

Fish remains, mostly otoliths, from the non-marine early Miocene of Otago, New Zealand

WERNER SCHWARZHANS, R. PAUL SCOFIELD, ALAN J.D. TENNYSON,
JENNIFER P. WORTHY, and TREVOR H. WORTHY



Schwarzahns, W., Scofield, R.P., Tennyson, A.J.D., Worthy, J.P., and Worthy, T.H. 2012. Fish remains, mostly otoliths, from the non-marine early Miocene of Otago, New Zealand. *Acta Palaeontologica Polonica* 57 (2): 319–350.

Fish remains described from the early Miocene lacustrine Bannockburn Formation of Central Otago, New Zealand, consist of several thousand otoliths and one skeleton plus another disintegrated skull. One species, *Mataichthys bictenatus* Schwarzahns, Scofield, Tennyson, and T. Worthy gen. et sp. nov., an eleotrid, is established on a skeleton with otoliths in situ. The soft embedding rock and delicate, three-dimensionally preserved fish bones were studied by CT-scanning technology rather than physical preparation, except where needed to extract the otolith. Fourteen species of fishes are described, 12 new to science and two in open nomenclature, representing the families Galaxiidae (*Galaxias angustiventris*, *G. bobmcdownalli*, *G. brevicauda*, *G. papilionis*, *G. parvirostris*, *G. tabidus*), Retropinnidae (*Prototroctes modestus*, *P. vertex*), and Eleotridae (*Mataichthys bictenatus*, *M. procerus*, *M. rhinoceros*, *M. taurinus*). These findings prove that most of the current endemic New Zealand/southern Australia freshwater fish fauna was firmly established in New Zealand as early as 19–16 Ma ago. Most fish species indicate the presence of large fishes, in some cases larger than Recent species of related taxa, for instance in the eleotrid genus *Mataichthys* when compared to the extant *Gobiomorphus*. The finding of a few otoliths from marine fishes corroborates the age determination of the Bannockburn Formation as the Altonian stage of the New Zealand marine Tertiary stratigraphy.

Key words: Pisces, Eleotridae, Galaxiidae, Retropinnidae, *Mataichthys*, otoliths, freshwater, Miocene, New Zealand.

Werner Schwarzahns [wwschwarz@aol.com], Ahrensburger Weg 103, 22359 Hamburg, Germany;

R. Paul Scofield [pscofield@canterburymuseum.com], Canterbury Museum, Rolleston Avenue, Christchurch, New Zealand 8013;

Alan J.D. Tennyson [alant@tepapa.govt.nz], Museum of New Zealand Te Papa Tongarewa, P.O. Box 467, Wellington, New Zealand;

Jennifer P. Worthy [jennykiwi@aapt.net.au] and Trevor H. Worthy [trevor.worthy@adelaide.edu.au], School of Biological, Earth and Environmental Sciences, University of New South Wales, New South Wales 2052, Australia; current address: School of Earth and Environmental Sciences, University of Adelaide, South Australia 5005, Australia.

Received 23 December 2010, accepted 24 March 2011, available online 31 March 2011.

Introduction

New Zealand is the emergent part of a continental fragment termed Zealandia that is separated from Australia to the west by at least 1600 km of ocean. The Tertiary fossil record of the terrestrial and freshwater biota of Zealandia is depauperate, with the first and only window to the terrestrial biota being afforded by the St Bathans Fauna from late early–middle Miocene Manuherikia Group in Central Otago, New Zealand (Fig. 1; Worthy et al. 2007). Vertebrates were first noticed in these strata by Douglas et al. (1981) and the fauna is now known to contain a diverse terrestrial biota that includes crocodylians, lizards, more than 35 taxa of birds, and mammals (Molnar and Pole 1997; Worthy et al. 2006, 2007, 2008, 2009, 2010a, b; Hand et al. 2007; Jones et al. 2009; Lee et al. 2009; Scofield et al. 2010; Tennyson et al. 2010). Although the St Bathans Fauna was

deposited in a lacustrine setting, work to date has concentrated on the terrestrial fauna. Among the vertebrates, the fossil assemblage is dominated by fish remains, including numerous disarticulated bones and otoliths, mostly sagittae. Identification of the diversity and identity of these fishes has significance for understanding the overall palaeoecological setting in which the St Bathans Fauna was deposited. In this paper, a first attempt at this is made by surveying the diversity of otoliths in the fauna and an articulated otolith-bearing fish is described.

Institutional abbreviations.—AMS, Australian Museum, Sydney, New South Wales, Australia; BMNH, Natural History Museum, London, United Kingdom; NIWA, National Institute of Water and Atmosphere, New Zealand; NMNZ, Museum of New Zealand Te Papa Tongarewa (formerly National Museum of New Zealand), Wellington, New Zealand; SAMA, South Australian Museum, Adelaide, South Australia.

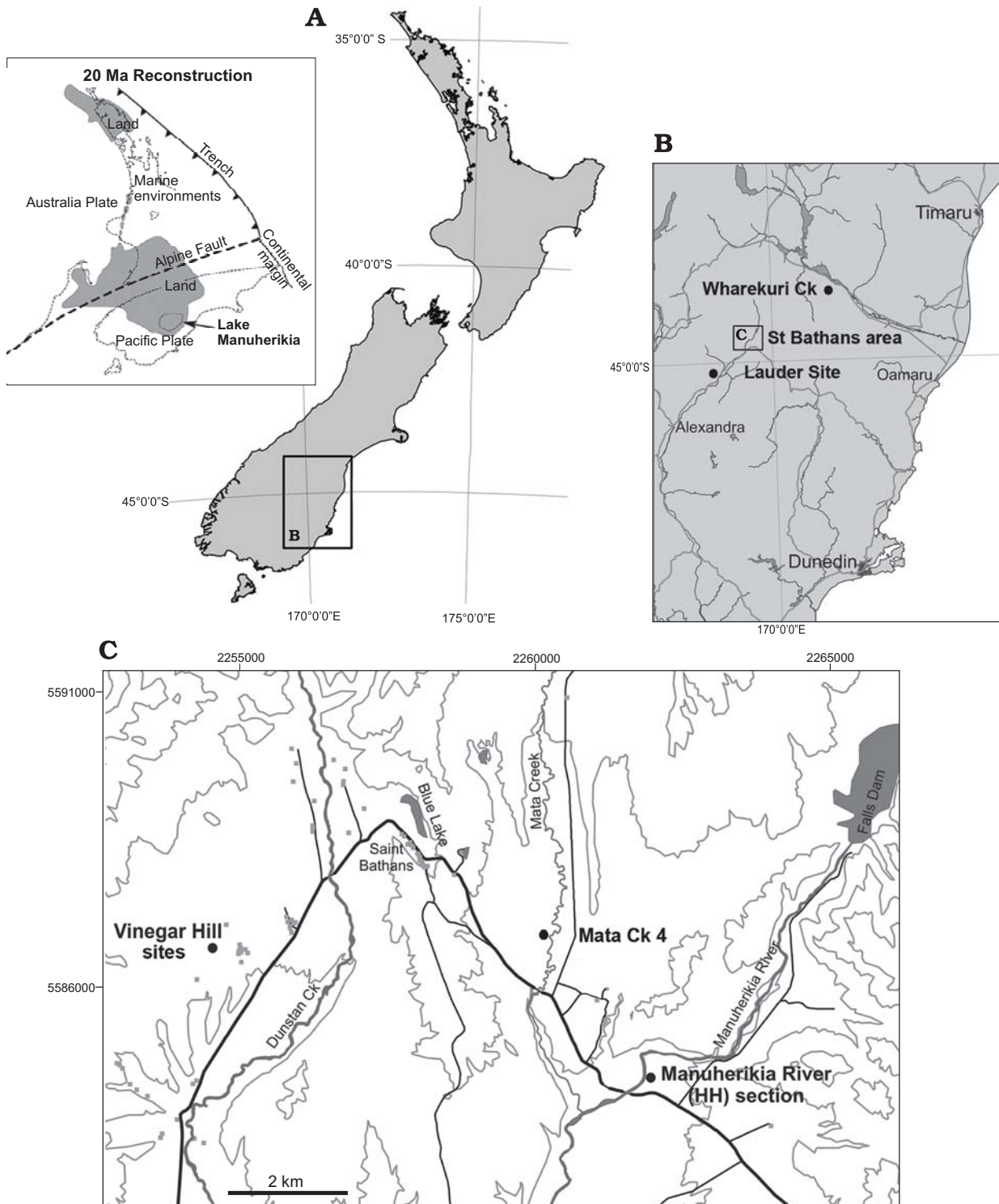


Fig. 1. Location maps with a palaeogeographic reconstruction of Zealandia in the early Miocene to show the location of Lake Manuherikia. **A.** Location map of New Zealand. **B.** Location of Lauder Site and the St Bathans area in Otago with the location sites indicated. **C.** Detailed map of the St Bathans area. The location map is derived from Worthy et al. (2007) and the palaeogeographic reconstruction is modified from that given for 20 Ma by Bunce et al. (2009).

lia, Australia; SMF, Senckenberg Museum, Frankfurt/Main, Germany; WAM, Western Australian Museum, Perth, West Australia, Australia; ZMH, Zoological Museum, Hamburg, Germany; ZMUC, Zoological Museum, Copenhagen, Denmark.

Other abbreviations.—CaL, cauda length; OH, otolith height; OL, otolith length; OsL, ostium length; OT, otolith thickness; SL, standard length, SuL, sulcus length; TL, total length. Roman numbers in fin ray counts refer to spinous rays, Arabic numbers to soft rays.

Geological setting

Sedimentology

The Lake Manuherikia freshwater fish fossils reported here derive from the Miocene Bannockburn Formation sediments deposited into the palaeolake Manuherikia. This lake covered an area of about 5600 km² (Douglas 1986), which is more than the combined area of all modern New Zealand lakes, and was surrounded by a broad (extensive) fluvial plain with major channels and interchannel flood-basins with deltas formed at major points of sediment entry to the lake. The stratigraphy and a palaeogeographical reconstruction of the Manuherikia Group fluvial Dunstan Formation and overlying lacustrine Bannockburn Formation was described by Douglas (1986) and Lee et al. (2009). Up to 700 m of sediments accumulated in and around this lake basin, which, although fairly shallow, must have been slowly subsiding in order to allow the accumulation of such a thickness. The basal Dunstan Formation sediments are a succession of alluvial conglomerate, sandstone, mudstone, and lignite interpreted to be a river to swamp succession. Overlying the top-most lignite-bearing part of Dunstan Formation, the lower 10 m of the Bannockburn Formation consists of fine silty sandstone, green claystone, calcareous mudstone and marl (Lee et al. 2009; Fig. 2). Fine-grained sandstone e.g., beds HH1d, HH1a, HH1b, locally include a basal conglomerate of quartz granules (<15 mm), rip-up clasts (angular marl pebbles) up to 8 cm in diameter, and fossil vertebrates, and they preserve ripple structures. Biogenic carbonate, thought to have been precipitated during the photosynthetic activities of cyanobacteria, coats rip-up clasts and fossils in these conglomerates. Bivalves (Hyriidae), ostracods, tubular microbial carbonate and carbonate stromatolitic fragments are locally present. Distinctive fine-grained cream to pale greenish-grey marl beds and calcareous mudstone up to 40 cm thick contain 1–3 mm diameter branching rootlet casts, infilled with green clay. Marl beds intensely disrupted by plant root, animal burrowing, or desiccation brecciation are preserved as weakly cemented nodules enclosed by mottled greenish grey clay. Interbedded green claystone containing abundant root traces probably represent shallow lake deposition within the zone of nearshore plant growth. A laterally extensive bed at 6.7 m (Fig. 2) comprises a single layer of paired hyriid valves in about 5 mm of fine sand interbedded in marl, that probably represents a death assemblage following aerial exposure and receding water during a drought event. These marl and sandstone interbeds indicate a rapidly oscillating shoreline. The sandstone with their basal conglomerate are interpreted as littoral current and/or storm wave-sorted deposits, whose initial input into the lake resulted from a flood event ripping up desiccated shoreline muds and mixing these and terrestrial vertebrate fossils with the lacustrine organisms.

The upper part of the lacustrine association (10–25 m; Fig. 2) is dominated by greyish green mudstone and lami-

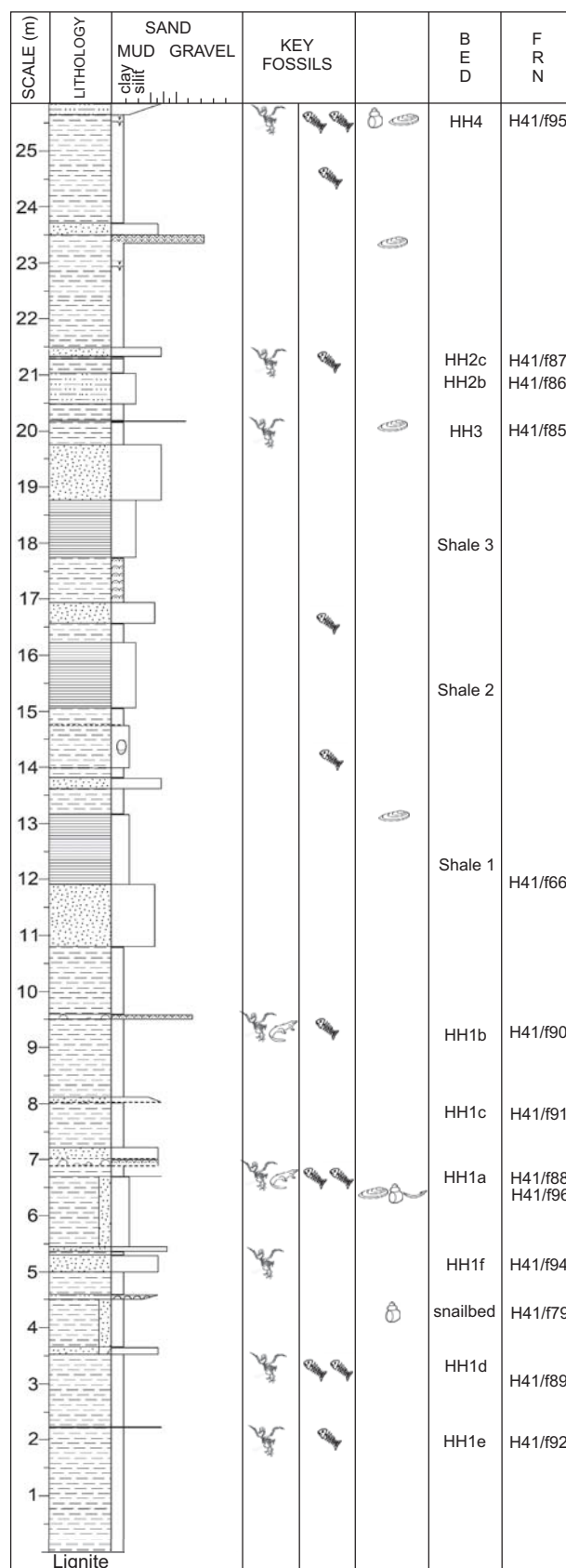


Fig. 2. Stratigraphic section showing the basal part of the Bannockburn Formation at the Manuherikia River location, New Zealand. FRN, Fossil Record Number in the archival Fossil Record File of the Geological Society of New Zealand.

nated shale with subordinate silty mudstone, and shelly and microbial carbonate beds. Blocky-weathering green mudstone contains abundant 1–2 mm wide vertical rootlet-like structures. Hyriid bivalve moulds occur in the shale, and rare horizons of hyriid shells or fragments are present. The green mudstone supported abundant aquatic plants and is interpreted as a nearshore facies, as in a palustrine association (Lee et al. 2009). Occasional lenses of thin shelly lags (HH3 and HH4) contain fish and bird bones, together with molluscs and algal carbonate fragments. Local concentrations of carbonate sand contain ostracods and gastropods, including hydrobiids and planorbids (?*Glyptophysa* sp.). Thin strata of stromatolites, e.g., at 23.5 m on Fig. 2, associated with carbonate sands and composed of laminated microcrystalline calcite, are comparable with various forms described from other Manuherikia Valley localities (Lindqvist 1994). Laminated shale, very dark grey—greenish grey when freshly exposed, contain fine organic matter and abundant mica flakes. Scattered fish vertebrae, spines, and scales are commonly preserved, as are compressed hyriid bivalve moulds. The shale beds, typically grading upward into green mudstone, were probably deposited in the deeper lacustrine profundal zone, perhaps during times of higher lake level and increased input of mica-rich sediment from tributary rivers.

Palynological evidence constrains the age of the Bannockburn Formation to the local Altonian Stage, or 19–16 Ma, which corresponds to the upper Burdigalian Age (Mildenhall 1989; Mildenhall and Pocknall 1989; Pole and Douglas 1998; Pole et al. 2003; Cooper 2004). Palynological data, including an increase in charcoal frequency and a rise to prominence of casuarinas (Casuarinaceae) pollen with associated eucalypts (Myrtaceae) and palms (Arecaceae), suggest the Bannockburn Formation was deposited in a lake surrounded in a seasonally drier woodland environment than that in which the underlying Dunstan Formation was deposited, leading to it being assigned to the Casuarinaceae biozone (Pole and Douglas 1998: fig. 6; Pole et al. 2003; Lee et al. 2009). Several pollen taxa of *Nothofagus* (mainly *Fuscospora* and *Brassospora*), podocarps (Podocarpaceae), and araucarias (Araucariaceae), indicate substantial complexity to the vegetation with nearby tall forests. This fossil flora indicates that the area was warmer than it is today, possibly with a climate similar to northern New Zealand. A markedly warmer climate is also indicated by the occurrence of a mekosuchine crocodile. Molnar and Pole (1997) note that the southernmost crocodiliform alive today, *Caiman yacare*, ranges as far as 35° south in Argentina. The abundance of desiccation features and evidence of mass die-offs of hyriid molluscs, however, suggests that drought perhaps was a dominant climatic feature in the region as it is today.

Localities

The fossils described here derive from exposures near the small village of St Bathans (Manuherikia River Section, Mata Creek, Vinegar Hill), Lauder, and Wharekuri Creek in the Waitaki Valley, all in Otago, New Zealand (Fig. 1).

Manuherikia River Section.—This section is exposed on the true left side of the Manuherikia River, Otago, at 44.90794°S, 169.85822°E. The fish remains described here derive from several beds in the lower 25 m of the section (Fig. 2), introduced in stratigraphic succession as follows.

Bed HH1d: 3.52–3.64 m above base of the Bannockburn Formation, c. 10 cm thick white fine sand layer underlain by 2–3 cm thick conglomerate of mud rip-up clasts coated in biogenic carbonates, stromatolite fragments, calcified rootlet casts, and vertebrate remains including fish bones and otoliths and rare bird bones and eggshell. Fossil Record Number in the archival Fossil Record File of the Geological Society of New Zealand H41/f89.

Bed HH1a: 6.88–7.0 m above base of Bannockburn Formation, a c. 5–10 cm thick sandy conglomerate of mud rip-up clasts coated in biogenic carbonates, stromatolite fragments, hyriid clam fragments and other rare molluscs, and abundant vertebrate remains including fish bones and otoliths, and common bird bones and eggshell. This, the most fossiliferous bed for vertebrates in the section, is overlain by fine sand up to 20 cm thick with preserved ripples. There are no articulated remains and most fossil bones show varying degrees of rounding due to erosion by tumbling in the littoral environment. Fossil Record File Number H41/f88.

Bed HH1b: 9.5–9.58 m above base of Bannockburn Formation, c. 10 cm thick sandy conglomerate. Very similar to bed HH1a, but which includes coarser material with clasts up to 8 cm and fossil bones are generally more worn. Material from this bed was quarried in two localities, the first where it was exposed on the river bank (NZ Fossil Record File Number H41/f90) and the second about 50 m across the river terrace at the foot of the hill in what is termed the Trench Excavation, at 44.90780°S; 169.85844°E (Fossil Record File Number H41/f0103).

Bed HH4: About 30 m downriver of HH1a and HH1b at 44.907861°S 169.857233°E, this bed is 25.63–25.83 m above the base of the Bannockburn Formation. It was a lens varying from 5–15 cm thick in a clay-silt layer marked by abundant fragmented gastropods (*Glyptophysa* sp.). At its base, infilled mud cracks attested to an episode of drying of the lake bed immediately before the deposition of this bed which is interpreted as an infilled channel scour feature. Fossil Record File Number H41/f0095.

Mata Creek, Site 4.—On the west bank of Mata Creek at 44.8847°S, 169.8384°E, an obvious white sand layer about 15 cm thick exposed in the cliff (Fig. 8D), contained in 2010 a cross section of a small channel about 1 m long. This channel, given the NZ Fossil Record File Number H41/108, deepened to about 30–40 cm thick protruding into the green clays below the sand. It had a fine conglomerate of rip-up clasts and bones in its basal 1–2 cm. The fish skeleton remains were found in the fine sands immediately above the conglomerates in this channel deposit. The relationship of this bed to the upper boundary of the underlying Dunstan Formation was not determined, but it probably lies in the zone 10–40 m above it.

Vinegar Hill.—The deposits at Vinegar Hill are exposed on the sides of a valley created by nineteenth century gold sluicing of the Dunstan Formation, and their section is shown in Fig. 3. We report fish remains from 2 sites in the lower part of the Bannockburn Formation:

Site 1: The most northwestern exposure in the valley at 44.87712°S, 169.74930°E. The fossils were located in a 1–5 cm thick layer of unconsolidated clean white sand with small white quartz pebbles or in its immediate bounding clay beds interpreted to be at c. 55.5 m on the section mapped by Douglas (1986) (Fig. 3). Fossil Record File Number H41/f0113.

