incisor-like jaw teeth, and also large specimens tend to have a strongly-developed, eel-like, muscular dome behind the occiput.

All these species thus have "anguilliform-like" characteristics, that could be interpreted as providing adaptation for life in a "crevice" habitat filled with aquatic vegetation and debris. Small eye size is reflected in a high ratio of forebrain/optic lobes in the brain of the three New Zealand species compared with most other New Zealand Galaxiidae (Cadwallader, 1975; Fig. 4). Comparable data have not been published for the Australian species.

There is thus a suite of characters affecting several independent morphological systems in which there are
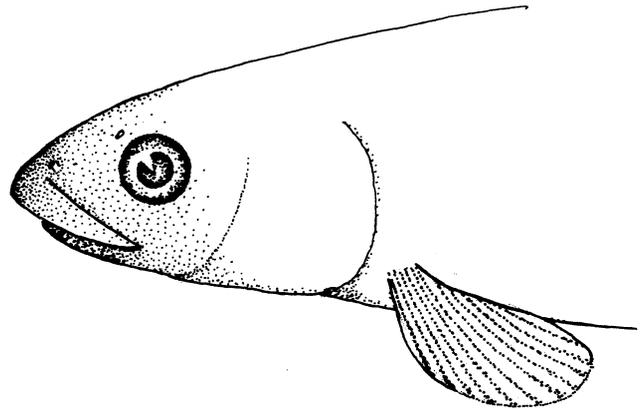

Fig. 3. Rotated and down-turned pectoral fin, as in *Galaxias postvectis* (compare with Fig. 1).

clear similarities between the four species. The issue for resolving the species' relationships and generic taxonomy is to determine the extent to which these various characters indicate homologies based on phylogenetic relationship in two or more species and/ or are convergent similarities that are due only to the adoption of a similar life style.

Not all of these distinctive characters are uniquely present in these species in the Galaxiidae. The Tasmanian *G. parvus* Frankenberg, for instance, has long tubular nostrils, pelvic fins of reduced size with fewer than seven pelvic rays, and a somewhat rounded caudal fin (McDowall & Frankenberg, 1981); it is commonly called "swamp galaxias" (Fulton, 1990). *Galaxias rekohua* Mitchell, newly described from the Chatham Islands of New Zealand (Mitchell, 1995), has strongly developed flanges on the caudal peduncle with dorsal, caudal and anal fins nearly confluent. Several species of *Galaxias* have elongate, tubular, cigar-shaped body form though, more often than not, these are species adapted for swifter-flowing streams and life within a boulder/cobble substrate (e.g., *G. brevipinnis*, *G. paucispondylus* Stokell in New
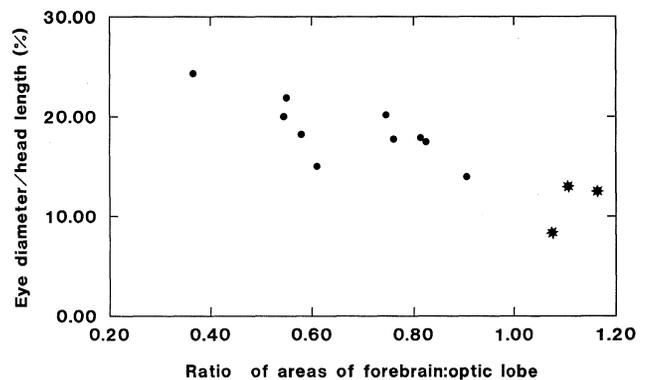

Fig. 4. Relationship between eye size and relative sizes of forebrain and optic lobe in New Zealand *Galaxias* (•) and *Neochanna* (*) (data from Cadwallader, 1975).
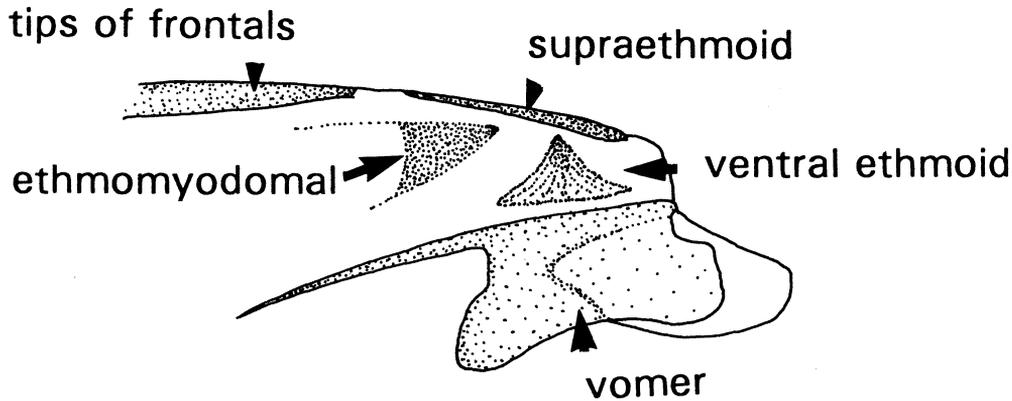
Fig. 5. Lateral view of ethmoid region in *Galaxias fasciatus* (note ventral position of vomer).

Zealand—McDowall, 1970). *Galaxias prognathus* Stokell and *G. paucispondylus* have small eyes, also, though not as small as in the mudfishes (McDowall, 1970). However, the mudfishes have both a higher level of modification in each these various characters, and have all of them together, and thus a unique combination of derived characters.

3. Osteology: Examination of the osteology of galaxiids reveals distinctive, independent specialisations in at least two character complexes in the four mudfishes.

Vomerine-ethmoid region of cranium: McDowall (1969) drew attention to a suite of particularly distinctive osteological characters in the ethmoid region of the three New Zealand species of *Neochanna*.

In most *Galaxias*, the frontals extend forwards over the orbits, but become well separated anteriorly, as they diverge over the ethmoid region. The ethmoid region (Fig. 5, 6A) consists of a block of cartilage that is a central brace for the anterior cranium and upper jaw. On top of the ethmoid cartilage is a perichondral supraethmoid which lies anterior to the tips of the frontals and behind the tip of the cranium; below the ethmoid cartilage is an endoskeletal ventral ethmoid. There is sometimes a small ethmomyodomal. The vomer is a flattish bone, almost butterfly-shaped, which sits directly below the ventral ethmoid, and has a posterior shaft that extends back to join the parasphenoid. The ethmoid cartilage has two blunt cartilaginous spurs on each side. One of these, the "maxillary spur" is low on the ethmoid cartilage which projects anterolaterally just above the wings of the vomer to form a brace for the head of the maxilla; this, in turn, rests inside the ascending process of premaxilla. Thus, this spur supports the medial upper jaw. The spurs are also well separated in *Galaxias* (Fig. 6B). In all four mudfishes the ascending process of the premaxilla fits between the forward projecting arms of the Y-

shaped anterior ethmoid cartilage and vomer. The ascending process of the premaxilla projects back and up towards but not over the anterior ethmoid region. The other, "palatine spur," originates higher on the ethmoid cartilage, and projects antero-lateroventrally to meet a cup-shaped anteromedially, inward and upward pointing tip of the palatine.

