Fordyce, R. E. 2006. New light on New Zealand Mesozoic reptiles.
Geological Society of New Zealand newsletter 140: 6-15.

The text below differs from original print format, but has the same content.

New light on New Zealand Mesozoic reptiles

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Jeff Stilwell and coauthors recently (early 2006) published the first report of dinosaur bones from Chatham Island. The fossils include convincing material, and the occurrence promises more finds. Questions remain, however, about the stratigraphic setting. This commentary summarises the recent finds, considers earlier reports of New Zealand Mesozoic vertebrates, and reviews some broader issues of Mesozoic reptile paleobiology relevant to New Zealand.

The Chatham Island finds

A diverse team reports on the Chathams finds. Jeff Stilwell (fig. 1 here) is an invertebrate paleontologist with research interests on Gondwana breakup and Southern Hemisphere Cretaceous-early Cenozoic molluscs (e.g. Stilwell & Zinsmeister 1992), including Chatham Islands (1997). Several authors are vertebrate paleontologists – Chris Consoli, Tom Rich, Pat Vickers-Rich, Steven Salisbury, and Phil Currie – with diverse experience of dinosaurs. Rupert Sutherland and Graeme Wilson (GNS) are well-known for their research on tectonics and biostratigraphy.

The Chathams article describes a range of isolated bones attributed to theropod ("beast-footed," carnivorous) dinosaurs, including a centrum (main part or body of a vertebra), a pedal phalanx (toe bone), the proximal head of a tibia (lower leg bone, at the knee joint), a manual phalanx (finger bone) and a manual ungual (terminal "claw" of a finger). On names of groups, fig. 2 here gives a simple guide to dinosaur classification. Specimens are catalogued in the GNS collections. Those outside the field of vertebrate paleontology might be sceptical that isolated and sometimes incomplete bones can be identified as to position (e.g. vertebra, limb) or to species. However, this approach has been thoroughly tested since Georges Cuvier proposed the idea of "correlation of parts" – that, because organisms can be viewed as integrated whole entities, a species may be identified from only a fragment of a skeleton. In vertebrate paleontology, as in human forensic pathology, the identification of single bones is based on knowledge of more-complete specimens. There is a wealth of

Fig 1 *Jeff Stilwell in the field Seymour Is Antarctica* photo E Fordyce

supporting information in the global literature (e.g. Weishampel et al. 2004, Farlow & Brett-Surmann 1997), and the technique is widely and successfully used. Of the Chathams bones, the phalanges are compellingly dinosaurian, although it is also possible that the ungual phalanx is from the foot of a large bird. The vertebral centrum does not seem to represent a marine reptile (plesiosaur, mosasaur). For this incomplete element, the authors state that position in the vertebral column and orientation are uncertain, but their conclusion that it was from a medium-sized theropod about 4 m long and 3 m high suggests far more confidence. The fragment of tibia (reportedly proximal, and thus figured upside down) cannot reasonably belong to other than dinosaur.

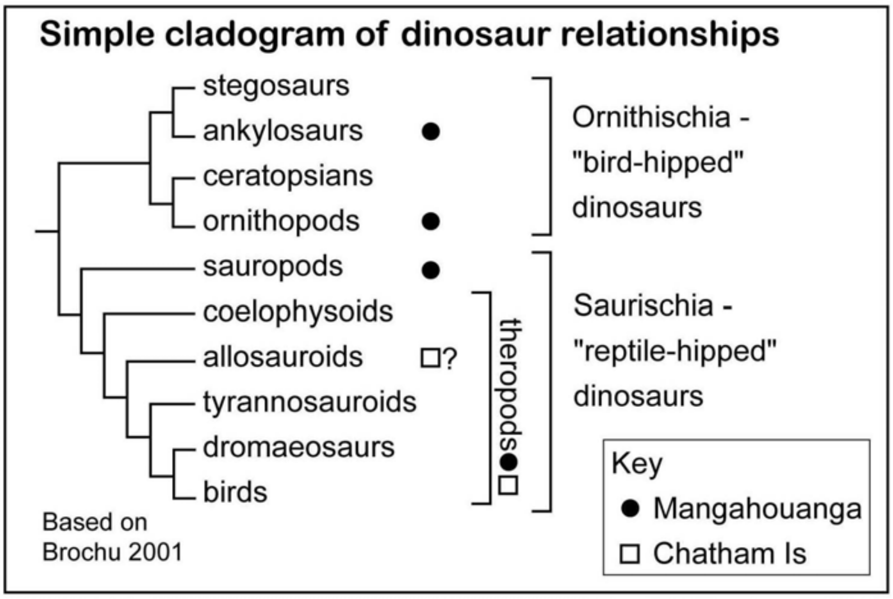

Fig 2 Simple cladogram of dinosaur relationships, based on Brochu(2001). Symbols indicate groups reported from the New Zealand Cretaceous

