*diversity*

*Review*

# A Review of *Galaxias* (Galaxiidae) Fossils from the Southern Hemisphere

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**Abstract:** The Galaxiidae is a Southern Hemisphere family of freshwater fish, considered to be of Gondwanan origin based on the current distribution of species in New Zealand, Australia (including Tasmania), New Caledonia, Africa, South America, and on some associated and subantarctic islands. The fossil record of galaxiids is extremely sparse and geographically restricted. The only galaxiid fossils currently known come from several Miocene lakes in southern New Zealand. They include more than 100 articulated fishes, some remarkably preserving soft parts such as eyes and skin, skulls and jaw components, and more than 200 isolated otoliths. Common coprolites and in situ preserved gut content at one site (Foulden Maar) indicate the different diets of larvae and adult fish. These discoveries reveal a diverse *Galaxias* fauna, the presence of lake-locked populations, ontogenetic diet shifts, and representatives of several non-migratory *Galaxias* lineages associated with inland streams and lakes. There are at least six *Galaxias* species based on macrofossils and six separate otolith-based species from varied volcanic and regional lacustrine environments. This diversity points to southern New Zealand as a centre of biodiversity and speciation in Galaxiidae in the early to late Miocene.

**Keywords:** Miocene; articulated skeletons; otoliths; coprolites; taphonomy; paleoecology; biogeography; New Zealand; fossil *Konservat-Lagerstätte*

## 1. Introduction

As demonstrated by the papers in this Special Issue, freshwater fishes of the family Galaxiidae (Galaxiiformes) have two striking features: a marine migratory larval phase and an exclusively Southern Hemisphere (Gondwanan) distribution. An unusually broad spread of one *Galaxias* species across several southern lands came to the notice of the earliest biogeographers, including Darwin himself. A remarkably prescient passage from the 6th edition of his *Origin of Species* is worthy of quotation in full:

> *"It was formerly believed that the same fresh-water species never existed on two continents distant from each other. But Dr. Günther has lately shown that the Galaxias attenuatus [sic; now Galaxias maculatus] inhabits Tasmania, New Zealand, the Falkland Islands, and the mainland of South America. This is a wonderful case, and probably indicates dispersal from an Antarctic centre during a former warm period. This case, however, is rendered in some degree less surprising by the species of this genus*

> *having the power of crossing by some unknown means considerable spaces of open ocean: thus there is one species common to New Zealand and to the Auckland Islands, though separated by a distance of about 230 miles. On the same continent fresh-water fish often range widely, and as if capriciously; for in two adjoining river-systems some of the species may be the same, and some wholly different."* ([1], pp. 374–375)

The subsequent text sees Darwin wrestle with alternative explanations for these biogeographical observations, including whirlwinds, river capture, floods and uplift. However, Darwin was missing at least two crucial pieces of knowledge, one biological and the other geological: life history variation within galaxiids (ancestral diadromy versus derived stream-residence) and plate tectonics. Dispersal and vicariant explanations characterized the vigorous and polarized debate that was to continue for over 100 years [2]. In the 1990s, molecular genetics started to provide evidence for many unrecognized stream-resident species whose ancestors had lost diadromy [3,4], and DNA sequence data on which to construct time-calibrated phylogenies that answered many biogeographical questions, both among [5–7] and within continents [8–10].

Fossils provide empirical evidence that can be used to time-calibrate and constrain phylogenetic hypotheses used in phylogeographic studies and help in modelling rates of morphological evolution or speciation [11]. They are of central importance to biogeographic reconstruction, as they give definitive, dated evidence for existence of ancestral forms on a particular landmass or in a sea, crucial to understanding Gondwanan history [12,13]. A key limitation, however, is the need to know definitively that a fossil is a true ancestor, and not a related, but separate, evolutionary lineage [5]. Despite the fact that galaxiids currently occur on most southern landmasses, their fossils are few, and are currently restricted to New Zealand [14–18].

About 21 species of galaxiid are currently recognized in the modern New Zealand fauna [19,20]. The exact number is difficult to determine, with several undescribed non-diadromous lineages possessing only tag-names (e.g., [5]). Some of the five diadromous species have land-locked populations in inland lakes throughout New Zealand. There are three major extant lineages: (i) *Galaxias maculatus* (Jenyns 1842) (diadromous inanga and dune-lake derivatives); (ii) *Neochanna* (mudfish, five freshwater resident species); (iii) a larger clade comprising the deep-bodied (three diadromous species), pencil (five freshwater resident species) and *G. brevipinnis*-like (diadromous koaro and six or more recently derived freshwater resident species) galaxiids [5,20]. A New Caledonian species appears to be recently derived from New Zealand *G. brevipinnis* Günther 1866 [5].

Molecular phylogenetic analysis of *G. maculatus* populations from Chile, Tasmania and New Zealand suggests Miocene (or later) links among these Gondwanan landmasses, and therefore a likely dispersive origin for New Zealand inanga [6]. New Zealand crown-group mudfish date from the mid-Miocene, probably with late Oligocene Australian origins [5]. The third larger *brevipinnis*-like clade likely has two separate Australian origins in the late Oligocene and late Miocene [5].

Recent work on Miocene freshwater deposits in South Island, New Zealand has revealed many fish fossils, some of which likely constitute new galaxiid taxa. These fossils are of major importance in understanding the evolutionary history of galaxiids in New Zealand specifically and the Southern Hemisphere in general [5,12,14,21,22]. To date, all fossils of *Galaxias* occur at early to late Miocene localities in Otago, southern New Zealand (Figure 1). In part, this may reflect a combination of paleontological effort and taphonomic bias.

This paper reviews the history of the discovery of galaxiid fossils in New Zealand and describes the fossil sites in terms of location, stratigraphy, sedimentology and age. It lists the galaxiid species, records the number and type of fossils and their preservation (body fossils, otoliths and coprolites) from each site. These fossils reveal aspects of paleodiversity and paleoecology including population structure and diet, and provide information on the biogeographic history of Galaxiidae in New Zealand.

## 2. History of Discovery of Galaxiidae Fossils in New Zealand

The earliest mention of fossil galaxiids from New Zealand was by Oliver ([23], p. 284), concerning three fish skeletons, "apparently *Galaxias*" that he had collected from lacustrine diatomite beds at Frasers Gully, Dunedin in 1929 (Figure 1, Table 1). Two of these specimens are held in the collections of Museum of New Zealand Te Papa Tongarewa in Wellington. Stokell [24] described and illustrated the part and counterpart of another specimen collected by GM Thomson from the same locality. He noted that it resembled living *Galaxias* species but did not formally name it. At the time, the Frasers Gully diatomite beds were regarded as Pliocene: they are now known to be of mid to late Miocene age (c. 13–11 Ma) [25]. Whitley ([26], p. 34) proposed "the new name *kaikorai*" for this "interesting fossil *Galaxias*" based upon Stokell's description and illustration [24] (Plates xi–xii) though apparently without seeing either the specimens mentioned by Oliver or that collected by Thomson. The latter fish, held in the collections of the Department of Geology, University of Otago (OU6330, 6331) was designated as the holotype. Further specimens were collected from the same locality (Kaikorai Leaf Beds, Frasers Gully) by Campbell and students from the 1970s to the 1990s.

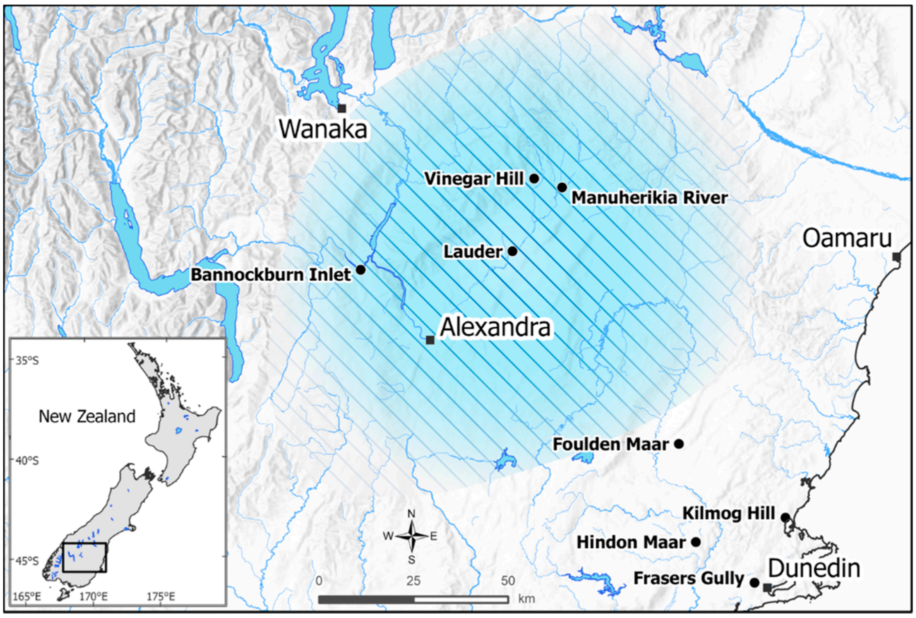

**Figure 1.** Locality map showing sites for *Galaxias* fossils in Otago, New Zealand. Shaded area shows approximate extent of Lake Manuherikia in the early Miocene.