The four mudfishes though somewhat variable, nevertheless show a consistent series of differences (Fig. 6B, C). There are no endoskeletal median ethmoid ossifications (supraethmoid, ventral ethmoid, ethmomyodomal). In the Australian, brown and black mudfishes, the frontals meet anteromedially and project forwards across the ethmoid cartilage to its front. The vomer is large and somewhat Y-shaped from above (conforming to the anterior ethmoid cartilage which is also Y-shaped), and it folds upwards around the anterior of the ethmoid cartilage to almost meet the tips of the frontals. The maxillary spur, that is cartilaginous in *Galaxias* and the Australian mudfish, becomes ossified in these three New Zealand mudfishes, providing an increasingly robust support for the upper jaw.

The ethmoid cartilage and vomer have the same shape and ossification in the Canterbury mudfish, but the frontals do not project forwards, to cover the ethmoid cartilage and almost meet the vomer anterodorsally, as they do in the other three species.

The anterior tip of the palatine retains its association with the lateral spur of the ethmoid cartilage in Tasmanian, brown and Canterbury mudfishes. However, in the black mudfish additional ossification of the ethmoid cartilage has extended to include the "palatine spur" and the anteromedial surface of the palatine has established a firm association with the side of the vomer/ethmoid ossification, further strengthening the anterior of the cranium (Fig. 6C).

Thus, though varying somewhat in details, there is in all four mudfishes a unique and consistent turning
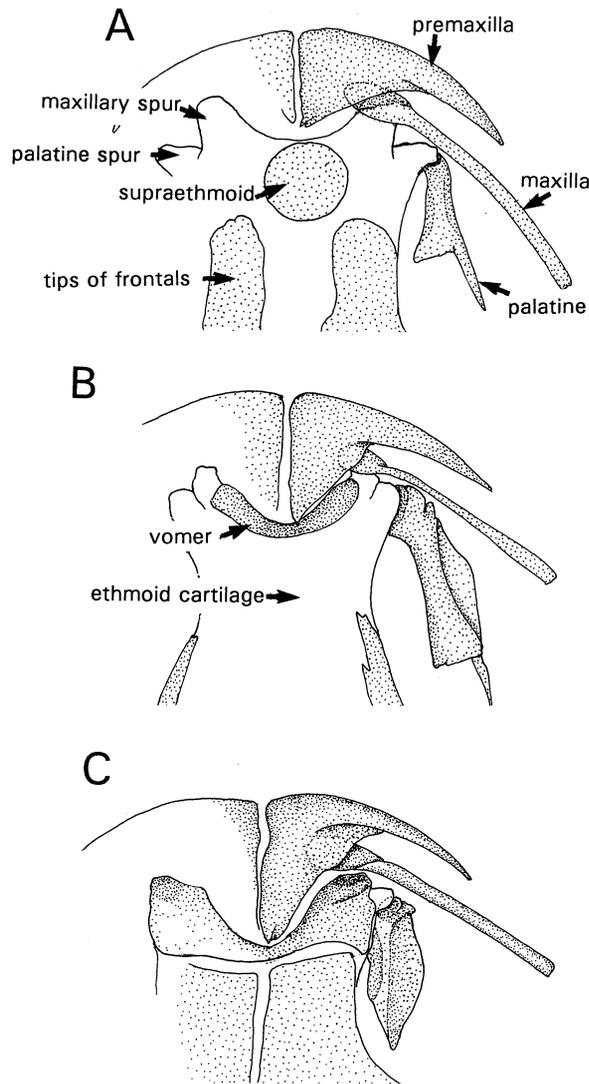
Fig. 6. Osteology of the ethmoid region in: **A**, *Galaxias fasciatus*; **B**, *Neochanna burrowsius*; **C**, *N. diversus*.

upwards of a Y-shaped vomer to enfold the anterior of the cranium, and increased ossification of the junction between, and a closer association between the upper jaw, palatine, and ethmoid/vomerine region of the cranium.

Ecologically these structural features make sense in a fish that lives in intimate relationship with the substrate and/or in debris-strewn waterways, as is true of all four species. The structure appears to be designed to strengthen and consolidate the upper jaw/ethmoid region of the cranium by increasing ossification and providing closer proximity of bones.

Pectoral girdle: In most *Galaxias*, the pectoral girdle consists primarily of the perimeter of a broad semicircle (Fig. 7A). The post-temporal connects dorsally with the supraoccipital, and in a series the post-temporal, supracleithrum, and cleithrum curve outwards and backwards, downwards, and then forwards and inwards following the body wall immediately behind the opercular

opening, running nearly parallel to the opercular membrane. There is a weak pectoral symphysis in the mid-ventral isthmus, where the pointed tips of the two cleithra meet (Fig. 8A). The coracoid is a substantial L-shaped bone that lies largely medial to the cleithrum, and has a long horizontal ramus that extends forwards to meet inside the tips of the cleithrum at about the pectoral symphysis. Thus the two cleithra and two coracoids (left and right) all meet at or near, and form, the mid-ventral pectoral symphysis. The shorter, vertical ramus of the coracoid projects upwards inside, and meets the cleithrum and a small scapula which sits above the four pectoral radials; the scapula and radials support the bases of the pectoral fin rays, the first ray on the scapula and the others on the radials.

In all four mudfishes, the form of the coracoid and the relationships of the coracoid and cleithrum are distinctly different. The post-temporal, supra-cleithrum and cleithrum (Fig. 7B), form an arc about parallel to the opercular membrane, similar to that of other galaxiids. But the coracoid is a much smaller bone, that is essentially triangular in shape, having lost the vertical ramus. The horizontal ramus is short and meets the cleithrum about half its length back from the pectoral symphysis, and so reaches nowhere near the tips of the cleithra and is quite separate from the pectoral symphysis. Ossification in the coracoid does not meet that of the scapula, but the coracoid and scapula form ossifications in a cartilaginous plate that supports the radials and thence the fin rays. In only *N. diversus*, at the junction between the anterior tip of the coracoid and the cleithrum, there is a distinct, small knob that forms the articulation with the coracoid (Fig. 8B).

Study of other *Galaxias* suggests that the form and articulations of the coracoid are specialisations uniquely derived in the four mudfishes. There are other *Galaxias* with distinctly lateral pectoral fins, such as *G. parvus* (Tasmania) and *G. maculatus* (Australia, New Zealand and South America). These are mid-water swimming species. They retain the L-shaped coracoid, which joins the cleithrum at the pectoral symphysis, as in *G. truttaceus, G. brevipinnis* and *G. fasciatus*. Thus there has not been modification of the pectoral skeleton in response to the more lateral placement of the pectoral fins. All four mudfishes thus appear to have a uniquely modified pectoral girdle in the shape of the coracoid and its articulation with the cleithrum.