Site 2: The exposure of Bannockburn Formation furthest down the western side of the valley at 44.87808°S, 169.74975°E. Here the sampled bed was stratigraphically about 1.8 m above small cliffs of lignite silts (1.5 m thick), or the beach lagoon silts of the uppermost Dunstan Formation, and so is at about 54 m on the section (Fig. 3). The sampled bed was c. 20 cm thick sandy green clay with fish and rare bird bone worn fragments overlain by c. 6 cm of unconsolidated sand, of which the lower 1 cm was orange-stained with common fish bones. Fossil Record File Number H41/f0111.

Wharekuri Creek, Waitaki Valley.—Wharekuri Creek is a minor tributary of the Waitaki River. About 2 km upstream, slivers of Manuherikia Group strata are exposed on the steep sides of Wharekuri Creek. The sampled outcrop is a small exposure of mudstone presumed to be of the Bannockburn Formation at 44.67858°S; 170.35848°E, where a thin cobble layer in the clays suggested some sorting of sediments. Only a small, c. 12 kg sample, was taken which revealed rare freshwater molluscs (*Glyptophysa* sp.), rare fragments of bird bones, and the rare otoliths reported here. Fossil Record File Number I40/f0386. The relationship of this exposure to the Dunstan Formation is not discernable due to the ruptured nature of the beds, although lignites attributed to the latter formation are nearby, so a lower Bannockburn Formation is likely.

Lauder shell bed.—Just west of the township of Lauder on the rail line is an exposure of the Bannockburn Formation in the western face of the first cutting passed through at 45.05674°S; 169.66353°E (Lindqvist 1994). The sampled bed was a thin layer (c. 1 cm) of molluscs (two species of tiny hydrobiids and rare hyriid clams) in the gently dipping sequence. Fish remains, including otoliths, were uncommon and bird bone fragments were rare. Fossil Record File Number is G41/f9508. The relationship of this exposure of the Bannockburn Formation to the underlying boundary with the Dunstan Formation is unknown.

Methods

Excavation.—Fossil beds were exposed by removal of the overburden, and then excavated by trowel. Sample sizes vary for each location as, in some, samples were taken primarily for recovery of terrestrial vertebrates. So, for example, several tones of sediment were processed for Bed HH1a,

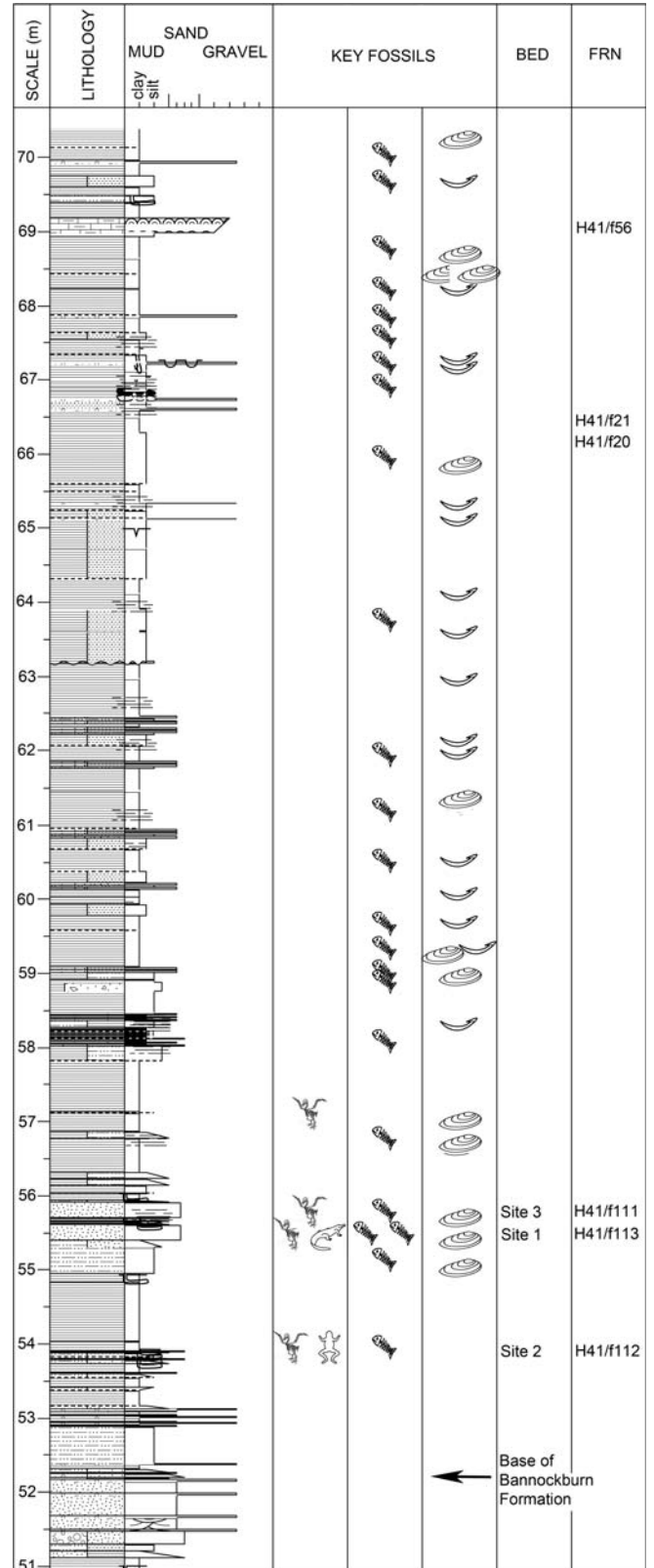


Fig. 3. Stratigraphic section at the Vinegar Hill location showing the position of Sites 1 and 2 relative to the basal part of the Bannockburn Formation (52.3–70 m; Lauder Member) after Douglas (1986) in the context of other fossil records (H41/f20 and H41/f21, H41/f56) and a vertebrate bearing Site 3 (H41/f111). FRN is Fossil Record Number in the archival Fossil Record File of the Geological Society of New Zealand.

whereas from Wharekuri, Lauder, and bed HH1d only 10–20 kg of sediment was processed, specifically for their otolith content. All sediment was collected and washed through 1 mm mesh sieves and dried. The fossil concentrate was sorted a few grains at a time, under a low-power binocular microscope, and all otoliths and other fossils separated from it. The otoliths described here were sent to WS for identification and description.

The studied material is deposited in the National Museum of New Zealand, Wellington, except for a few specimens remaining with the senior author for his comparative collection. Type material has been catalogued with numbers NMNZ S.52707 to 52753.

Scanning.—The CT scans were performed on each block of the skeleton at Christchurch Hospital, Christchurch, New Zealand, using a Siemens Somatom Definition X-ray machine (120 kV and 400 mA, and 0.4 mm slice thickness, voxel dimensions 0.16 mm × 0.16 mm × 0.16 mm). CT data were imported into the Mimics medical imaging software (Materialise N.V., Leuven, Belgium) and a 3D digital reconstruction of each block was created. The individual reconstructions were then tidied, smoothed and stitched together using Adobe Photoshop (Adobe Systems Inc., Mountain View, CA).

Otolith morphology.—The terminology of sagittae otoliths is from Schwarzhans (2010), based on morphological nomenclature established by Koken (1884) and Weiler (1942), with minor amendments by Schwarzhans (1978). The caudal colliculum has a different form in the family Moridae, being transformed into a narrow, ridge-like feature. Deng et al. (2010) have shown that the macula of the saccular sensory epithelium of *Antimora rostrata* “has an elaborate structure”, which is reflected in the unusual sulcus morphology found in the otoliths of this family. For optimal comparison purposes, Figs. 4–7, 10–13 show otoliths from the right side. Photos of left otoliths have been mirror-imaged. The classification of the systematic part follows Nelson (2006).

Systematic palaeontology

Class Osteichthys Huxley, 1880

Subclass Actinopterygii Klein, 1885

Order Salmoniformes Bleeker, 1859

Suborder Galaxioidei Berg, 1937

Family Galaxiidae Bonaparte, 1832

Several galaxiid fish skeletons have been recorded from New Zealand lake sediments from the early to late Miocene of Otago and the Pleistocene of Gisborne (see McDowall 2009, 2010). Of all these finds, only one location has yielded adequate preservation that allowed specific identification—the Foulden Diatomite of the Foulden Maar of early Miocene age (Lindqvist and Lee 2009). A fossil from this site was described as *Galaxias effusus* Lee, McDowall, and Lindqvist, 2007 with a size of about 12 cm SL and 14 cm TL, which is towards the smaller size of living galaxiids. The Foulden Diatomite is about 5 My older than the Bannockburn Formation (23 Ma versus 19–16 Ma) and given the specific environment, size and distribution of its occurrence *Galaxias effusus* is not likely to represent one of the species described here based on otoliths. McDowall and Pole (1997) reported a large specimen of about 38 cm length from the Bannockburn Formation, and McDowall (2010) stated that it is quite unlike any living species, but insufficient detail has been preserved to permit formal description. Additional material from the Bannockburn Formation has been reported by Lee et al. (2007), but McDowall (2010: 22), considers that: “distinct taxa are likely to have been involved though again insufficient detail is present to permit formal description”. It must be assumed though that among these specimens there will be representatives correlating with the otolith-based species described below. A further fossil galaxiid has been described from the late Miocene of the Kaikorai Valley near Dunedin (Oliver 1936) as *Galaxias kaikorai* Whitley, 1956. McDowall (1976) concluded though that the fish from the Kaikorai Valley could not be distinguished from the extant species *G. brevipinnis*.

Genus *Galaxias* Cuvier, 1816

Type species: Galaxias fasciatus Gray, 1842, by subsequent monotypy, River Thames, New Zealand; Recent.

Galaxias angustiventris Schwarzhans sp. nov.

Fig. 4F–H.

Etymology: From Latin *angustus*, narrow and *venter*, belly; referring to the narrow ventral field on the inner face below the sulcus.

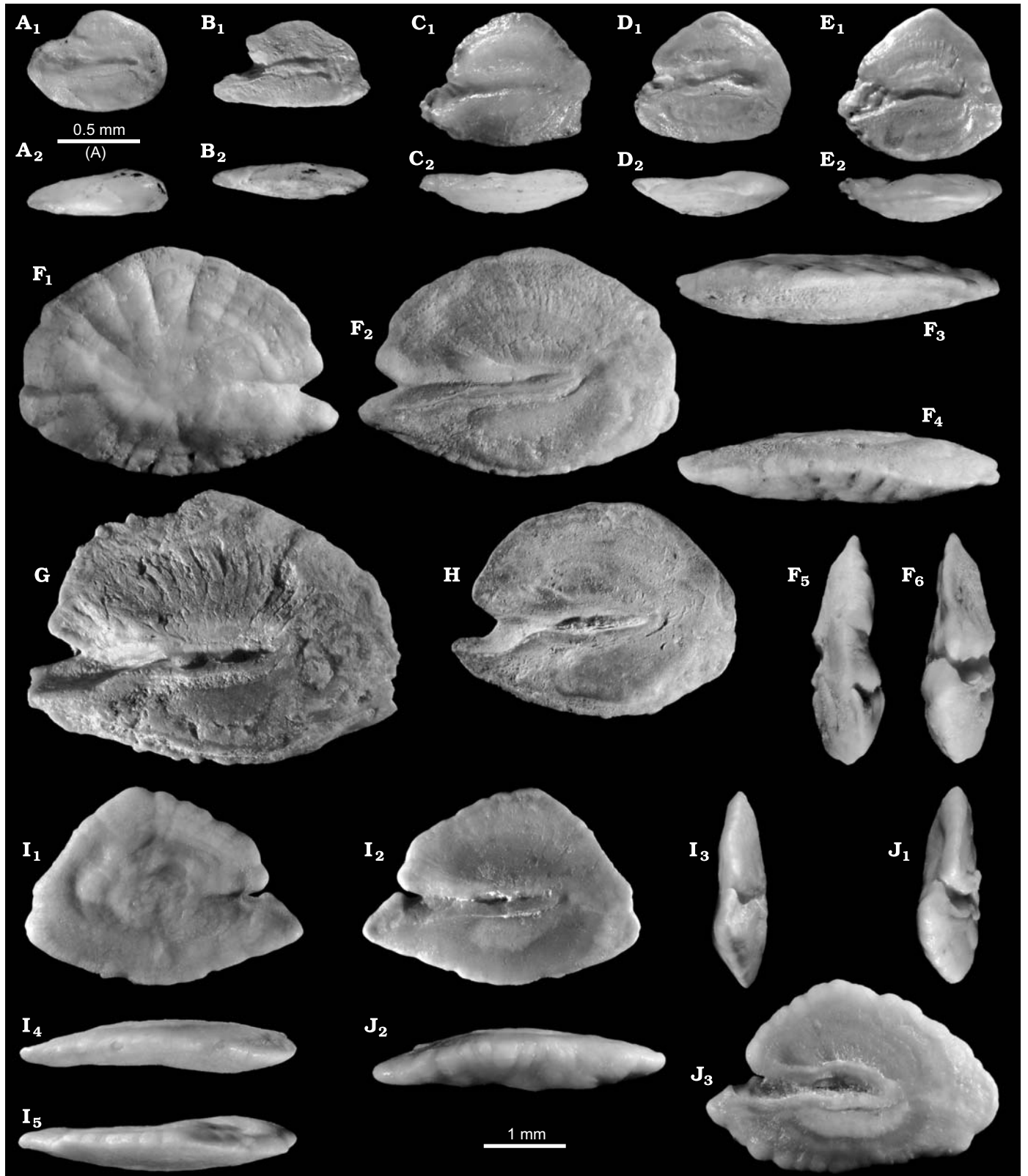
Type material: Holotype: NMNZ S.52707 (Fig. 4F). Paratypes: three specimens, NMNZ S.52708 (Fig. 4G, H).

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

Type horizon: HH1a bed, Bannockburn Formation, early Miocene.

Diagnosis.—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 in-

Fig. 4. Otoliths of Recent galaxiid fishes from Australia (A, B, D, E), New Zealand (C) and the early Miocene of New Zealand (F–J, Bannockburn Formation, Manuherikia River). A. *Lepidogalaxias salamandroides* Mees, 1961, Recent, Western Australia, collection W. Schwarzhans, donated by WAM, inner face (A₁), dorsal view (A₂). B. *Galaxias olidus* Günther, 1866, Recent, South Australia, collection W. Schwarzhans, donated by SAMA, inner face (B₁), dorsal view (B₂). C. *Galaxias fasciatus* Gray, 1842, Recent, New Zealand, North Island, collection W. Schwarzhans, donated by NMNZ, inner face (C₁), dorsal view (C₂). D. *Galaxias maculatus* (Jenyns, 1842), Recent, Western Australia, collection W. Schwarzhans, donated by WAM, inner face (D₁), dorsal view (D₂). E. *Galaxias occidentalis* Ogilby, 1899, Recent, Western Australia, collection W. Schwarzhans, donated by WAM, inner face (E₁), dorsal view (E₂). →



F–H. *Galaxias angustiventris* Schwarzahns sp. nov. **F.** Holotype, NMNZ S.52707, early Miocene, Bannockburn Formation, Manuherikia River, HH1a, outer face (F₁), inner face (F₂), dorsal (F₃), ventral (F₄), posterior (F₅), and anterior (F₆) views. **G.** Paratype, NMNZ S.52708a, inner face, early Miocene, Bannockburn Formation, Manuherikia River, HH1a. **H.** Paratype, NMNZ S.52708b, inner face, early Miocene, Bannockburn Formation, Manuherikia River, HH1a. **I–J.** *Galaxias brevicauda* Schwarzahns sp. nov. **I.** Holotype, NMNZ S.52709 early Miocene, Bannockburn Formation, Manuherikia River, HH1a, outer face (I₁), inner face (I₂), anterior (I₃), ventral (I₄), and dorsal (I₅) views. **J.** Paratype, NMNZ S.52710, early Miocene, Bannockburn Formation, Manuherikia River, HH1a, anterior view (J₁), ventral view (J₂), inner face (J₃).

ner face narrow with distinct furrows below sulcus and close to rim of otolith.

Description.—Moderately compressed otoliths with regularly rounded outline except for shallow ventral rim and small, but sharply pointed rostrum. Size up to 4.5 mm. Excisura sharp, short; antirostrum short, broad. Dorsal rim occasionally undulating. OL:OH = 1.3–1.4; OH:OT about 3.2.

Inner face slightly convex with short, narrow, slightly deepened, inferior sulcus. Ostium narrow, anteriorly open, deeper than cauda; cauda straight, terminating far from posterior tip of otolith. OL:SuL about 1.5; CaL:OsL about 1.0. Dorsal field wide, often somewhat irregularly ornamented, with broad but indistinct depression. Ventral field narrow, with furrow below sulcus and furrow close to ventral rim.

Outer face flat with several short radial furrows on dorsal field and occasional few very short furrows along ventral rim of otolith.

Remarks.—*Galaxias angustiventris* is similar to *G. brevicauda* Schwarzhans sp. nov. with both species having otoliths with a short cauda terminating far from the posterior tip of the otolith. It differs from the latter mainly in the rounded dorsal rim, the large dorsal field and narrow ventral field, the short rostrum, the wide excisura, the presence of a ventral furrow close to the ventral rim of the otolith and the slightly more thick appearance (OH:OT about 3.2 versus 3.8).

None of the otoliths known from the living species of the genus shows a similarly short cauda (for comparison see Fig. 4A–E). It is therefore possible that the two species represent an extinct genus of the family Galaxiidae.

Stratigraphic and geographic range.—Bannockburn Formation, Manuherikia River.

Galaxias brevicauda Schwarzhans sp. nov.

Fig. 4I–J.

Etymology: From Latin *brevis*, short and *cauda*, technical term of the rear part of the sulcus; referring to the short cauda of the sulcus.

Type material: Holotype: NMNZ S.52709 (Fig. 4I). Paratype: One specimen, NMNZ S.52710, (Fig. 4J).

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

Type horizon: HH1a bed, Bannockburn Formation, early Miocene.

Diagnosis.—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.

Description.—Moderately compressed otoliths with triangular outline and shallow ventral rim. Size up to 3.5 mm. Rostrum sharp, massive; excisura narrow, short; antirostrum short, broad. Posterior tip angular, nearly symmetrically expressed to rostrum. Mid-dorsal angle on dorsal rim variable slightly before or behind midpoint of otolith. All rims undulating. OL:OH = 1.4–1.5; OH:OT about 3.8.

Inner face slightly convex, smooth, with short, narrow, slightly deepened, inferior sulcus. Ostium narrow, anteriorly open; cauda straight, terminating far from posterior tip of otolith. OL:SuL = 1.5–1.7; CaL:OsL about 1.0. Dorsal field wide, with broad depression with sharp ventral border to sulcus. Ventral field narrow, with furrow below sulcus but now furrow close to ventral rim.

Outer face slightly concave with few short radial furrows on dorsal field.

Remarks.—*Galaxias brevicauda* belongs to a species-group with otoliths having a short cauda terminating far from the posterior tip of the otolith, like *G. angustiventris* (see that species for further comparison).

Stratigraphic and geographic range.—Bannockburn Formation, Manuherikia River.

Galaxias bobmcdowalli Schwarzhans sp. nov.

Fig. 5A–L.

Etymology: Named in honour of the late Robert M. McDowall (1939–2011) for his many contributions to the knowledge of Recent and fossil fresh water fishes of New Zealand.

Type material: Holotype: NMNZ S.52711 (Fig. 5A). Paratypes: 24 specimens (19 specimens NMNZ S.52712, HH1a bed; 2 specimens NMNZ S.52713, HH1b bed, trench excavation; 3 specimens NMNZ S.52714, Vinegar Hill, site 2) (Fig. 5B–I).

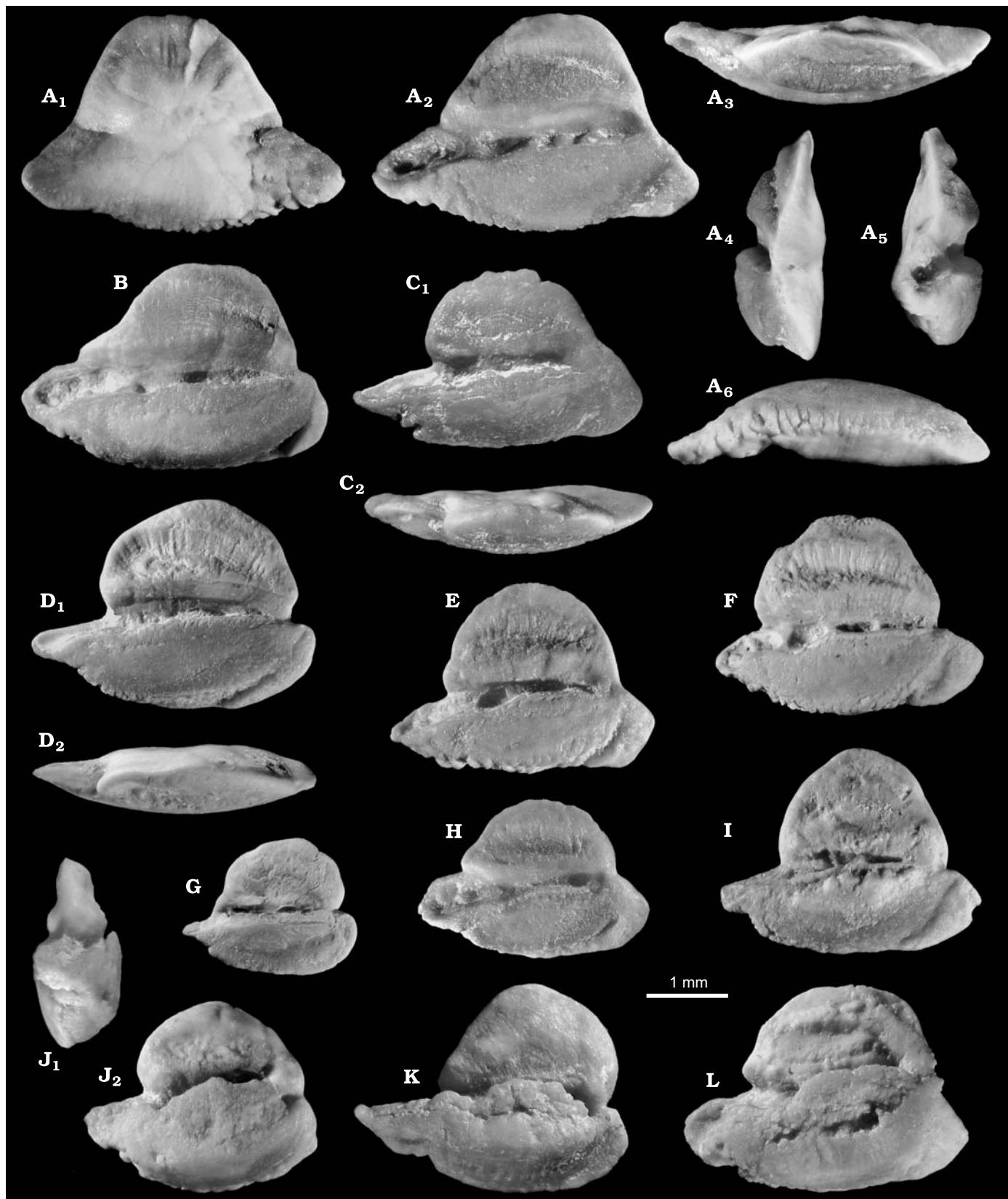
Type locality: Home Hills Station, Manuherikia River near St Bathans, Otago.