In 1962, a University of Otago student, Cecilia Travis, collected two small fish fossils from a site near Middlemarch, now referred to as Foulden Maar (Figure 1), and figured these in her MSc thesis [27]. Both specimens were identified by Stokell as *G. kaikorai* Whitley 1956. McDowall [16] re-examined the holotype of *G. kaikorai*, the two incomplete specimens collected by Oliver from the same locality, and the two Middlemarch specimens. He concluded that the Frasers Gully specimens could not be distinguished from the living species *G. brevipinnis*, and that the Middlemarch specimens resembled the extant *G. vulgaris* Stokell 1949. In 1976, Martin Browne, another University of Otago student, collected small, slender, articulated and nearly entire fish from Kilmog Hill, 25 km north of Dunedin (Figure 1).

McDowall and Pole [17] described a large but incomplete articulated fish skeleton from near Bannockburn (Figure 1) as a galaxiid, probably genus *Galaxias*. Several jaw and other cranial fragments were collected from Bannockburn Inlet in 2004 by Daphne Lee and Manya Krysta [14].

In 2005, Daphne Lee and Jon Lindqvist collected a well-preserved, articulated specimen from a newly exposed small mining pit at Foulden Maar near Middlemarch (= the site studied by C Travis), which became the holotype for *Galaxias effusus* Lee, McDowall, Lindqvist 2007 [14]. Since then, many more articulated specimens, including larvae and juveniles, have been collected from this and a nearby larger mining pit [28].

The first formal study of freshwater fossil otoliths from New Zealand yielded 230 galaxiid otoliths from several sites near St Bathans (Figure 1). These were subsequently described as six new species of *Galaxias* [18].

Field work carried out since 2015 has yielded several compressed but complete specimens of *Galaxias* adults, juveniles and larvae from the newly recognized Hindon Maar Complex, about 25 km west of Dunedin (Figure 1) [29].

## 3. Material Studied, Fossil Localities and Ages

All fossil *Galaxias* specimens investigated in this study come from lake deposits in Otago, southern New Zealand. We provide numbers of specimens, locality and stratigraphic information including Fossil Record File (FRF) numbers for each site. The New Zealand Fossil Record Electronic Database (FRED) (https://www.fred.org.nz/) administered by the Geoscience Society of New Zealand and GNS Science catalogues fossil localities by giving each a number prefixed with the NZMS260 map sheet number, followed by a running locality number (Table 1). Most of the *Galaxias* specimens are held in the collections of the Geology Museum, University of Otago (OU). One specimen is held at the Department of Botany, University of Queensland. Two fish and 230 otoliths are held in the collections of the Museum of New Zealand Te Papa Tongarewa (formerly National Museum of New Zealand), Wellington, New Zealand (NMNZ).

**Table 1.** Details for *Galaxias* fossils from New Zealand.

| Locality | Fossil Record Number | Species | Preservation | Age | References |
|---|---|---|---|---|---|
| Foulden Maar | I43/f8503 | *G. effusus* | articulated larvae, juveniles and adults | early Miocene (23 Ma) | [14,16,30] |
| Bannockburn Inlet, Bannockburn Fm. | F41/f217 | *Galaxias* n. sp. 'Bannockburn Inlet' | isolated cranial bones, one partial specimen | early Miocene (19–16 Ma) | [14,17,31] |
| Manuherikia River, Bannockburn Fm. | H41/f089<br>H41/f090<br>H41/f096 | *G. angustiventris*<br>*G. brevicauda*<br>*G. papilionis*<br>*Galaxias* sp. | otoliths;<br>otoliths;<br>otoliths;<br>otoliths | early Miocene (19–16 Ma) | [18] |
| Manuherikia River and Vinegar Hill, Bannockburn Fm. | H41/f0112<br>H41/f0113 | *G. bobmcdowalli*<br>*G. parvirostris* | otoliths;otoliths | early Miocene (19–16 Ma) | [18] |
| Lauder, Bannockburn Fm. | G41/f9508 | *G. tabidus* | otoliths | early Miocene (19–16 Ma) | [18] |
| Hindon Maar | I44/f0392 | *Galaxias* n. sp. 'Hindon' | larvae, juveniles, adults | middle Miocene (14 Ma) | [29] |
| Frasers Gully, Kaikorai Leaf Beds | I44/f145 | *G. kaikorai* Whitley | articulated adults | middle Miocene (13–11 Ma) | [14,16,23] |
| Kilmog Hill, 'Kaikorai Leaf Beds' | I44/f015 | *Galaxias* n. sp. 'Kilmog Hill' | nearly entire fishes | middle Miocene (13–11 Ma) | [14,32] |

### *3.1. Foulden Maar (I43/f8503), Earliest Miocene, 23 Ma*

The oldest galaxiid fossils known come from Foulden Maar (Table 1), a 23-million-year-old *Konservat-Lagerstätte* near Middlemarch, Otago [30,33,34]. Foulden Maar is a partly eroded maar crater infilled by 120 m of laminated, fossiliferous freshwater diatomite, which consists almost entirely of a single species of pennate diatom [35,36]. The c. 1 km-diameter maar lake was a closed system, fed by groundwater and meteoric water and surrounded by a tephra rim, with anoxic bottom waters, which captured and preserved plants and animals from the lake and the surrounding evergreen, Lauraceae-dominated rainforest. There is no evidence of disturbance of the anoxic lake beds by currents, scavenging or bioturbation and individual laminae can be traced for tens to hundreds of metres across the basin [28,33,35]. The fossils include a myriad of leaves, flowers, fruits, seeds, representatives of about 20 families of arthropods and at least 3 types of fish. A detailed account of the geological setting, sedimentology and crater stratigraphy of Foulden Maar is presented by Lindqvist and Lee [33] and Kaulfuss [35]; Lee et al. [30] provide a review of the biodiversity and paleoecology.

Articulated, sometimes partly pyritized fish remains are relatively common at Foulden Maar and include the holotype of *Galaxias effusus* (Figure 2) and more than 100 further galaxiid fossils (not all collected) from small surface mining pits [28]. Almost all are preserved as complete, laterally compressed skeletons (Figures 2 and 3A,C), except for two dorsal-ventrally compressed specimens (Figure 3D). Field observations suggest they are randomly distributed throughout the exposed diatomite sequence, which represents c. 10,000 years of the lake's evolution. The in situ anteroposterior axes of 51 specimens measured show no preferred orientation and there is no indication of mass-mortality layers [28]. The maximum observed body length is 140 mm.

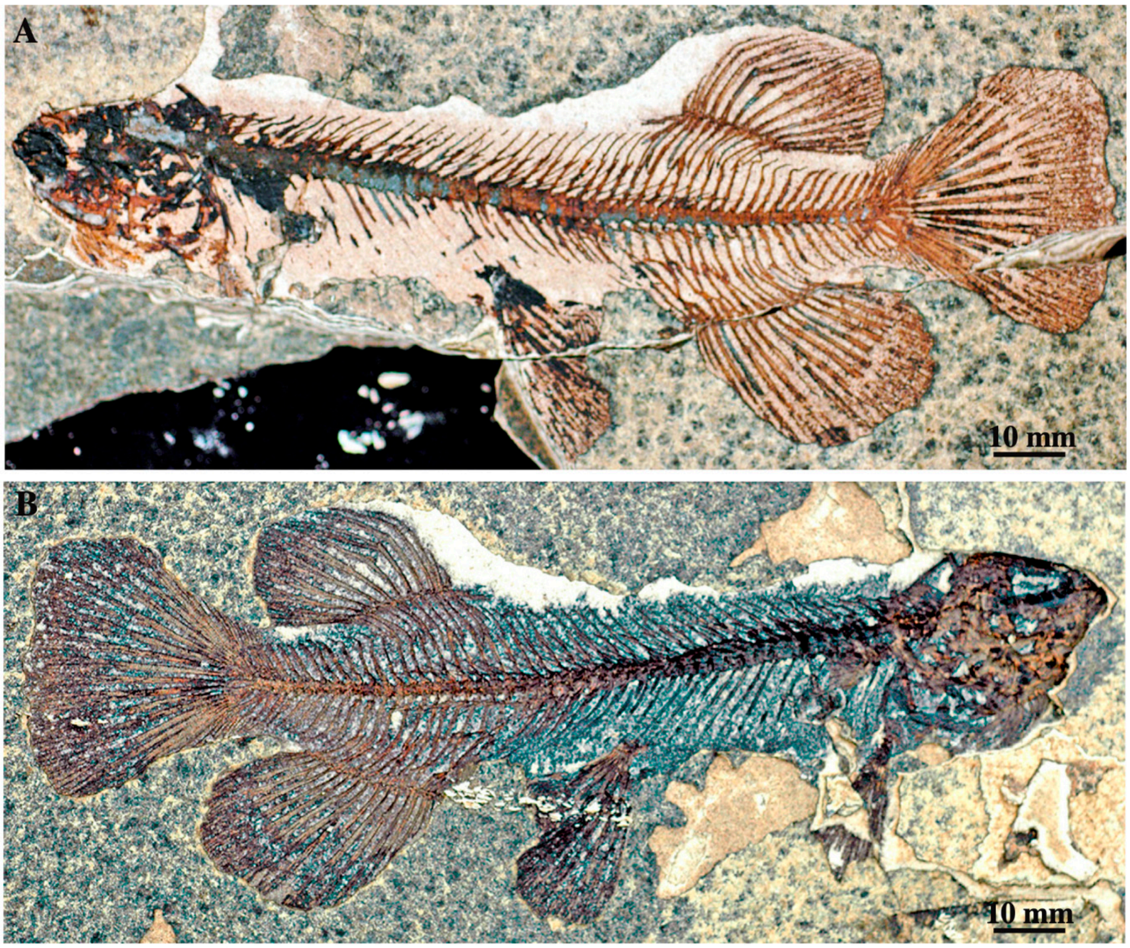

**Figure 2.** Foulden Maar, early Miocene. *Galaxias effusus* Lee, McDowall & Lindqvist 2007. (**A**,**B**), Part and counterpart of holotype (OU22650).