The stratigraphic setting is intriguing. The bones are from a coastal outcrop of Takatika Grit on the northern part of Chatham Island (see also Campbell et al. 1993: 60). This unit is a thin (~10 m) marine unit, with abundant phosphorite nodules, greensand and volcanogenic debris, resting unconformably on basement schist. Stilwell et al. (2006: fig. 2) divide the unit into 14 beds, of which 8 contain bone (although p 249 states 3 bone horizons). The article title will be taken widely to mean that the KT boundary is present in this sequence, will ensure wide citation, and will likely smooth the path to more research funding. Note, though, that the authors actually state: “The grit may represent, in part, an allochthonous accumulation of reworked uppermost Cretaceous sediments and fossils that were deposited post K–T boundary, in the Danian. However, the mixed latest Cretaceous–earliest Tertiary age of associated microfossils indicate that the K–T boundary may be present below the exposed bone-rich beds…” It’s interesting to read “may be present,” given the lack of a firm Haumurian (late

Cretaceous) or older age for the grit. Later (p 248), it is stated that the Takatika Grit is significant for allowing reconstruction of paleoenvironment and biota from just before the KT boundary, hinting at a Cretaceous age after all. Readers would have been served better had ages been indicated directly on the stratigraphic column of Stilwell et al.: fig. 2. I await a more-conclusive statement on age.

For now, we can assume that Cretaceous terrestrial bones were reworked into Paleocene shallow marine sediments. Is that really possible? Yes; dinosaur bones and remains of other terrestrial organisms have been collected many times from shallow marine strata. Consider, for example, Late Cretaceous dinosaurs from shallow marine Tahora Formation of Mangahouanga Stream, Hawkes Bay (Molnar and Wiffen 1994), and Late Eocene terrestrial mammal bones from shallow marine La Meseta Formation of Seymour Island, Antarctica (Reguero et al. 2002).

As with many good stories, there is an earlier history. Campbell et al. (1993: 62-64) mentioned the presence of reptile bones, possibly dinosaurian (see their fig. 4.30), in the Takatika Grit, but didn't offer a firm identification. Before that, in 1991, University of Canterbury Geosciences student Evan Meek reported bone associated with phosphorite horizons in the Grit, and collected several fragments of presumed plesiosaur bone now held in the Geology Museum at University of Otago.

Some points made by Stilwell et al. don't stand close scrutiny. For example, it is implied twice in the introduction to the paper that the dinosaurs are from an oceanic island, and on p 249 the authors emphasise that the dinosaurs are from an isolated setting nearly 1000 km east of New Zealand. These statements miss the point. "Oceanic" is correct in the sense that Chatham Island is now distant from mainland New Zealand, but in the geological sense and especially in the paleobiogeographic sense it is misleading, and the authors should know better: Chatham Island is based on New Zealand continental crust, not oceanic crust. Some dinosaur afficionados likely to read Stilwell et al. without knowledge of New Zealand geology could be confused needlessly by such wording. Stilwell et al. (their fig. 4) indeed show Chatham Island as continuous with what is now South Island, as also indicated in Fig. 3 of this review (based in turn on reconstructions by King).