Type horizon: HH1a bed, Bannockburn Formation, early Miocene.

Other material.—176 specimens (133 specimens [3 altered or deformed], NMNZ S.52715, Home Hills Station, Manuherikia River near St Bathans, HH1a bed [Fig. 5J, L]; 19 specimens [2 altered or deformed], NMNZ S.52716, Home Hills Station, Manuherikia River near St Bathans, HH1b bed [Fig. 5K]; 11 specimens, Home Hills Station, Manuherikia River near St Bathans, HH1d; 6 specimens, Vinegar Hill, site 1; 8 specimens, Vinegar Hill, site 2).

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

Fig. 5. Otoliths of the galaxiid fish *Galaxias bobmcdowalli* sp. nov. **A.** Holotype, NMNZ S.52711, early Miocene, Bannockburn Formation, Manuherikia River, HH1a, outer face (A₁), inner face (A₂), dorsal (A₃), posterior (A₄), anterior (A₅), and ventral (A₆) views. **B.** Paratype, NMNZ S.52712a, early Miocene, Bannockburn Formation, Manuherikia River, HH1a, inner face. **C.** Paratype, NMNZ S.52712b, early Miocene, Bannockburn Formation, Manuherikia River, HH1a, inner face (C₁), dorsal view (C₂). **D.** Paratype, NMNZ S.52712c, early Miocene, Bannockburn Formation, Manuherikia River, HH1a, inner face (D₁), dorsal view (D₂). **E.** Paratype, NMNZ S.52712d, early Miocene, Bannockburn Formation, Manuherikia River, HH1a, inner face. **F.** Paratype, NMNZ S.52713a, early Miocene, Bannockburn Formation, Manuherikia River, HH1a, inner face. **G.** Paratype, NMNZ S.52712e, early Miocene, Bannockburn Formation, Manuherikia River, HH1a, inner face. **H.** Paratype, NMNZ S.52712f, early Miocene, Bannockburn Formation, Manuherikia River, →



HH1a, inner face. **I.** Paratype, NMNZ S.52712g, early Miocene, Bannockburn Formation, Manuherikia River, HH1a, inner face. **J.** Teratologically deformed specimens, NMNZ S.52715a, early Miocene, Bannockburn Formation, Manuherikia River, HH1a, anterior view (**J₁**), inner face (**J₂**). **K.** Teratologically deformed specimens, NMNZ S.52715b, early Miocene, Bannockburn Formation, Manuherikia River, HH1a, inner face. **L.** Teratologically deformed specimens, NMNZ S.52716a, early Miocene, Bannockburn Formation, Manuherikia River, HH1a, inner face.

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.

Description.—Moderately compressed to moderately elongate, robust otoliths with triangular outline and shallow ventral rim. Size up to 4 mm. Rostrum long, sharp, massive, sometimes anteriorly thinning; excisura wide, short; antirostrum indistinct. Posterior tip massive, pointed, inferior, similarly expressed as rostrum, but not as long and sharp. Dorsal rim high, highest at about its midpoint, rarely with distinct angle. Ventral rim shallow, often with concavity below rostrum and posterior tip. Rims smooth, ventral rim sometimes delicately crenulated. OL:OH = 1.3–1.65; OH:OT = 2.4–2.9.

Inner face markedly to strongly convex, with long, narrow, deepened, nearly median sulcus. Ostium moderately narrow, anteriorly open; cauda very narrow, straight, terminating close to posterior tip of otolith, sometimes almost joined to postdorsal incision. OL:SuL = 1.1–1.25; CaL:OsL = 1.4–1.7. Dorsal field wide, with broad, fairly deep depression. Ventral field moderately wide, with ventral furrow below close to ventral rim and often joined to it along the mid-ventral portion. Its posterior stretch curving upward and inward, seemingly ‘cutting off’ posterior tip.

Outer face slightly concave, rather smooth.

Variability and ontogeny.—Otoliths of *G. bobmcdowalli* are remarkable for their high variability, which affects the thickness of the inner face below the sulcus, the expression of rostrum and inferior posterior tip, which range from about equally long to the rostrum being considerably longer than the posterior tip, and particularly expression of the excisura-like incision of the posterior rim, which ranges from nearly absent to about as deep as the excisura of the anterior rim. The variation of rostrum and posterior tip as well as variations of the thickness of the otolith are reflected in a large variability of measurements and their relations such as OL:OH and OH:OT.

Another remarkable aspect, not only in the case of *G. bobmcdowalli*, but most other otoliths (see later) is the predominance of large otoliths from truly adult specimens. It is therefore difficult to understand ontogenetic changes in this species. The few smaller specimens available (Fig. 5G) show mostly thinner otoliths, often combined with less curvature of the inner face, and a weaker posterior tip.

A further interesting aspect with otoliths of *G. bobmcdowalli*, again also observed in some other common otolith-based species (see later) is the occasional occurrence of teratologically deformed specimens. The cause of these deformations is unknown, but they seem to follow a particular trend in all observed specimens (Fig. 5J–L) in the sense that the ventral field becomes overly thickened and the sulcus, particularly the cauda, shielded by a ridge growing over it from the ventral field. Due to the thickening the sulcus becomes very deep and its opening only visible from a dorsal view. The exuberantly grown material shows some difference in structure from the “normal” otolith surface.

Remarks.—*Galaxias bobmcdowalli* represents the most common galaxiid otolith in the Bannockburn Formation with the widest distribution, missing only from the HH4 bed, Wharekuri Creek and the Lauder shell bed. It belongs to a species group with otoliths having a long cauda terminating close to the posterior tip of the otolith, closer in fact than observed in most Recent *Galaxias* species (for comparison see Fig. 4A–E). Otoliths of *G. bobmcdowalli* are easily recognized by their robust appearance with the triangular outline, the long, sharp rostrum, the distinct inferior posterior tip and the depression or incision of the posterior rim at the level of the cauda. They most closely resemble otoliths of *G. papilionis* Schwarzhans sp. nov., from which they differ in the stronger curvature of the inner face, the greater thickness (OH:OT = 2.4–2.9 versus 3.2–3.5), the long rostrum, the more regular triangular dorsal rim (versus expanded postdorsally) and the less pronounced posterior incision.

Stratigraphic and geographic range.—Bannockburn Formation, Manuherikia River and Vinegar Hill.

Galaxias papilionis Schwarzhans sp. nov.

Fig. 6A–D.

Etymology: From Latin *papilio*, butterfly, referring to the shape of the dorsal and ventral fields resembling the wings of a butterfly.

Type material: Holotype: NMNZ S.52717 (Fig. 6A). Paratypes: 11 specimens (8 specimens NMNZ S.52718, HH1d bed; 3 specimens NMNZ S 52719, HH1a bed), (Fig. 6B–D).

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

Type horizon: HH1d bed, Bannockburn Formation, early Miocene.

Diagnosis.—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.

Description.—Compressed thin otoliths with high-bodied outline. Size up to 3 mm. Rostrum short, thin, pointed, with ventral concavity or indentation; excisura wide; antirostrum indistinct. Posterior tip inferior, broadly rounded, with deep, broad incision joining to tip of cauda. Dorsal rim high, rounded, postdorsally expanded. Ventral rim moderately deep, posteriorly expanded. All rims smooth. OL:OH = 1.05–1.25; OH:OT = 3.2–3.5.

Inner face almost flat, smooth, with long, narrow, deepened, nearly median sulcus. Ostium very narrow, anteriorly open; cauda similarly narrow, straight, its posterior tip reaching posterior rim of otolith and joined to postdorsal incision, resulting in a posterior “excisura” and a posterior sulcus opening. OL:SuL = 1.1–1.2; CaL:OsL = 1.7–2.3. Dorsal field wide, with broad, shallow depression. Ventral field wide, with no distinct ventral furrow.

Outer face flat, rather smooth.

Variability and ontogeny.—The expression of the short ros-

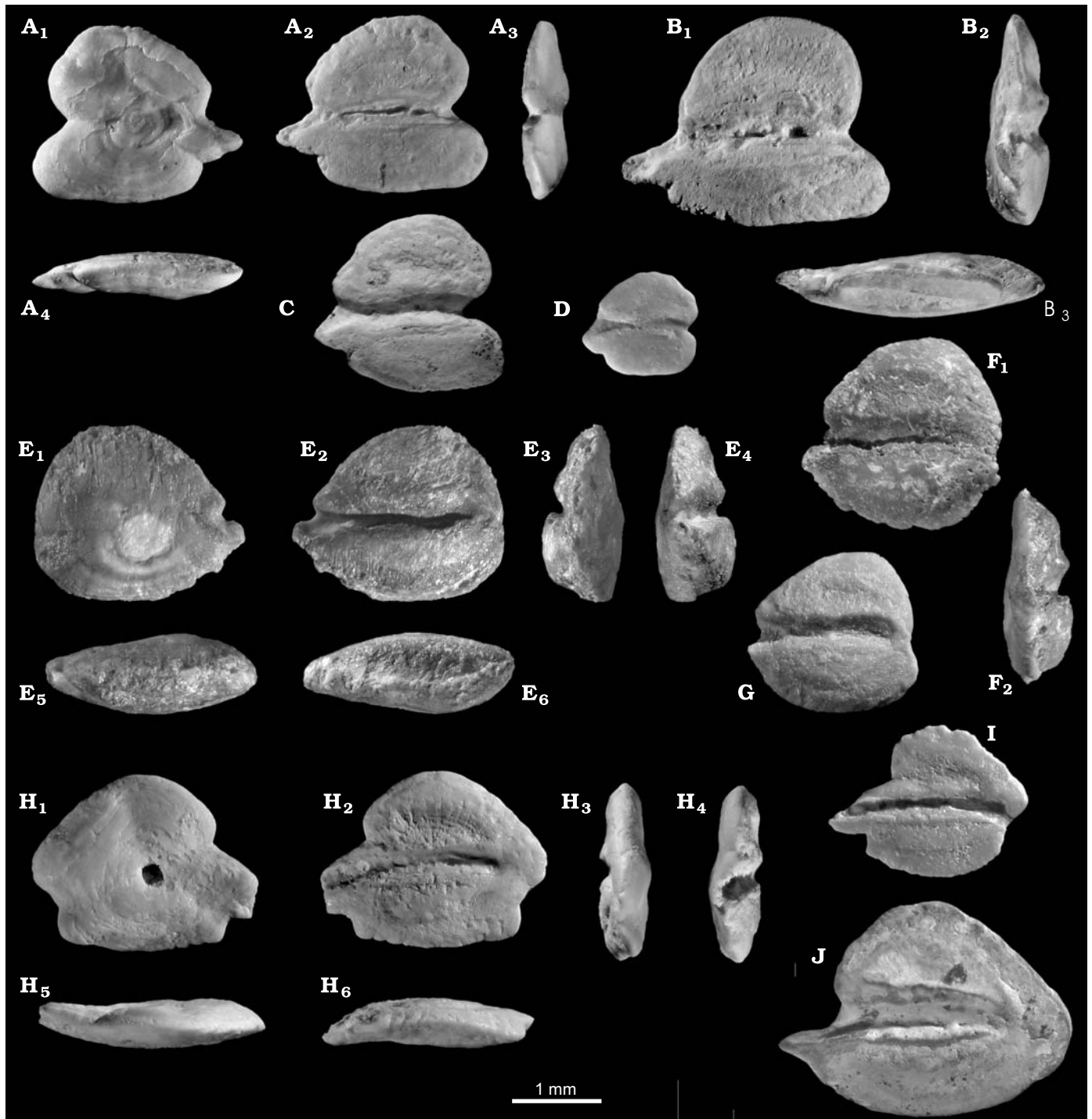


Fig. 6. Otoliths of galaxiid fishes from the early Miocene Bannockburn Formation of New Zealand: HH1d, Manuherikia River (A, C, D); HH1a, Manuherikia River (B); HH4, Manuherikia River (J); Vinegar Hill, site 2 (F, G); Lauder shell bed, west of Lauder (H, I). **A–D.** *Galaxias papillionis* Schwarzahns sp. nov. **A.** Holotype, NMNZ S.52717, outer face (A₁), inner face (A₂), anterior view (A₃), ventral view (A₄). **B–D.** Paratypes. **B.** NMNZ S.52719a, inner face (B₁), anterior view (B₂), dorsal view (B₃). **C.** NMNZ S.52718a, inner face. **D.** NMNZ S.52718b, inner face. **E–G.** *Galaxias parvirostris* Schwarzahns sp. nov. **E.** Holotype, NMNZ S.52720, outer face (E₁), inner face (E₂), posterior (E₃), anterior (E₄), dorsal (E₅), and ventral (E₆) views. **F.** Paratype, NMNZ S.52721a, inner face (F₁), anterior view (F₂). **G.** Paratype, NMNZ S.52721b, inner face. **H–I.** *Galaxias tabidus* Schwarzahns sp. nov. **H.** Holotype, NMNZ S.52723, outer face (H₁), inner face (H₂), posterior (H₃), anterior (H₄), dorsal (H₅), and ventral (H₆) views. **I.** Paratype, NMNZ S.52724a, inner face. **J.** *Galaxias* sp., NMNZ S.52725a, inner face.

trum is variable to some extent as well as the excisura of the posterior rim. The latter is less well developed in small specimens.

Remarks.—*Galaxias papilionis* looks like *G. bobmcdowalli* taken to an extreme. It differs in the flat inner face, the very short, fragile, pointed rostrum and the deep posterior

“excisura” with both dorsal and ventral rims expanding over it. Interestingly, *G. papilionis* represents the earliest *Galaxias* species occurring in the Bannockburn Formation near its base in the HH1d bed. It is rather rare in the next sampled bed up-section, the HH1a bed, but it is uncertain whether this represents a stratigraphic event or an ecological one.

Stratigraphic and geographic range.—Bannockburn Formation, Manuherikia River.

Galaxias parvirostris Schwarzhans sp. nov.

Fig. 6E–G.

Etymology: From Latin *parvus*, small, and rostrum, technical term for the anterior tip of the otolith below the sulcus, referring to the short rostrum.

Type material: Holotype: NMNZ S.52720, (Fig. 6E). Paratypes: 3 specimens (2 specimens NMNZ S.52721, same location as holotype, 1 specimen NMNZ S.52722, Home Hills Station, Manuherikia River near St Bathans, HH1a bed) (Fig. 6F–G).

Type locality: Vinegar Hill, site 2, Otago.

Type horizon: Bannockburn Formation, early Miocene.

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.

Description.—Compressed thick otoliths with rounded outline. Size up to 2.5 mm. Rostrum short, blunt; excisura small; antirostrum indistinct. Posterior tip broadly rounded. Dorsal rim high, rounded, postdorsally pronounced. Ventral rim moderately deep, rounded. All rims smooth. OL:OH = 1.05–1.2; OH:OT = 2.2–2.8.

Inner face markedly convex, somewhat rugged, with long, narrow, deepened, nearly median sulcus. Ostium very narrow, anteriorly open; cauda similarly narrow, straight, reaching close to posterior rim of otolith. OL:SuL = 1.05–1.1; CaL:OsL = 2.5–3.0. Dorsal field wide, with small, shallow depression. Ventral field wide, with indistinct ventral furrow at some distance from ventral rim of otolith.

Outer face flat to slightly convex, rather smooth.

Remarks.—*Galaxias parvirostris* is a rare species almost exclusively known from the location Vinegar Hill: only one specimen was found in the HH1a bed of the Manuherikia River location, which is the richest otolith bearing level in the Bannockburn Formation. It is easily recognized and best distinguished from other species by the rounded outline, the thick appearance and the very short rostrum and ostium.

Stratigraphic and geographic range.—Bannockburn Formation, Manuherikia River and Vinegar Hill.

Galaxias tabidus Schwarzhans sp. nov.

Fig. 6H–I.

Etymology: From Latin *tabidus*, melting, diminishing, referring to the anterior and posterior indentations of the ventral rim.

Type material: Holotype: NMNZ S.52723 (Fig. 6H). Paratypes: 2 specimens NMNZ S.52724 (Fig. 6I).

Type locality: West of Lauder, Otago.

Type horizon: Lauder shell bed, early Miocene.

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.

Description.—Moderately compressed thin otoliths. Size up to 2.5 mm. Rostrum short, pointed; no excisura, small; instead about 100° angular indentation of anterior rim above ostium. Dorsal rim high, rounded, anteriorly pronounced, posteriorly regularly inclining. Posterior tip median, above tip of cauda. Ventral rim shallow, with two 90–100° indentations, one anteriorly below rostrum, the other below posterior tip. Rims slightly undulating. OL:OH = 1.3; OH:OT about 3.5.

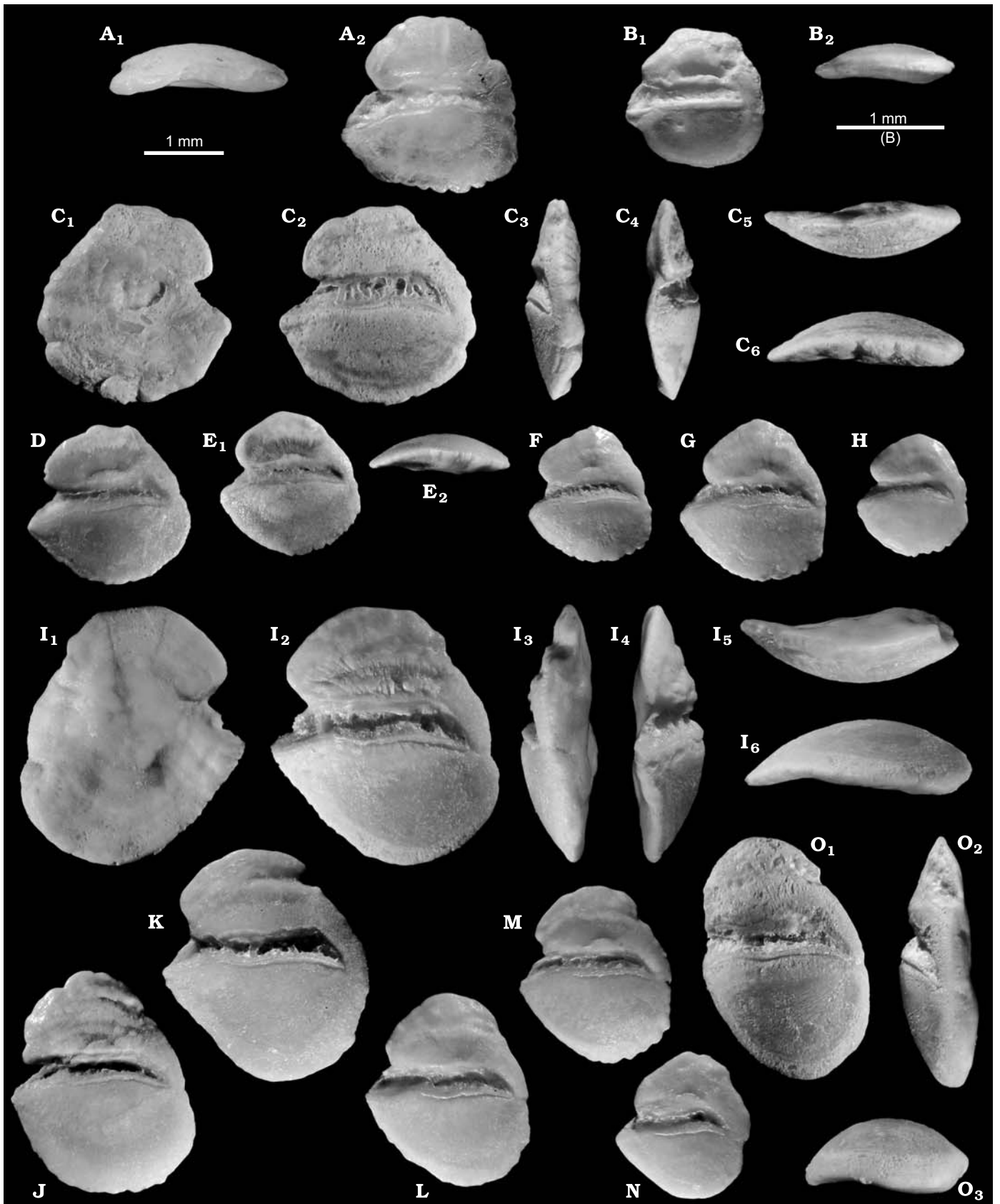
Inner face nearly flat, only slightly curved at the rostrum, smooth, with long, narrow, moderately deepened, nearly median sulcus. Ostium very narrow, anteriorly open; cauda similarly narrow, straight, reaching close to posterior rim of otolith below its posterior tip. OL:SuL = 1.1–1.15; CaL:OsL about 2.5. Dorsal field wide, with small, shallow depression. Ventral field wide, with indistinct ventral furrow far from ventral rim of otolith.