The fish bones at Foulden Maar are generally dissolved (decalcified) and are preserved as impressions or as soft brown to black residual material, often with somewhat diffuse outline and associated pyrite. No otoliths are preserved. Many of the fish fossils preserve brown to black "shadows", which can be interpreted as chemically and/or biologically (e.g., by bacteria) altered soft tissue of the living fish. Some specimens preserve the original skin pattern (Figure 3B).

In addition to juvenile and adult specimens of *Galaxias*, several larvae have been found. They are preserved as elongate, 35–40 mm in length, very faint, light-brown body traces with relatively large eyes and different levels of notochord and fin development (Figure 3E,G). As in the literature on extant *Galaxias*, the full complement of fin rays in all fins has been used as a distinguishing character between larval stages and juveniles (e.g., [37]).

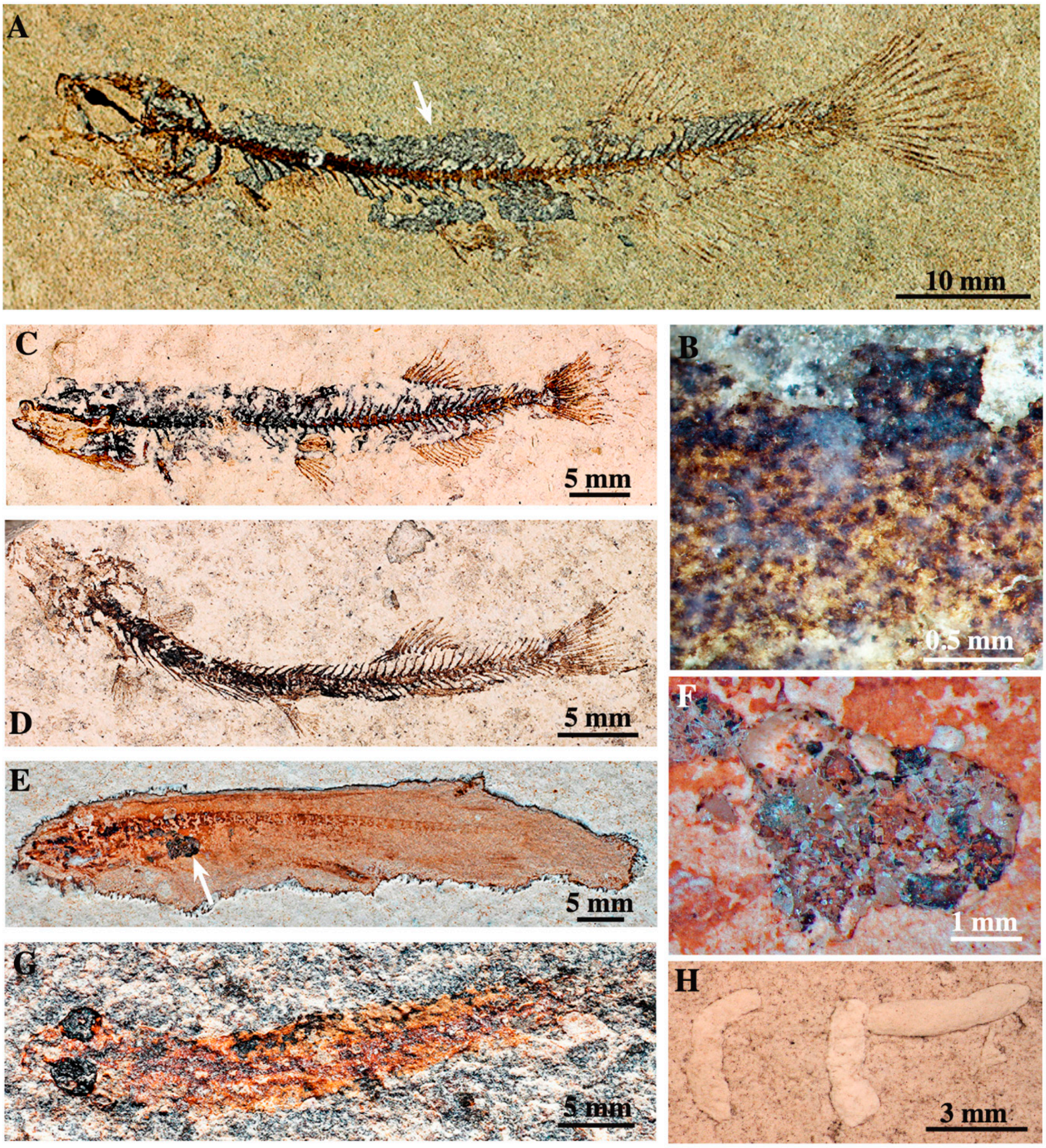

**Figure 3.** Foulden Maar, early Miocene, *Galaxias effusus*. (**A**), Articulated skeleton with skin partially preserved (OU22914); (**B**), Close-up of specimen A showing skin pattern with dark spots and blotches (photographed under ethanol); (**C**), Articulated, laterally compressed adult (OU22915); (**D**), Articulated adult with dorso-ventrally compressed head region (OU22916); (**E**), Juvenile *Galaxias* with body outline and gut contents (arrow) preserved (OU22698); (**F**), Close-up of specimen in E, showing gut content consisting of mineral grains, organic detritus, arthropod fragments and sponge spicules; (**G**), *Galaxias* larva prior to development of fins and skeleton (OU22697); (**H**), Three small coprolites produced by diatom-feeding *Galaxias* larvae.

An assignment of these larvae to *Galaxias* seems highly likely, based on the similarity in morphology and size to larvae of extant species (Bob McDowall, personal communication, 2009). Only two specimens of non-galaxiid fish (*Anguilla* sp. and an unidentified taxon) have been found in the maar.

### *3.2. Lake Manuherikia Localities*

One articulated skeleton, disarticulated skeletal elements and more than 200 fossil otoliths assigned to species of *Galaxias* were collected from four sites around the margins of the extensive paleolake Manuherikia, which covered an area of more than 5600 km$^2$ in Central Otago and was connected to the sea by streams and river systems [38]. All fossils are derived from fine-grained sandstones, siltstones and calcareous mudstones of Bannockburn Formation, described in detail elsewhere [38].

#### 3.2.1. Bannockburn Inlet (F41/217), Early Miocene, 19–16 Ma

An incomplete decalcified skeleton of a relatively large but slender *Galaxias* was collected from a carbonaceous silt near Bannockburn (Table 1). The specimen with an estimated length of 383 mm was described and figured by McDowall and Pole [17] who suggested that it was similar in overall body shape to extant *G. maculatus*.

Numerous disarticulated skeletal elements considered to be from galaxiids were collected from a shaley mudstone at another Bannockburn locality. They include several dentaries and a possible premaxilla with what are interpreted as stout, bluntly pointed, curved uniserial teeth (Figure 4A–D herein; Figure 6A–C in Lee et al. [14]). These are similar to the uniserial teeth seen in *Galaxias* or *Retropinna*; in particular, the “blunt, recurved shape” resembles the teeth of large specimens of *Galaxias argenteus* (Gmelin 1789). The adult fish from which they came may have reached a length of 500 mm, close to the size of the largest living *Galaxias*. The size, absence of scales and presence of other associated bones including parasphenoids and subopercular make the assignment to *Galaxias* likely [14].

#### 3.2.2. Manuherikia River, Near St Bathans (H41/f089, H41/f096, H41/f090), Early Miocene, 19–16 Ma

More than 200 isolated otoliths have been obtained by sieving calcareous fine-grained sandstone within the basal Bannockburn Formation from four horizons (HH1a, HH1b, HH1d and HH4) in a c. 25-m thick stratigraphic section along the banks of the Manuherikia River [18] (their Figure 2). They represent five different *Galaxias* otolith-based species: *G. angustiventris* Schwarzhans 2012, *G. brevicauda* Schwarzhans 2012, *G. bobmcdowalli* Schwarzhans 2012, *G. papilionis* Schwarzhans 2012 and *G. parvirostris* Schwarzhans 2012; all five species occur together at one stratigraphic level (HH1a).