Discussion

While it might be argued that all of the "systems" indicating similarity between the four mudfishes, and their differences from *Galaxias*, are associated with a changed mode of life, the distinctive features of the mudfishes involve several organ systems and include diverse aspects of general morphology (body form, tail and fin shapes, nostrils, eye size), upper jaw/vomerine/ ethmoid osteology, and pectoral girdle. In particular, the osteological details associated with at least two organ

A

B

post-temporal

supracleithrum

scapula

cleithrum

coracoid

radials
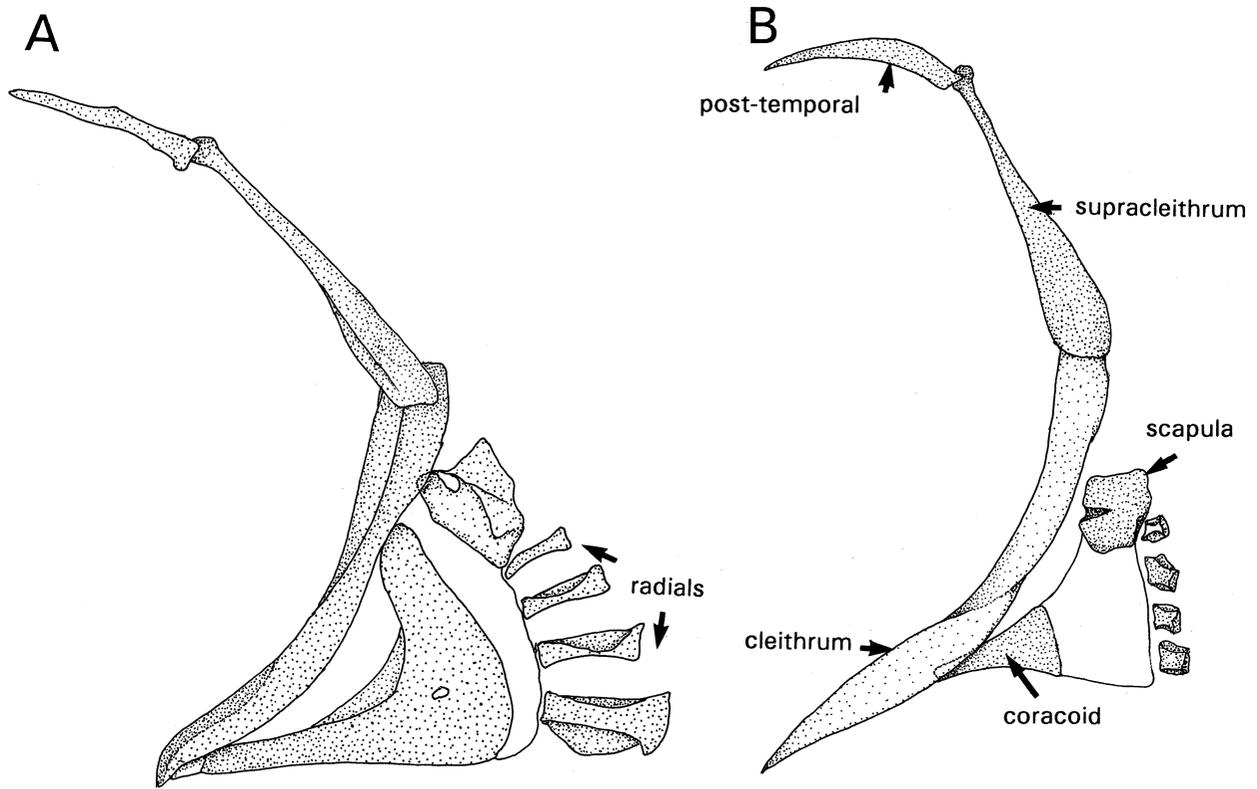
Fig. 7. Lateral view of osteology of pectoral girdle in: **A**, *Galaxias fasciatus*; **B**, *Neochanna diversus*.

A   **B**

pectoral symphysis
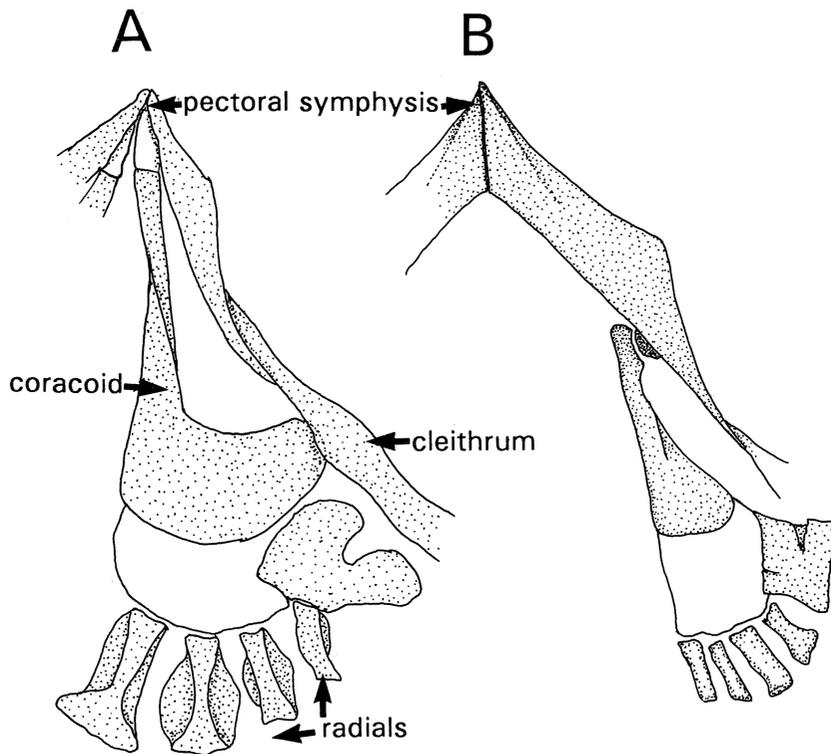
coracoid

cleithrum

radials

Fig. 8. Ventral view of osteology of pectoral girdle in: **A**, *Galaxias fasciatus*; **B**, *Neochanna diversus*.
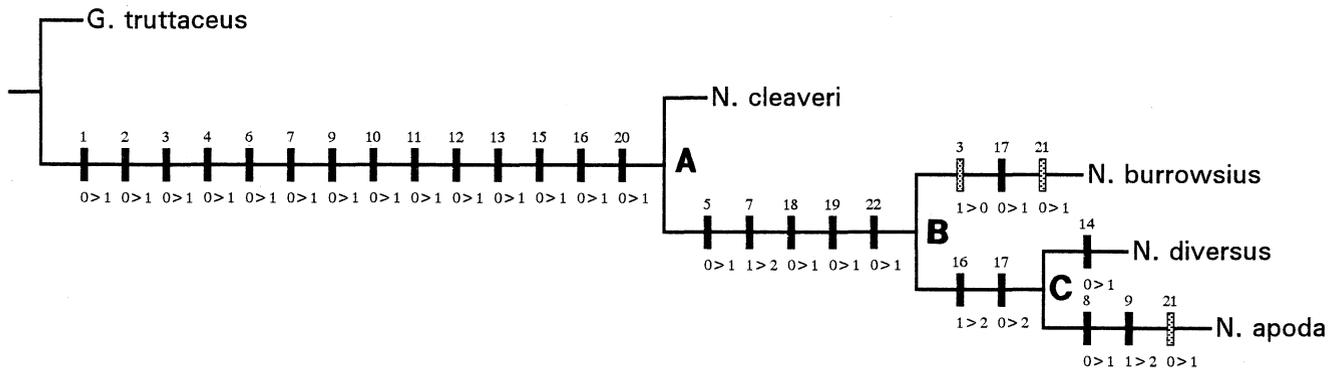
Fig. 9. Cladogram showing hypothesised relationships of *Neochanna* species (length 28, consistency index 0.92, retention index 0.75). A black box indicates an apomorphic character; a shaded box indicates a homoplastic character. Superscripts refer to characters and subscripts indicate direction.

systems are distinctive and very similar in all four species. This suggests that the four mudfishes have a common derivation, and that they are more closely related to each other than any one or more of them is related to other Galaxiidae. They are thus considered to form a monophyletic group. It is appropriate that the Tasmanian mudfish be transferred from *Galaxias* to *Neochanna* to reflect this relationship.

