


Editorial

Evolutionary Genetics and Biogeography of Galaxiid Fishes (Teleostei: Galaxiiformes: Galaxiidae)

Graham P. Wallis 

Department of Zoology, University of Otago, P.O. Box 56, Dunedin 9054, New Zealand; g.wallis@otago.ac.nz

1. Introduction

Since the dawn of the discipline, biogeographers have wondered at the widespread distribution of galaxiid fishes throughout temperate regions of the Southern Hemisphere [1,2]. Much of the endemic flora and fauna was at first shoe-horned into familiar groups by colonists. Galaxiids were variously classified as trouts, gudgeons, minnows and pikes, compounding the problem of how they became so widely dispersed, before their discrete taxonomic identity and diadromous life history became clear [3,4]. Further important clarification of taxonomy and natural history became the life's work of the late Bob McDowall [5–9]. Application of molecular techniques has helped to clarify galaxiid species boundaries and provided evidence for many new species, particularly stream-resident species whose ancestors lost diadromy [10–16]. More recently, DNA sequence data have formed the basis for time-calibrated phylogenies that answer some biogeographical questions and resolve the evolution of diadromy and its loss [17–20]. These give a better baseline for further investigating the evolutionary biology of this fascinating group of fishes and some of the interesting features that they show [21–24].

2. Palaeontology

Next to taxonomy and current distribution, fossils form a foundation to all evolutionary and biogeographic study. Given the widespread distribution of galaxiids across the Gondwanan continent, it is perhaps surprising that all undisputed galaxiid fossils found so far [25–28] herald from present-day New Zealand, a small remnant of the continent Zealandia [29–31]. This may in part reflect the importance of the region as a centre of origin, given that the group is predominantly cool-temperate in current distribution, and climates have been warmer over most of the last 50 million years since the Eocene. Apart from a New Caledonian species, galaxiids are limited to southern parts of South America, Africa and Australasia [8], and genetic diversity within the diverse *G. vulgaris* [32] and *G. olidus* [12,13] complexes show strikingly higher genetic diversity to the south. Additionally, the extensive system of Miocene freshwater lakes with marine links, making up part of what is today Otago (South Island, New Zealand), offered wonderful conditions for preservation, with fine sediments in a low-energy environment.

In this Special Issue, Kaulfuss et al. [33] review the history of these fossil discoveries, describing the location, stratigraphy, sedimentology and age of the sites. They list the galaxiid species found, and the number and type of fossils and their preservation type (body fossils, otoliths, coprolites). In addition to eight named species known from fossils alone, the authors give preliminary descriptions of four or five likely new species. These fossils provide an important record of the paleodiversity and paleoecology of the region, as well as the biogeographic history of galaxiids in New Zealand.

3. Biogeography

Molecular analyses of extant galaxiid species suggest a mix of vicariant and dispersive origins at a global level [15,17,20,29,31]. Within New Zealand, the dynamic nature of the geology, especially rapid fault movement, uplift and erosion, has driven major changes



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in hydrology. Waters, Burridge et al. [34] review 20 years of research focused on the effects of the changing topography on the galaxiid fauna. On a broad scale, two species of pencil galaxiid (*G. paucispondylus*, *G. divergens*) and two mudfish (*N. burrowsius*, *N. apoda*) either side of the Southern Alps probably arose in allopatry with uplift along the Alpine Fault over the last 5+ myrs [35]. In particular, several likely incidences of river capture have been inferred from combining geological and molecular analyses through ‘reciprocal illumination’. These changes of course have led to isolation and subsequent divergence of some lineages, such as the Teviot and Nevis Valley galaxiids [36], which are of conservation significance and possibly merit species status. Even in Australia, where such geological processes are slower and more subtle, there is evidence of hydrological evolution leading to biological evolution. For example, *G. oliros*, sister to the *G. olidus* complex, likely formed as an inland remnant in the Douglas Basin once the Murray-Darling cut its new and current path to the sea through the Murray Gorge to the west. The fast-evolving mtDNA genome has been key to dating such events, even those as recent as the last glaciation. For example, populations of both *G. divergens* and *G. vulgaris* ‘northern’ show parallel divergence between the upper Clarence and Wairau rivers (Marlborough, New Zealand), following glacial retreat and severing of links between the two systems. Vera-Escalona, Delgado et al. [15] review population genetic structure of South American galaxiids, including how de-glaciation has led to river reversals from Atlantic to Pacific sides of South America. *G. maculatus* shows a strong signal of reduced diversity in areas that were glaciated despite its diadromous life history enabling rapid re-colonisation. *G. platei* shows an east–west split across the Andes of about 1.5 myrs, and similar evidence of retreat to glacial refugia, but its post-glacial re-colonisation has been rapid for a strictly freshwater species.