Outer face flat, smooth.

Remarks.—*Galaxias tabidus* is restricted in distribution to the Lauder shell bed, which is probably stratigraphically younger than the other Bannockburn locations sampled and represents a different facies, many kilometres from the deltaic environment of the sites near St Bathans. Its otoliths are easily recognized by the very distinctive shape of the ventral rim, which resembles otoliths of the Recent New Zealand species *G. fasciatus* Gray, 1842 (see Fig. 4C), the “pseudo”-excisura above the ostium and the thin, fragile appearance with an almost flat inner face and a long sulcus.

Stratigraphic and geographic range.—Bannockburn Formation, Lauder.

Fig. 7. Otoliths of Recent retropinnid fishes from Australia (A, B) and their early Miocene counterparts from New Zealand (C–O, Bannockburn Formation). **A.** *Prototroctes maraena* Günther, 1864, Recent, New South Wales, collection W. Schwarzhans, donated by AMS, ventral view (A₁), inner face (A₂). **B.** *Retropinna semoni* (Weber, 1895), Recent, South Australia, collection W. Schwarzhans, donated by SAMA, inner face (B₁), ventral view (B₂). **C–H.** *Prototroctes modestus* Schwarzhans sp. nov. from early Miocene, Bannockburn Formation (C–G, Manuherikia River, HH1a; H, Wharekuri Creek, Aviemore). **C.** Holotype, NMNZ S. 52726, outer face (C₁), inner face (C₂), posterior (C₃), anterior (C₄), dorsal (C₅), and ventral (C₆) views. **D–H.** Paratypes. **D.** NMNZ S.52727a, inner face. **E.** NMNZ S.52727b, inner face (E₁), ventral view (E₂). **F.** NMNZ S.52727c, inner face. **G.** NMNZ S.52727d, inner face. →



H. NMNZ S.52728, inner face. I–O. *Prototroctes vertex* Schwarzhans sp. nov. from early Miocene, Bannockburn Formation, Manuherikia River, HH1a. I. Holotype, NMNZ S.52729, outer face (I₁), inner face (I₂), posterior (I₃), anterior (I₄), dorsal (I₅), and ventral (I₆) views. J–N. Paratypes NMNZ S.52731a–e, inner face. O. Deformed specimen NMNZ S.52732a, inner face (O₁), posterior view (O₂), ventral view (O₃).

Galaxias sp.

Fig. 6J.

Material.—2 specimens NMNZ S.52725. Home Hills Station, Manuherikia River near St Bathans, Otago, HH4 bed, Bannockburn Formation, early Miocene.

Remarks.—These two otoliths from the highest stratigraphic interval sampled for the Bannockburn Formation at the Manuherikia River location, are characterized by a rounded triangular outline with a moderately long, sharp rostrum and an inferior posterior tip. The sulcus is positioned median on the inner face with a moderately long cauda terminating at some distance from the posterior rim of the otolith. These otoliths represent the only galaxiid otoliths at HH4, the highest sampled bed of the Bannockburn Formation at the Manuherikia River section, and likely represent yet a further undescribed species.

Family Retropinnidae McCulloch, 1927

The first fossil fish skeletons of the genus *Prototroctes* were recorded from the middle Pleistocene of New Zealand from near Gisborne by McDowall et al. (2006a), based on the diagnostic strengthened bounding rays in the caudal fin. McDowall et al. related the mid-Pleistocene skeletons to the recently extinct *P. oxyrhynchus* Günther, 1870, but the more backward location of the dorsal fin halfway between pelvic and anal fins could in fact point to their being from a distinct species. When considering the many otoliths of *Prototroctes* found in the Bannockburn Formation (see below), it may seem reasonable to assume that some of the material recorded as unspecified galaxiid skeletal remains by Lee et al. (2007) could in fact represent specimens of *Prototroctes*.

Genus *Prototroctes* Günther, 1864

Type species: *Prototroctes maraena* Günther, 1864, by monotypy, Southern Australia; Recent.

Prototroctes modestus Schwarzahns sp. nov.

Fig. 7C–H.

Etymology: From Latin *modestus*, modest, referring to the inconspicuous outline of the otolith.

Type material: Holotype: NMNZ S.52726 (Fig. 7C). Paratypes: 16 specimens (15 specimens NMNZ S.52727, same location as holotype; 1 specimen NMNZ S.52728, Wharekuri Creek near Aviemore, Otago, early Miocene, Bannockburn Formation) (Fig. 7D–H).

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

Type horizon: HH1a bed, Bannockburn Formation, early Miocene.

Diagnosis.—Thin otoliths with compressed outline and regularly rounded ventral rim. OL:OH = 0.95–1.05. Dorsal rim without postdorsal indentation.

Description.—Compressed, thin otoliths with broadly rounded ventral rim. Size up to 2.5 mm. Rostrum massive, pointed, moderately long; excisura narrow, not deep; antirostrum short. Posterior rim broadly rounded, somewhat oblate postdorsally.

Dorsal rim short, high, highest behind midpoint. Rims smooth or delicately crenulated. OH:OT = 3.7–3.8.

Inner face markedly convex, with long, narrow, deepened, slightly suprmedian sulcus. Ostium as narrow as cauda, very short, anteriorly open; cauda slightly swinging, terminating close to posterior rim of otolith, with ventrally pointed tip. OL:SuL about 1.1; CaL:OsL = 2.0–2.5. Dorsal field small, with small, ventrally well marked depression. Ventral field wide, smooth, with faint ventral furrow moderately close to ventral rim.

Outer face flat to slightly concave, rather smooth.

Remarks.—Of the two species of the genus recorded here in the Bannockburn Formation, *P. modestus* is less common, the other being *P. vertex* Schwarzahns sp. nov. (see below for differentiation). Otoliths of *P. modestus* closely resemble those of the Recent *P. maraena* Günther, 1864 (Fig. 7A) from southern Australia, except for the more deeply and gently curved ventral rim and the different proportions of the dorsal rim. Otoliths of the recently extinct *P. oxyrhynchus* Günther, 1870 from New Zealand are not known. Otoliths of *Retropinna semoni* (Weber, 1895) (Fig. 7B), representing the other Recent genus of the family, are smaller, like the fishes themselves, and show a straight cauda with a rounded tip (versus swinging cauda with a ventrally pointed tip).

Stratigraphic and geographic range.—Bannockburn Formation, Manuherikia River and Wharekuri Creek.

Prototroctes vertex Schwarzahns sp. nov.

Fig. 7I–O.

Etymology: From Latin *vertex*, twist, referring to the inclined, twisted axis of the otolith.

Type material: Holotype: NMNZ S.52729 (Fig. 7I). Paratypes: 25 specimens (21 specimens NMNZ S.52731, same location as holotype; 4 specimens NMNZ S.52730, same location as holotype, HH1b bed, trench excavation) (Fig. 7J–N).

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

Type horizon: HH1a bed, Bannockburn Formation, early Miocene.

Other material.—1265 specimens: 1131 specimens (2 deformed, NMNZ S.52732, Fig. 7O), Home Hills, Manuherikia River near St Bathans, HH1a bed; 20 specimens, Home Hills Station, Manuherikia River near St Bathans, HH1b; 33 specimens, Vinegar Hill, site 1, 81 specimens, Vinegar Hill, site 2.

Diagnosis.—Compact, very compressed otoliths with inclined, twisted vertical otolith axis. OL:OH = 0.7–0.9. Ventral rim deep, posteriorly pronounced. Dorsal rim high, anteriorly pronounced, usually with marked postdorsal indentation.

Description.—Compact, very high-bodied otoliths with deep, regularly rounded, posteriorly pronounced ventral rim. Size up to nearly 3 mm. Rostrum short, stout; excisura moderately deep, broad; antirostrum short, blunt. Posterior rim inclined, ventrally pronounced, gently curving. Dorsal rim high, highest anteriorly, with marked indentation postdorsally. Rims smooth or slightly undulating. OH:OT = 3.5–3.8.

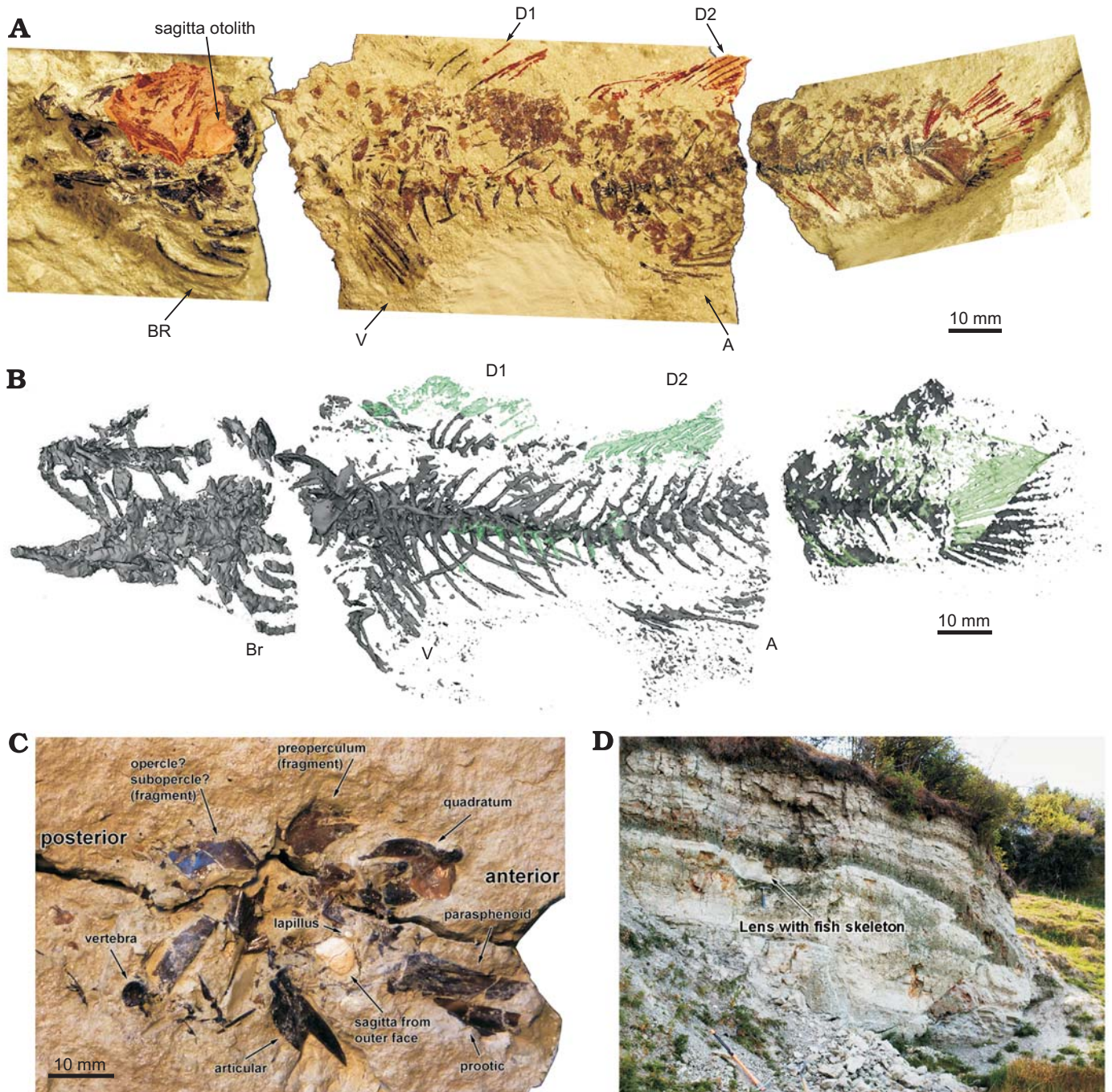


Fig. 8. Skeleton finds of eleotrid fishes and field location. **A.** Skeleton of *Mataichthys bictenatus* Schwarzahns, Scofield, Tennyson, and T. Worthy gen. et sp. nov., holotype, photograph of slabs with information about counterslabs (red) and splinter with otic capsule (red) and otolith in situ (red) spliced in digitally, NMNZ S.52752, location 4, Mata Creek, Bannockburn Formation, early Miocene. Photographs of slab and counterslabs mounted. **B.** Skeleton of *M. bictenatus*, CT-scans of slabs with information about counterslabs (green) spliced in digitally, same specimen as top row. Note that CT-scan images can be distorted and are not used for morphometrics. CT of slabs and counterslabs mounted. **C.** Head slab of *M. bictenatus*, found associated with specimen above, with otolith in situ, NMNZ S.52753. **D.** Photograph of Mata Creek location depicting sedimentary lense from which the fish slabs originated.

Inner face strongly convex, somewhat twisted due to inclined vertical axis of otolith. Sulcus long, narrow, deepened, slightly supramedian. Ostium as narrow as cauda, very short, anteriorly open; cauda slightly swinging, terminating close to posterior rim of otolith, with ventrally pointed tip. OL:SuL about 1.1; CaL:OsL = 1.8–2.3. Dorsal field anteriorly expanded, high. Dorsal depression ventrally well marked, open-

ing posteriorly to the indentation of the posterior-dorsal rim. Ventral field wide, smooth, with faint ventral furrow moderately close to ventral rim.

Outer face flat to slightly concave, smooth.

Variability and ontogeny.—The variability of the otoliths of this species is moderate, mainly confined to variations of the expression of the dorsal rim and slight variations in the ratio

OL:OH, the most compressed and probably deformed shape being depicted in Fig. 7O. Ontogenetic changes are more prominent with the typical expression of the dorsal rim usually not apparent in otoliths smaller about 1.8 mm long. Also there is a clear trend of decreasing index OL:OH with size.

Remarks.—The compressed form with the inclined vertical otolith axis and the twisted inner face as well as the peculiar shape of the dorsal rim all distinguish *P. vertex* from *P. modestus*. Smaller, diagnostically less mature and less compressed specimens of *P. vertex*, however, are not always easy to distinguish from those of the more rare *P. modestus*.

Stratigraphic and geographic range.—Bannockburn Formation, Manuherikia River and Vinegar Hill.

Order Perciformes Bleeker, 1859

Suborder Gobioidi Jordan and Evermann, 1896

Family Eleotridae Bleeker, 1877

Several fossil fish skeletons have been reported (McDowall et al. 2006b; McDowall 2009, 2010) as unidentified species of the eleotrid genus *Gobiomorphus* from the Bannockburn Formation from Fiddlers Flat (equals the Manuherikia River Section, fossil record number H41/f66; Fig. 2) and Vinegar Hill, in beds close to those from which the otoliths described below derive, and from Pleistocene sediments of Gisborne.

Otoliths of Recent eleotrid species have rarely been figured in the literature. We have therefore figured an appropriate selection of otoliths from Recent species from the Indo West-Pacific for comparison purposes (Figs. 11, 12). Otoliths of the Gobioidi, including those of Eleotridae, are easily recognized by the “shoe-sole-shaped” sulcus with an undivided colliculum located somewhat inclined on the centre of the inner face and not opening anteriorly. The otolith shape is more or less rectangular; the inner face is flat to slightly convex, with a distinct ventral line and usually a distinct dorsal depression.

Generally, eleotrid otoliths do not differ greatly from those of other gobioid families, particularly the Gobiidae, although most otoliths of eleotrids lack the postdorsal projection seen in many gobiids, and they often show a postventral projection that is very rarely observed in gobiids (see also Reichenbacher and Weidmann 1992; Schwarzhans 2010).

Certain groups of distinct otolith morphologies can be observed in the Recent Eleotridae from the Indo West-Pacific, as follows.

(i) A group containing the genera *Butis*, *Bostrychus*, and *Ophiocara* (Fig. 11A–I), all of the subfamily Butinae, are characterized by a trapezoidal outline with pronounced pre-ventral and postventral projections. Another character of the otoliths of these genera is the location of the sulcus, which reaches close to the anterior-ventral rim of the otolith and sometimes almost opens to it. This character is interpreted as plesiomorphic.

(ii) The otoliths of the genera *Gobiomorphus* and *Philypnodon* (Fig. 11K–S) of the subfamily Eleotrinae are largely similar to the above group in outline, but the sulcus stays at

the centre of the inner face and does not approach the anterior rim. This group is endemic to Australia and New Zealand. Another endemic cave eleotrid from NW-Australia (*Milyeringa*) could belong to the same group (Fig. 12P).

(iii) Another group comprises mostly genera from the subfamily Eleotrinae including *Belobranchnus*, *Bunaka*, *Giurus*, *Mogurnda*, *Allomogurnda*, and *Hypseleotris* (Fig. 12A–I) and possibly also *Calumia* (Fig. 11 J). These all have compressed otoliths with a ratio OL:OH ranging from 0.8 to 1.1, which is the main difference from the otoliths of group 2 (versus ratio OL:OH 1.2–1.4).

(iv) Finally, a fourth group of eleotrid genera includes *Eleotris*, *Culius*, and *Oxyeleotris* (Fig. 12J–O) that is characterized by more elongate otoliths, typically with a postdorsal instead of a postventral projection. Their otoliths do not show any significant distinction from many gobiid genera.

The eleotrid otoliths described here from the new extinct genus *Mataichthys* resemble most those of the genera *Gobiomorphus* and *Philypnodon*, which together with the endemic *Grahamichthys* (otoliths not known) represent the extant fresh water eleotrids in New Zealand and temperate Australia.

Genus *Mataichthys* Schwarzhans, Scofield, Tennyson, and T. Worthy nov.

Type species: *Mataichthys bictenatus* Schwarzhans, Scofield, Tennyson, and T. Worthy sp. nov.; see below.

Etymology: After Mata Creek and the fish-rich rocks therein, where the holotype was found: “mata”, as a noun in Maori can refer to a receptacle packed with preserved fish or birds, or a rock or stone, among other things (Williams 1971). Gender masculine.

Diagnosis.—An extinct genus of the family Eleotridae with the following combination of characters: body depth at ventral fin base about 16% SL; total vertebrae 28 (12 precaudal, 16 caudal); dorsal fin rays VI in first dorsal and I+10 in second dorsal; ventral fins separate, with I+7 rays; anal fin rays I+6 or 7, origin under 13th vertebra and under 4th ray of D2; caudal skeleton with 3 separated epurals; ctenoid body scales with alternating primary and secondary short and stout peripheral cteni of equal length; otoliths with median sulcus, pronounced postventral and variably developed anterior-ventral projections.

Species included.—*Mataichthys* comprises one species based on a skeleton find with otoliths in situ and many isolated otoliths of the same species, namely *M. bictenatus* and three more otolith-based species allocated purely on otolith correlation (*M. procerus*, *M. rhinoceros*, and *M. taurinus*) all from the early Miocene of the Bannockburn Formation, Otago, New Zealand.