Where in the Galaxiidae these four mudfishes have their closest relationships is at present uncertain. The Tasmanian mudfish is clearly the least specialised of the four species, and one of its probably primitive characteristics is its retention of a diadromous life cycle (Fulton, 1986; McDowall, 1988). If diadromy is a primitive feature of the family that reflects its ancient salmoniform relationships (McDowall, 1993), then it is also likely that the closest relatives of the mudfishes are other diadromous *Galaxias*. The Tasmanian mudfish is much the least specialised of the mudfishes.

The data generated two nominally equally valid cladograms, only one of which is shown in Fig. 9. In the alternative the positions of *N. burrowsius* (Phillipps, 1926) and *N. diversus* were switched (*N. burrowsius* and *N. apoda* together shared a common ancestor with *N. diversus*). The characters that supported these alternative arrangements were:

- presence (*N. burrowsius*) or absence (*N. diversus* and *N. apoda*) of pelvic girdles and fins, and
- whether there are 16 principal caudal fin rays as in most species of *Galaxias*, or less than 16 rays.

Characters that support the cladogram are discussed below, including reasons why the phylogenetic evidence based on pelvic girdle and fins is preferred to that from caudal fin ray counts (see "NODE C"), below. Nodes mentioned are inserted in Fig. 9 as capital letters.

NODE A: Taking the diadromous species of *Galaxias* discussed above as an outgroup, *Neochanna* (now including *N. cleaveri*, as well as *N. burrowsius, N. diversus* and *N. apoda*) stands as a monophyletic group (Fig. 9) defined by the following characters:

a. vomer folds up the anterior wall of the ethmoid cartilage (Fig. 6B) (Character State CS.1 in Table 1);
b. loss of endoskeletal ethmoid ossifications (CS.2 in Table 1);
c. frontals advance across the ethmoid cartilage to the anterior of the cranium (in all but *N. burrowsius*) (Fig. 6B) (CS.3);
d. anterior tubular nostrils elongated, anteriorly directed (Fig. 1A-D) (CS.6);
e. eyes small (Figs 1A-D, 2E) (CS.7);
f. endopterygoid teeth reduced (though this is a poor indicator of relationships as it is variable within at least *N. diversus*, in which teeth are sometimes absent, but if present are few and small) (CS. 9)
g. pectoral fins small, laterally positioned (Fig. 1A-D) (CS. 10,11);
h. coracoid articulates with cleithrum well back from the pectoral symphysis (Fig. 7B, 8B) (CS. 12);
i. pelvic fins reduced (Figs 1A-D, 2D) (CS. 16).

NODE B: Synapomorphies that define a subgroup comprising the three New Zealand mudfishes—*N. burrowsius, N. diversus* and *N. apoda*—include:

j. maxillary spurs in ethmoid cartilage ossified (Fig. 6B) (CS. 5);
k. pelvic fin rays reduced from 7 to 5 or fewer (*N. burrowsius*), or fins and girdles lost (*N. apoda* and *N. diversus*) (CS.17);
l. dorsal and anal fins long and low, with fin rays subequal in length along fin (alternate character is fins high and rounded with central rays longest, as in the Australian mudfish) (Fig. 1A-D) (CS. 18);
m. flanges on upper and lower margins of caudal peduncle extend forwards from caudal fin to reach bases of dorsal and anal fins, the three fins becoming more or less confluent (Fig. 1A-D) (CS. 19);
n. loss of diadromous life history with no marine life stage (CS. 22).

These characters establish the three New Zealand species as a monophyletic group and therefore suggest a single derivation from an ancestry common with that of the Australian *N. cleaveri*.

An alternative hypothesis could be that the advance of the frontals (CS. 3) is a synapomorphy common to *N. cleaveri*, *N. apoda* and *N. diversus*, with the condition in *N. burrowsius* plesiomorphic. This would require that the putative synapomorphies, listed above as uniting the three New Zealand species (CS. 5, 17, 18, 19, 22), each evolved twice, and this is rejected as being far less parsimonious. The condition of the frontals in *N. burrowsius* is therefore seen as secondary and its similarity to *Galaxias* a homoplasy.

NODE C: If a group comprising the three New Zealand mudfishes is accepted as monophyletic, then their inter-relationships are interpreted as *N. apoda* and *N. diversus* together being a sister group of *N. burrowsius*, on the basis of the following characters:

o. eye size further reduced (Fig. 2E) (CS. 2);
p. pelvic fins and girdle completely lost (present though reduced in *N. burrowsius*) (Fig. 1B-D) (CS. 16)
q. caudal peduncle is also reduced in length (Fig. 1B-D), but was not included in the cladistic analysis because of broad overlap.

This hypothesis requires reduction of the number of principal caudal rays from the standard 16 in most galaxiids independently in both *N. apoda* (13–16 rays) and *N. burrowsius* (11–14 rays) (it remains at 16 in *N. diversus*). The alternative is that reduction in caudal fin rays is a synapomorphy in these two species, but this requires independent total loss of the pelvic fins and girdle in *N. apoda* and *N. diversus*, and still requires independent retreat of the frontals from above the ethmoid cartilage in *N. burrowsius*. Since caudal fin ray number in *N. apoda* is sometimes the standard 16 and sometimes less, the process of loss can be seen occurring in that species and independent reduction in both *N. apoda* and *N. burrowsius* is therefore likely.

I have not found unique independently derived specialisations in the Australian *N. cleaveri*, by comparison either with other *Neochanna* or with *Galaxias*. This is not true of the New Zealand species, in which the following autapomorphies are evident:

Autapomorphies in *N. apoda* include:
• flattened, incisor-like teeth in jaws (CS. 8);
• total loss of endopterygoid teeth (CS. 9);
• also, dorsal and anal fin bases are much elongated and increased ray counts (Fig. 1D, 2B & C); and
• caudal peduncle is very short (Fig. 1D, 2A)

Autapomorphies in *N. diversus* include:
• closer association between palatine and side of ethmoid cartilage (Fig. 6B) (CS. 4);
• presence of knob on cleithrum for articulation of coracoid (Fig. 8B) (CS. 14);
• broad pectoral symphysis (Fig. 8B) (CS. 15).

Autapomorphies in *N. burrowsius* include:
• retreat of frontals from above ethmoid cartilage (CS. 3);
• reduction in caudal fin ray count to only 13–14 (CS. 21).

Biogeography of the genus *Neochanna*

Trans-Tasman range of *Neochanna*: The close phylogenetic relationships between the Australian and New Zealand mudfishes, hypothesised above, raises biogeographical implications only hinted at in previous studies (McDowall, 1970; McDowall & Frankenberg, 1981). Any hypothesis employing land-based mechanisms of vicariance/dispersal for *Neochanna* implies an ancient, probably late Mesozoic/early Tertiary, land connection between Australia and New Zealand involving the former existence of Gondwana and its subsequent fragmentation and dispersal around the southern hemisphere. A scenario involving the occurrence of the common ancestors of the Australian and New Zealand mudfishes on Gondwana, and their separation by a vicariance event occurring perhaps as long as 85 million years ago (Cooper, 1989), is conceivable, and perhaps consistent with scenarios presented for the biogeography of other taxa common to Australia and New Zealand.

However, given the fact that the Australian mudfish is diadromous and thus has a marine juvenile life-stage probably lasting several months, and given the fact that ocean currents sweep across the Tasman Sea from Australia to New Zealand, an origin of the mudfishes in Australia, with dispersal to New Zealand in these ocean currents is an equally likely scenario. This is consistent with the hypothesised phylogeny of the genus, in which the Australian species is the most primitive and the sister group of the three more derived New Zealand species.