4. Morphological Differentiation and Plasticity

As well as having a wide latitudinal range, galaxiids can be found in a wide range of aquatic habitats, including soft-bottomed volcanic and rocky post-glacial lakes; riffles and pools in river margins and small fast-flowing streams; intermittent and permanent water-courses; tidal inlets, swamps, estuaries and streams. Fossils abound in the Otago volcanic maar sites, and the type location for *G. anomalus* Stokell is a farm drain. *G. brevipinnis* shows great climbing ability, traversing vertical faces of concrete dams and weirs, penetrating far up-river systems and waterfalls to high altitudes. Other species, like *G. prognathus*, may be able to survive drought conditions in the hyporheos; *Neochanna* mudfish and *Lepidogalaxias* go one step further, aestivating in dried mud deposits. A review of the South American galaxiids by Cussac, Barrantes et al. [37] exemplifies the breadth of habitats occupied. These sorts of tolerances and behaviours have protected some threatened species from competition and predation by brown trout in particular, which prefer cooler more predictable conditions, and are excluded from sections above waterfalls in streams [38], unless deliberately transferred there. Adaptability to different habitats can be found within species, such as *G. gollumoides* McDowall and Chadderton, originally described from a swamp on Stewart Island, New Zealand, but common in lowland and upland sections of streams in Southland, New Zealand.

Dunn, O’Brien et al. [39] address phenotypic plasticity in *G. gollumoides* driven by wetland and stream habitats using reciprocal transfer experiments and detailed morphometric analysis over 3+ years. In the wild, adult *G. gollumoides* in streams tend to have smaller and flatter heads with smaller eye orbits than the stockier wetland fish. Using wetland and stream larvae raised to adulthood in either flowing or still tanks, wetland larvae raised in stream-like conditions converged toward the stream MDS centroid for 19 morphological characters, consistent with adaptive plasticity. The stream larvae raised in still conditions, however, diverged away from both centroids, though convergent on wetland in dimension 2 alone. Sample sizes and effects were small, so conclusions should be treated with caution, but convergence in higher-flow regions likely reflects more constraint on morphology. The limits to body form are likely narrow in more rapid flow, just as marine vertebrates

show convergence of body form for streamlining. The paper also contrasts ontogenetic trends for fin characters between the two forms, showing a variety of convergent, divergent and parallel trajectories.

Counter-intuitively, phenotypic plasticity is of great potential evolutionary significance: it increases the breadth of environments in which the organism can survive. As such, it can be the starting point for morphological divergence, differentiation and ultimately speciation. If body form is persistently pushed towards one end of the spectrum of plastic response, then concomitant genetic change will occur that begins to lock that phenotype in place, and indeed adapt it further by Darwinian selection. This scenario can be thought of as genes being the “followers of evolution” [40]. Two other papers in this issue also draw attention to plasticity of *G. maculatus*, in relation to its widespread distribution [15,37]

This mode of evolution has probably been important in the evolution of fishes in general [41], given their remarkable morphological plasticity, including the *G. vulgaris* group (sensu Allibone and Wallis [10]), which divide naturally into flathead and roundhead groups [11,42–44]. A second paper by Dunn, O’Brien et al. [45] focuses on how lentic and lotic habitats alternatively impact upon morphological differentiation in flathead *G. vulgaris*, roundhead *G. gollumoides* and the ancestral diadromous *G. brevipinnis* form. Each species showed some significant intraspecific morphological differentiation across several of a subset of 25 out of 35 morphological characters. Nineteen characters showed convergence across all species; only one character was significantly divergent (body width at vent). Lentic Galaxias had longer bodies, stouter caudal peduncles, longer and narrower pectoral fins, and longer, wider heads with larger mouths. These results likely reflect widespread phenotypic plasticity, but could also include some longer-term genotypic adaptation to local hydrological conditions, the fore-runner of speciation. The results parallel findings in other *Galaxias*, *Paragalaxias* and *Neochanna*.