#### 3.2.3. Vinegar Hill, Near St Bathans (H41/f112, H41/f113), Early Miocene, 19–16 Ma

Isolated fish bones and rare fish skeletons are present throughout a 30-m composite section at Vinegar Hill [18] (their Figure 3) although none are assigned to *Galaxias*. Twenty-one otoliths referred to two new species of *Galaxias*: *G. bobmcdowalli* Schwarzhans 2012 and *G. parvirostris* Schwarzhans 2012 were described from two stratigraphic horizons about 1.5 m apart [18] (Figure 3, Table 1). *G. parvirostris* is also present (single specimen) at the Manuherikia River site.

#### 3.2.4. Lauder, Central Otago (G41/f9508), Early Miocene, 19–16 Ma

Three otoliths of a new species of *Galaxias*, *G. tabidus* Schwarzhans 2012 were collected from a thin shell bed at a site near Lauder [18]. According to Schwarzhans et al. [18], the otolith morphology resembles that of the extant species, *G. fasciatus* Gray 1842.

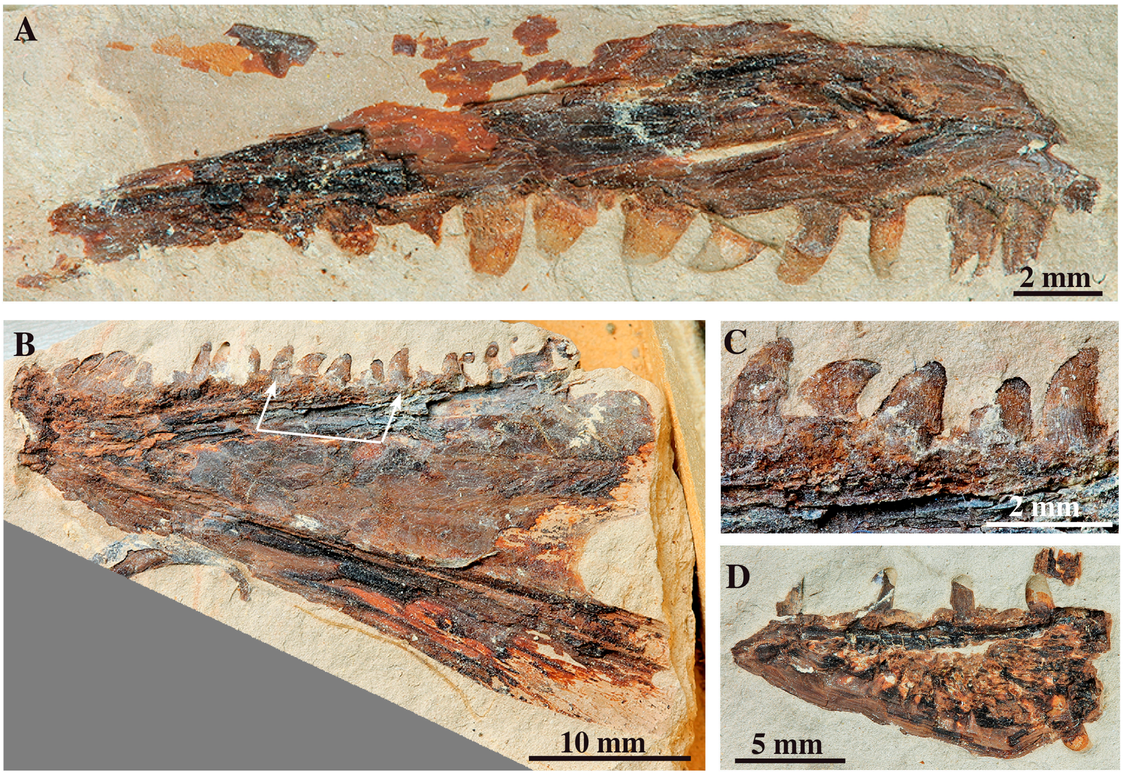

**Figure 4.** Bannockburn Formation, Lake Manuherikia, early Miocene. (**A**–**D**), Bannockburn Inlet, *Galaxias* n. sp. 'Bannockburn Inlet'. (**A**), Premaxilla (OU22617); (**B**), Fragment of dentary (OU22665); (**C**), Close-up of B, showing uniserial, stout, bluntly-pointed, curved teeth (OU22664); (**D**), Fragment of dentary (OU22664).

### 3.3. *Hindon Maar (I44/f0392) Middle Miocene, c. 14 Ma*

Articulated, compressed fish fossils are relatively common in carbonaceous mudstone and diatomite at the Hindon Maar *Konservat-Lagerstätte* [29] (Table 1) sometimes preserved with soft tissue such as skin and eyes. The eyes appear as dark black spots and the body outline and mouthparts are traced as a black shadow around the skeleton (Figure 5A,E). The bones exhibit various degrees of pyritization from none to completely pyritized and in some cases exhibit signs of decalcification (Figure 5A–C). No otoliths have been observed. Notable at this site is the exquisite preservation of highly-mineralized acrodin tooth caps [39], several detached (Figure 5D). Adult specimens reaching up to 180 mm body length, juveniles and c. 40 mm long larvae of *Galaxias* are present (Figure 5F), confirming that these fish were lake-locked and non-diadromous, completing their life cycle within the lake. As for Foulden Maar (above), the Hindon Maar from which these fossils were recovered was a small (c. 1 km diameter) and isolated inland lake, with *Galaxias* dominating and only one other type of fish (the freshwater eel *Anguilla*) found to date.

### 3.4. *Frasers Gully, Kaikorai Valley, Dunedin (I44/f0145) Middle Miocene, 13–11 Ma*

Small articulated and compressed galaxiids (Figure 6) are relatively common in the laminated tuffaceous diatomite exposed in the banks of Frasers Creek [25,32] where they occur with an abundance of plant fossils, mainly leaves but also fruits and seeds. The section at Frasers Gully (Table 1) is exposed intermittently in the bed and sides of the small creek over a distance of a few hundred metres (Benson unpublished MS) [32] (reproduced as their Figure 15). The beds include tuffaceous and/or clayey diatomite, carbonaceous lenses, pebbly sandstone, tuffaceous sandstone and volcaniclastic conglomerates [32]. The base of the Kaikorai Leaf Beds is not exposed, but Grange [40] gives a thickness of 80 feet (c. 25 m) of diatomite from drill-hole data. It is likely that the Kaikorai Leaf Beds infill a small maar crater although geophysical investigations and drilling are needed to confirm this.