Choosing between these scenarios is not simple. Some would argue that congruence of distribution patterns between disparate and unrelated taxonomic groups points
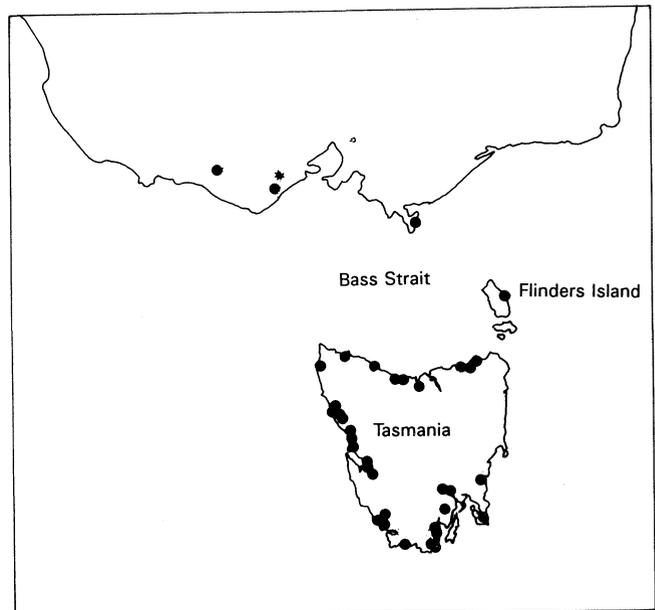

Fig. 10. Distribution of Australian mudfish, *Neochanna cleaveri* (* Wye River).

conclusively to a common vicariance-related, explanation for the distributions (Croizat *et al.*, 1974; Rosen, 1974; Craw, 1989). I am not, however, of the view that such common patterns necessarily have the same explanations or that dispersal explanations should be invoked only when phylogenies are inconsistent with possible patterns of vicariance suggested by other taxa (Croizat *et al.*, 1974; Rosen, 1974; see McDowall, 1978; Andersson, 1996). Berra *et al.* (1996) have recently reported on results of electrophoretic comparisons of populations of *G. maculatus* from Australia, New Zealand and South America, and they concluded that in this diadromous species differences between populations over its vast range are so slight as to suggest recent, and even continuing, gene flow—though this is not a new idea (McDowall & Whitaker, 1975; McDowall, 1978). The only way this is possible is by transoceanic dispersal in the southern ocean. If this is possible for *G. maculatus* between Australia/New Zealand and South America, dispersal of the diadromous Australian mudfish from eastern Australia to New Zealand is also highly conceivable.

Distribution of the Australian species: The Australian mudfish occurs primarily in Tasmania, though there are records from Flinders Island (Bass Strait—Green, 1984), and in coastal, southern Victoria (Jackson & Davies, 1982; Koehn & O'Connor, 1990; Koehn & Raadik, 1991—Fig. 10). Freshwater fish distributions that span Bass Strait occur also in other Australian species. Some are diadromous, like *G. maculatus, G. brevipinnis* and *G. truttaceus* (Galaxiidae—McDowall & Frankenberg, 1981), *Prototroctes maraena* Günther (Prototroctidae—McDowall, 1996a), *Anguilla australis* Richardson and *A. reinhardtii* Richardson (Anguillidae—Beumer, 1996), and *Pseudaphritis urvillii* Cuvier and Valenciennes (Bovichtidae—Andrews, 1996). Others, however are not diadromous, such as *Galaxiella pusilla* (Mack) (Galaxiidae—McDowall & Frankenberg, 1981) and *Nannoperca australis* Günther (Nannopercidae—Kuiter *et al.*, 1996). The distributions of the diadromous species may be explained by either dispersal of marine life stages through the sea across Bass Strait, between the Australian mainland and Tasmania, or by the known presence of a land connection across the strait as recently as the Pleistocene (<14,000 years before present—Davies, 1974). The same alternative dispersal explanations are unlikely to apply to the non-diadromous species and the land bridge scenario is a much more likely explanation for these.

Choosing between these scenarios to explain the distribution of the Australian mudfish (which is diadromous—Fulton, 1986) is, again, not simple; either mechanism seems equally plausible. Koehn & Raadik (1991) suggested that the known distribution of the Australian mudfish in Victoria "closely conforms to the region formerly encompassed by a land bridge" across Bass Strait, and from that I infer that they favoured a causal relationship. They thought that if the occurrence of the fish in Victoria was due to marine dispersal, "the species would be expected to be more widely distributed", thus tending to discount the role of diadromy in the

species' presence in Victoria. On the other hand, they stated that "geomorphological conditions that existed during and after the last glaciation... restricted non-diadromous freshwater species" as a result of which "only diadromous species inhabit the short coastal streams. The diadromous life cycle of *G. cleaveri* accounts for its distribution in the Wye River" (Fig. 10*). They thereby apparently attribute the range of the species in Victoria to diadromy. Moreover, they were also equivocal about the nature of its diadromy, suggesting that the "more restricted distribution of *Galaxias cleaveri* [compared with other diadromous *Galaxias* species] suggests that the larvae may be confined to estuaries". Thus they appear to attribute the presence of the Australian mudfish in Victoria to the presence of a land connection, but its distribution in Victoria perhaps to a diadromous life cycle and therefore perhaps dispersal through the sea. Dispersal across Bass Strait by a marine stage of the Australian species seems, to me, a viable option.

Distribution and biogeography of the New Zealand species: Any interpretation of New Zealand historical biogeography must be structured around the fact that its land mass has had a "rough tectonic history" (Gibbs, 1989). In particular, there was very little emergent land during the Oligocene, about 30 million years ago, perhaps so little that virtually the entire biota dates from post-Oligocene dispersal to New Zealand, if Pole (1994) is correct. Thus, all terrestrial and freshwater taxa must, at least, have passed through a very severe evolutionary bottleneck, with intensive and extensive taxonomic "winnowing" and extinction at that time (Cooper, 1989; Cooper & Cooper, 1995). What we observe, today, results from speciation and dispersal of the survivors of that event/period, as well as the addition of taxa that have dispersed to the New Zealand region since then and have speciated as the land area increased again. The effects of any more ancient events, and in particular the supposed influences of "terranes" of allochthonous origins on the distributions of biotic elements (Gibbs, 1989) are bound to have been profoundly altered by the reduced land area of the Oligocene, as well as later marine transgression, mountain building, land connections and volcanism, to the extent that today's taxa and their distributions are unlikely still to reflect their origins in such terranes (Cooper, 1989; Cooper & Cooper, 1995).

If we assume a single ancestry/common derivation of the New Zealand species as shown in the cladogram in Fig. 9, then the biogeography of the genus *Neochanna* in New Zealand is structured around the speciation and divergence of that single ancestral stock. Distributions of the three New Zealand mudfishes are entirely allopatric, with:

- *Neochanna diversus* present in the north of the North Island;
- *N. apoda* in the western and southern North Island and West Coast of the South Island, and
- *N. burrowsius* in the eastern South Island (Fig. 11).