Both of these papers [39,45] show the dangers of basing taxonomy of closely related species on morphology alone: convergence of body form may result in under-splitting whereas divergence due to intraspecific differentiation could lead to over-splitting. Full resolution of the number of galaxiid species in the *vulgaris* group in New Zealand, *olidus* group in Australia and *zebratus* group in South Africa will require detailed genetical data, though even then, it is difficult to decide where to draw the line with allopatric replacements. One criterion might be to demand evidence of additional morphological (or other adaptive) differentiation despite parallel existence in similar environments [46]. Past hybridization, particularly through river capture [34,36,47,48] or human modification [49] might conflate these attempts, but a genomic biogeographic approach should allow this history to be resolved.

5. Conservation

The papers in this Special Issue show how galaxiids are a distinctive evolutionary element in global fish diversity, as well as playing important functional roles in the freshwater ecosystems of southern lands. From both viewpoints, we should cherish and protect remaining populations. Introduced salmonids have been recognized as a threat for many years [8], and these continue to increase with expanding aquaculture and damming followed by stocking of reservoirs [15]. In addition, there is a growing list of more recently introduced species threatening galaxiid populations worldwide, including carp, catfish, characins, cyprinodontiforms and atherinopsids [37]. Volcanic lakes of North Island New Zealand were once burgeoning with lake forms of *G. brevipinnis*, an important resource to Maori, but now decimated by trout [50]. Intensification of farming, particularly dairying in New Zealand, has further marginalized mudfish populations and increased run-off into waterways. As a result, nitrification and pesticide residues threaten remaining galaxiid populations. Recent years has seen the added threat of climate change, which has contributed to the loss of northern population of *G. maculatus* in Chile and Argentina, exacerbated by enabling the southern spread of invading species [37].

6. Parasitology

Since nearly every non-parasitic metazoan has at least one species-specific metazoan parasite, the global diversity of the latter group probably exceeds that of the former. In a review of galaxiid parasites, Paterson, Viozzi et al. [51] show that at least half of all species have parasites described from them. The number of parasites discovered in a species reflects the geographic range of that species and intensity of research, with 23 parasite species described from *G. maculatus* across 14 studies. The wide range of parasites found in galaxiids includes several macroparasites (e.g., acanthocephalans, cestodes, copepods, molluscs, monogeneans, nematodes, trematodes, leeches) and microparasite groups (e.g., myxozoans, ciliates). The authors support idea of an online database of species and their hosts, and a broadening of attitudes to treat parasites as an important component of diversity in themselves, rather than simply threats to the fish species that they infest.

7. Future Work

Reviews in this Special Issue show different degrees of knowledge for different aspects of galaxiid biology. We have a much fuller picture of taxonomy, phylogeny and phylogeography, thanks to application of molecular genetics [15,34,37]. There may well be isolated populations of non-migratory forms yet to be discovered [52], and the African situation needs more work [53]. Genomic data will clarify finer-scale relationships and structure in more detail, and assess the importance of past hybridisation in the evolution of the group [49,54]. More importantly, genomics will allow us to address the underlying genetic basis of diadromy, more specifically its loss [55,56]. Genes involved in species becoming stream-resident are excellent examples of speciation genes in the true sense of the word, since long-term landlocking almost inevitably leads to allopatric speciation. Genomics will also allow us to address the underlying basis of physiological adaptation, particularly related to changing osmotic [57] and disease [55] challenges.