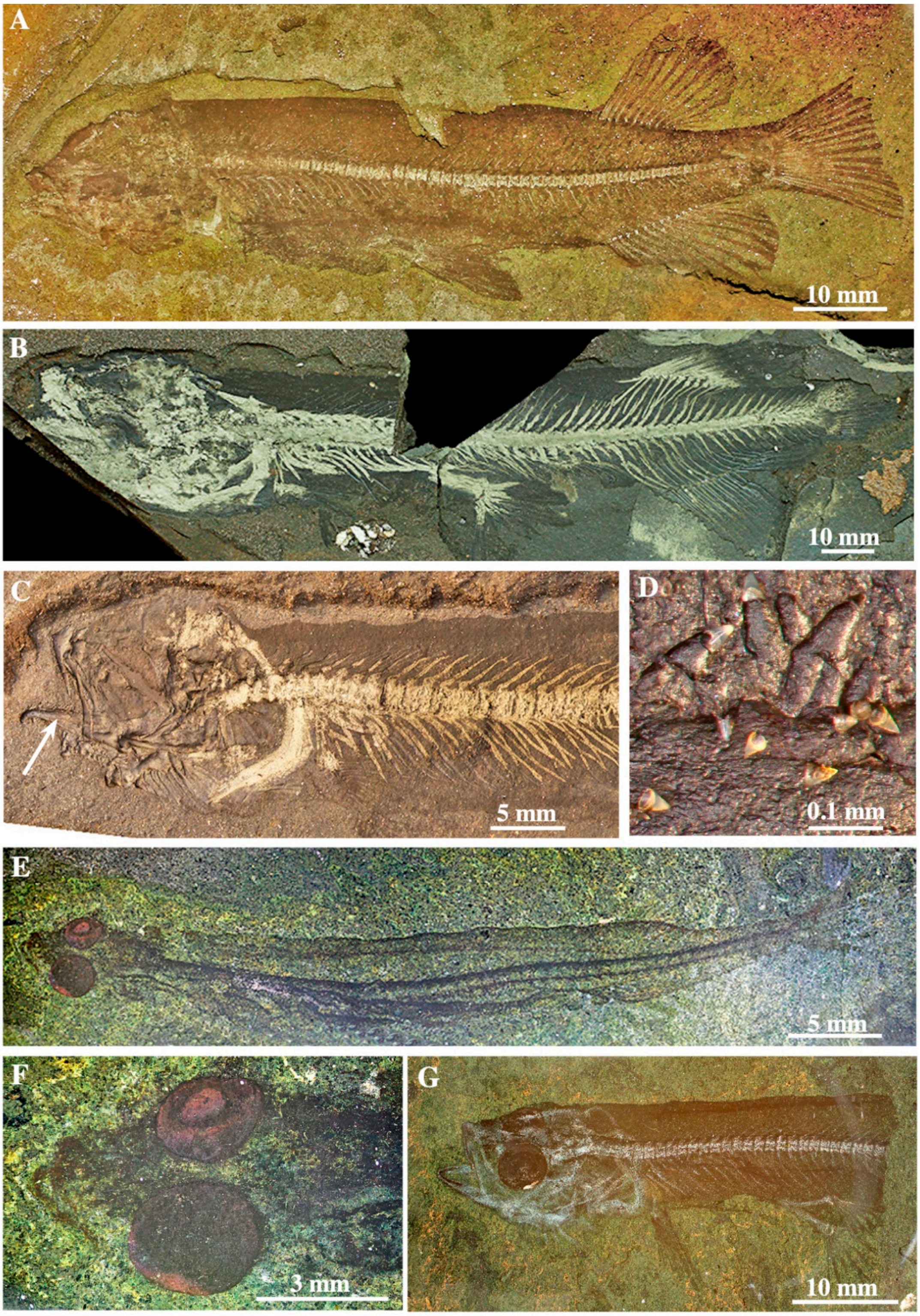

**Figure 5.** Hindon Maar, middle Miocene, *Galaxias* n. sp. 'Hindon'. (**A**), Articulated adult with soft-tissue preservation (OU22881); (**B**), Articulated adult with soft-tissue preservation and pyritized skeleton (OU22840); (**C**), Articulated adult with partly pyritized skeleton and cranial elements (OU22872); (**D**), Close-up of C, showing stout, conical, teeth with detached acrodin caps; (**E**), *Galaxias* larva, fins and

skeleton not yet developed (OU22850); **F**, Close-up of E, showing preservation of large eyes and mouthparts. **G**, Juvenile specimen with cranial osteology, eyes and skin pattern preserved (OU22846). ((**E**–**G**) photographed under ethanol).

### 3.5. *Kilmog Hill (I44/f015) Middle Miocene, 13–11 Ma*

Ten small articulated compressed specimens (Figure 7) were collected from a finely laminated diatomite at a site that is no longer exposed in a rotated slump block on Kilmog Hill, 25 km north of Dunedin (Table 1). The c. 20-cm thick bed of fish-bearing diatomite occurs in the upper part of a 12-m thick sequence of non-marine lapilli tuff beds of the Dunedin Volcanic Group [32] (their Figure 7). The diatomite probably formed in a small, localized pond that formed in between episodes of volcanic activity in a near-shore volcanic environment.

## 4. Systematic Paleontology

Class Osteichthyes Huxley, 1880
Subclass Actinopterygii Klein, 1885
Order Galaxiiformes
Suborder Galaxioidei Berg, 1937
Family Galaxiidae Bonaparte, 1832
*Galaxias* Cuvier, 1816
Type species: *Galaxias fasciatus* Gray, 1842

### 4.1. *Assignment of the Fossils to Galaxias*

The assignment of fossils to *Galaxias* is drawn from absence of scales, comparative morphology, freshwater habitat and their Southern Hemisphere location. The posteriorly-placed single dorsal fin is particularly characteristic of the group. Fossil otoliths are identified as belonging to *Galaxias* on the basis of the following combination of characters: otolith outline triangular or ellipsoidal-triangular with inferior rostral and posterior tips; sulcus narrow, long with a short, slightly widened and anteriorly open rostrum and a narrower, longer cauda that is slightly upward oriented and can show a weakly flexed tip. We present a synopsis of the eight formally named species and several possible new species:

### 4.2. *Macrofossils*

#### 4.2.1. *Galaxias kaikorai* Whitley 1956 (Figure 6A–E)

Diagnosis: Galaxiid fish with relatively slender form with posterior dorsal fin origin distinctly more anterior than anal fin origin, abdominal pelvic fins, vertebral count in excess of 50, caudal neural and haemal spines laterally flattened, caudal fin truncate with sharply angled or only slightly rounded fin tips, 262 mm estimated maximum total length. No otoliths preserved.

Holotype: OU6330, 6331, Geology Museum, University of Otago.

Age: middle Miocene, 13–11 Ma.

Material included: NM6162/1, NM6162/2 (Oliver 1936); OU6330, OU6331 (Holotype, part and counterpart); OU22473a,b, OU22474, OU22475a,b, OU22476, OU22477, OU22478, OU22479, OU22480.

Remarks: A full description and illustration of the holotype is given in Stokell [24]. Further comments on individual specimens from the type locality were made in Lee et al. [14] (p. 130). The total body lengths of three of the fossils were estimated by McDowall [16] as 173–222 mm, 146–203 mm and 176–262 mm using body proportions of two living taxa (*G. brevipinnis* and *G. vulgaris*).

McDowall [16] suggested that *G. kaikorai* could not be distinguished on the basis of morphology from the living *G. brevipinnis.* However, a re-evaluation of the holotype and topotypes, coupled with the realization that these fossils were Miocene in age, rather than Pliocene, led to the decision to reinstate the name *Galaxias kaikorai* [14] for these 13–11 Ma lacustrine fish.

Nearest modern taxon: *G. brevipinnis* [16].

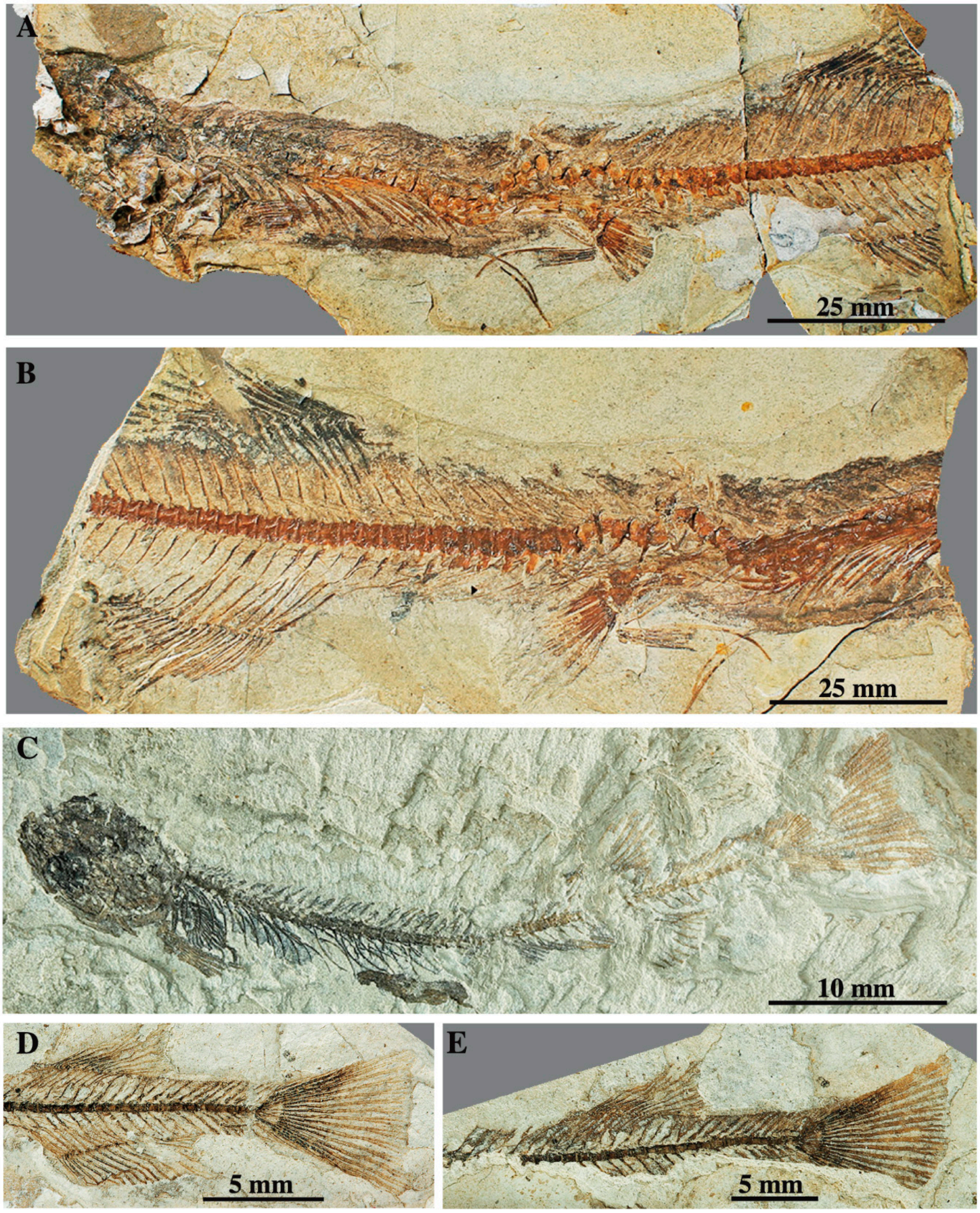

**Figure 6.** Frasers Gully, Kaikorai Leaf Beds, middle Miocene. *Galaxias kaikorai* Whitley 1956. (**A**,**B**), Part and counterpart of holotype (part OU6330, counterpart OU6331); (**C**), Articulated, complete adult specimen (OU22478); (**D**,**E**), Partially preserved fish (OU22477.2, OU22477.1).