None of the three species is diadromous (though their common ancestor may have been), so that their present distributions will probably not have been affected by
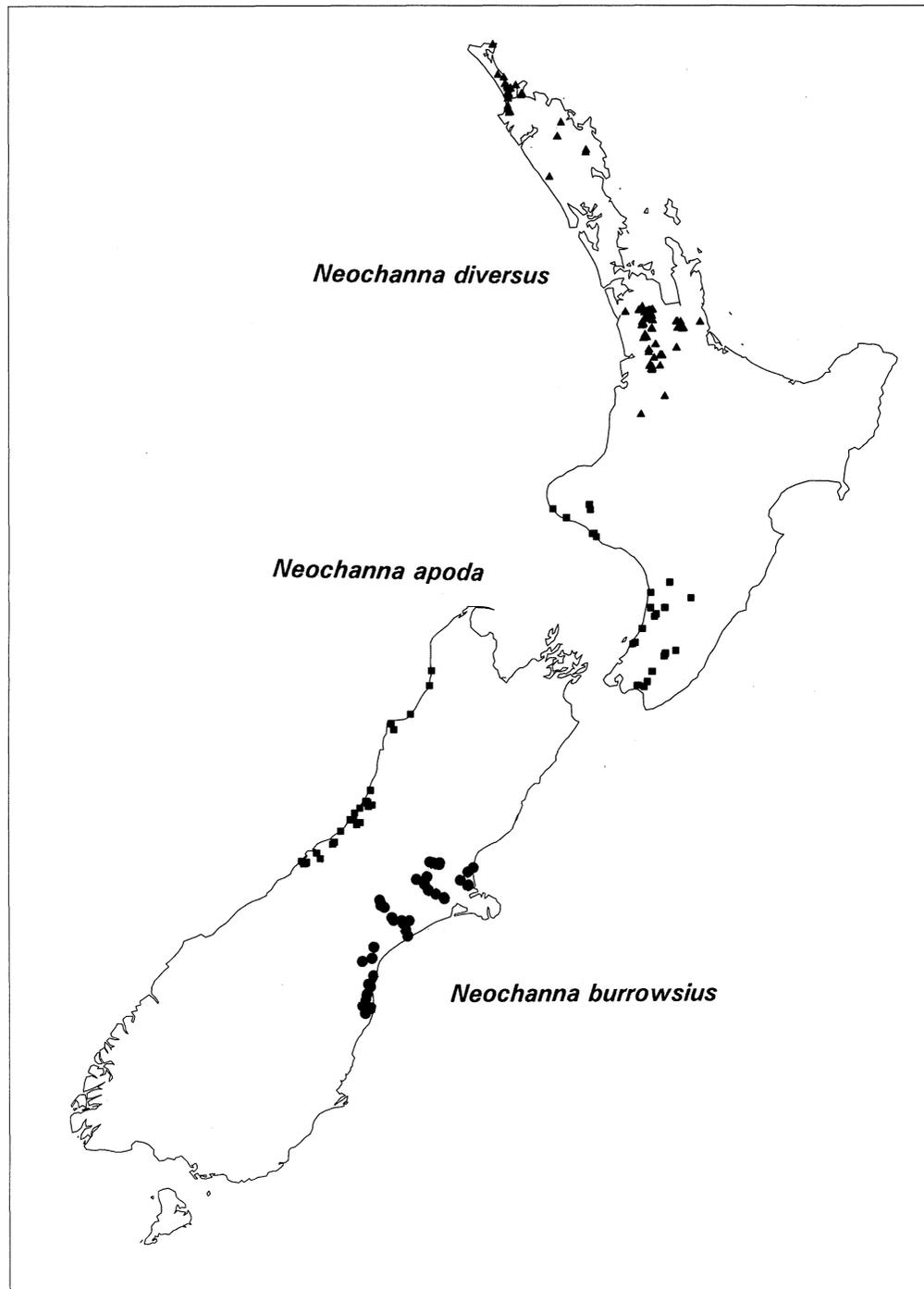
Fig. 11. Distribution of the three New Zealand mudfishes, *Neochanna apoda, N. burrowsius,* and *N. diversus* (data from NIWA New Zealand Freshwater Fish Database).

recent or continuing dispersal of marine life stages through the sea. They are likely therefore to reflect, at least in part, the geological history of the landscape— probably over lat Tertiary to Recent times. Likely influential events in this geological history include the following:

• the fact, noted above, that most of the New Zealand region was submerged beneath ocean during Oligocene times, about 30 million years ago with emergent land of minimal size, (Cooper, 1989, and Cooper & Cooper, 1995 show only several relatively small emergent islands—Fig. 12);

• the Kaikoura orogeny during the Pliocene and early Pleistocene, that resulted in the uplifting of the present mountain ranges of New Zealand, particularly of the Southern Alps (which bisect the South Island distributions of *N. apoda* to the

north-west of the Alps and *N. burrowsius* to the south-east) (Fig. 11);

• formation of the Canterbury Plains during the late Pliocene and Pleistocene, as the product of extensive erosion and outwash from the rising Southern Alps;

• extensive marine transgression across the now southern half of the North Island during the Pliocene and early Pleistocene, when there was sea across the present North Island almost as far north as Lake Taupo; however, parts of the south-western present North Island are thought to have been connected to the northern tip of the South Island at that time, but separated by sea from the rest of the North Island (Fig. 13);

• re-emergence from the sea of the above area, and the closure of all sea connections across central New Zealand during the Pleistocene, at a time of lowered sea levels (Fig. 14);

• later reopening of the sea connection across central New Zealand at what is now known as Cook Strait;

• extensive Pleistocene to Recent glaciation, with permanent snow and ice to low levels, especially along the West Coast of the South Island;
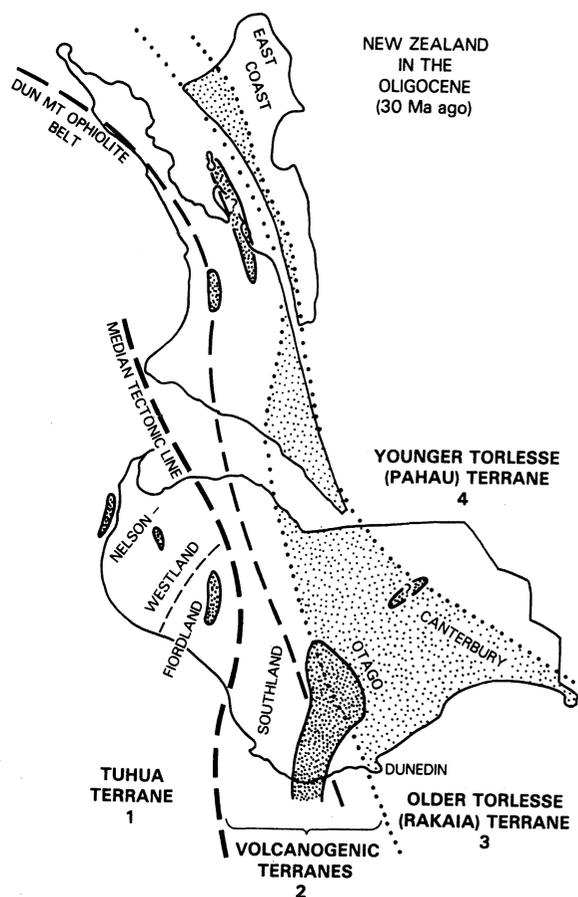

Fig. 13. New Zealand during the Pliocene, showing extensive marine transgression across the southern North Island (redrawn from Lewis & Carter, 1994).

