Systematic Revision of the
Mountain Galaxias, *Galaxias olidus* Günther, 1866
Species Complex (Teleostei: Galaxiidae)
in Eastern Australia

*Galaxias olidus* Günther, 1866 - holotype

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Some of the morphological diversity in the *Galaxias olidus* sensu lato species complex.

(Image credits: Rudie Kuiter, Neil Armstrong, and Tarmo Raadik)
ABSTRACT

Australia is one of the world’s top megadiverse countries based on the number of species and levels of endemism of plants and animals, however, the continuing loss of biodiversity, particularly in freshwater environments, is one of the most serious environmental problems. The Australian freshwater fish fauna, defined as relatively well known, has been described as depauperate when compared with other land masses of similar size and climate. This disparity has been proposed as a consequence of relative differences in environmental and geological factors, and degree of isolation, however, it may also be due to differing taxonomic effort, with an overall decline in freshwater taxonomic research noted since the 1970s and a dramatic reduction in expertise since the mid 1980s.

Molecular research since the 1980s has detected species-level genetic diversity in many obligate freshwater fishes, all previously defined primarily on morphological assessments alone. None of these studies have yet been supported by morphological reappraisals to resolve the taxonomy of the species complexes, with some unresolved for over 20 years. The molecular data strongly suggest that the current taxonomic framework for Australian freshwater fishes is incomplete, under represents true levels of species diversity by at least 2–3 fold, and our basic knowledge of the number and diversity of freshwater fishes is largely deficient.

The Galaxiidae are arguably the most widespread family of Southern Hemisphere freshwater fish, and represent almost half of the species of southern-temperate affinity in Australia. They are relatively morphologically conservative and were considered reasonably well studied morphologically, though recent molecular studies have indicated significant species-level diversity in a nonmigratory species in southern New Zealand and one in South Africa.

The nonmigratory Mountain Galaxias, *Galaxias olidus*, of mainland Australia has a broad geographic range across discrete river systems, and is highly vulnerable to isolation and hence genetic divergence. A taxonomic history of multiple species consolidated into a single taxon, suggesting high levels of morphological variability, combined with recent morphological and ecological data, is strongly suggestive of *Galaxias olidus* constituting an unresolved, cryptic species complex. The aim of the current study is to investigate levels of genetic diversity within this obligate freshwater fish to assess species boundaries, to undertake a morphometric and meristic analysis of individuals to determine if genetically identified candidate taxa can be morphologically defined, and, if so, to revise the taxonomic framework of the complex, providing redescriptions of any valid nominal taxa and formal description of new taxa.

A comprehensive comparative dataset of study material was initially compiled following an evaluation of existing data and specimens. This material consisted of a small amount of existing
specimens from museum collections, but was supplemented by a large collection of fresh material from an extensive field sampling program which undertook intensive collecting at a fine spatial scale across the geographic range of the species.

*Galaxias olidus* sensu lato was not supported as a single, well-defined diagnosable species by allozyme analyses (54 loci), but was instead found to comprise a complex of 15 candidate species, most found in sympathy to parapatry (possibly recent sympathy), all diagnosable from one another by multiple fixed differences. Finer-scale genetic substructure was also evident within three candidate species, indicating genetically distinct subpopulations which, with minor exception, appeared to conform to drainage boundaries. Putative hybridization, though detected, appears to be uncommon amongst the candidate species, and was only found between three taxa-pairs, with one taxon common to all pairs.

An additional, though unexpected, result was the discovery of high levels of genetic heterogeneity within samples of *Galaxias brevipinnis* s.l. from mainland Australia used as outgroups, which suggests, for the first time, the presence of an unresolved species complex within this taxon.

Based on multivariate analysis the 15 allozymically defined candidate species in *Galaxias olidus* s.l. were able to be unequivocally diagnosed from each other by unique differences in their morphology, with the majority diagnosable by two independent datasets (morphometrics (29 characters) and meristics (17 characters)), and additional, less consistent morphological characters. When combined with significant molecular characters, each species could be identified on the basis of two, usually three, independent measures of diagnosability and four are considered distinct biological species in sympathy or parapatry and 11 as evolutionary species in allopatry, in the absence of evidence of recent sympathy or parapatry. *Galaxias olidus* s.s. remains the most variable taxon in the complex.

The combined approach of using multiple, independent lines of evidence provides the greatest chance of identifying robust and diagnosable species, particularly in cryptic species complexes where subtle morphological differences that are taxonomically important are masked by other phenotypic variation, and where traditional, morphologically based, studies often fail.

Following taxonomic reappraisal *Galaxias olidus* Günther (sensu strictu) is retained and redefined, two species previously synonymised with *G. olidus* (*Galaxias fuscus* Mack and *Galaxias ornatus* Castelnau) are revised and reinstated as valid species, and 12 new species are described. All taxa are closely related in a monophyletic lineage (to the exclusion of other described species investigated in the genus on mainland Australia), distinct from *Galaxias brevipinnis* and *Galaxias maculatus* (includes *G. occidentalis* and *G. rostratus*) lineages, and form a grouping of morphologically similar taxa designated as the *Galaxias olidus* complex.
Many morphological characters were found to overlap between species in this complex, and though all were useful in multivariate diagnosis of taxa (i.e. in combination provided discrimination in multidimensional space), many (e.g. meristic characters) were less useful as taxonomic characters in species descriptions. This is due to the high level of morphological conservatism in this complex of species, often with only subtle differences between taxa. Consequently, field-based diagnosis of species relies heavily on combinations of proportionate ratios of characters.