#### 4.2.2. *Galaxias effusus* Lee, McDowall and Lindqvist 2007 (Figures 2 and 3)

Diagnosis: Galaxiid fish with posterior dorsal fin origin nearly above anal fin origin, abdominal pelvic fins, vertebral count of perhaps 45–46, complete series of supraneurals back to dorsal fin origin and epineurals back to below dorsal fin, caudal neural and haemal spines laterally flattened;

unpaired fins, dorsal, anal, and caudal, distinctively large and rounded. 140 mm total length. No otoliths preserved.

Holotype: OU22650, Geology Museum, University of Otago.

Age: earliest Miocene, 23 Ma.

Type locality: Foulden Hills Diatomite, Foulden Maar, near Middlemarch, Otago.

Material included: OU7103, OU7104 (Figures 1 and 2 in [27]); OU22644a,b, OU22645, OU22646 [14] (pp. 129–130); about 100 additional specimens in OU collections.

Remarks: A full description and illustration of the holotype is given in Lee et al. ([14], pp. 115–117, Figure 4; and five further specimens are described on pp. 129–130). The total body length of most other skeletons from this site (c. 50 specimens measured) is <80 mm, i.e., they are distinctively smaller than *G. effusus*. Further study is needed to confirm whether this indicates the presence of a second, smaller species of *Galaxias* or a high mortality rate of sub-adult individuals.

Nearest modern taxon: *G. argenteus* [14].

#### 4.2.3. *Galaxias* n. sp. 'Hindon' (Figure 5)

Galaxiid adults, juveniles and larvae of slender, elongate specimens with 160 mm maximum total length. No otoliths preserved. These specimens have not yet been formally described but are likely to represent a separate species as they occupied a very small, isolated, land-locked paleolake.

Age: c. 14 Ma

Remarks: About 20 specimens have been collected from Hindon Maar. They differ in morphology from the two species described from Kilmog Hill and Frasers Gully but further study is needed for them to be formally described. They are eight million years younger than *G. effusus* from Foulden Maar and slightly older than *G. kaikorai.*

Material included: OU22839–OU22885.

#### 4.2.4. *Galaxias* n. sp. 'Kilmog Hill' (Figure 7)

Small galaxiid adults preserved as part and counterpart, examined and described by Bob McDowall [14] (their Appendix A). Slender-bodied fish with 44–55 mm total body length and the general body morphology of *Galaxias kaikorai*. No otoliths preserved. These specimens have not yet been formally described.

Age: 13–11 Ma

Remarks: About 10 specimens have been collected from the Kilmog Hill site. They resemble *G. kaikorai* but may represent a separate species.

Material included: OU22654, OU22655, OU22657, OU22658, OU22659, OU22481, OU22667 [14] (p. 130), OU22485, OU22487, OU22488.

#### 4.2.5. *Galaxias* n. sp. 'Bannockburn Inlet' (Figure 4)

Large, slender galaxiid lacking head. Estimated length 383 mm.

Age: early Miocene, 19–16 Ma.

Locality: Bannockburn Inlet

Material: SL812, Department of Botany, University of Queensland (Figure 1 in [17]).

Remarks: Other isolated cranial elements from the same locality (Figure 4) might represent the same species but more articulated material is needed to confirm this association.

### *4.3. Otolith-Based Species*

#### 4.3.1. *Galaxias angustiventris* Schwarzhans 2012 (Figure 8A)

Diagnosis: Otolith with oval outline with regularly rounded dorsal and posterior rims. Ventral rim shallow. Rostrum short, sharp; excisura sharp, moderately wide. Ostium narrow; cauda terminating far from posterior tip of otolith. Ventral field on inner face narrow with distinct furrows below sulcus and close to rim of otolith. Size up to 4.5 mm.

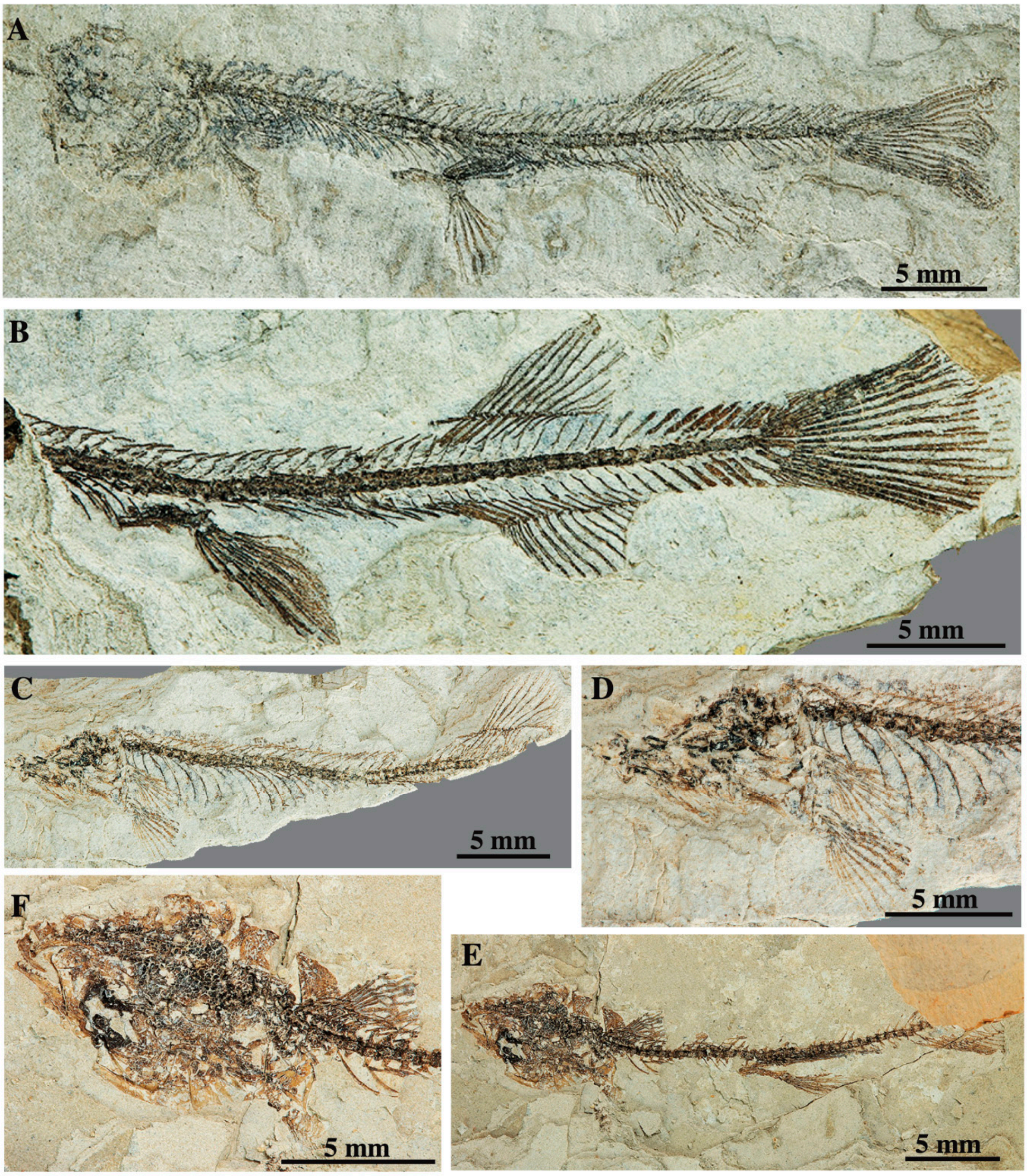

**Figure 7.** Kilmog Hill, middle Miocene. *Galaxias* n. sp. 'Kilmog Hill'. (**A**), Complete small adult (OU22481); (**B**), Partial specimen showing fin morphology (OU22654); (**C**), Partial adult (OU22658); (**D**), Close-up of C; (**E**), Adult fish with large head (OU22659); (**F**), Close-up of E showing teeth and eye partly preserved.

Holotype: NMNZ S.52707 (Figure 4F in [18]).
Age: early Miocene, 19–16 Ma.
Type locality: Home Hills Station, Manuherikia River near St Bathans, Otago.

Remarks: Schwarzhans et al. [18] (p. 326) noted that "none of the otoliths known from living species of the genus show a similarly-short cauda" and suggested that this species and *G. brevicauda*

Schwarzhans 2012 might belong to an extinct genus within Galaxiidae. However, otoliths are undescribed for some lineages of galaxiids [5].

#### 4.3.2. *Galaxias brevicauda* Schwarzhans 2012 (Figure 8B)

Diagnosis: Otolith with triangular outline with obtuse mid-dorsal angle, marked rostrum and similarly marked and inferior posterior angle. Ventral rim shallow. Rostrum massive, sharp; excisura sharp, narrow. Ostium narrow; cauda terminating far from posterior tip of otolith. Ventral field on inner face narrow with distinct furrow below sulcus but not near ventral rim of otolith. Size up to 3.5 mm.