To a certain extent, genomics releases us from the tyranny of model species; this freedom is important in allowing us to build a fuller understanding of diversity across all forms of life. Galaxiids have much to offer the full range of biological research with their fascinating life-history, biogeography and evolution. The biggest challenge of the next few decades will be preserving their dwindling populations under the manifold threats to freshwater ecosystems [58].

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References

1. Darwin, C. *The Origin of Species*, 6th ed.; (Reprint); J.M. Dent & Sons: London, UK, 1872.
2. McDowall, R.M. Generalized tracks and dispersal in biogeography. *Syst. Zool.* **1978**, *27*, 88–104. [[CrossRef](#)]
3. Stokell, G. The systematic arrangement of the New Zealand Galaxiidae. Part I. Generic and sub-generic classification. *Trans. R. Soc. N. Z.* **1945**, *75*, 124–137.

4. Stokell, G. *Freshwater Fishes of New Zealand*; Simpson & Williams: Christchurch, New Zealand, 1955.
5. McDowall, R.M. The galaxiid fishes of New Zealand. *Bull. Mus. Comp. Zool. Harv.* **1970**, *139*, 341–431.
6. McDowall, R.M. The galaxiid fishes of South America. *Zool. J. Linn. Soc.* **1971**, *50*, 33–73. [[CrossRef](#)]
7. McDowall, R.M.; Frankenberg, R.S. The galaxiid fishes of Australia. *Rec. Aust. Mus.* **1981**, *33*, 443–605. [[CrossRef](#)]
8. McDowall, R.M. *New Zealand Freshwater Fishes. A Natural History and Guide*; Heinemann Reed: Auckland, New Zealand, 1990.
9. McDowall, R.M. *The Reed Field Guide to New Zealand Freshwater Fishes*; Reed Publishing: Auckland, New Zealand, 2000.
10. Allibone, R.M.; Wallis, G.P. Genetic variation and diadromy in some native New Zealand galaxiids (Teleostei: Galaxiidae). *Biol. J. Linn. Soc.* **1993**, *50*, 19–33. [[CrossRef](#)]
11. Allibone, R.M.; Crowl, T.A.; Holmes, J.M.; King, T.M.; McDowall, R.M.; Townsend, C.R.; Wallis, G.P. Isozyme analysis of *Galaxias* species (Teleostei: Galaxiidae) from the Taieri River, South Island, New Zealand: A species complex revealed. *Biol. J. Linn. Soc.* **1996**, *57*, 107–127. [[CrossRef](#)]
12. Adams, M.; Raadik, T.A.; Burrige, C.P.; Georges, A. Global biodiversity assessment and hyper-cryptic species complexes: More than one species of elephant in the room? *Syst. Biol.* **2014**, *63*, 518–533. [[CrossRef](#)] [[PubMed](#)]
13. Raadik, T.A. Fifteen from one: A revision of the *Galaxias olidus* Günther, 1866 complex (Teleostei, Galaxiidae) in south-eastern Australia recognises three previously described taxa and describes 12 new species. *Zootaxa* **2014**, *3898*, 1–198. [[CrossRef](#)] [[PubMed](#)]
14. Coleman, R.A.; Hoffmann, A.A.; Raadik, T.A. A review of *Galaxiella pusilla* (Mack) (Teleostei: Galaxiidae) in south-eastern Australia with a description of a new species. *Zootaxa* **2015**, *4021*, 243–281. [[CrossRef](#)]
15. Vera-Escalona, I.; Delgado, M.L.; Habit, E.; Ruzzante, D.E. Historical and contemporary diversity of galaxiids in South America: Biogeographic and phylogenetic perspectives. *Diversity* **2020**, *12*, 304. [[CrossRef](#)]
16. Nelson, N.J.; Briskie, J.V.; Constantine, R.; Monks, J.; Wallis, G.P.; Watts, C.; Wotton, D.M. The winners: Species that have benefited from 30 years of conservation action. *J. R. Soc. N. Z.* **2019**, *49*, 281–300. [[CrossRef](#)]
17. Waters, J.M.; Dijkstra, L.H.; Wallis, G.P. Biogeography of a southern hemisphere freshwater fish: How important is marine dispersal? *Mol. Ecol.* **2000**, *9*, 1815–1821. [[CrossRef](#)]
18. Waters, J.M.; Lopez, J.A.; Wallis, G.P. Molecular phylogenetics and biogeography of galaxiid fishes (Osteichthyes: Galaxiidae): Dispersal, vicariance, and the position of *Lepidogalaxias salamandroides*. *Syst. Biol.* **2000**, *49*, 777–795. [[CrossRef](#)]