Comparisons.—The separation of the ventral fins in the fossil skeleton suggests assignment of *Mataichthys* to Eleotridae (ventral fins are fused in Gobiidae, separate in Eleotridae) and this is further supported by characters of the caudal skeleton and the otoliths. Amongst Eleotridae, the extant *Gobiomorphus* and *Philypnodon* are considered related genera by Hoese and Gill (1993), although Thacker and Hard-

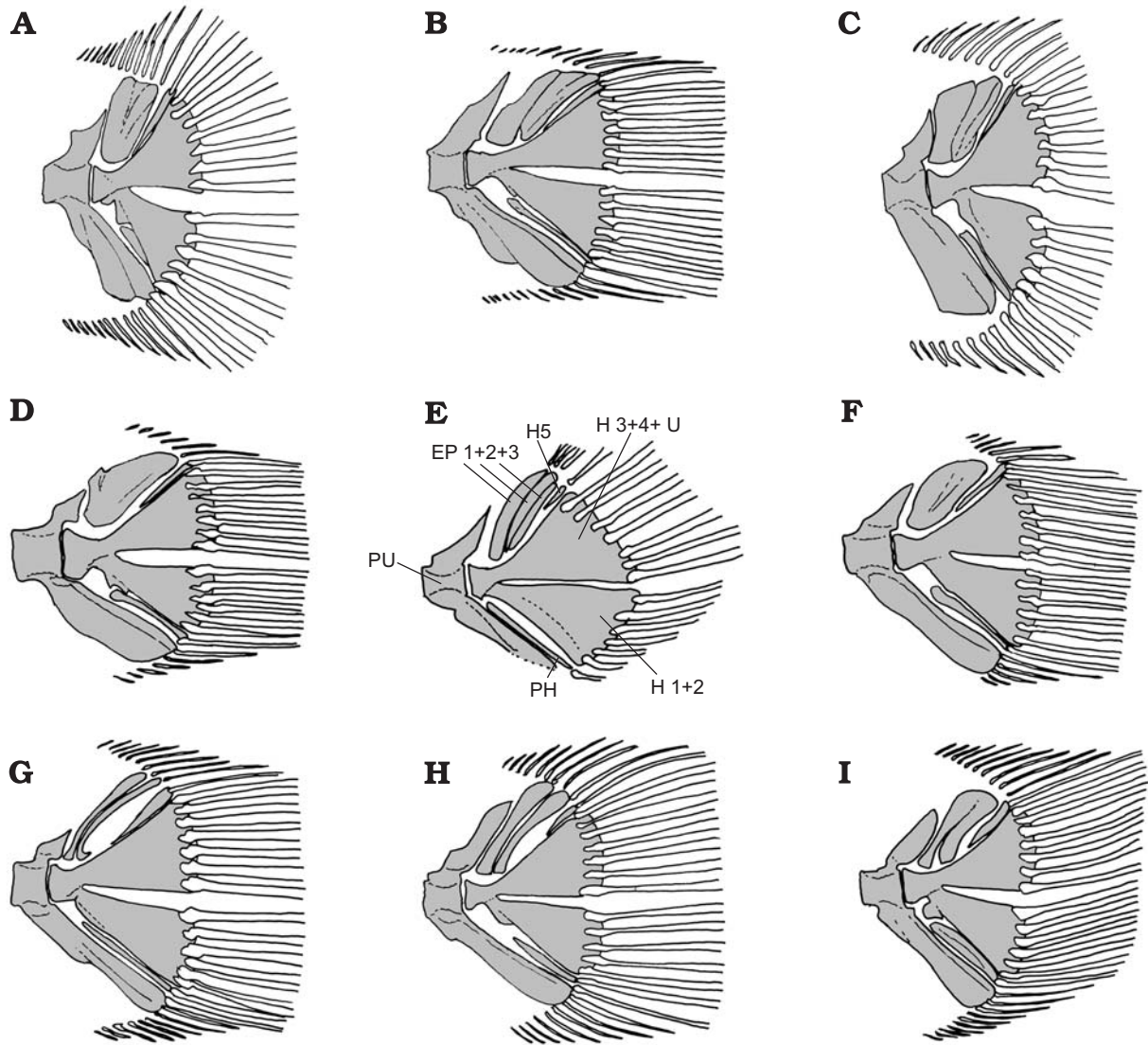


Fig. 9. Comparison of the caudal skeleton of Miocene *Mataichthys bictenatus* and Recent eleotrids based on x-rays (scaled to same size). **A.** *Gobiomorphus gobioides* (Valenciennes, 1837), NMNZ P.32815. **B.** *Gobiomorphus australis* (Krefft, 1864), ZMUC Jrn.374. **C.** *Gobiomorphus cotidianus* McDowall, 1975, NMNZ P.12719-B. **D.** *Philypnodon grandiceps* (Krefft, 1864), ZMUC Jrn.115. **E.** *Mataichthys bictenatus* Schwarzahns, Scofield, Tennyson, and T. Worthy gen. et sp. nov. (holotype, NMNZ S.52752, location 4, Mata Creek, Bannockburn Formation, early Miocene). **F.** *Butis humeralis* (Valenciennes, 1837), ZMUC Jrn.93. **G.** *Ophiocara porocephala* (Valenciennes, 1837), ZMUC Jrn.101. **H.** *Ophieleotris aporos* (Bleeker, 1854), ZMUC P.781801. **I.** *Culius fuscus* (Bloch and Schneider, 1801), ZMUC P.781283. Abbreviations: EP, epurals; H 1+2, fused hypurals 1 and 2; H 3+4+ U, fused urostylar complex and hypurals 3 and 4; H 5, hypural 5; PH, parhypural; PU 2, preural centre 2.

man (2005) do not interpret them as closely related. Both genera, however, are endemic to New Zealand and temperate Australia and are found in freshwater and marginal marine environments (diadromous). The high total number of vertebrae (27–29 in *Gobiomorphus* and *Philypnodon*), the anal fin origin far behind D2 origin (under 4th to 5th ray of D2 in *Gobiomorphus* and *Philypnodon*) and the general structure of the otolith (groups with *Gobiomorphus* and *Philypnodon*, see above) are shared features.

The specific organization of the caudal skeleton with its three broad, narrowly separated epurals is closest to the structure observed in *Gobiomorphus*, but there the 2nd and 3rd epurals are fused or nearly fused, whereas in *Mataichthys* all three epurals are separate. In *Butis* and *Philypnodon* all

epurals are fused. *Bostrychus* (see Winterbottom 1993) has three narrow epurals of which the 2nd and 3rd are fused at the base. *Ophiocara* and *Ophieleotris* have only two narrow and separate epurals. For detailed figures see Fig. 9 and Hoese and Gill (1993) on eleotrid phylogeny.

Another character separating *Mataichthys* from *Gobiomorphus* (and *Philypnodon*) is the low number of anal fin rays (I+6 or 7 versus I+8–10). Few eleotrids have such low counts (i.e., *Ophiocara*). However, the skeleton of the type specimen of *Mataichthys bictenatus* Schwarzahns, Scofield, Tennyson, and T. Worthy sp. nov. (see below) is not well enough preserved in this region to be certain. The number of ventral fin rays (I+7) is higher than in *Gobiomorphus* and *Philypnodon* (I+5–6).

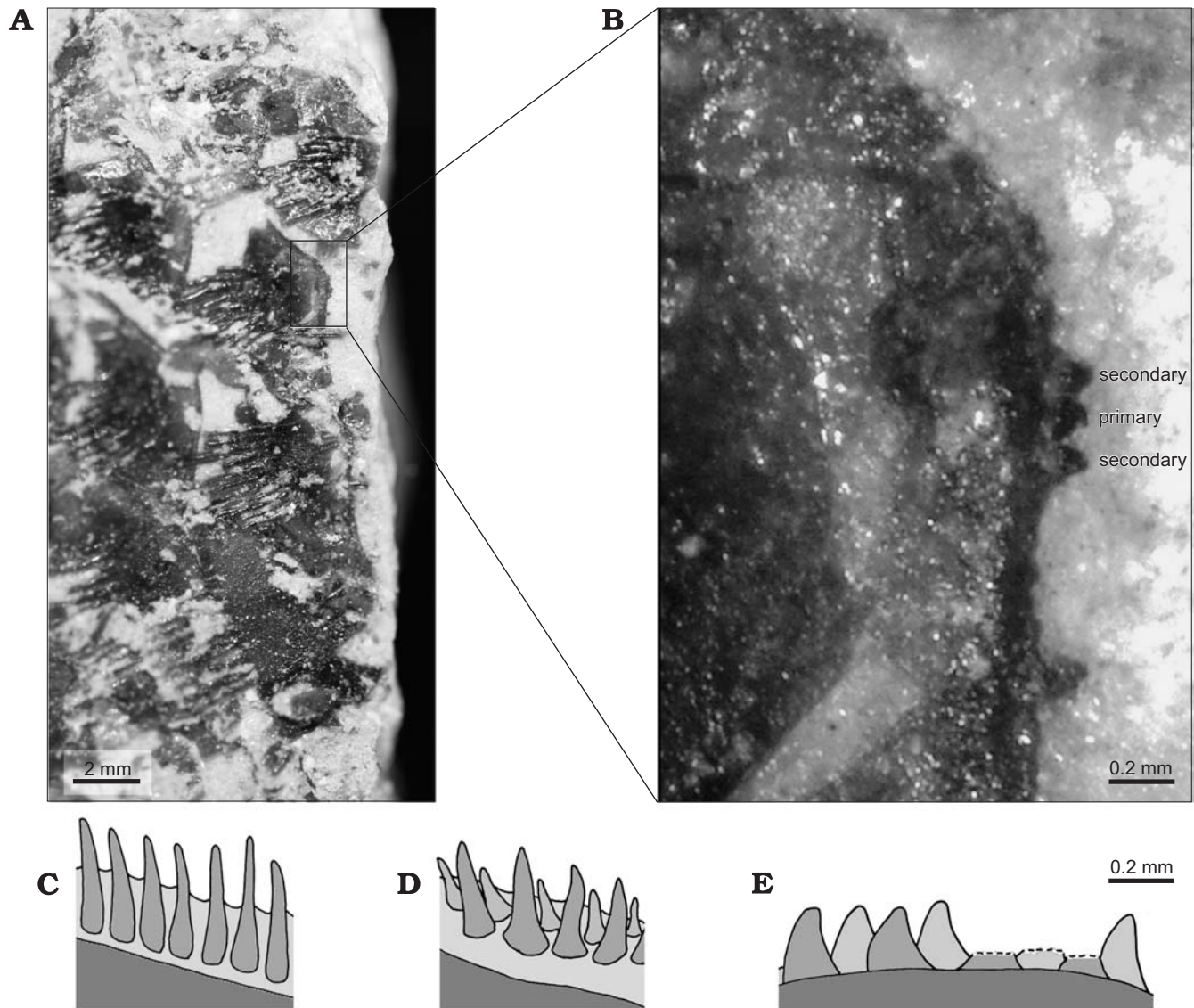
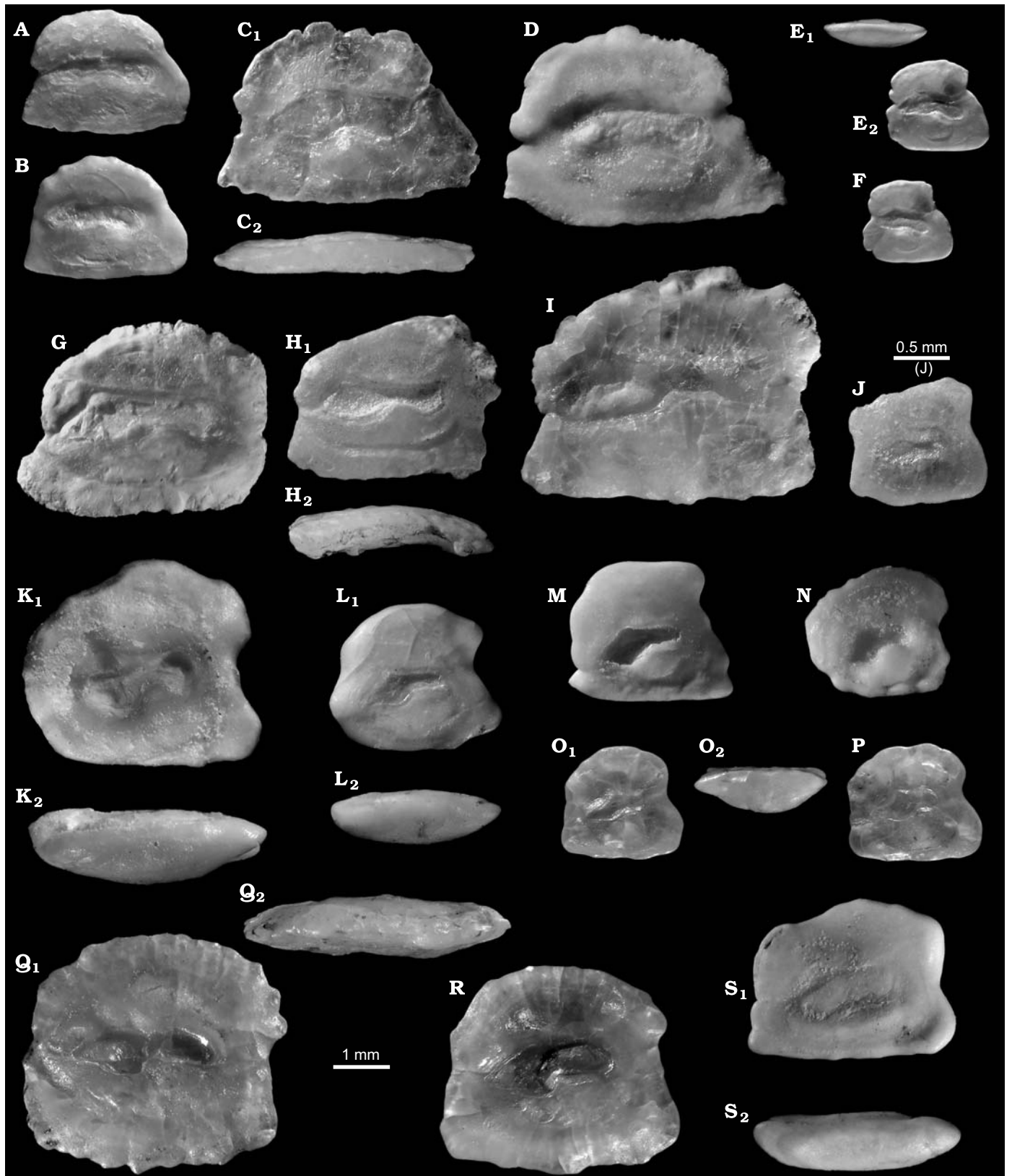


Fig. 10. Comparison of the body scale morphology of Miocene *Mataichthys bictenatus* with Recent eleotrids. **A**, *Mataichthys bictenatus* Schwarzahns, Scofield, Tennyson, and T. Worthy gen. et sp. nov. (holotype, NMNZ.S.52752, location 4, Mata Creek, Bannockburn Formation, early Miocene). **B**. Close-up of *Mataichthys bictenatus* depicting few preserved alternating primary and secondary cteni. **C–E**. Schematic drawings of the insertion of cteni on body scales in *Gobiomorphus gobioides* (Valenciennes, 1837) (from McDowall et al. 2006b) (**C**), *Eleotris* sp. (from Roberts 1993) (**D**), and *Mataichthys bictenatus* (**E**).

As in *Gobiomorphus* species the scales of *Mataichthys bictenatus* are peripherally ctenoid ornamented (Roberts 1993). They differ in that the single row of cteni have alternating primary and secondary peripheral short and stout cteni of equal length (Fig. 10), which are inserted in two bands at an upper and lower level with their bases overlapping. Scales

of *Gobiomorphus* species (Roberts 1993; McDowall et al. 2006b) show a single row of primary cteni (Fig. 10). The only record of alternating primary and secondary cteni among Recent eleotrids has been reported in *Eleotris* by Roberts, though many more eleotrid genera have yet to be investigated for this character, but these show much smaller

Fig. 11. Otoliths of recent eleotrid fishes from the Indo West-Pacific for comparison. **A**, **B**. *Butis amboinensis* (Bleeker, 1853), Recent, New Britain, ZMUC P.781670-72, inner face. **C**. *Butis butis* (Hamilton, 1822), Recent, Sumatra, collection W. Schwarzahns, donated by ZMH, inner face (C_1), ventral view (C_2). **D**. *Butis melanostigma* (Bleeker, 1849), Recent, Singapore, BMNH 1970.7.22.192-204, inner face. **E**, **F**. *Butis koilomatodon* (Bleeker, 1849), Recent, Hainan, China, collection W. Schwarzahns, donated by SMF, ventral view (E_1), inner face (E_2 , F). **G**. *Bostrychus sinensis* (Lacepède, 1801), Recent, China, collection W. Schwarzahns, donated by ZMH, inner face. **H**. *Bostrychus strigogenys* (Nichols, 1937), Recent, 04°26'S–136°53'E, WAM 31254-001, inner face (H_1), ventral view (H_2). **I**. *Ophiocara porocephala* (Valenciennes, 1837), Recent, Manus Island, Bismarck Archipelago, ZMUC P.781771-78, inner face. **J**. *Calumia profunda* Larson and Hoese, 1980, Recent, 00°35'S–130°19'E, WAM 32930-004, inner face. **K**. *Gobiomorphus australis* (Krefft, 1864), Recent, New South Wales, ZMUC collection Steel 1912, inner face (K_1), ventral view (K_2). **L**. *Gobiomorphus basalis* (Gray, 1842), Recent, Hutt river, Wellington, BMNH 1964.12.21.17-18, inner face (L_1), ventral view (L_2). **M**. *Gobiomorphus breviceps* (Stockell, 1939), Recent, Karopororo, New Zealand, →



BMNH 1964.4.30.67-68, inner face. **N.** *Gobiomorphus hubbsi* (Stockell, 1959), Recent, Orongorongo river, New Zealand, BMNH 1964.4.30.69-70, inner face. **O, P.** *Gobiomorphus cotidianus* McDowall, 1975, 2 specimens, Recent, Hawkes Bay, New Zealand, collection W. Schwarzhans, donated by Gerry Closs, inner face (O₁, P), ventral view (O₂). **Q, R.** *Gobiomorphus gobioides* (Valenciennes, 1837), 2 specimens, Recent, Kakanui estuary, New Zealand, collection W. Schwarzhans, donated by Don Jellyman, inner face (Q₁, R₁), ventral view (Q₂). **S.** *Philypnodon grandiceps* (Krefft, 1864), Recent, New South Wales, collection W. Schwarzhans, donated by AMS, inner face (S₁), ventral view (S₂).

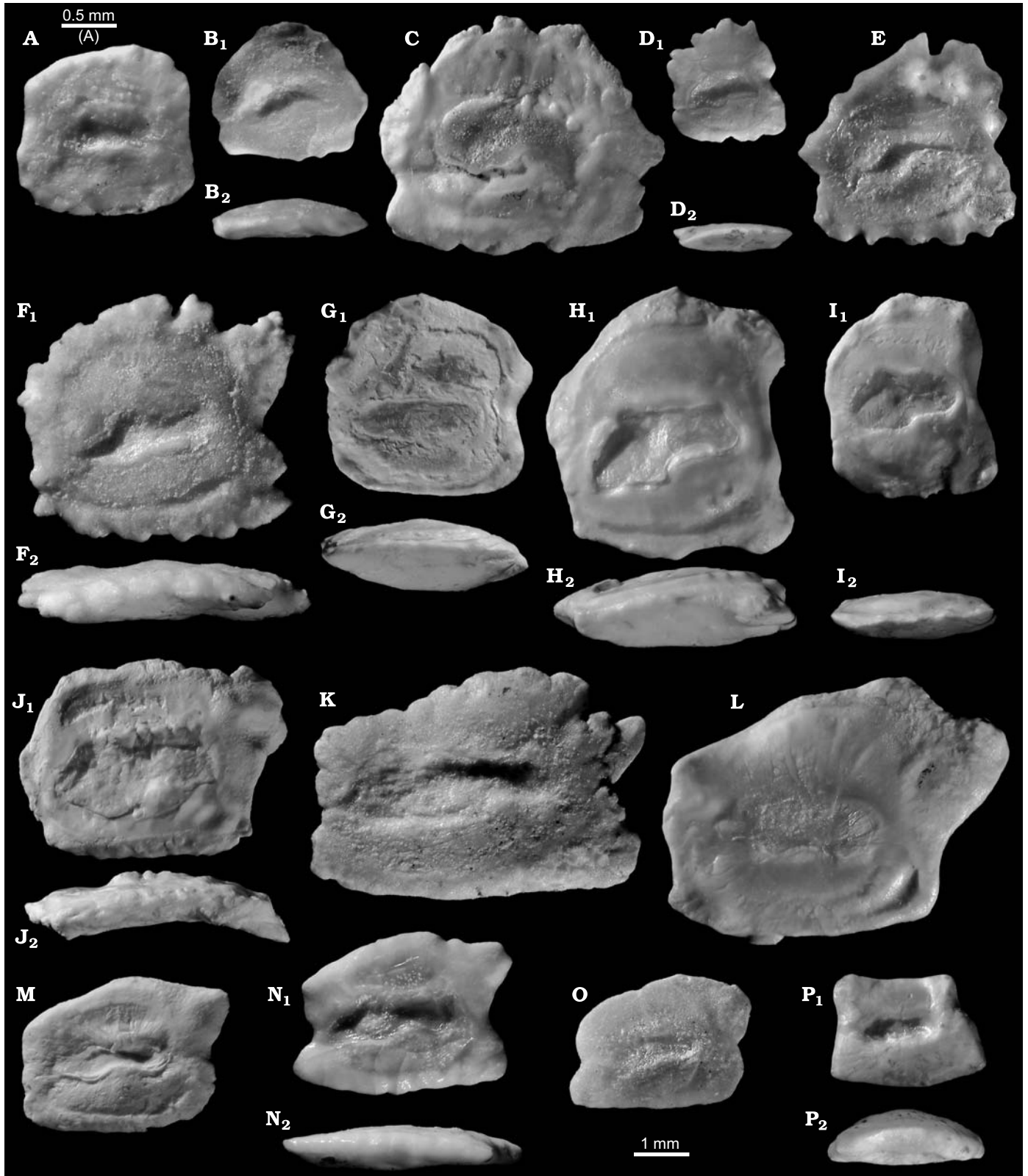


Fig. 12. Otoliths of recent eleotrid fishes from the Indo West-Pacific for comparison. **A.** *Allomogurnda nesolepis* (Weber, 1907), Recent, 04°11'S–144°46'E, WAM 29605-008, inner face. **B.** *Belobranchus belobranchus* (Valenciennes, 1837), Recent, 10°16'S–150°43'E, WAM 31634-005, inner face (B₁), ventral view (B₂). **C.** *Bunaka gyrinoides* (Bleeker, 1853), Recent, Ponape, collection W. Schwarzhans, donated by ZMH, inner face. **D.** *Giurus margaritaceus* (Valenciennes, 1837), Recent, 03°16'S–138°41'E, WAM 31753-002, inner face (D₁), ventral view (D₂). **E.** *Giurus hoedti* (Bleeker, 1854), Recent, 01°51'S–136°33'E, WAM 31041-003, inner face. **F.** *Mogurnda aurofodinae* Whitley, 1938, Recent, 03°34'S–142°57'E, WAM 29838-001, inner face (F₁), ventral view (F₂). **G.** *Mogurnda mogurnda* (Richardson, 1844), Recent, northern Australia, collection W. Schwarzhans, donated by WAM, inner →

secondary than primary cteni (Fig. 10). Clearly, the specialization of cteni in *Mataichthys* differs from *Eleotris*.

The otoliths of *Mataichthys* resemble those of the *Gobiomorphus*–*Philypnodon* group (see above) with the median sulcus and the roughly trapezoidal outline. However, *Gobiomorphus* otoliths are more rounded in outline than *Mataichthys* otoliths, and with less pronounced anterior-ventral and posterior-ventral projections. Otoliths of *Philypnodon* are more similar in outline (see Fig. 11K–S).

Species of *Mataichthys* apparently grew to a large size, possibly up to 25 cm long, judging from otolith sizes that exceed the in situ otolith of the holotype of *M. bictenatus* and comparison with a similarly sized modern species of *Gobiomorphus*, *G. gobioides*. *Philypnodon* species do not attain such sizes.

Mataichthys may be considered a plesiomorphic genus related to *Gobiomorphus* and *Philypnodon*. The separation of the three epurals of the caudal skeleton (versus the 2nd and 3rd usually fused in extant species), the trapezoidal outline of the otolith (versus rectangular to rounded in extant species of *Gobiomorphus*) and possibly the high number of ventral fin rays (I+7 versus I+5–6) are considered plesiomorphic characters. The low number of anal fin rays (I+6 or 7 versus I+8–10) and the presence of alternating primary and secondary peripheral cteni on the scales (versus only primary cteni), however, are regarded as autapomorphic features indicating that *Mataichthys* may be sister group to *Gobiomorphus*, but not within the lineage of extant species of that genus.