The identification of 15 species within the *Galaxias olidus* complex indicates substantial genetic divergence has occurred in this group of fishes in eastern Australia. The overall pattern of genetic substructuring within, and shallow to relatively deep divergence between species, is characteristic of this group having a long association with, and having undergone extensive evolution in isolation within, Australian freshwater drainages. In addition, the increased level of diversity found in the genus *Galaxias* (from this study and elsewhere) provides additional support for the long evolutionary history of the Galaxiidae.

The basic knowledge of species-level diversity is deficient for Australian freshwater fishes, and may be larger than previously suggested, with numbers of species in some taxa under represented by up to 15 fold. This lack of essential taxonomic knowledge is a fundamental and serious impediment to assessing species loss and in implementing effective strategies for biodiversity conservation. This is particularly critical in the Galaxiidae, where the spread of highly predatory alien salmonids in freshwater systems in the Southern Hemisphere has led to local extinctions and significantly altered galaxiid distributions, and is highly likely to have resulted in the extinction of undiscovered unique lineages, worthy of recognition as species, in small and remote catchments.

More broadly, the lack of knowledge of Australian freshwater fish diversity also compromise assessments of diversity and areas of high endemism at the global scale and confound efforts to define effective freshwater ecoregions for biodiversity conservation.
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<tbody>
<tr>
<td>ACT</td>
<td>Australian Capital Territory</td>
</tr>
<tr>
<td>AMS</td>
<td>Australian Museum, Sydney</td>
</tr>
<tr>
<td>ANCOVA</td>
<td>Analysis of co-variance</td>
</tr>
<tr>
<td>ANOVA</td>
<td>Analysis of variance</td>
</tr>
<tr>
<td>AWRC</td>
<td>Australian Water Resources Council</td>
</tr>
<tr>
<td>$\beta$</td>
<td>Regression coefficient</td>
</tr>
<tr>
<td>BMNH</td>
<td>British Museum of Natural History, London</td>
</tr>
<tr>
<td>cytB</td>
<td>Cytochrome B</td>
</tr>
<tr>
<td>DD</td>
<td>Drainage Division</td>
</tr>
<tr>
<td>DFA</td>
<td>Discriminant Functions Analysis</td>
</tr>
<tr>
<td>DTT</td>
<td>Diagnosable Terminal Taxon or Taxa</td>
</tr>
<tr>
<td>EBU</td>
<td>Evolutionary Biology Unit</td>
</tr>
<tr>
<td>EC</td>
<td>Electrical conductivity units</td>
</tr>
<tr>
<td>FD</td>
<td>Fixed Difference</td>
</tr>
<tr>
<td>GDR</td>
<td>Great Dividing Range</td>
</tr>
<tr>
<td>LCF</td>
<td>Length to caudal fork</td>
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<tr>
<td>LHS</td>
<td>Left Hand Side</td>
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<tr>
<td>MANOVA</td>
<td>Multivariate analysis of variance</td>
</tr>
<tr>
<td>masl</td>
<td>Metres above sea level</td>
</tr>
<tr>
<td>MDB</td>
<td>Murray-Darling Basin Drainage Division</td>
</tr>
<tr>
<td>mtDNA</td>
<td>Mitochondrial DNA</td>
</tr>
<tr>
<td>MRT</td>
<td>Multivariate Regression Tree</td>
</tr>
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<td>NEC</td>
<td>North East Coast Drainage Division</td>
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<tr>
<td>Nei D</td>
<td>Nei's Distance</td>
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<tr>
<td>NJ</td>
<td>Neighbour Joining</td>
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<tr>
<td>NMNZ</td>
<td>National Museum of New Zealand, Wellington</td>
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<tr>
<td>NMV</td>
<td>Museum Victoria, Melbourne</td>
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<td>New South Wales</td>
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<td>NZ</td>
<td>New Zealand</td>
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<tr>
<td>OTU</td>
<td>Operational Taxonomic Unit</td>
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<tr>
<td>partim</td>
<td>Latin, in part, partly</td>
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<tr>
<td>PCA</td>
<td>Principal Components Analysis</td>
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<td>Principal Co-ordinates Analysis</td>
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<td>RB</td>
<td>River Basin</td>
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<td>RHS</td>
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<td>SAG</td>
<td>South Australian Gulf Drainage Division</td>
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<td>South-east Australia</td>
</tr>
<tr>
<td>SEC</td>
<td>South East Coast Drainage Division</td>
</tr>
<tr>
<td>SL</td>
<td>Standard Length</td>
</tr>
<tr>
<td>s.l.</td>
<td>Latin, sensu lato, in the broad sense</td>
</tr>
<tr>
<td>sp. nov.</td>
<td>Latin, species novum, new species</td>
</tr>
<tr>
<td>s.s.</td>
<td>Latin, sensu strictu, in the strict sense</td>
</tr>
<tr>
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<td>Tasmania</td>
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<tr>
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<td>Unweighted Pair-Group Method of arithmetic Averages</td>
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