19. Waters, J.M.; Rowe, D.L.; Burrige, C.P.; Wallis, G.P. Gene trees versus species trees: Reassessing life-history evolution in a freshwater fish radiation. *Syst. Biol.* **2010**, *59*, 504–517. [[CrossRef](#)]
20. Burrige, C.P.; McDowall, R.M.; Craw, D.; Wilson, M.V.H.; Waters, J.M. Marine dispersal as a pre-requisite for Gondwanan vicariance among elements of the galaxiid fish fauna. *J. Biogeogr.* **2012**, *39*, 306–321. [[CrossRef](#)]
21. Berra, T.M.; Pusey, B.J. Threatened fishes of the world: *Lepidogalaxias salamandroides* Mees, 1961 (Lepidogalaxiidae). *Environ. Biol. Fish.* **1997**, *50*, 201–202. [[CrossRef](#)]
22. Suter, H.C.; Kennedy, M.; Young, G. Neoteny or not? The distribution of the hypophysial duct within the Galaxioidea. *J. Fish. Biol.* **2004**, *64*, 1217–1225. [[CrossRef](#)]
23. Waters, J.M.; McDowall, R.M. Phylogenetics of the Australasian mudfishes: Evolution of an eel-like body plan. *Mol. Phylogenet. Evol.* **2005**, *37*, 417–425. [[CrossRef](#)] [[PubMed](#)]
24. Wallis, L.J.; Wallis, G.P. Extreme positive selection on a new highly-expressed larval glycoprotein (LGP) gene in *Galaxias* fishes (Osmeriformes: Galaxiidae). *Mol. Biol. Evol.* **2011**, *28*, 399–406. [[CrossRef](#)]
25. McDowall, R.M. Notes on some *Galaxias* fossils from the Pliocene of New Zealand. *J. R. Soc. N. Z.* **1976**, *6*, 17–22. [[CrossRef](#)]
26. McDowall, R.M.; Pole, M. A large galaxiid fossil (Teleostei) from the Miocene of Central Otago, New Zealand. *J. R. Soc. N. Z.* **1997**, *27*, 193–198. [[CrossRef](#)]
27. Lee, D.E.; McDowall, R.M.; Lindqvist, J.K. *Galaxias* fossils from Miocene lake deposits, Otago, New Zealand: The earliest records of the Southern Hemisphere family Galaxiidae (Teleostei). *J. R. Soc. N. Z.* **2007**, *37*, 109–130. [[CrossRef](#)]
28. Schwarzahns, W.; Scofield, R.P.; Tennyson, A.J.D.; Worthy, J.P.; Worthy, T.H. Fish remains, mostly otoliths, from the non-marine early Miocene of Otago, New Zealand. *Acta Palaeontol. Pol.* **2012**, *57*, 319–350. [[CrossRef](#)]
29. Wallis, G.P.; Trewick, S.A. New Zealand phylogeography: Evolution on a small continent. *Mol. Ecol.* **2009**, *18*, 3548–3580. [[CrossRef](#)] [[PubMed](#)]
30. Mortimer, N.; Campbell, H. *Zealandia: Our Continent Revealed*; Penguin and GNS: Auckland/Lower Hutt, New Zealand, 2014.
31. Wallis, G.P.; Jorge, F. Going under down under? Lineage ages argue for extensive survival of the Oligocene marine transgression on Zealandia. *Mol. Ecol.* **2018**, *27*, 4368–4396. [[CrossRef](#)]
32. Wallis, G.P.; Judge, K.F.; Bland, J.; Waters, J.M.; Berra, T.M. Genetic diversity in New Zealand *Galaxias vulgaris sensu lato* (Teleostei: Osmeriformes: Galaxiidae): A test of a biogeographic hypothesis. *J. Biogeogr.* **2001**, *28*, 59–67. [[CrossRef](#)]
33. Kaulfuss, U.; Lee, D.E.; Robinson, J.H.; Wallis, G.P.; Schwarzahns, W.W. A review of *Galaxias* (Galaxiidae) fossils from the Southern Hemisphere. *Diversity* **2020**, *12*, 208. [[CrossRef](#)]
34. Waters, J.M.; Burrige, C.P.; Craw, D. River capture and freshwater biological evolution: A review of galaxiid fish vicariance. *Diversity* **2020**, *12*, 216. [[CrossRef](#)]
35. Craw, D.; Upton, P.; Burrige, C.P.; Wallis, G.P.; Waters, J.M. Rapid biological speciation driven by tectonic evolution in New Zealand. *Nat. Geosci.* **2016**, *9*, 140–145. [[CrossRef](#)]
36. Waters, J.M.; Wallis, G.P.; Burrige, C.P.; Craw, D. Geology shapes biogeography: Quaternary river-capture explains New Zealand's biologically 'composite' Taieri River. *Quat. Sci. Rev.* **2015**, *120*, 47–56. [[CrossRef](#)]