Stevens and Hicks (2009), in an analysis of mitochondrial DNA, concluded that the seven living species of *Gobiomorphus* in New Zealand are descendants of a single lineage that separated from the two temperate Australian species and the sister genus *Philypnodon*. They postulate that the origin of the New Zealand *Gobiomorphus* lineage resulted from a single dispersal event from Australia some 16 to 28 Myr ago and felt that this finding is corroborated by unidentified skeleton findings interpreted to belong to *Gobiomorphus* (McDowall et al. 2006b). While there is nothing in our findings in the Bannockburn Formation that would contradict Stevens and Hicks' (2009) logic, the identification of *Mataichthys* shows that the history of freshwater eleotrids in the Miocene of New Zealand was more complex, and included lineages which are now extinct.

Stratigraphic and geographic range.—Bannockburn Formation, Manuherikia River and Vinegar Hill.

Mataichthys bictenatus Schwarzhans, Scofield, Tennyson, and T. Worthy sp. nov.

Figs. 8–10, 13A–O.

?2006 *Gobiomorphus* sp.; McDowall et al. 2006b: fig. 3.

Etymology: For the bictenate nature of the scales, meaning alternating primary and secondary peripheral cteni—a feature unlike any modern *Gobiomorphus* species (Roberts 1993; McDowall et al. 2006b).

Type material: Holotype: NMNZ S.52752, skeleton with otolith in situ (Figs. 8A, B, 9E, 10A, B, E). Paratypes: 55 otolith specimens, NMNZ S.52733–34, Home Hills Station, Manuherikia River near St Bathans, Otago, early Miocene, Bannockburn Formation, HH1a bed (Fig. 13A–O).

Type locality: Location 4 at Mata Creek near St Bathans, Otago.

Type horizon: Bannockburn Formation, early Miocene.

Other material.—One fragmentarily preserved skull with otoliths (sagitta, lapillus) in situ (NMNZ S.52753, Fig. 8C), same location as holotype. 6454 otolith specimens: 5599 specimens same location as paratypes; 519 specimens Manuherikia River, HH1b bed, trench excavation; 17 specimens Manuherikia River, HH4; 78 mostly juvenile specimens Manuherikia River, HH1d; 59 specimens, Vinegar Hill, site 1; 182 specimens, Vinegar Hill, site 2.

Comment.—*Mataichthys bictenatus* is by far the most common fish species in the Bannockburn Formation as evidenced by the abundance of its otoliths. It is also the only species known from skeletal remains with otoliths in situ. The Mata Creek number 4 location has yielded a complete fish skeleton and a somewhat disintegrated and distorted isolated skull from *M. bictenatus*, both with otoliths in situ. The specimens were found at the base of a small low-relief channel less than 1 m wide and 20 cm thick (Fig. 8D), probably representing a scour fill in a nearshore lake environment. The complete fish skeleton was excavated in three pieces plus a number of smaller counterslab pieces and has a total length of about 18 cm. The specimen represents a rare opportunity in fish palaeontology to identify and describe a new species based on a skeleton with otoliths in situ. The embedding rock is soft and the fish bones often thin and fragile. It was therefore decided to take a CT-scan of the skeleton prior to preparation, which was then prepared to uncover fin rays for meristic counts and the otolith. The description of the skeleton was substantially aided by the use of the CT-scans. Due to relatively poor exposure of a large part of the head, the description of the skeleton is based mainly on meristic counts, the description of the caudal skeleton and morphometric measurements wherever possible. The presence of the otolith

face (G₁), ventral view (G₂). **H.** *Mogurnda furva* Allen and Hoese, 1986, Recent, 06°25'S–143°19'E, WAM 31685-001, inner face (H₁), ventral view (H₂). **I.** *Hypseleotris compressus* (Kreff, 1864), Recent, Cape York, Australia, BMNH 67.5.6.52-60, inner face (I₁), ventral view (I₂). **J.** *Culius fuscus* (Forster, 1801), Recent, Viti Levu, collection W. Schwarzhans, donated by ZMH, inner face (J₁), ventral view (J₂). **K.** *Oxyeleotris lineolatus* (Steindachner, 1867), Recent, northern Australia, collection W. Schwarzhans, donated by WAM, inner face. **L.** *Oxyeleotris caeca* Allen, 1996, Recent, 06°35'S–143°30'E, WAM 31208-001, inner face. **M.** *Oxyeleotris aruensis* (Weber, 1911), Recent, Aru Island, SMF 6746-52, inner face. **N.** *Oxyeleotris marmorata* (Bleeker, 1852), Recent, Borneo, Kapuas, BMNH 1982.3.29.219, inner face (N₁), ventral view (N₂). **O.** *Eleotris acanthopoma* Bleeker, 1853, Recent, 21°34'S–165°31'E, WAM 31370-001, inner face. **P.** *Milyeringa veritas* Whitley, 1945, Recent, northern Western Australia, collection W. Schwarzhans, donated by WAM, inner face (P₁), dorsal view (P₂).

in situ allowed us to link the skeleton with the most numerous taxon represented by otoliths.

Diagnosis.—Skeleton: Vertebrae 12+16 = 28, second dorsal I+10, ventral I+7, anal I+6 (or 7, assuming one missing), origin of anal under the 4th ray of the second dorsal, caudal skeleton with hypurals 1+2 fused and hypurals 3+4+urostylar fused, 3 epurals broad narrowly separated, hemal spine on last vertebra short. Otolith: OL:OH = 1.3–1.5 in specimens larger than 3.5 mm long. Anterior-ventral and posterior-ventral projections distinct, often pointed. Dorsal rim moderately high, regularly rounded.

Description of skeleton.—Standard length (SL) of the only complete specimen about 17.5 cm, which is larger than most extant species of the genus *Gobiomorphus*, except for *G. gobioides*. Body slender; body depth at ventral fin base about 16% SL. Head length about 27% SL. Vertebrae 28, 12 precaudal and 16 caudal. First dorsal fin (D1) with 6 spines. Second dorsal fin (D2) with 1 spine and 10 rays, the rays being incompletely preserved. Anal fin with 1 spine and 6 rays (plus 1 probably missing). Pelvic fin poorly preserved. Ventral fins presumably separate, not fused as in gobiids, judging from the regular shape of the fin, with 1 spine and 7 rays. Caudal fin rays 15, thereof 1 only as imprint (not visible on CT). Anal fin origin under 13th vertebra and under 4th ray of D2. Predorsal length about 40 % SL; preanal length about 65% SL; distance origin D1 to origin D2 about 16% SL. Upper jaw length about 13% SL. From base of ventral fin to anal fin origin about 35% SL. Scales ctenoid, with single row of cteni, having alternating primary and secondary short and stout peripheral cteni of equal length, about 4–6 mm in size depending on location on body, 9–10 vertical scale rows at anal fin origin (Fig. 10).

Vertebrae with long neural and haemal spines. Neural spine on last caudal vertebra short, haemal spine on last caudal vertebra long, uniformly broad. Caudal skeleton (Fig. 9) with hypurals 1+2 fused and hypurals 2+4 and urostylar fused (typical gobioid caudal skeleton). Hypural 5 small, parhypural long, 3 epurals broad, narrowly placed, but not fused (third epural as imprint). Vertebrae 3 to 12 with long ribs, longest on vertebrae 5 and 6, vertebrae 4 to 12 with epipleural spines. Head bones mostly covered in matrix or poorly visible on CT-scan except for parts of supraoccipital, opercle, parasphenoid, pterygoid, maxilla, premaxilla, dentale and frontal. Premaxilla and dentale with small conical multiserial teeth, however only partly preserved. Mouth open and gill cover probably also open indicating suffocation of fish prior to sediment embedment. Branchiostegal rays 5+. A partly disinte-

grated skull (NMNZ S.52753) has revealed a well preserved quadratum and articular.

Description of otolith.—Robust, moderately elongate otoliths up to nearly 6.5 mm long (Fig. 13A–O). OL:OH = 1.3–1.5 in otoliths from 3.5 to 6.5 mm, 1.1–1.3 in otoliths from 1 to 3 mm long; OH:OT = 3.0–3.3. Anterior-ventral and posterior-ventral projections distinct, often pointed, the posterior one often more strongly developed. Dorsal rim moderately high, regularly rounded. Ventral rim nearly straight, horizontal. Anterior and posterior rims inclined, anterior rim straight or slightly convex, rarely concave, posterior rim usually concave. Rims irregularly undulating, crenulated in juveniles.

Inner face nearly flat, with somewhat rugged surface. Sulcus with median position, moderately large and deepened, typical shoe-sole shape, slightly inclined. OL:SuL 1.6–2.0. Dorsal field high, with well marked dorsal depression. Ventral field narrower, somewhat elevated, with distinct ventral furrow. Ventral furrow close to ventral rim anteriorly, curving upward and away from ventral rim posteriorly.

Outer face slightly convex with small central umbo, irregularly ornamented or smooth.

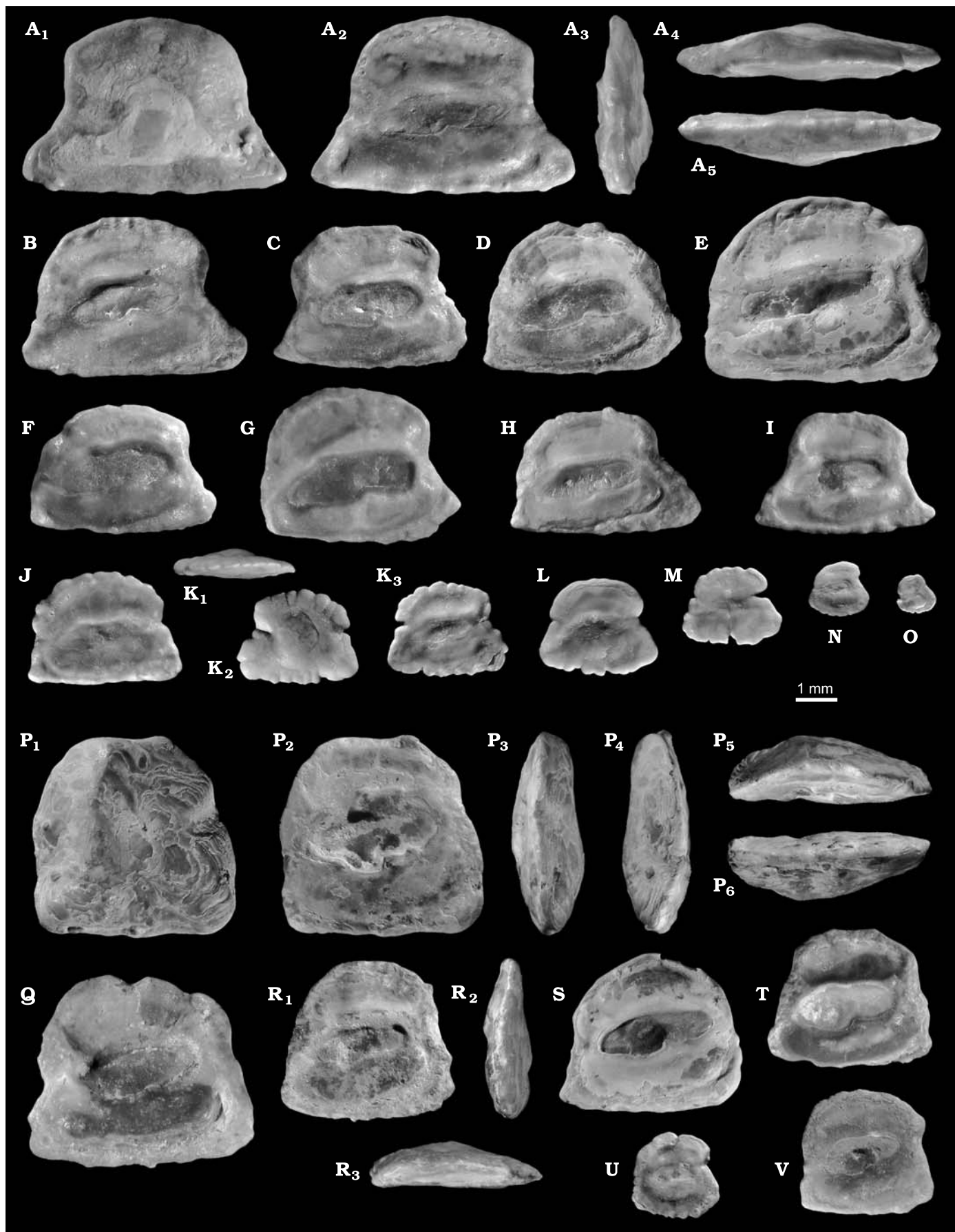
Variability and ontogeny of otoliths.—Otoliths of *M. bictenatus* exhibit a rather wide range of morphological variation, mostly associated with details of the outline, particularly of the anterior part of the otolith. The anterior rim is usually straight to slightly concave with a more or less well developed anterior-ventral rostrum-like projection. In some instances the anterior rim is slightly convex and the anterior-ventral corner nearly without projection. The strength of the posterior-ventral projection is also variable to some extent, but never lost. The variability of the ratios OL:OH and OL:SuL is larger than would typically be expected from Recent comparative eleotrid otoliths.

Ontogenetic effects are mostly associated with more ornamentation in smaller otoliths. Also the index OL:OH increases significantly with increasing size.

Otolith deformations.—Etched or deformed specimens, which are altered to such an extent that they could easily be regarded as representing different species, are fairly common. The deformations are usually expressed by over-thickening of the otolith, particularly by a convex inner face and a deep sulcus. Similar effects have been observed in a few otoliths of *Galaxias bobmcdowalli* (see above). Some typically deformed specimens are figured on Fig. 14, of which two (Fig. 14Q, S) are considered to represent *M. bictenatus*. The cause of all these observed deformations is not known.

Etched specimens are even more common and are mostly

Fig. 13. Otoliths of eleotrid fishes from the early Miocene Bannockburn Formation. A–O. *Mataichthys bictenatus* Schwarzahns, Scofield, Tennyson, and T. Worthy gen. et sp. nov., paratypes, Manuherikia River, HH1a. A. NMNZ S.52733a, outer face (A₁), inner face (A₂), posterior (A₃), dorsal (A₄), and ventral (A₅) views. B–I. NMNZ S.52733b–i, inner face. J. NMNZ S.52734a, inner view. K. NMNZ S.52734b, dorsal view (K₁), outer face (K₂) and inner face (K₃). L–O. NMNZ S.52734c–f, inner face. P–V. *Mataichthys procerus* Schwarzahns gen. et sp. nov. P–U. Manuherikia River (P–Q, T–U, HH4; R, HH1a; S, HH1d). V. Vinegar Hill, site 2. P. Holotype, NMNZ S.52735, outer face (P₁), inner face (P₂), posterior (P₃), anterior (P₄), dorsal (P₅), and ventral (P₆) views. Q–V. Paratypes. Q. NMNZ S.52736a, inner face. R. NMNZ S.52737a, inner face (R₁), posterior view (R₂), dorsal view (R₃). S. NMNZ S.52738a, inner face. T, U. NMNZ S.52736b–c, inner face. V. NMNZ S.52739a, inner face. →



characterized by smoothed and thick otolith rims. Specifically the dorsal rim, which is usually thinner than the ventral rim, becomes eroded and reduced first. Also as a result, the sulcus appears to be much larger than usual, mostly because of the erosion of the otolith rim, but also as a result of etching of the sulcus margins. A typical example is shown (Fig. 14O) and another rather extremely etched specimen (Fig. 14P). Both specimens are thought to represent *M. bictenatus*.

It is unclear what has caused the etching as well as the deformation of these otoliths, whose numbers are well above those expected from better known marine otolith assemblages. Judging from the good preservation of the otoliths, the deformation probably originated in the living fish, so may be the expression of some sort of illness. The etching is almost certainly of secondary origin, and has occurred either as a result of transport and physical erosion of the otolith prior to embedding or, possibly more likely judging from appearance and also in comparison to observations from marine environments, a result of chemical/marginal solution etching. In the case of the latter, a possible explanation could, for instance, be that the fish had been a prey item and etching occurred during the passage through the intestinal tract.

Comparisons.—Only one species of *Gobiomorphus* attains a similar size; *G. gobioides* from New Zealand reaches up to 25 cm SL. The following comparison therefore focuses primarily on these two species. *Mataichthys bictenatus* differs in the lower number of anal fin rays (I+6 or 7 versus I+9–10), the higher number of ventral fin rays (I+7 versus I+5–6), the separation of the epurals (versus all three joined), the slightly more slender shape (body depth at ventral fin base about 16% SL versus 25% SL), the longer predorsal length (45% SL versus 38% SL), the distance origin D1 to origin D2 about 16% SL (versus 19% SL) and the presence of marked posterior-ventral and often also anterior-ventral projections in the otolith (versus rounded anterior- and posterior-ventral joints).

McDowall et al. (2006b) figured and described a fish skeleton imprint preserved in somewhat distorted dorsal view from the Bannockburn Formation near Fiddlers Flat, which is the Manuherikia River section (see fossil record number H41/f66 in Fig. 2). It is about 16 cm long and they reported that it had 26 to 28 vertebrae (some uncertainty due to preservation). Its fins and caudal skeleton are poorly preserved. One fin, interpreted as pectoral, seems to contain at least 13 rays, but this is clearly incomplete due to preservation. Another fin-imprint, probably representing a dorsal fin (D2), has almost disintegrated. Given the proximity of location and stratigraphy, the little information retrievable from

the McDowall et al. (2006b) specimen does not contradict a tentative association with *M. bictenatus*.

Remarks.—*Mataichthys bictenatus* is by far the most common fish species in the Bannockburn Formation. Its otoliths are abundant in all levels of the Manuherikia River section and at Vinegar Hill. Exceptions are the poorly sampled Wharekuri Creek site and the Lauder shell bed, where the latter is probably younger stratigraphically and where *M. bictenatus* seems to be replaced by another species tentatively placed in the genus (gen. aff. *Mataichthys* sp., see below). The majority of otoliths were found at Manuherikia River, bed HH1a. Interestingly, this location is dominated by large, adult otoliths usually longer than 3 mm, many of which are poorly preserved, deformed or etched. In contrast, the HH1d bed about 3.5 m deeper in the section has yielded almost exclusively juvenile specimens of the same species below 2.5 mm in length and mostly of excellent preservation. This difference is probably the result of different facies and taphonomic environments, which are not yet understood.

Stratigraphic and geographic range.—Bannockburn Formation, Manuherikia River and Vinegar Hill.

Mataichthys procerus Schwarzahns sp. nov.

Fig. 13P–V.

Etymology: From Latin *procerus*, high-bodied, referring to the high-bodied shape of the otolith.

Type material: Holotype: NMNZ S.52735 (Fig. 13P). Paratypes: 23 specimens (7 specimens NMNZ S.52736, same location as holotype, HH4 bed; 7 specimens, NMNZ S.52737, same location as holotype, HH1a bed; 6 specimens NMNZ S.52738, same location as holotype, HH1d bed; 3 specimens NMNZ S.52739, Vinegar Hill, site 2) (Fig. 13Q–V).

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

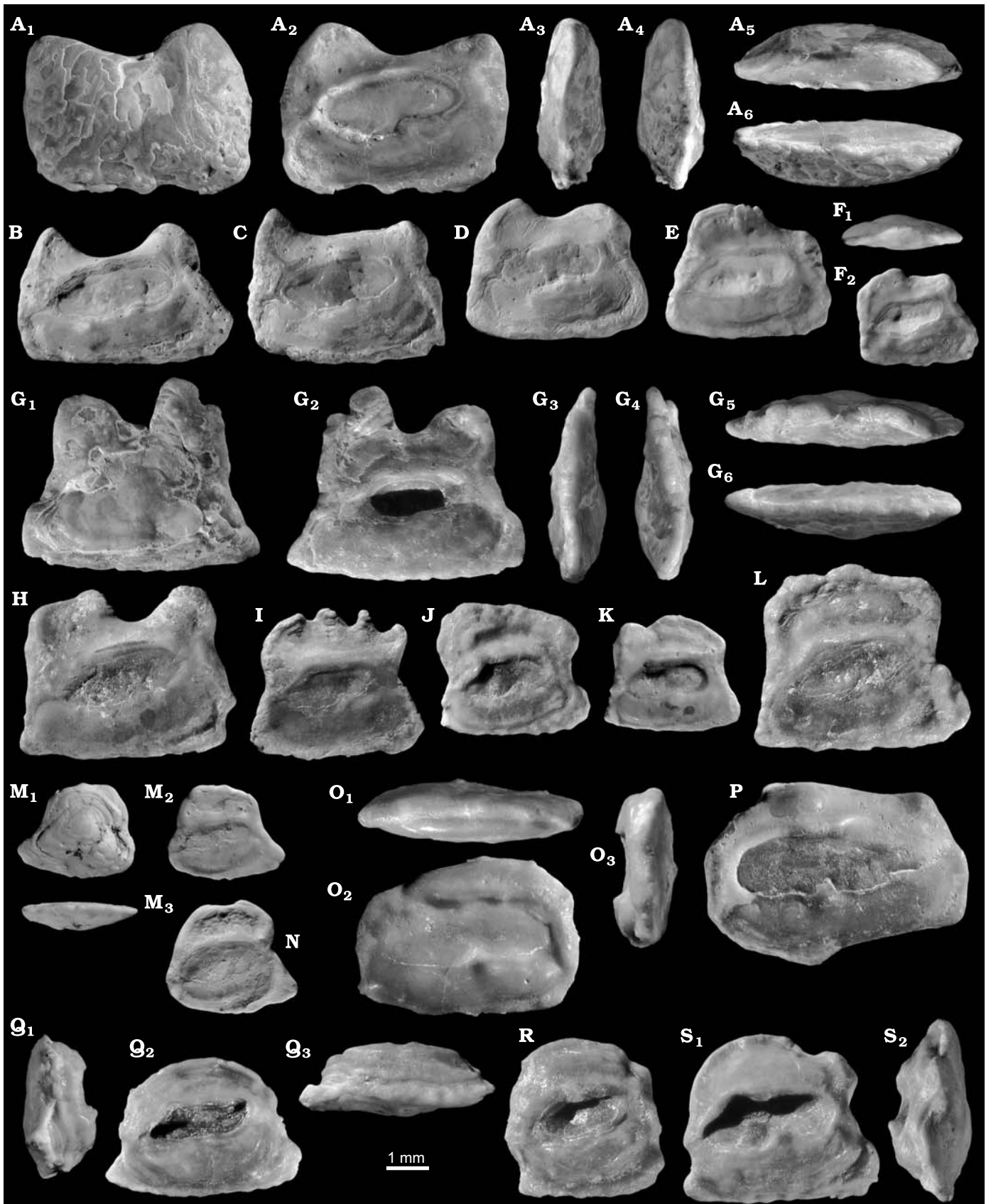
Type horizon: HH4 bed, Bannockburn Formation, early Miocene.