Fig. 12. The New Zealand area during the Oligocene (c. 30 million years ago): dark stippling indicates areas considered to have been above sea level (from Cooper, 1989).
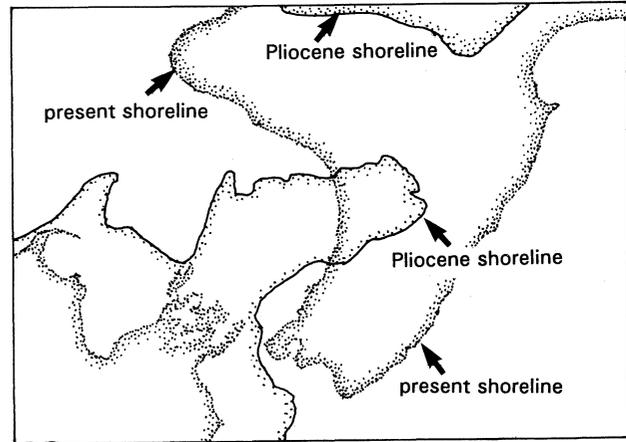
• intensive Pleistocene to recent volcanism in the central/northeastern North Island (from about 25,000 years ago).

(These events are described variously by Suggate *et al.*, 1978; Fleming, 1979; Gage, 1980; Stevens, 1980; Wilson & Walker, 1985; Cooper, 1989; Wilson & Houghton, 1993; Lewis & Carter, 1994; Cooper & Cooper, 1995.)

In examining the biogeography of the mudfishes in New Zealand, it is important to know the extent to which present distributions are a product of these various known geo-historical events that affected the landscape and its biota, as opposed to the influences of any more ancient processes.

The three species of *Neochanna* could have been isolated on the various Oligocene islands (Fig. 12), and have spread from these centres as the New Zealand land mass emerged from the sea during the mid-Tertiary. Such a scenario would probably have required a distinct "Canterbury" island (Cooper, 1989, shows a possible such land area—Fig. 12), particularly if the phylogeny of New Zealand mudfishes, with the Canterbury mudfish a sister group of the two others, as presented in Fig. 9, is accepted.

Alternatively, however, the total allopatry of the three species is consistent with the hypothesis that their distributions reflect relatively recent (late Tertiary and since) geological history. Where distributions seem consistent with such more recent events, it is probably appropriate in the first instance to assume that there are causal relationships. The scenario developed here is offered on that basis, and again under the assumption that the phylogenetic relationships of the three species to the Australian species, and to each other, are as proposed above (Fig. 9), i.e. that *N. apoda* and *N. diversus* are sister species, and together form a sister group of *N. burrowsius*.

How far spread *Neochanna* was in New Zealand prior to the uplift of the Southern Alps is, of course, unknown.
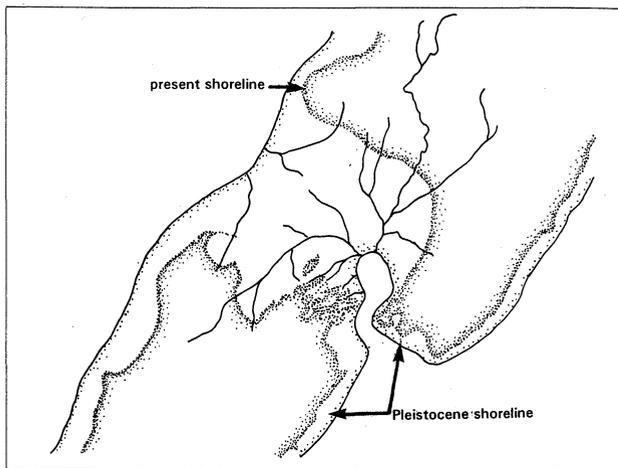
Fig. 14. Central New Zealand during the Pleistocene, indicating likely confluences of river systems between North and South Islands as a result of lowered sea levels (redrawn from Fleming, 1979).

One possibility is that the common ancestor of *N. apoda* and *N. diversus*, and perhaps the common ancestor of all three species, was widespread, perhaps as far north as the Waikato and even Northland prior to the Pliocene marine transgression across the southern North Island (Fig. 13). *Neochanna burrowsius* is now separated from *N. apoda* in the South Island by the Southern Alps, the uplift of which can be interpreted as a major vicariant event (Fig. 11).

The present distribution of *N. diversus* (Northland, south through the Hauraki Plains, and Waikato as far as the Mokau River) equates closely with the proto-North Island of Pliocene times of extensive marine transgression (Fig. 13: Fleming, 1979; Lewis & Carter, 1994), which may suggest that the fish was already in that area before the marine transgression developed. *Neochanna diversus* does not occur in the eastern North Island (Bay of Plenty), and this is consistent with the east coast of the North Island having not adopted its present connections to the remainder of the North Island until less than 10 million years ago (Cooper, 1989). Mudfish may never have reached the region. Alternatively, if there were any populations of mudfish there, they may have been extirpated by events relating to volcanism known to have occurred in the central/eastern North Island over the past 25,000 years (Wilson & Houghton, 1993; Wilson & Walker, 1985; McDowall, 1996b). Other non-diadromous North Island freshwater fishes that might have been expected in the north-east (Bay of Plenty/East Cape) are notably sporadic in distribution east of about the longitude of Coromandel (McDowall, 1990, 1996b), and so absence of mudfish is not inconsistent with this.

The Pliocene marine transgression of the southern North Island would have excluded all freshwater fishes (and all other terrestrial and freshwater biota) from that

area, but *N. apoda* may have occupied the continuous land from the Wellington peninsula southwards through the northern West Coast of the South Island (Fig. 13), to the northwest of the Southern Alps. Following retreat of the seas, re-emergence of the southern North Island, and perhaps also with bridging of Cook Strait as recently as 10,000–20,000 years ago (Lewis & Carter, 1994), there was ample opportunity for *N. apoda* to disperse north into the southern and western North Island, undoubtedly assisted by confluence of river systems that drained the south-western North Island and northern South Island (Fig. 14). As a result, *N. apoda* now occurs along the west coast of the North Island almost as far north as Cape Egmont (or did until locally extirpated by human impacts), in the Wairarapa in and south of the Manawatu River system, as well as widely in the West Coast of the South Island (Fig. 11). The northern part of this distribution equates closely with river systems that are believed formerly to have drained the emergent land before Cook Strait took its present conformation in quite recent times (Fig. 14). Distribution of *N. apoda* extends well south along the West Coast of the South Island. There seem to be no existing habitat-suitability reasons why the fish should not occur further south. However, as Main (1989) has shown, extensive Pleistocene glaciation probably extirpated all terrestrial and freshwater life in the southern West Coast, including any populations of *N. apoda*. This mudfish occurs there only north of about the estimated limits of low elevation glaciation.

Neochanna burrowsius occurs only as far south as the Waitaki River, and is thus confined largely to the Canterbury Plains. Dispersion of *N. burrowsius* southwards, as the plains were formed by erosion and outwash of gravels from the uplifting Southern Alps to the west during the late Pliocene, Pleistocene to Present, seems a likely scenario. Its absence south of the Waitaki, i.e. in the ancient, long emergent, Otago peneplain to the south, suggests that it was never present there. Nor does it occur in Central Otago or the Southland Plains, where there are plenty of apparently suitable habitats. The absence of any mudfish from southern New Zealand is consistent with a more northern origin of *N. burrowsius* with dispersion south as far as the Waitaki, as the Canterbury Plains were formed during late Pliocene to recent times.