37. Cussac, V.E.; Barrantes, M.E.; Boy, C.C.; Górski, K.; Habit, E.; Lattuca, M.E.; Rojo, J.H. New insights into the distribution, physiology and life histories of South American galaxiid fishes, and potential threats to this unique fauna. *Diversity* **2020**, *12*, 178. [[CrossRef](#)]
38. McIntosh, A.R.; McHugh, P.A.; Dunn, N.R.; Goodman, J.M.; Howard, S.W.; Jellyman, P.G.; O'Brien, L.K.; Nystrom, P.; Woodford, D.J. The impact of brown trout on galaxiid fishes in New Zealand. *N. Z. J. Ecol.* **2010**, *34*, 195–206.
39. Dunn, N.R.; O'Brien, L.K.; Closs, G.P. Phenotypically induced intraspecific variation in the morphological development of wetland and stream *Galaxias gollumoides* McDowall and Chadderton. *Diversity* **2020**, *12*, 220. [[CrossRef](#)]
40. Schwander, T.; Leimar, O. Genes as leaders and followers in evolution. *Trends Ecol. Evol.* **2011**, *26*, 143–151. [[CrossRef](#)]
41. Seehausen, O.; Wagner, C.E. Speciation in freshwater fishes. *Annu. Rev. Ecol. Syst.* **2014**, *45*, 621–651. [[CrossRef](#)]
42. McDowall, R.M.; Wallis, G.P. Description and redescription of *Galaxias* species (Teleostei: Galaxiidae) from Otago and Southland. *J. R. Soc. N. Z.* **1996**, *26*, 401–427. [[CrossRef](#)]
43. Waters, J.M.; Wallis, G.P. Mitochondrial DNA phylogenetics of the *Galaxias vulgaris* complex from South Island, New Zealand: Rapid radiation of a species flock. *J. Fish Biol.* **2001**, *58*, 1166–1180. [[CrossRef](#)]
44. Crow, S.K.; Waters, J.M.; Closs, G.P.; Wallis, G.P. Morphological and genetic analysis of *Galaxias* 'southern' and *G. gollumoides*: Interspecific differentiation and intraspecific structuring. *J. R. Soc. N. Z.* **2009**, *39*, 43–62. [[CrossRef](#)]
45. Dunn, N.R.; O'Brien, L.K.; Burrige, C.P.; Closs, G.P. Morphological convergence and divergence in *Galaxias* fishes in lentic and lotic habitats. *Diversity* **2020**, *12*, 183. [[CrossRef](#)]
46. Crandall, K.A.; Bininda-Emonds, O.R.P.; Mace, G.M.; Wayne, R.K. Considering evolutionary processes in conservation biology. *Trends Ecol. Evol.* **2000**, *15*, 290–295. [[CrossRef](#)]
47. Waters, J.M.; Craw, D.; Youngson, J.H.; Wallis, G.P. Genes meet geology: Fish phylogeographic pattern reflects ancient, rather than modern, drainage connections. *Evolution* **2001**, *55*, 1844–1851. [[CrossRef](#)] [[PubMed](#)]
48. Carrea, C.; Anderson, L.V.; Craw, D.; Waters, J.M.; Burrige, C.P. The significance of past interdrainage connectivity for studies of diversity, distribution and movement of freshwater-limited taxa within a catchment. *J. Biogeogr.* **2014**, *41*, 536–547. [[CrossRef](#)]