Other material.—444 specimens: 7 specimens, same location as holotype, HH4; 9 specimens, HH1b; 398 specimens, HH1a; 5 specimens, Vinegar Hill, site 1; 25 specimens, Vinegar Hill, site 2.

Diagnosis.—OL:OH = 1.0–1.2 in specimens longer than 3 mm. Anterior-ventral and posterior-ventral projections feeble or absent. Dorsal rim high, regularly rounded.

Description.—Robust, compressed, high-bodied otoliths up to about 5.5 mm long. OH:OT = 3.0–3.4. No or very feeble anterior-ventral projection, indistinct to moderately developed posterior-ventral projection. Dorsal rim high, regularly rounded. Ventral rim nearly straight, horizontal. Anterior

Fig. 14. Otoliths of eleotrid fishes from the early Miocene Bannockburn Formation. **A–F, H.** *Mataichthys rhinoceros* Schwarzahns sp. nov., Manuherikia River, HH4. **A.** Holotype, NMNZ S.52740, outer face (A₁), inner face (A₂), posterior (A₃), anterior (A₄), dorsal (A₅), and ventral (A₆) views. **B–F.** Paratypes, NMNZ S.52741a–e, dorsal view (F₁), inner face (B–E, F₂). **H.** Paratype, NMNZ S.52744, inner face. **G, I–L.** *Mataichthys taurinus* Schwarzahns sp. nov., Manuherikia River, HH1a. **G.** Holotype, NMNZ S.52742, outer face (G₁), inner face (G₂), posterior (G₃), anterior (G₄), dorsal (G₅), and ventral (G₆) views. **I–L.** Paratypes, NMNZ S.52743a–d, inner face. **M, N.** Gen. aff. *Mataichthys* sp., NMNZ S.52745a, b, Lauder shell bed, west of Lauder, outer face (M₁), inner face (M₂, N), ventral view (M₃). **O, P.** *Mataichthys* sp. (etched specimens, probably of *Mataichthys bictenatus* Schwarzahns, Scofield, Tennyson, and T. Worthy gen. et sp. nov.), Manuherikia River, HH1a. **O.** NMNZ S.52746a, dorsal view (O₁), inner face (O₂), posterior view (O₃). **P.** NMNZ S.52746b, inner face. →



Q–S. *Mataichthys* sp., deformed specimens, Manuherikia River, HH1a. Q, S. Probably of *Mataichthys bictenatus* Schwarzahns, Scofield, Tennyson, and T. Worthy gen. et sp. nov. Q. NMNZ S.52747a, anterior view (Q₁), inner face (Q₂), ventral view (Q₃). S. NMNZ S52747c, inner face (S₁), posterior view (S₂). R. Probably of *Mataichthys procerus* Schwarzahns sp. nov., NMNZ S.52747b, inner face.

and posterior rims blunt, slightly inclined, straight. Rims irregularly undulating, crenulated in juveniles.

Inner face nearly flat, with somewhat rugged surface. Sulcus with median position, moderately large and deepened, typical shoe-sole shape, slightly inclined. OL:SuL 1.6–1.8. Dorsal field high, with mostly well marked dorsal depression. Ventral field narrower, somewhat elevated, with distinct ventral furrow at moderate distance from ventral rim.

Outer face slightly convex with small precentral umbo, irregularly ornamented or smooth.

Remarks.—Otoliths of *M. procerus* are the second most common eleotrid species in the Bannockburn Formation after *M. bictenatus* with which it occurs. The main differences are the more compressed shape with the lower index OL:OH (1.0–1.2 versus 1.3–1.5) in adults (larger than 3 mm, not apparent in smaller specimens) and the much less pronounced anterior-ventral and posterior-ventral projections. Small specimens below 2 mm long may not always be distinguishable because the index OL:OH of both species converge as a result of allometric ontogenetic growth in *M. bictenatus* leaving the shape of the ventral and posterior rims the only useful distinguishing characters.

As for *M. bictenatus*, a few altered/deformed otoliths with thickened inner faces and deepened sulci have also been observed in *M. procerus*. One such specimen tentatively attributed to *M. procerus* is shown in Fig. 14R.

Stratigraphic and geographic range.—Bannockburn Formation, Manuherikia River and Vinegar Hill.

Mataichthys rhinoceros Schwarzahns sp. nov.

Fig. 14A–F.

Etymology: Referring to the resemblance of the dorsal rim of the otolith to the dorsal head profile of a rhinoceros.

Type material: Holotype: NMNZ S.52740 (Fig. 14A). Paratypes: Twelve specimens, NMNZ S.52741 and 52744, same location as holotype (Fig. 14B–F).

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

Type horizon: HH4 bed, Bannockburn Formation, early Miocene.

Other material.—99 specimens: 30 specimens, same location as holotype, HH4; 69 specimens, HH1a; 2 specimens HH1b.

Diagnosis.—OL:OH = 1.3–1.5 (OH measured at highest point of dorsal rim) in specimens longer than 4 mm. Anterior-ventral projection feeble or absent, posterior-ventral projection feeble to pronounced. Dorsal rim with broad and deep central concavity leaving only horn-like projections anterior and posterior.

Description.—Robust, moderately elongate otoliths up to nearly 5.5 mm long. OL:OH = 1.3–1.5 in specimens from 4 to 5.5 mm, 1.2–1.25 in specimens from 2.5 to 3.5 mm long; OH:OT = 2.5–2.8. No or very feeble anterior-ventral projection, indistinct to moderately developed posterior-ventral projection. Dorsal rim with deep and broad half-moon shaped depression, leaving only horn-like projections at anterior-dorsal and posterior-dorsal terminations. Ventral rim nearly straight,

horizontal. Anterior rim blunt to broadly rounded, posterior rim blunt or inclined, straight. Rims irregularly undulating.

Inner face nearly flat, with somewhat rugged surface. Sulcus with median position, moderately large and deepened, typical shoe-sole shape, slightly inclined. OL:SuL 1.6–1.8. Dorsal field narrow, with dorsal depression opening to concavity of dorsal rim. Ventral field narrow, somewhat elevated, with distinct ventral furrow at moderate distance from ventral rim.

Outer face slightly convex with small central umbo, smooth.

Remarks.—Otoliths of *M. rhinoceros* are easily recognized by the peculiar dorsal rim with the deep, concave depression and the horn like anterior and posterior projections. In proportions they resemble *M. bictenatus*, but differ further in the feeble or absent anterior-ventral projection. Small specimens tend to have the dorsal depression less well developed (hence a lower index OL:OH of 1.2–1.25) and those below 2.5 mm in length can probably not be distinguished from *M. bictenatus*.

Mataichthys rhinoceros represents the most common species of the genus in the HH4 bed in the Bannockburn Formation at the Manuherikia River section, whereas *M. bictenatus* is the most common *Mataichthys* species at all lower levels at this location. Apart from in the HH4 level, *M. rhinoceros* has also been found in a lower relative frequency in the HH1a bed.

Stratigraphic and geographic range.—Bannockburn Formation, Manuherikia River.

Mataichthys taurinus Schwarzahns sp. nov.

Fig. 14G–L.

Etymology: From Latin *taurinus*, bull-like, referring to the resemblance of the dorsal rim of the otolith to the horns of a bull.

Type material: Holotype: NMNZ S.52742 (Fig. 14G). Paratypes: Eight specimens, NMNZ S.52743, same location as holotype (Fig. 14H–L).

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

Type horizon: HH1a bed, Bannockburn Formation, early Miocene.

Further material.—128 specimens: 116 specimens, same location as holotype; 10 specimens, same location as holotype, HH1b bed, trench excavation.

Diagnosis.—OL:OH = 1.15–1.25. Anterior-ventral and posterior-ventral projections moderately pronounced, usually almost symmetrical. Dorsal rim high, thin, dentate or with central concavity of variable depth. OL:SuL 1.7–2.4.

Description.—Robust, high-bodied otoliths up to 5.5 mm long. OH:OT = 3.2–3.6. Anterior-ventral and posterior-ventral projections mostly distinct and symmetrically developed, or posterior-ventral projection more strongly. Dorsal rim high, thin, dentate or with central concavity of variable depth, usually deep in large specimens. Anterior-dorsally pronounced expansion in the absence of a central dorsal incision. Ventral rim nearly straight, horizontal. Anterior rim blunt, slightly concave, sometimes with anterior-dorsal lobe, posterior rim blunt, with marked concavity at level of cauda. Rims irregularly undulating.

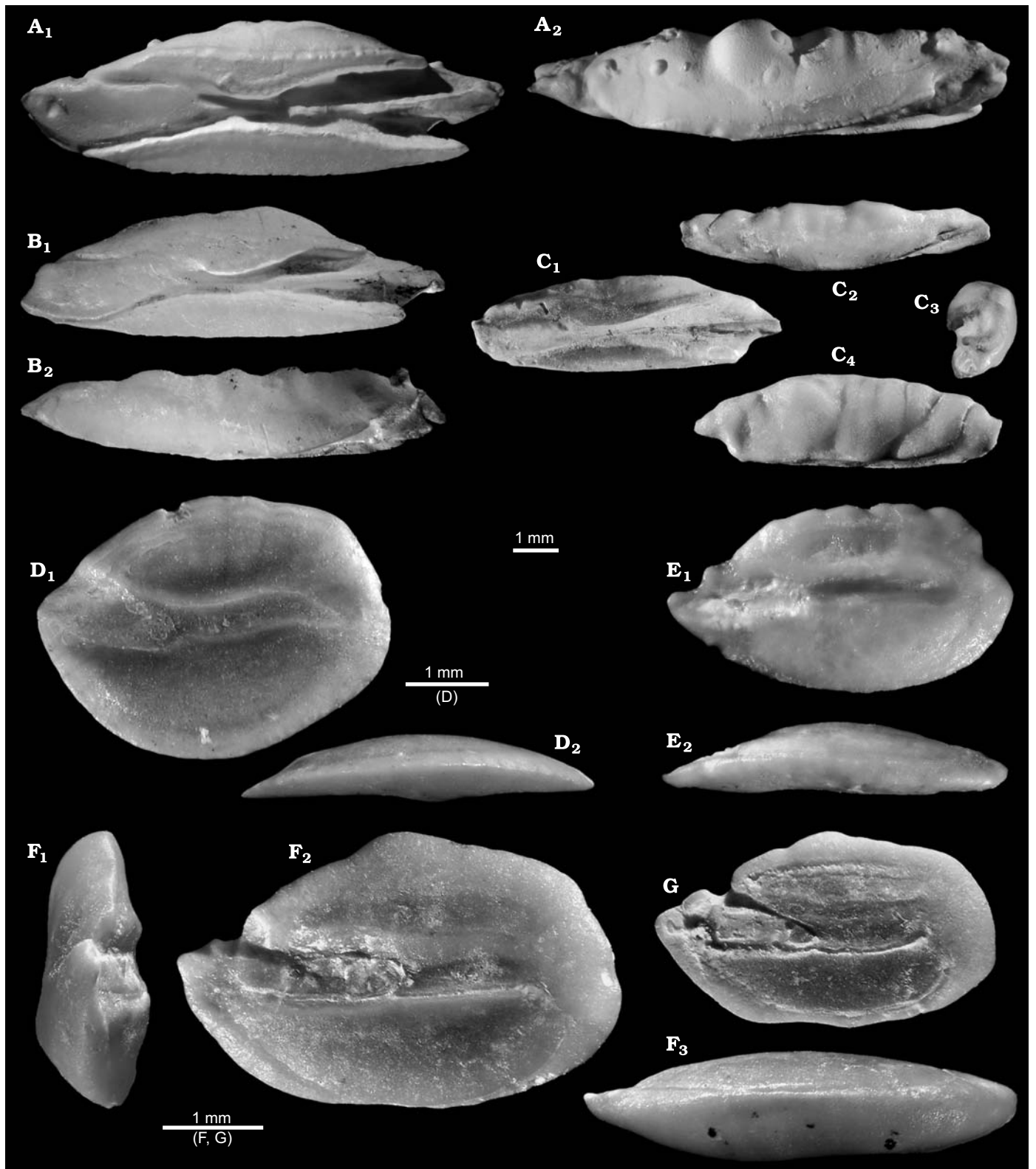


Fig. 15. Otoliths of marine fishes from the early Miocene Bannockburn Formation and from selected recent fishes for comparison. **A.** *Eeyorius hutchinsi* Paulin, 1986, Recent, off Tasmania, 41°00'S–147°23'E, WAM 27564-003, paratype, inner face (A₁), dorsal view (A₂). **B.** *Lotella rhacina* (Bloch and Schneider, 1801). **B.** Recent, of Western Australia, collection W. Schwarzhans, donated by WAM, inner face (B₁), dorsal view (B₂). **C.** NMNZ S.52748, Manuherikia River, HH1a, inner face (C₁), dorsal view (C₂), posterior view (C₃), outer face (C₄). **D.** *Lactarius sigmoidalis* (Frost, 1933), NMNZ S.52749, Manuherikia River, HH1a, inner face (D₁), ventral view (D₂). **E.** *Bleekeria viridianguilla* (Fowler, 1931), Recent, Jakarta, SMF 15768, inner face (E₁), ventral view (E₂). **F.** **G.** Genus aff. *Bleekeria sagittiformis* (Schwarzhans, 1980), Manuherikia River. **F.** NMNZ S.52750, HH1b, anterior view (F₁), inner face (F₂), ventral view (F₃). **G.** NMNZ S.52751, HH1a, inner face.

Table 1. Distribution of otoliths in the studied sections and samples.

Locations	Manuherikia River				Vinegar Hill		Aviemore	Lauder	Total
	HH1d	HH1a	HH1b	HH4	Site 1	Site 2			
Galaxiidae									
<i>Galaxias angustiventris</i>		4							4
<i>Galaxias brevicauda</i>		2							2
<i>Galaxias bobmcdowalli</i>	11	153	21		6	11			202
<i>Galaxias papilionis</i>	9	3							12
<i>Galaxias parvirostris</i>		1				4			5
<i>Galaxias tabidus</i>								3	3
<i>Galaxias</i> sp.				2					2
Retropinnidae									
<i>Prototroctes modestus</i>		16					1		17
<i>Prototroctes vertex</i>		1153	24		33	81			1291
Eleotridae									
<i>Mataichthys bictenatus</i>	78	5654	519	17	59	182			6509
<i>Mataichthys procerus</i>	6	468	9	15	5	28			531
<i>Mataichthys rhinoceros</i>		112	2	43					157
<i>Mataichthys taurinus</i>		212	10						222
gen. aff. <i>Mataichthys</i> sp.								11	11
etched and deformed specimens		1153	33	28	4	7			1225
Otoliths from marine fishes									
Moridae									
<i>Lotella rhacina</i>		1							1
Lactariidae									
<i>Lactarius sigmoidalis</i>		1							1
Ammodytidae									
gen. aff. <i>Bleekeria sagittiformis</i>		1	1						2
Total	104	8934	619	105	107	313	1	14	10197

Inner face nearly flat, with mostly smooth surface. Sulcus with median position, not very large, moderately deepened, typical shoe-sole shape, slightly inclined. Dorsal field high, with dorsal depression opening into incision of dorsal rim. Ventral field narrow, somewhat elevated, with distinct ventral furrow at moderate distance from ventral rim.

Outer face slightly convex with small central umbo, smooth.

Remarks.—Otoliths of *M. taurinus* resemble *M. procerus* in their compressed, high-bodied appearance, which is expressed in the low index OL:OH of less than 1.3. They differ in the thin dorsal rim with its dentations or, more commonly, central incision. Specimens 3.5 mm long and smaller tend not to have developed this dorsal incision, but are still often recognizable by their anterior-dorsal lobe. Specimens below 2.5 mm long may not always be distinguishable. Due to its dorsal incision, otoliths of *M. taurinus* may at times also resemble those of *M. rhinoceros*, particularly when eroded. The main difference is the more compressed shape (index OL:OH = 1.15–1.25 versus 1.3–1.5 in specimens longer than 3.5 mm) and the thin, narrowly incised dorsal rim (versus broad concavity and thick rim).

Stratigraphic and geographic range.—Bannockburn Formation, Manuherikia River.

Genus aff. *Mataichthys* sp.

Fig. 14M, N.

Material.—Eleven specimens, NMNZ S.52745, West of Lauder, Otago, early Miocene, Lauder shell bed.

Remarks.—A number of rather small specimens from Lauder, not exceeding 3 mm long, probably represent yet another eleotrid species, tentatively placed in *Mataichthys*, and characterized by the regularly rounded anterior rim and the massively expanded posterior-ventral projection. The sulcus is rather narrow and small. With the present material, it is not certain whether these otoliths are from juveniles of a large *Mataichthys* species like those from the other sampled sites in the Bannockburn Formation, or represent adults of a smaller species, possibly of the genus *Gobiomorphus*, which could be indicated by the regularly rounded anterior rim, a character found in otoliths of several Recent species of the genus (Fig. 11K–R). More material from Lauder is required to answer this question.

Altered/deformed and etched *Mataichthys* otoliths.

Fig. 14O–S.

Material.—Etched specimens: 1133 specimens (3 specimens, NMNZ S.52746, Home Hills Station, Manuherikia River near St Bathans, Otago, early Miocene, Bannockburn Formation, HH1a bed; 1059 further specimens, HH1a bed; 26 specimens HH1b bed, trench excavation; 28 specimens, HH4 bed; 4 specimens, Vinegar Hill, site 1; 7 specimens, Vinegar Hill, site 2), altered/deformed specimens: 98 specimens (91 specimens, NMNZ S.52747, Home Hills Station, Manuherikia River near St Bathans, Otago, early Miocene, Bannockburn Formation, HH1a bed; 7 specimens HH1b bed, trench excavation).

Remarks.—As already mentioned and briefly described under *M. bictenatus*, a number of etched and deformed *Mataichthys* otoliths are present in the samples. These are sometimes so diverse in form that they could be regarded as representing distinct species.

The etching effects are notable, as they have resulted in the erosion of the otolith rims in such a way that the ventral projections are abraded, the ventral furrow of the inner face joins to the ventral rim of the otolith or the dorsal depression of the inner face has nearly disappeared through downward erosion of the dorsal rim. The same etching effects widen the sulcus margins. These etching effects are different from the usual mechanical erosion often observed in fossil otoliths in that the otoliths still appear well preserved, so that the effects probably result from some chemical etching (see also discussion under *M. bictenatus*).

The alterations observed and thought to represent deformations are always similar in nature, i.e., unusual thickening of the ventral field, reduction of the dorsal rim and deepening of the sulcus.

Otoliths of marine fishes

Gadiformes Goodrich, 1909

Moridae Goode and Bean, 1896

Genus *Lotella* Kaup, 1858

Type species: *Lotella schlegeli* Kaup, 1858 (= *Lota phycis* Temminck and Schlegel, 1846). Type by monotypy. *Lotella schlegeli* is an unneeded substitute for *Lota phycis*. Nagasaki, Japan.

Lotella rhacina (Bloch and Schneider, 1801)

Fig. 15C.

Material.—One specimen, NMNZ S.52748, Home Hills Station, Manuherikia River near St Bathans, Otago, HH1a bed, Bannockburn Formation, early Miocene.

Remarks.—This is the first record of the genus and species in the fossil record. Bed HH1a was mined from beneath a 2 m thick cover bed of Holocene fluvial gravels, so there is no possibility of contamination from a Recent occurrence. A Recent otolith of *L. rhacina* is figured for comparison (Fig. 15B) to illustrate the somewhat unexpected occurrence of the Recent species obtained from sediments of early Miocene age. In an analysis of species time spans based on otoliths, Schwarzhans

(2010) showed that only about 10% of species of marine fishes recorded from the early Miocene (19–16 Ma) of the North Sea Basin can be attributed to extant species. For further comparison, a Recent otolith of the related temperate Australian morid *Eeyorius hutchinsi* Paulin, 1986 is figured (Fig. 15A).

Stratigraphic and geographic range.—Bannockburn Formation, Manuherikia River; otherwise only known from the Recent, marine, New Zealand.

Perciformes Bleeker, 1859

Lactariidae Jordan, 1923

Genus *Lactarius* Valenciennes in Cuvier and Valenciennes, 1833

Type species: *Lactarius delicatulus* Valenciennes, 1833 (= *Scomber lactarius* Bloch and Schneider, 1801). Type by monotypy (also by absolute tautonymy of cited synonym); *Lactarius delicatulus* is an unneeded replacement for *Scomber lactarius*. Tranquebar, India.

Lactarius sigmoidalis (Frost, 1933)

Fig. 15D.