Mesozoic terrestrial reptiles

The article on the Chathams dinosaurs is one of many on Mesozoic, mainly Cretaceous, reptiles from New Zealand. Our record of marine reptiles is highly informative, yet the more fragmentary record of dinosaurs – perhaps a shoe-box full of bones in contrast to a shipping-container full of marine reptiles – arouses interest because of implications to ecology and paleogeography. Early geologists hinted inconclusively at the presence of terrestrial reptiles. For example, Haast (1870: 189) commented, about Cretaceous reptiles at Waipara, "There was also, what I consider to be, the distal or lower portion of the femur, which, judging from the articulation, evidently had some affinities with terrestrial remains, such as the Iguanodon a herbivorous terrestrial reptile, of enormous size, and living in the Northern Hemisphere, in the wealden and greensand (Cretaceous) period" [original spellings and capitals retained]. Later, an anonymous author, most likely Hector (in McKay 1877: 41), referred to the tooth of a "megalosauroid . . . land saurian", apparently also from Waipara. The identity of these specimens was not elaborated on and, by 1900, there was still no firm evidence of dinosaurs in New Zealand. In following decades, many people assumed that those reptiles had never actually been here, and the absence of evidence was taken as evidence of absence. Fleming (1962: 93), however, cautioned in generalising about the absence of fossil land vertebrates, particularly as some living forms, such as tuatara, must have had a long Tertiary record in spite of a lack of fossils.

As it happens, in 1958, Don Haw had already discovered reptile bones in Cretaceous shallow marine strata of Mangahouanga Stream, Hawkes Bay (Haw 2002), stimulating the now widely-recognised field programme of Joan and Pont Wiffen and associates including Crabtree, McKee, and Moisley. The first formal report of a New Zealand dinosaur was by Ralph Molnar (1981), who described an isolated vertebra recovered by the Wiffen group from Mangahouanga. The bone did not match any of the marine reptiles already known from New Zealand. Molnar, a Brisbane-based dinosaur paleontologist trained in USA, convincingly argued that the vertebra recovered by Wiffen was from the tail of a theropod dinosaur. Later finds, reviewed by Molnar and Wiffen (1994) and Wiffen (1996), include fragments of other dinosaurs: the partial rib from a sauropod (large quadrupedal plant-eating saurischian), the pelvis of a hypsilophodontid (an small bipedal ornithopod), a fragment of ankylosaur (armoured ornithopod), and the phalanx of a probable theropod (but possibly a large bird). Reptiles other than dinosaurs are known from Mangahouanga, including a protostegid marine turtle (Wiffen 1981), and a fragment of pterosaur (Wiffen and Molnar 1988). Beyond the primary literature, these discoveries are well-covered in popular books (e.g. Stace and Eagle 2001).

What of New Zealand localities other than Chatham Island and Mangahouanga Stream? The only other described putative dinosaur is an isolated manual phalanx (finger bone) from the Huriwai Measures (Puraroan, Late Jurassic), south of the Waikato River mouth. This single small bone was identified as probable theropod (Molnar et al. 1998); it represents the first tetrapod vertebrate described from the New Zealand Jurassic.

There are hints of other tetrapod fossils from our Mesozoic, although these are not necessarily dinosaurian and some may actually represent marine groups. Fleming et al. (1971) mentioned the "teeth having Labyrinthodont characters" earlier reported by Hector (1880, 1886) and Worley (1894) from unspecified formations (probably Triassic) at Nugget Point, South Otago, and Wairoa district, Nelson. These could represent ichthyosaurs or, alternatively, an amphibian. Fordyce et al. (2003) recently reported a bone fragment from a large "labyrinthodont" amphibian (strictly, a sterospondyl) from the basal Triassic south of Mataura.

Mesozoic marine reptiles

The New Zealand record of marine reptiles, particularly Piripauan-Haumurian (Late Cretaceous), is significant at a global level, thanks to some rather complete and informative specimens. The key groups are plesiosaurs and mosasaurs, while the main localities are Mangahouanga Stream, Haumuri Bluff-Conway, Waipara, and Shag Point. For a historical overview, and details of some of the important species, one starts with the monograph of

Welles & Gregg (1971). That document arose from Welles' visit to New Zealand in the late 1960s (Gregg 1997) to start a new phase of study on Cretaceous reptiles after a break of about 70 years since the days of Hutton. Welles and Gregg reviewed the early contributions of Owen, Haast, Hector (especially 1874), and Hutton, and the productive field work of the indefatigable Alexander McKay. The monograph also gave details of unpublished early research, and discussed the tragic loss of fossils collected by McKay and sent overseas for study. A notable contribution of Welles and Gregg was to name and describe a new species of mosasaur (sea-lizard), *Prognathodon waiparaensis*, based on a partial skull recovered from just below the KT boundary in the Waipara River section at Laidmore-Claremont. The taxonomy in the Welles and Gregg monograph is specialised, and when I read the article as a graduate student seeking an introduction to reptile anatomy and classification, I found it not very helpful; other sources, such as books by A.S. Romer, were more rewarding. (For more recent works, see Callaway & Nicolls 1997, and many articles in Journal of Vertebrate Paleontology.)