49. Esa, Y.B.; Waters, J.M.; Wallis, G.P. Introgressive hybridization between *Galaxias depressiceps* and *Galaxias* sp D (Teleostei: Galaxiidae) in Otago, New Zealand: Secondary contact mediated by water races. *Conserv. Genet.* **2000**, *1*, 329–339. [[CrossRef](#)]
50. McDowall, R.M. *Ikawai: Freshwater Fishes in Māori Culture and Economy*; Canterbury University Press: Christchurch, New Zealand, 2011.
51. Paterson, R.A.; Viozzi, G.P.; Rauque, C.A.; Flores, V.R.; Poulin, R.P. A global assessment of parasite diversity in galaxiid fishes. *Diversity* **2021**, *13*, 27. [[CrossRef](#)]
52. Watts, R.J.; Storey, A.W.; Hebbert, D.R.; Edward, D.H.D. Genetic and morphological differences between populations of the western minnow, *Galaxias occidentalis*, from two river systems in south-western Australia. *Mar. Freshw. Res.* **1995**, *46*, 769–777. [[CrossRef](#)]
53. Chakona, G.; Swartz, E.R.; Chakona, A. The status and distribution of a newly identified endemic galaxiid in the eastern Cape Fold Ecoregion, of South Africa. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **2018**, *28*, 55–67. [[CrossRef](#)]
54. Wallis, G.P.; Cameron-Christie, S.R.; Kennedy, H.L.; Palmer, G.; Sanders, T.R.; Winter, D.J. Interspecific hybridization causes long-term phylogenetic discordance between nuclear and mitochondrial genomes in freshwater fishes. *Mol. Ecol.* **2017**, *26*, 3116–3127. [[CrossRef](#)] [[PubMed](#)]
55. Wallis, G.P.; Wallis, L.J. A preliminary transcriptomic study of galaxiid fishes reveals a larval glycoprotein gene under strong positive selection. In *Evolutionary Biology: Genome Evolution, Speciation, Coevolution and Origin of Life*; Pontarotti, P., Ed.; Springer: Heidelberg, Germany, 2014; Chapter 3; pp. 47–68.
56. Delgado, M.L.; Manosalva, A.; Urbina, M.A.; Habit, E.; Link, O.; Ruzzante, D.E. Genomic basis of the loss of diadromy in *Galaxias maculatus*: Insights from reciprocal transplant experiments. *Mol. Ecol.* **2020**, *29*, 4857–4870. [[CrossRef](#)] [[PubMed](#)]
57. Ruiz-Jarabo, I.; González-Wevar, C.A.; Oyarzún, R.; Fuentes, J.; Poulin, E.; Bertrán, C.; Vargas-Chacoff, L. Isolation driven divergence in osmoregulation in *Galaxias maculatus* (Jenyns, 1848) (Actinopterygii: Osmeriformes). *PLoS ONE* **2016**, *11*, e0154766. [[CrossRef](#)]
58. Chilcott, S.; Freeman, R.; Davies, P.E.; Crook, D.; Fulton, W.; Hamr, P.; Jarvis, D.; Sanger, A. Extinct habitat, extant species: Lessons learned from conservation recovery actions for the Pedder galaxias (*Galaxias pedderensis*) in south-west Tasmania, Australia. *Mar. Freshw. Res.* **2013**, *64*, 864–873. [[CrossRef](#)]