Holotype: NMNZ S.52709 (Figure 4I in [18]).

Age: early Miocene, 19–16 Ma.

Type locality: Home Hills Station, Manuherikia River near St Bathans, Otago.

Remarks: Possibly from an extinct galaxiid, as for *G. angustiventris* (see above).

#### 4.3.3. *Galaxias bobmcdowalli* Schwarzhans 2012 (Figure 8C)

Diagnosis: Triangular outline with high mid-dorsal angle, sharp and long rostrum and less sharp inferior posterior angle. Ventral rim very shallow. Excisura moderate; often excisura-like incision of posterior rim at level of caudal tip. Ostium short; cauda longer than ostium, almost reaching posterior tip of otolith. Ventral field on inner face moderately wide, with distinct ventral furrow near ventral rim of otolith, often joined to it mid-ventrally. Size up to 4 mm.

Holotype: NMNZ S.52711 (Figure 5A in [18]).

Age: early Miocene, 19–16 Ma.

Type locality: Home Hills Station, Manuherikia River near St Bathans, Otago.

Remarks: This is the most common and widely distributed type of galaxiid otolith in the Lake Manuherikia fauna (202 of 230 specimens are assigned to *G. bobmcdowalli*) and they occur at five of the seven galaxiid-bearing sites. *Galaxias bobmcdowalli* and *G. papilionis* represent a morphological pattern characterized by a distinct triangular outline and a long cauda that reaches very close to the distinctly indented posterior rim of the otolith or sometimes even appears to be opening to it. There are no extant morphologies observed in galaxiid otoliths with such a distinctive development of the caudal tip and the posterior rim.

#### 4.3.4. *Galaxias papilionis* Schwarzhans 2012 (Figure 8D)

Diagnosis: Otolith with high-bodied outline with expanded dorsal and ventral rims. Inner face almost flat. Rostrum short and thin. Excisura broad; posterior rim with deep and wide excisura-like incision joining up with the caudal tip. Ostium narrow, short; cauda longer than ostium, opening towards posterior rim of otolith. Ventral field on inner face wide, without distinct ventral furrow. Size up to 3 mm.

Holotype: NMNZ S.52717 (Figure 6A in [18]).

Age: early Miocene, 19–16 Ma.

Type locality: Home Hills Station, Manuherikia River near St Bathans, Otago.

Remarks: This species is based on the holotype and 11 paratypes. It is remarkable for the most extreme incision of the posterior rim of the otolith and appears to be related to *G. bobmcdowalli* (see above).

#### 4.3.5. *Galaxias parvirostris* Schwarzhans 2012 (Figure 8E)

Diagnosis: Thick otoliths with compressed, rounded outline with very short rostrum. Inner face convex. Excisura small. Posterior rim rounded. Ostium narrow, short; cauda longer than ostium, terminating close to posterior rim of otolith. Ventral field on inner face wide, with indistinct ventral furrow. Size up to 2.5 mm.

Holotype: NMNZ S.52720 (Figure 6H in [18]).

Age: early Miocene, 19–16 Ma.

Type horizon: Vinegar Hill, near St Bathans, Otago.

Remarks: A rare species: four specimens known from Vinegar Hill and one from Home Hills Station. *G. parvirostris* differs from all other otolith-based species found at Lake Manuherikia by the thick appearance and the rounded outline with a very short rostrum.

#### 4.3.6. *Galaxias tabidus* Schwarzhans 2012 (Figure 8F)

Diagnosis: Thin otoliths with moderately compressed outline with short rostrum. Ventral rim with angular indentations anteriorly below rostrum and posteriorly below posterior tip. Inner face almost flat. No excisura; instead angular indentation of anterior rim above ostium. Ostium narrow, short; cauda longer than ostium, terminating close to posterior rim of otolith. Ventral field on inner face wide, with indistinct ventral furrow far from ventral rim of otolith. Size up to 2.5 mm.

Holotype: NMNZ S.52723 (Figure 6H in [18]).

Age: early to middle Miocene

Type locality: West of Lauder, Otago.

Remarks: Restricted to a 10-mm thick horizon in which tiny hydrobiid molluscs are found.

Nearest modern taxon: *G. fasciatus* [18].

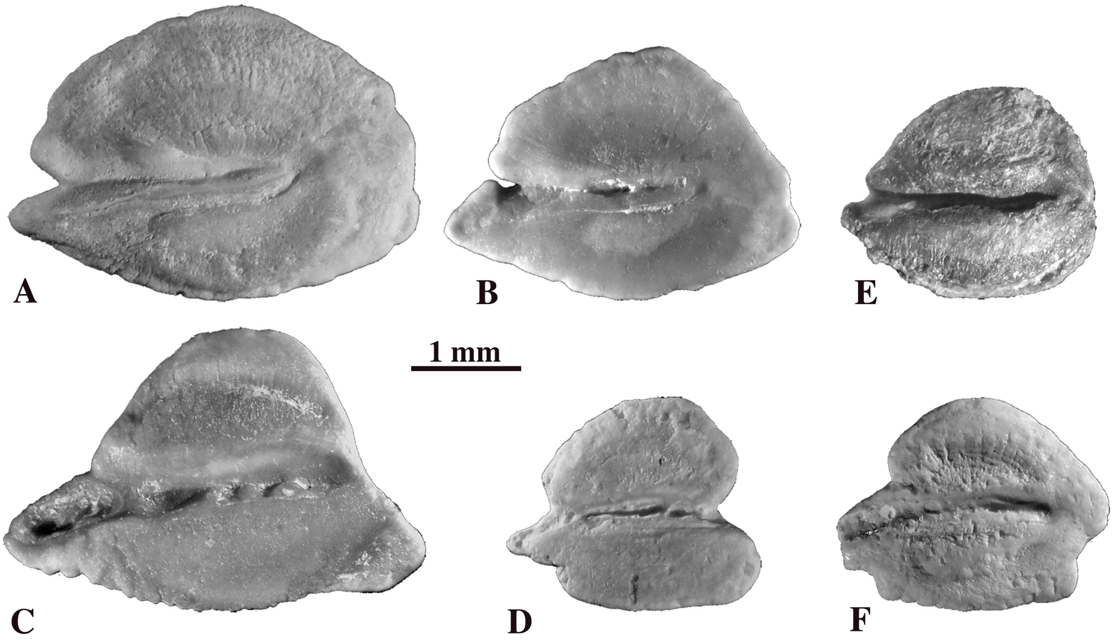

**Figure 8.** Bannockburn Formation, Lake Manuherikia, early Miocene, otolith-based *Galaxias* species. (**A–D**), Manuherikia River; (**A**), *G. angustiventris* Schwarzhans 2012, inner face of otolith of holotype (NMNZ S.52707); (**B**), *G. brevicauda* Schwarzhans 2012, inner face of otolith of holotype (NMNZ S.52709); (**C**), *G. bobmcdowalli* Schwarzhans 2012, inner face of otolith of holotype, (NMNZ S.52711); (**D**), *G. papilionis* Schwarzhans 2012, inner face of otolith of holotype (NMNZ S.52717); (**E**), Vinegar Hill, *G. parvirostris* Schwarzhans 2012, inner face of otolith of holotype (NMNZ S.52720); (**F**), Lauder, *G. tabidus* Schwarzhans 2012, inner face of otolith of holotype (NMNZ S.52723).

#### 4.3.7. *Galaxias* sp.

Material: Two otoliths figured in Schwarzhans et al. (Figure 6J in [18])

Age: early Miocene, 19–16 Ma.

Locality: Home Hills Station, Manuherikia River near St Bathans, Otago.

Remarks: These are likely to represent a further undescribed species [18].

### *4.4. Coprolites*

All coprolites studied come from Foulden Maar, where they are frequently found in laminated diatomite [28]. Some of these were identified as fecal remains of swimming waterfowl, possibly ducks [33], whereas other coprolites consisting of disarticulated fish (galaxiid) remains indicate the presence of a larger predator or scavenger in the paleolake. Two out of 10 types of coprolite recognized from this site were assigned with some confidence to *Galaxias* [18].

The most common type of coprolite at Foulden Maar is 3–30 mm long, brown to black, ovoid/ovate/elongate/sub-circular in shape, and consists of abundant leaf debris, woody fragments, sponge spicules, arthropod remains and autochthonous (i.e., derived from the maar lake) mineral grains. These are almost certainly galaxiid coprolites, based both on their abundance in the sediment and on the diet of modern *Galaxias* species, which consume a range of terrestrial and aquatic arthropods and would have ingested plant detritus, sponge spicules and mineral grains as they foraged in shallow zones at the lake margin. This is confirmed by stomach content found in situ in one sub-adult *Galaxias* (Figure 3E,F), which has the same composition as the coprolites.