Material.—One specimen, NMNZ S.52749, Home Hills Station, Manuherikia River near St Bathans, Otago, HH1a bed, Bannockburn Formation, early Miocene.

Remarks.—*Lactarius sigmoidalis* represents a common species in the late Oligocene and early Miocene of New Zealand, ranging stratigraphically from Duntroonian to Lillburnian (about 25 to 12 Ma). It is thus of limited stratigraphical relevance.

Stratigraphic and geographic range.—Bannockburn Formation, Manuherikia River; otherwise in marine strata of New Zealand from Duntroonian, late Oligocene, to Lillburnian, middle Miocene of Canterbury, Otago and Southland, southern Island, New Zealand.

Ammodytidae Bonaparte, 1832

Genus *Bleekeria* Günther, 1862

Type species: *Bleekeria kallelepis* Günther, 1862. Type by monotypy. Madras, India.

Genus aff. *Bleekeria sagittiformis* (Schwarzhans, 1980)

Fig. 15F, G.

1980 *Trachinoideorum sagittiformis* Schwarzhans; Schwarzhans 1980: figs. 496–498.

Material.—Two specimens: one specimen NMNZ S.52750, Home Hills Station, Manuherikia River near St Bathans, Otago, early Miocene, Bannockburn Formation, HH1b bed, trench excavation; one specimen NMNZ S.52751, same location, HH1a bed.

Remarks.—Recently obtained otoliths of the extant genus *Bleekeria* of the family Ammodytidae (*Bleekeria viridiana* (Fowler, 1931), Fig. 15E), indicate that these enigmatic otoliths are better placed in Ammodytidae and close to the genus *Bleekeria*. Three species of this group have been reported from the Miocene of New Zealand, and all seem to have a rather restricted stratigraphic range: gen. aff. *B. sagittiformis*

from the Altonian (18–16.3 Ma), gen. aff. *B. latisulcatus* (Frost, 1924) from the Clifdenian and Lillburnian (16.3–11.3 Ma), and gen. aff. *B. ultimus* (Schwarzshans, 1980) from the Waiauian (11.3–10.4 Ma). The discovery of gen. aff. *B. sagittiformis* in the Manuherikia River section thus supports the Altonian age of the Bannockburn Formation of 19–16.3 Ma.

Stratigraphic and geographic range.—Bannockburn Formation, Manuherikia River; otherwise in marine strata of New Zealand from Altonian, early Miocene, of Canterbury, southern Island.

Discussion

Evolutionary significance of the otolith assemblage from the Bannockburn Formation.—This is the first record of otoliths from non-marine/lacustrine strata of New Zealand, and allows the first comprehensive assessment of the early Miocene non-marine fish fauna of that region, since many of the previous skeleton records did not allow specific identification (except for the description of *Galaxias effusus* Lee, McDowall, and Lindqvist, 2007 from the older Foulden Maar). The key finding is that many major southern endemic freshwater fish groups are already present in the fauna.

The early Miocene Galaxiidae include at least six species and represent the most species-rich group, just as they do in the modern New Zealand fauna (McDowall 2010). In terms of fossil abundance, however, they are behind Eleotridae and Retropinnidae. Only one of the six species, *G. tabidus*, significantly resembles living species such as *G. fasciatus* or *G. maculatus*. Two of the six species, *G. angustiventris* and *G. brevicauda*, have otoliths that are quite different from otoliths of extant *Galaxias* species and might well represent a separate, possibly extinct genus. Three species are remarkable for the large size of their otoliths, namely *G. angustiventris*, *G. brevicauda* and *G. bobmcdowalli*, and these probably originate from fishes longer than 30 cm. The otoliths of the other three species, *G. papilionis*, *G. parvirostris* and *G. tabidus*, probably originate from smaller species, but adults may still have reached 15+ cm long, based on comparison with Recent taxa.

The early Miocene Retropinnidae are represented by two species of *Prototroctes*, a genus with only a single species in the modern New Zealand fauna, *P. oxyrhynchus*, which has been extinct for about 80 years (McDowall 2010). Otoliths of this Recent species are not known and hence comparison is based on the second species of the genus, *P. maraena*, still extant in southern Australia. One of the fossil *Prototroctes* species, *P. vertex*, is very common; the other, somewhat smaller species, *P. modestus*, is much rarer. Otoliths of *P. vertex* are larger than those from the Recent *P. maraena* and indicate a rather larger fish, reaching more than 30 cm long.

Otoliths from fishes of the family Eleotridae are the most common in the Bannockburn Formation and are dominated

by a single species, *Mataichthys bictenatus*, which is also unique in that a skeleton with otoliths in situ has been found. The other three species, *M. procerus*, *M. rhinoceros* and *M. taurinus*, are much rarer, but they all share the large otolith size that indicates fish reaching up to 20–25 cm in adults. This is a significant observation, because few Recent eleotrids attain such sizes, and in the fresh waters of New Zealand only one, *Gobiomorphus gobioides*, “the giant bully”, reaches 25 cm long (McDowall 2010). The eleotrids from the Bannockburn Formation, however, are assigned to an extinct lineage, *Mataichthys*, rather than the Recent *Gobiomorphus* lineage.

In conclusion, there are two main findings about the fish fauna of the Bannockburn Formation: first, the remarkably large size of the otoliths, and therefore the fishes too, and second, the presence of extinct fossil groups such as *Mataichthys*, but possibly also certain species of *Galaxias* (*G. angustiventris* and *G. brevicauda*). Together, both findings indicate a diverse fish fauna in the Manuherikia lake of early Miocene age of a specific and more complex composition than might be expected by comparison with today.

Certain Recent freshwater fishes of New Zealand have not been observed in the Bannockburn Formation despite the large sample sizes reported here, namely *Cheimarrichthys* (Pinguipedidae) and *Anguilla* (Anguillidae). The obvious reason could of course be that they were (not yet) present in the early Miocene of New Zealand, or that the environment of fossilization was unfavourable to yield such otoliths from their modes of life, as might be the case for the ‘torrent fish’ *Cheimarrichthys*. However, *Anguilla* eels are found in all freshwater habitats connected to the sea in New Zealand today, so our data suggests that they were absent from Lake Manuherikia. Also, there are other endemic genera in the families represented that have not been found, i.e., *Neochanna* (Galaxiidae), *Retropinna* and *Stokella* (Retropinnidae), and *Grahamichthys* (Eleotridae). McDowall and Lee (2005; see also McDowall 2009, 2010) reported two large scales 12 mm in diameter assumed to be from a species of Percichthyidae from the Bannockburn Formation. Percichthyidae contain a number of endemic freshwater genera and species in Australia, but are absent from New Zealand today. The large number of otoliths now obtained from the Bannockburn Formation does not support the presence of a percichthyid in the deposits sampled by us. Therefore, it appears that either the subject scales were derived from a fish not represented by otoliths or are from a marine fish, such as *Lactarius*.

Palaeoecological interpretation.—Most specimens and the richest associations of otoliths have been obtained from the Manuherikia River section, particularly from the HH1a bed (Table 1). This was deposited in a nearshore lake environment in the vicinity of a braided river inflow. The sediments may have dried out at times, as evidenced by desiccation features such as mud cracks and hyriid mussel enriched layers. It is possible that the unusual density of otoliths in these

strata was enhanced by activities of animals preying on fish, probably mostly birds but also crocodylians, which would tend to rest near the shore. Gulls, herons, palaelodids and accipitrids, all potential fish predators, are known from the St Bathans Fauna (Scofield et al. 2010; Worthy et al. 2007, 2010b). Otoliths are known to be ejected in regurgitation pellets by birds or to pass through their intestines. Such processes could also help explain the etching observed in several eleotrid otoliths.

The richness of fish species in the fossil deposits may be due to the comingling of remains of dominant lacustrine fishes with some riverine fishes brought in by the streams, or by the addition of prey remains. The latter is the most likely explanation for the rare presence of otoliths of marine fishes. Other explanations, such as occasional incursion of marine fishes into the lake, appear unlikely because of the type of marine fishes observed, and erosion and re-deposition of otoliths from older marine sediments in the vicinity is unlikely, because the fossils we report show no evidence of transport (erosion) and otoliths do not typically endure such events very well.

Biostratigraphic interpretation.—The Bannockburn Formation has been dated as early to early middle Miocene based on palynology (see Mildenhall 1989; Mildenhall and Pocknall 1989; Pole and Douglas 1998; Pole et al. 2003) with a range from 19 to 16 Ma and thus is part of the Altonian stage of the marine New Zealand Tertiary (included in the Burdigalian age of the international geological time scale). This finding is now corroborated by the occurrence of two marine fish taxa, namely *Lactarius sigmoidalis* and genus aff. *Bleekeria sagittiformis*, the latter so far being stratigraphically restricted to the Altonian.

The small otolith fauna from the Wharekuri Creek site has some species in common with bed HH1a, which supports the interpretation, based on lithological similarity, that this exposure is part of the Bannockburn Formation. The exposures, here and elsewhere in the Waitaki Valley, have been separated from those to the south by the late Miocene uplift of several thousand metres forming the intervening Hawkdun Range. In contrast, the otolith association from the Lauder shell bed differs significantly from the rich Manuherikia River beds and also from the Vinegar Hill locations. In fact, it appears that not a single species is found in common between Lauder and the other locations sampled (Table 1). This might reflect either a different environment at Lauder or, more likely that the Lauder shell bed is stratigraphically younger than the sediments of the two other locations.

Acknowledgements

For support in obtaining Recent comparative otoliths we thank Gerald Allen and Sue Morrison (WAM, Perth), the late C.J.M. Glover (SAMA), John Paxton (AMS), Don Jellyman (NIWA), Peter Castle (NMNZ), Oliver Crimmen (BMNH), Jørgen Nielsen and Peter Møller (ZMUC), Horst Wilkens (ZMH), Farid Krupp (SMF). Carl Struthers (NMNZ) provided

x-rays of *Gobiomorphus* and Tammes Menne (ZMUC) provided x-rays of other eleotrids. We thank staff at Christchurch Hospital Radiology department for the use of the CT Scanners. Jørgen Nielsen (ZMUC) is thanked for his valuable comments on the description of *Mataichthys bictenatus* skeleton. We thank Barry Douglas for providing the measurements for the lower 7 m of the Manuherikia River Section (Fig. 2) and Jamie Wood for help in measuring the remainder of that section. We are particularly thankful for the continued generous support to this project by the owners of Home Hills Station, Ann and Euan Johnstone, and to John Templeton, the manager of Dunstanburn Station for access to Mata Creek. This research is part of the project DP0770660 funded by the Australian Research Council, and is also supported by the authors' institutions.

References

- Bunce, M., Worthy, T.H., Phillips, M.J., Holdaway, R.N., Willerslev, E., Haile, J., Shapiro, B., Scofield, R.P., Drummond, A., Kamp, P.J.J., and Cooper, A. 2009. The evolutionary history of the extinct ratite moa and New Zealand Neogene paleogeography. *Proceeding of the National Academy of Sciences U.S.A.* 106: 20646–20651.
- Cooper, R.A. (ed.) 2004. New Zealand Geological Timescale. *Institute of Geological and Nuclear Sciences Monograph* 22: 1–284.
- Deng, X., Wagner, H.-J., and Popper, A.N. 2010. The inner ear and its coupling to the swim bladder in the deep-sea fish *Antimora rostrata* (Teleostei: Moridae). *Deep-Sea Research I* 58: 27–37.
- Douglas, B.J. 1986. *Lignite resources of Central Otago. Manuherikia Group of Central Otago, New Zealand: stratigraphy, depositional systems, lignite resource assessment and exploration models.* 2 vols. 104 pp. New Zealand Energy Research and Development Committee Publication, Wellington.
- Douglas, B.J., Lindqvist, J.K., Fordyce, R.E., and Campbell, J.D. 1981. Early Miocene terrestrial vertebrates from Central Otago. *Geological Society of New Zealand newsletter* 53: 17.
- Frost, G.A. 1924. Otoliths of fishes from the Tertiary formation of New Zealand. *Transactions and Proceedings of the New Zealand Institute* 55: 605–614.
- Frost, G.A. 1933. Otoliths from the Tertiary formations of New Zealand. *Transactions and Proceedings of the New Zealand Institute* 63: 133–142.
- Hand, S.J., Beck, R., Worthy, T.H., Archer, M., and Sigé, B. 2007. Australian and New Zealand bats: The origin, evolution, and extinction of bat lineages in Australasia. *Journal of Vertebrate Paleontology* 27: 86A.
- Hoese, D. and Gill, A. 1993. Phylogenetic relationships of eleotridid fishes (Perciformes: Gobioidei). *Bulletin of Marine Science* 52: 415–440.
- Jones, M.E.H., Tennyson, A.J.D., Worthy, J.P., Evans, S.E., and Worthy, T.H. 2009. A sphenodontine (Rhynchocephalia) from the Miocene of New Zealand and palaeobiogeography of the tuatara (*Sphenodon*). *Proceedings of the Royal Society B* 276: 1385–1390.
- Koken, E. 1884. Über Fisch-Otolithen, insbesondere über diejenigen der norddeutschen Oligocän-Ablagerungen. *Zeitschrift der Deutschen geologischen Gesellschaft* 36: 500–565.
- Lee, D., Lindqvist, J., Mildenhall, D., Bannister, J., and Kaulfuss, U. 2009. Paleobotany, palynology and sedimentology of Late Cretaceous–Miocene sequences in Otago and Southland. *In*: I.M. Turnbull (ed.), *Field Trip Guides, Geosciences 09 Conference, Oamaru, New Zealand. Geological Society of New Zealand Miscellaneous Publication* 128B: FT 12-1–FT 12-39.
- Lee, D.E., McDowall, R.M., and Lindqvist, J.K. 2007. *Galaxias* fossils from Miocene Lake deposits, Central Otago, New Zealand: the earliest records of the Southern Hemisphere family Galaxiidae (Teleostei). *Journal of the Royal Society of New Zealand* 37: 109–130.
- Lindqvist, J.K. 1994. Lacustrine stromatolites and oncoids: Manuherikia Group (Miocene), New Zealand. *In*: J. Bertrand-Sarfati and C. Monty

- (eds.), *Phanerozoic Stromatolites II*, 227–254. Kluwer Academic Publishers, Dordrecht.
- Lindqvist, J.K. and Lee, D.E. 2009. High-sequence paleoclimate signals from Foulden Maar, Waipiata volcanic field, southern New Zealand: An early Miocene varved lacustrine diatomite deposit. *Sedimentary Geology* 222: 98–110.
- McDowall, R.M. 1976. Notes on some *Galaxias* fossils from the Pliocene of New Zealand. *Journal of the Royal Society of New Zealand* 6: 17–2.
- McDowall, R.M. 2009. Historical and ecological context, pattern and process, in the derivation of New Zealand's freshwater fish fauna. *New Zealand Journal of Ecology* 34: 1–10.
- McDowall, R.M. 2010. *New Zealand Freshwater Fishes: An Historical and Ecological Biogeography*. 449 pp. Springer, Heidelberg.
- McDowall, R.M. and Lee, D.E. 2005. Probable perciform fish scales from a Miocene freshwater lake deposit, Central Otago, New Zealand. *Journal of the Royal Society of New Zealand* 35: 339–344.
- McDowall, R.M. and Pole, M. 1997. A large galaxiid fossil (Teleostei) from the Miocene of Central Otago, New Zealand. *Journal of the Royal Society of New Zealand* 27: 193–198.
- McDowall, R.M., Kennedy, E.M., and Alloway, B.V. 2006a. A fossil southern grayling, genus *Prototroctes* (Teleostei: Retropinnidae), from the Pleistocene of north-eastern New Zealand. *Journal of the Royal Society of New Zealand* 36: 27–36.
- McDowall, R.M., Kennedy, E.M., Lindqvist, J.K., Lee, D.E., Alloway, B.V., and Gregory, M. 2006b. Probable *Gobiomorphus* fossils from the Miocene and Pleistocene of New Zealand (Teleostei: Eleotridae). *Journal of the Royal Society of New Zealand* 36: 97–109.
- Mildenhall, D.C. 1989. Summary of the age and palaeoecology of the Miocene Manuherikia Group, Central Otago, New Zealand. *Journal of the Royal Society of New Zealand* 19: 19–29.
- Mildenhall, D.C. and Pocknall, D.T. 1989. Miocene–Pleistocene spores and pollen from Central Otago, South island, New Zealand. *New Zealand Geological Survey Palaeontological Bulletin* 59: 1–128.
- Molnar, R. and Pole, M. 1997. A Miocene crocodylian from New Zealand. *Alcheringa* 21: 65–70.
- Nelson, J.S. 2006. *Fishes of the World. Fourth Edition*. 600 pp. Wiley & Sons, Hoboken, New Jersey.
- Oliver, W.R.B. 1936. The Tertiary flora of the Kaikorai Valley, Otago, New Zealand. *Transactions and Proceedings of the Royal Society of New Zealand* 66: 284–304.
- Pole, M. and Douglas, B.J. 1998. A quantitative palynostratigraphy of the Miocene Manuherikia Group, New Zealand. *Journal of the Royal Society of New Zealand* 28: 405–420.
- Pole, M.S., Douglas, B., and Mason, G.M. 2003. The terrestrial Miocene biota of southern New Zealand. *Journal of the Royal Society of New Zealand* 33: 415–426.
- Reichenbacher, B. and Weidmann, M. 1992. Fisch-Otolithen aus der oligo-/miozänen Molasse der West-Schweiz und der Haute-Savoie (Frankreich). *Stuttgarter Beiträge zur Naturkunde, B* 184: 1–83.
- Roberts, C.D. 1993. Comparative morphology of spined scales and their phylogenetic significance in the Teleostei. *Bulletin of Marine Science* 52: 60–113.
- Schwarzahns, W. 1978. Otolith-morphology and its usage for higher systematical units, with special reference to the Myctophiformes s.l. *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie* 15: 167–185.
- Schwarzahns, W. 1980. Die tertiäre Teleosteer-Fauna Neuseelands, rekonstruiert anhand von Otolithen. *Berliner Geowissenschaftliche Abhandlungen Reihe A, Geologie und Palaeontologie* 26: 1–211. [1984: Fish otoliths from the New Zealand Tertiary (English translation). 269 pp. *Report of the New Zealand Geological Society* 113]
- Schwarzahns, W. 2010. *The Otoliths from the Miocene of the North Sea Basin*. 352 pp. Backhuys Publishers, Leiden.
- Scofield, R.P., Worthy, T.H., and Tennyson, A.J.D. 2010. A heron (Aves: Ardeidae) from the early Miocene St Bathans fauna of southern New Zealand. *Records of the Australian Museum* 62: 89–104.
- Stevens, M.I. and Hicks, B.J. 2009. Mitochondrial DNA reveals monophyly of New Zealand's *Gobiomorphus* (Teleostei: Eleotridae) amongst a morphological complex. *Evolutionary Ecology Research* 11: 109–123.
- Thacker, C.E. and Hardman, M.A. 2005. Molecular phylogeny of basal gobioid fishes: Rhyacichthyidae, Odontobutidae, Xenisthmidae, Eleotridae (Teleostei: Perciformes: Gobioidi). *Molecular Phylogenetics and Evolution* 37: 858–871.
- Tennyson, A.J.D., Worthy, T.H., Jones, C.M., Scofield, R.P., and Hand, S.J. 2010. Moa's Ark: Miocene fossils reveal the great antiquity of moa (Aves: Dinornithiformes) in Zealandia. *Records of the Australian Museum* 62: 105–114.
- Weiler, W. 1942. Die Otolithen des rheinischen und nordwestdeutschen Tertiärs. *Abhandlungen des Reichsamts für Bodenforschung, Berlin* 206: 1–140.
- Whitley, G. 1956. New fishes from Australia and New Zealand. *Proceedings of the Royal Zoological Society of New South Wales* 1954–55: 34–38.
- Williams, H.W. 1971. *Dictionary of the Maori Language, 7th ed.* xl + 499 pp. Legislation Direct, Wellington, New Zealand.
- Winterbottom, R. 1993. Search for the Gobioid sister group (Actinopterygii: Percomorpha). *Bulletin of Marine Science* 52: 395–414.
- Worthy, T.H., Hand, S.J., Nguyen, J.M.T., Tennyson, A.J.D., Worthy, J.P., Scofield, R.P., Boles, W.E., and Archer, M. 2010a. Biogeographical and phylogenetic implications of an early Miocene wren (Aves: Passeriformes: Acanthisittidae) from New Zealand. *Journal of Vertebrate Paleontology* 30: 479–498.
- Worthy, T.H., Hand, S.J., Worthy, J., Tennyson, A.J.D., and Scofield, R.P. 2009. A large fruit pigeon (Columbidae) from the early Miocene of New Zealand. *The Auk* 126: 649–656.
- Worthy, T.H., Tennyson, A.J.D., Archer, M., Musser, A., Hand, S.J., Jones, C., Douglas, B.J., McNamara, J.A., and Beck, R.M.D. 2006. Miocene mammal reveals a Mesozoic ghost lineage on insular New Zealand, southwest Pacific. *Proceeding of the National Academy of Sciences U.S.A.* 103: 19419–19423.
- Worthy, T.H., Tennyson, A.J.D., Archer, M., Scofield, R.P. 2010b. First record of *Palaelodus* (Aves: Phoenicopteriformes) from New Zealand. *Records of the Australian Museum* 62: 77–88.
- Worthy, T.H., Tennyson, A.J.D., Hand, S.J., and Scofield, R.P. 2008. A new species of the diving duck *Manuherikia* and evidence for geese (Aves: Anatidae: Anserinae) in the St Bathans Fauna (early Miocene), New Zealand. *Journal of the Royal Society of New Zealand* 38: 97–114.
- Worthy, T.H., Tennyson, A.J.D., Jones, C., McNamara, J.A., and Douglas, B.J. 2007. Miocene waterfowl and other birds from Central Otago, New Zealand. *Journal of Systematic Palaeontology* 5: 1–39.