Overall, the patterns of distribution and speciation of the three New Zealand mudfishes conform easily to a scenario established around the late Tertiary and subsequent geological history of New Zealand. In the absence of evidence to the contrary, the small radiation of these species appears to be of about that age; there is nothing presently known that suggests a much more ancient, Gondwana, origin. The prospect that the common ancestor of all four mudfishes in Australia and New Zealand was a Gondwana form, which survived the Oligocene bottleneck in New Zealand (Cooper & Cooper, 1995), and which dispersed and speciated in New Zealand in response to these same late Tertiary and subsequent geo-historical events, discussed above, cannot

be excluded. Dating of speciation events, particularly the separation of the Australian and New Zealand lineages, using DNA sequencing technology may provide an estimate of the time of divergence of the New Zealand species from *N. cleaveri* in Australia, and thereby throw light on this question, and allow a more rigorous choice of historical scenarios for the origins, distribution and speciation of the genus *Neochanna*.

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Appendix 1: Material examined includes unregistered material in the fish archive of the National Institute of Water and Atmospheric Research, and material from the collections of the Museum of New Zealand (NMNZ), as follows (* signifies cleared and alizarin-stained osteological preparations, for which fish lengths are given: this material is substantially the same as that used by McDowall, 1969).

Galaxias argenteus: *(1), Lake Brunner, Grey River system, N.Z., no date, 160 mm S.L.; (2), Pita Creek, Manakaiaua River, N.Z., ? January, 1984, 93–94 mm S.L.

Galaxias brevipinnis: *(2), Lake Kiriopukae, Waikaremoana, N.Z., 63–68 mm S.L.; (6), Ohau River, upper Waitaki River system, N.Z., 13 March, 1991, 66–87 mm S.L.; *(1), Kangaroo River, N.S.W., Australia, 8 January, 1976, 75 mm S.L.

Galaxias fasciatus: *(3), locality and date unknown, N.Z., 63–156 mm S.L.; (4), small drain feeding Mahakaiawa Stream, N.Z., 15 April, 1971, 51–114 mm S.L.

Galaxias maculatus: *(1), Waikanae River, N.Z., no date, 64 mm S.L.; (3), Otaki River, N.Z., 16 October, 1964, 65–70 mm S.L.

Galaxias postvectis: (3), Stony Creek, Kaniere River, Hokitika River system, Westland, N.Z., 147–189 mm S.L.

Galaxias truttaceus: (6), Lake Dudley, Tasmania, 25 February, 1978, 69–113 mm S.L.; *(2), locality unknown, Tasmania, no date, 62–79 mm S.L.; *(2), locality unknown, no date, 55–81 mm S.L.

Neochanna apoda: *(5) Kaipaitangata Stream, ? March, 1965, 58–69 mm S.L., spring at Dalefield, 2 July, 1968, 55–81 mm S.L., both locations Ruamahanga River system, N.Z.; (2) Opunake, N.Z., June, 1926, 146–152 mm, NMNZ P1557, (3) Rongotea, N.Z., February 1958, 85–100 mm, NMNZ P2485.

Neochanna burrowsius: *(1) and (16) Buchanan Creek, tributary of Waihao River, South Canterbury, N.Z., 6 July, 1976, 85 mm S.L. and 39–109 mm S.L.; (3) creek at Eiffelton, south of Ashburton, N.Z., no date; NMNZ P4891, 65–125 mm S.L.

Neochanna cleaveri: *(1) Pieman River, Tasmania, Australia, 28 January, 1964, 56.5 mm S.L.; *(2), unknown locality, Tasmania, Australia, no date, 60, 86 mm S.L.; (4), Derwent River, Tasmania, Australia, 20 March, 1987, 43–52 mm S.L.

Neochanna diversus: *(1), swamp, lower Waikato River, New Zealand, no date, 85 mm S.L.; (6), drain at Te Kauwhata, Waikato River, N.Z., 20 July, 1966, 27–45 mm; (22) swamp at Waiharara, Awanui River system, N.Z., 25 March, 1965, 40–134 mm, NMNZ P4898.

Table 1. Definition of primitive and derived character states: assignment of characters as primitive (0) or derived (1 & 2) is based on outgroup comparisons with *Galaxias* species, and is discussed in the text

1. Vomerine/ethmoid region of anterior cranium:
   0 vomer flat and lies largely below ethmoid cartilage;
   1 vomer folds up anterior wall of ethmoid cartilage to meet frontals (Fig. 6B).

2. Ethmoid ossification
   0 endoskeletal ethmoid ossifications present;
   1 no endoskeletal ethmoid ossifications.

3. Frontals:
   0 diverge anteriorly and do not reach forward to meet vomer;
   1 joined anteriorly and extend forward to meet vomer that folds up ethmoid cartilage.

4. Palatine spur on ethmoid cartilage:
   0 spur cartilaginous, no ossification;
   1 spur ossified.

5. Maxillary spur on ethmoid cartilage;
   0 spur cartilaginous, no ossification;
   1 spur ossified.

6. Anterior tubular nostrils:
   0 short and oblique;
   1 long and directed forwards.

7. Eyes:
   0 large;
   1 moderate;
   2 small.

8. Jaw teeth:
   0 sharp, recurved, fang-like;
   1 flattened and incisor-like.

9. Endopterygoidal teeth:
   0 large and numerous;
   1 variable, few and small, or absent;
   2 always absent.

10. Pectoral fin size:
    0 large;
    1 small.

11. Pectoral fin position:
    0 low on sides, facing downwards;
    1 high on sides, facing laterally.

12. Coracoid articulation in pectoral girdle:
    0 coracoids long, articulate with cleithrum at pectoral symphysis;

1 coracoids shortened, articulate with cleithrum well back from pectoral symphysis.

13. Coracoid shape:
    0 coracoid large and distinctly L-shaped, also articulating with cleithrum near scapula;
    1 coracoid small and triangular; does not articulate with cleithrum near scapula.

14. Cleithrum:
    0 cleithrum has no knob at articulation with anterior ramus of coracoid;
    1 cleithrum has bony knob at articulation with anterior ramus of coracoid.

15. Pectoral symphysis:
    0 narrow and weak;
    1 broad and strong.

16. Pelvic fin size:
    0 large, usually > 50% of pectoral-pelvic interval;
    1 small, usually < 50% of pectoral-pelvic interval;
    2 fins and girdle lacking.

17. Pelvic fin rays:
    0 usually 7 rays;
    1 usually 5 rays;
    2 no rays, fin lacking.

18. Dorsal and anal fin shape;
    0 fins high and rounded, bases short;
    1 fins long and low, distal margin nearly parallel to body profile, bases long.

19. Caudal peduncle flanges:
    0 flanges weak, not reaching rear of dorsal and anal fin bases;
    1 flanges long, confluent, or nearly confluent with dorsal and anal fin bases.

20. Caudal fin shape:
    0 caudal fin emarginate to truncate;
    1 caudal fin distinctly rounded.

21. Caudal fin rays:
    0 nearly always 16 rays; variation slight;
    1 13–16 rays, variable;
    2 11–14 rays, variable.

22. Diadromy:
    0 present;
    1 absent.

Table 2. Matrix of character states in *Galaxias truttaceus* (outgroup) and *Neochanna* species; 0 = ancestral condition, 1 & 2 = derived conditions, characters as numbered in Table 1.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Galaxias truttaceus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neochanna cleaveri	1	1	1	1	0	1	1	0	1	1	1	1	1	0	1	1	0	0	0	1	0	0
Neochanna burrowsius	1	1	0	1	1	1	2	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1
Neochanna apoda	1	1	1	1	1	1	2	1	2	1	1	1	1	0	1	2	2	1	1	1	1	1
Neochanna diversus	1	1	1	1	1	1	2	0	1	1	1	1	1	1	1	2	2	1	1	1	0	1