The second most common coprolites include 2–9 mm long fecal strings consisting almost entirely of frustules of pennate diatoms and minor amounts of fine organic detritus (Figure 3H). This type is most likely derived from galaxiid larvae, as in larval stages of some extant *Galaxias* species that are known to feed exclusively on algae before developing other feeding habits during juvenile stages [41].

## **5. Discussion**

### *5.1. Diversity of Miocene Galaxiids*

To date, fossils of eight species of *Galaxias* have been formally described from New Zealand: two species from body fossils (*G. kaikorai*, *G. effusus*) and six from isolated otoliths (*G. angustiventris, G. brevicauda, G. papilionis, G. bobmcdowalli, G. parvirostris, G. tabidus*) [14,18]. We recognize four other informal species based on macrofossil remains (*Galaxias* n. sp. 'Foulden'; *Galaxias* n. sp. 'Hindon', *Galaxias* n. sp. 'Kilmog Hill', *Galaxias* n. sp. 'Bannockburn Inlet') and a probable further otolith-based taxon from Lake Manuherikia [18]. Thus, a minimum of eight, and possibly up to 13 species of *Galaxias* were present in early to late Miocene lakes in southern New Zealand (Table 1).

There is currently no taxonomic overlap between taxa described from either otoliths or from body fossils. A possible exception is the large headless fish described from Bannockburn Inlet [17], which occupied the same shallow water habitats of Lake Manuherikia as the otolith-based taxa. It is unlikely that any of the fossil species from the four, small isolated volcanic lakes are conspecific with the otolith-based taxa from Lake Manuherikia.

The highest diversity (six, possibly seven species) of *Galaxias* has been reported from sediments of Lake Manuherikia [18], indicating that this very large (5600 km$^2$) and long-lived, early Miocene lake system with differentiated shallow lacustrine habitats and with access to the open sea via streams and river systems provided ideal conditions for diverse *Galaxias* to migrate and to thrive [15,18,38]. Habitat differentiation and warmer climate could also contribute to this high diversity, together with the fact that our fossils could be temporally separated by a few million years. By contrast, the diversity within small volcanic lakes was low, with only a single (different) species recorded from each of Foulden Maar, Hindon Maar, Frasers Gully and Kilmog Hill. However, the combined diversity of five species from these small lakes is comparable to that of lake-dwelling *Galaxias* in the extant New Zealand fauna. Although today's lakes do not harbor local endemics, the koaro travels well inland because of its climbing ability, and so has a high propensity to colonize lakes everywhere, including alpine tarns. Long-term land-locking and isolation has led to loss of diadromy and subsequent speciation in river systems. Diverse equivalents of today's pencil and koaro-like stream-resident forms (lineage iii; see Introduction) could have existed in local Miocene catchments, and a different form "captured" by each maar. Such strong local differentiation of *Galaxias* species across river systems in the region is still evident today [4,42,43].

The relatively diverse *Galaxias* fauna documented from comparatively few Miocene lakes sites in southern New Zealand suggests that these fishes may have been remarkably diverse in paleo-environments occupying streams and rivers throughout New Zealand, but rarely preserved in coarse-grained sediments of high energy riverine environments. The paleoclimate in southern New Zealand throughout the early to mid-Miocene was warm temperate to marginally subtropical, unlike the cool temperate conditions prevailing in Otago today [44]. The distribution of modern *Galaxias* extends into subtropical environments, but diversity is greatest at cooler temperatures and higher latitudes [19,20].

### *5.2. Paleolake Ecosystems and Diadromy*

Modern galaxiids in New Zealand occupy rivers, streams and creeks in habitats ranging from bouldery, gravelly and swift-flowing streams to boggy, silty and organic swamps. Three species are commonly found in lakes, and are often land-locked: *G. argenteus*, *G. fasciatus*, *G. brevipinnis.* The latter two, particularly the last (koaro), are noted as strong climbers when young [19,20] and it may be no coincidence that these taxa are the closest morphological matches to three of the fossil species (*G. effusus*, *G. kaikorai* and *G. tabidus*).

All galaxiid fossils (and all other freshwater fossil fish remains) reported from New Zealand to date are from lacustrine environments, where fine-grained sediments deposited in low-energy environments favoured the fossilisation of fish and other biota, in some cases with remarkable preservation of anatomical details such as body outline, skin pattern and eyes (Figures 3 and 5). Otoliths in general are preserved in alkaline clastic environments whereas most of the *Galaxias* body fossils are from biogenic sediments of slightly acidic depositional environments and these preservation differences may also contribute to the absence of taxonomic overlap.

Despite all fossil sites being former lakes, they represent distinctively different lacustrine environments and habitats in which the galaxiid species lived. At Foulden Maar and Hindon Maar, *Galaxias* occupied small (c. 1 km diameter), isolated lakes surrounded by a tephra rim and with deep, stratified water columns and narrow littoral zones at the lake margins. The anoxic bottom water was certainly not suitable for life, meaning that the habitat of *Galaxias effusus* and *Galaxias* n. sp. "Hindon" was restricted to the upper water column and the littoral zones.

Coprolites assigned to *Galaxias* and in situ gut contents with organic debris, arthropod remains, diatoms and mineral grains confirm that larvae, juveniles and adults of these species were foraging in the shallow water zone in the Foulden Maar paleolake and suggest that an ontogenetic shift in diet was already developed in early Miocene galaxiids. From sedimentological investigations [29,35] there is no indication of a connection of the Foulden Maar and Hindon Maar paleolakes to the regional drainage system. In combination with the co-occurring ontogenetic stages (larval to adult) this indicates that the two species at these sites were landlocked. The same may apply to *Galaxias kaikorai* from Frasers Gully, which also inhabited a small maar lake, although sedimentological studies are needed to confirm whether this lake was connected to streams.

At all three sites, *Galaxias* occurs in laminated diatomite that resulted from seasonal or annual algal blooms. It is therefore possible that the low diversity of *Galaxias* (one species at each site) and other fish (none to two species) in these maar lakes reflects fluctuating water quality and oxygen levels throughout the year, possibly in combination with poor accessibility to the lakes. Access to the isolated paleolakes could have been achieved by the fish climbing from adjacent waterways during occasional flood events or alternatively they may have been introduced by birds.

By contrast, the small *Galaxias* n. sp. 'Kilmog Hill' occupied a small and short-lived, possibly lava-dammed pond or small lake, in an environment characterized by volcanic disturbance and likely steep topographic gradients. This species may have had access to streams that flowed down the slopes of the Dunedin Volcano and was most likely diadromous, as no larvae or juvenile individuals have been discovered.

Ecosystems of the six (or seven) *Galaxias* species in Lake Manuherikia differed considerably from the species in maar lakes in being situated in a vast, regional lake system that was in existence for hundreds of thousands, possibly up to several million years, but changed in extent and depth over time in response to shifting base levels [15,18,38]. The sediments in which the galaxiids are preserved document differentiated shallow water and littoral habitats, which supported a relatively high diversity of galaxiids and representatives of at least three other families of fish: two species of Retropinnidae [18], five species of Eleotridae [18,45] and a species of Percichthyidae (a family no longer present in New Zealand) [46]. To date, no galaxiid fossils have been found in 'oil shales' corresponding to deeper water conditions in parts of the lake system. The galaxiids and other fish of the Lake Manuherikia ecosystem may have exhibited diadromous behaviour, with associated fluvial and floodplain sediments indicating outlets to the sea to the south and east [38]. It is interesting to note that some of the species (*Galaxias angustiventris*, *G. brevicauda* and the most abundant *G. bobmcdowalli*) are primarily known from relatively large otoliths (3–4.5 mm). These must have represented fish specimens in the range from 25–35 cm standard length or more when compared to extant otolith versus fish sizes in the genus (deduced from [47] and unpublished data of WWS). This is near the high end of sizes observed in extant galaxiid fishes, for instance the giant *G. argenteus* which can achieve sizes up to 40 cm. The large size of fishes occurring in Lake Manuherikia is also corroborated by exceptionally large eleotrid (Gobiiformes) otoliths of the fossil genus *Mataichthys*. *Galaxias* (and eleotrid) otoliths retrieved from the other localities (Vinegar Hill and Lauder) are much smaller, rarely exceeding 2.5 mm in length. Future geochemical study of the abundant otoliths may provide information on the time spent at sea by the galaxiid larvae.

## 6. Conclusions

At least eight to thirteen species of *Galaxias* have been discovered in early to late Miocene lacustrine sediments in southern New Zealand. These taxa are based on both isolated otoliths and articulated specimens, some of which retain soft tissue such as skin, eyes and gut contents. The oldest record of *Galaxias* is *G. effusus* from the earliest Miocene (23 Ma) Foulden Maar fossil-Lagerstätte.

The specimens from the Otago paleolakes represent the world's only *Galaxias* fossils known to date, despite the wide modern Southern Hemisphere (Gondwanan) distribution of the group. The relatively high diversity of *Galaxias* in Miocene New Zealand likely reflects speciation within extensive lake ecosystems and between more insular maar lakes, including land-locked non-diadromous taxa and migratory diadromous taxa. This diversity is in keeping with the general importance of ecological and life-history switches as drivers of speciation in freshwater fishes [48].

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