Much research on marine reptiles has been reported since 1971, and only a brief summary is given here. Material from Mangahouanga Stream (Wiffen and Moisley 1986) includes the new plesiosaur *Tuarangisaurus* and more material attributed to *Mauisaurus*, plus mosasaurs (Wiffen 1981a, 1990) including a *Prognathodon* and 3 new species: *Moanasaurus mangahouangae*, *Rikisaurus tehoensis*, and *Mosasaurus flemingi*. It would be surprising to find a diversity of closely related species (in this case, mosasaurs) of similar size in one assemblage, and whether all the latter mosasaurs are distinct is moot.

To consider fossils from northern South Island, Caldwell et al. (2005) reported new material of the mosasaur *Taniwhasaurus oweni* (including *T. haumuriensis* of previous authors) from Haumuri Bluff. Norton Hiller and Al Mannering at Canterbury Museum have made notable advances. Hiller et al. (2005) described rather complete and highly informative new material of the plesiosaur *Mauisaurus haasti* from Ngaroma, Conway River, clarifying the concept of a species named by James Hector, and confirming *M. haasti* as an elasmosaur (extreme long-necked plesiosaur). Because *Tuarangisaurus keyesi* and *Mauisaurus haasti* are not known from comparable material (the first is based on a skull, the latter on postcranial skeleton), it is not clear whether the 2 species are truly distinct. A possible third elasmosaur species may be represented by an indeterminate fragmentary elasmosaur (Hiller & Mannering 2004) from the classical locality of Claremont-Laidmore at Waipara. Yet more material is known from Waipara: most recently, Hiller & Mannering (2005) described a cluster of postcranial remains from a large concretion, apparently representing another elasmosaur distinct from *Mauisaurus haasti*. The species was not named because it lacks a skull – probably the single most important element on which to base a new species. The most-recently recovered Waipara reptile is a mosasaur, apparently a new *Prognathodon*, which includes the skull and jaws. The fossil is under preparation (see www.otago.ac.nz/geology/features/paleontology/).

From the south, the large plesiosaur *Kaiwhekea katiki* (Shag Point) was described by Cruickshank & Fordyce (2002) as a new genus in the mainly Jurassic family Cryptoclididae - a group in which the neck is significantly shorter than in elasmosaurs. *Kaiwhekea* is notable as (currently) being the only New Zealand Mesozoic reptile represented by an articulated and nearly complete skeleton, albeit with many bones represented by natural moulds. *Kaiwhekea* was compared with 2 other Gondwanan plesiosaurs, *Aristonectes* and *Morturneria*, also thought to be cryptoclidids. Later, Gasparini et al. (2003) showed that *Aristonectes* is probably a specialised elasmosaur. Where does *Kaiwhekea* belong? It is not an elasmosaur in the usual sense of the term. O'Keefe (2004) used cladistic analysis to show that *Kaiwhekea* might not belong in the Cryptoclididae, but rather in the specialised cryptocleidoid family Cimoliasauridae. It is trite but true to say that more research is needed.

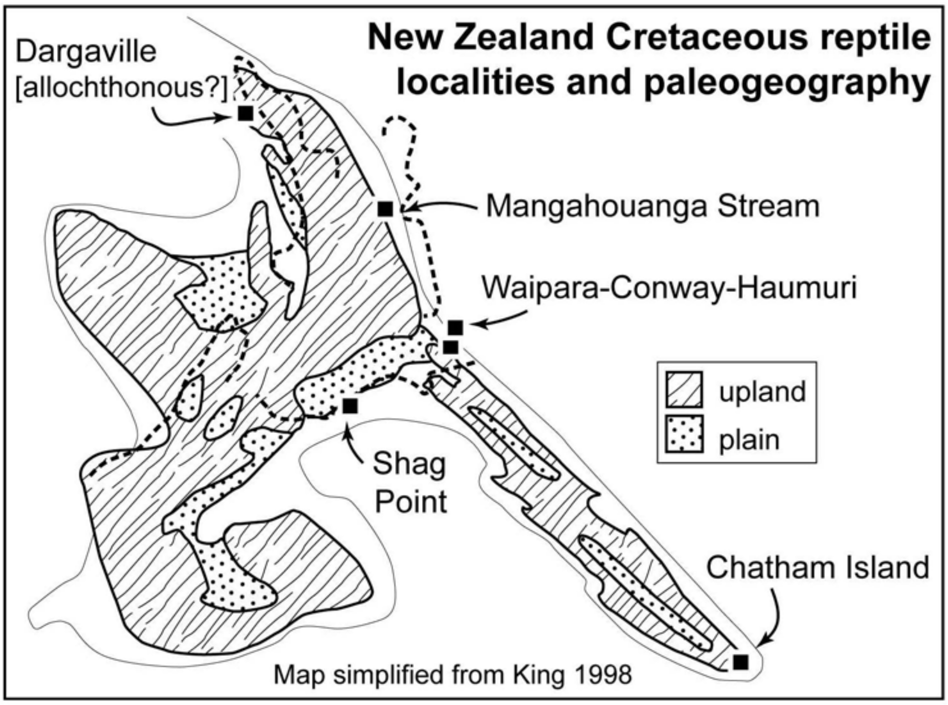

Figure 3. New Zealand Cretaceous reptile localities and paleogeography, based on Cruickshank and Fordyce (2002) with map simplified from King (1998).

Beyond mosasaurs and plesiosaurs, a third marine reptile group is known from the New Zealand Mesozoic, the dolphin-like Ichthyosauria. Fleming et al. (1971) reviewed the specimens, most of which were reported first in the 19th century. Probably the most tantalising fossil known by 1971 was the Late Triassic partial rostrum reported by Campbell (1965) from the Murihiku Supergroup. More Murihiku specimens have been found since, but they are too incomplete to identify (Fordyce 2003). Sachs & Grant-Mackie (2003) recently reported a fragment of snout of a presumed Cretaceous (and thus geologically young) ichthyosaur from Northland, giving hope of finding other more-complete material.

Mesozoic New Zealand – isolated in a high latitude setting

For the Jurassic and much of the Cretaceous, New Zealand was probably within or close to the polar circle (e.g. Lawver et al. 1992, Pole 1999, McLoughlin 2001, Schellart et al. 2006), implying significant seasonal variation in light and climate, and thus in biological productivity (plant growth). Further, by about 85 Ma (Piripauan; Cooper 2004), the Tasman Sea was opening, and the New Zealand landmass was presumably physically isolated from other parts of Gondwana. There are implications for dinosaur (and marine reptile) biology, as noted by Molnar and Wiffen (1994) for New Zealand, and by Rich et al. (2002) for southern Australia. In summary, in a high latitude setting, dinosaurs on an "island continent" would have had limited ability to migrate during winter cold and darkness. Marine reptiles would likely be affected by fluctuations in food caused by great seasonal variation in productivity. How many dinosaurs lived on Late Cretaceous New Zealand after separation from the Gondwana margin? Molnar (1981) noted that a small landmass would support only a small population of any one dinosaur species, and citing small population numbers that might barely be self-sustaining. His discussion, however, did not consider that home ranges of many organisms are not exclusive but may overlap; there may have been more dinosaurs on New Zealand than suggested by Molnar. It is intriguing also that some reptiles may represent late occurrences of groups otherwise reported earlier in the Northern Hemisphere fossils. Consider, for example, the Late Cretaceous plesiosaur *Kaiwhekea*, which apparently represents an otherwise mainly Jurassic lineage known from Europe, or the Early Cretaceous report of an *Allosaurus*-like dinosaur, presumably close to Jurassic forms from North America. Another "out of time" record is that of a supposed ceratopsian dinosaur from Victoria, which is older than the start of the great ceratopsian radiation of the northern Hemisphere. (Ceratopsians were "horned" herbivores, such as *Triceratops*.) Admittedly, those specimens known from nearly complete skeletons (*Kaiwhekea*) are more convincing than those based on single bones (the Australian *Allosaurus* and ceratopsian). Some of these issues were discussed further by Long (1998) and Rich and Rich (2000).

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