A probable theropod bone from the latest Jurassic of New Zealand

RALPH E. MOLNAR

Queensland Museum P.O. Box 3300 Brisbane, Queensland, 4101, Australia

JOAN WIFFEN

138 Beach Road Haumoana Hawke's Bay, New Zealand

BRENDAN HAYES

9A Esmonde Road Takapuna Auckland, New Zealand

Abstract A small bone found in the Huriwai Measures (Late Tithonian) south of the Waikato River, North Island, represents the first terrestrial tetrapod bone from the Jurassic of New Zealand. The bone, a phalanx, is hollow and is probably from a small theropod. Phalanges are not all uniform in form, and this one has a characteristic distal expansion that should permit identification should more complete specimens be found. Plant fossils from the Huriwai Measures suggest a forested environment. The specimen indicates that dinosaurs probably continuously inhabited what is now New Zealand at least from the Late Jurassic to the end of the Cretaceous.

Keywords Jurassic; Huriwai Measures; theropod; Tithonian; paleozoogeography; phalanges

INTRODUCTION

In early 1995, one of us (BH) found a small bone embedded in a small piece of coarse-grained, gritty, fawn arenite 3 km south of the Waikato River on the west coast of North Island. The piece of sandstone was not *in situ*. This is locality R13/ f284 in the Geological Society of New Zealand archival fossil record file. The rock also contained plant fossils. This region is mapped as the Jurassic Huriwai Group. The bone is probably a phalanx from a terrestrial tetrapod, and so represents the first evidence of terrestrial tetrapods from the Jurassic of New Zealand. The only other Jurassic tetrapod material from New Zealand is an ichthyosaur centrum, found at Kawhia well south of Port Waikato, now also at The University of Auckland Geology Department. This has not been formally described but is mentioned in Brazier et al. (1990). The latest continental reconstructions place New Zealand as part of the coast of Antarctica at 70°S during the Late Jurassic (Oxfordian) (Veevers et al. 1991). If so, then this element also represents the first Late Jurassic tetrapod from the Antarctic region of Gondwanaland. The specimen is held at The University of Auckland Geology Department, as AU13802, and a cast (QM F33573) is held by the Queensland Museum (Brisbane).

OCCURRENCE

Geology

The Mesozoic beds on the coast south of the Waikato River have been long known, having been first described by von Hochstetter (1864; English translation, 1959). The locality is mapped as the Huriwai Measures, Puaroan Stage (Late Tithonian), Late Jurassic (Purser 1961; Ballance 1988). These rocks consist of breccias, conglomerates, and coarse sandstones with thin coals, and farther inland the uppermost unit (Matira Sandstone) may extend into the lowest Cretaceous (Pocknall 1988). The Huriwai here is overlain, with a major unconformity, by coarse-grained Oligocene rocks that differ sufficiently in lithology so that the piece could confidently be referred to the Jurassic (Waterhouse 1978; Rodgers & Grant-Mackie 1988).

The presence of the plant material and the coarse-grained texture of the rock containing the bone indicate that it is derived from the Jurassic beds, not the overlying Cenozoic rock.

Associated flora and fauna and environment of deposition

An abundant flora has been recovered from the Huriwai, mostly *Cladophlebis* and *Taeniopteris* (Purser 1961), and horsetails, a liverwort, and conifer leaves and cones have also been recognised (Pocknall 1988). Rare animal fossils consist of bivalves, thought to be nonmarine (Purser 1961), with marine molluscs more abundant in the basal strata.

Ballance (1988) argued that the area of deposition was a prograding shoreline, backed by a coastal braided floodplain. He concluded that ferns—including tree ferns—and reeds grew in the region, but that the conifer material seemed to have been transported from farther inland. He interpreted the paleoclimate as cold, maybe with seasonal sea ice, a conclusion possibly consistent with Broekhuizen's suggestion (reported in Pocknall 1988)—based on the paleoflora—that the climate was cool-temperate to warmtemperate.

The region was subject to falls of volcanic ash, but far enough removed from the volcanoes that pyroclastic flows and lavas are absent (Ballance & Campbell 1993). A reconstruction of the braided floodplain delta is given in Ballance & Campbell (1993, fig. 4).

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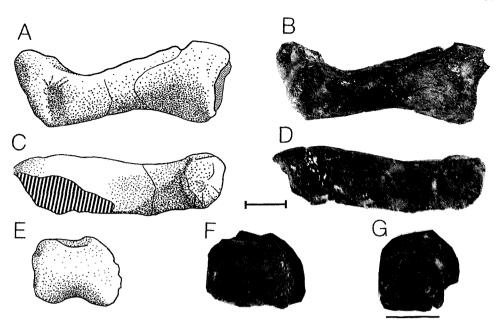


Fig. 1 Probable theropod manual phalanx (AU13802) from the Huriwai Measures, Port Waikato area, North Island: A, B oblique medial or lateral view, seen slightly from above, anterior to the left; C, D medial or lateral view, anterior to the right; E, F distal articular surface in distal view; G, broken shaft, showing that it is hollow. Shading in (A) indicates matrix on proximal end; hatching in (C) indicates broken region. Scale bar 2 mm for A–F, c. 2 mm for G.

DESCRIPTION

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The bone is stained black. It has the general form of tetrapod metapodials and phalanges, being elongate with proximal and distal expansions and flattened concave proximal and convex distal articular surfaces (Fig. 1). The distal articular surface is intact but part of the proximal articular region is broken, revealing amorphous material, without obvious bony structure (Fig. 1C, D). The distal articular face is cylindrical dorsally becoming weakly trochlear ventrally (Fig. 1E, F). The axis of curvature of the distal articular face is perpendicular to the long axis of the bone. This region projects to one side of the bone (medial?), but not the other (Fig. 1A, B). The shaft is triangular in section, with the apex directed dorsally giving the shaft laterodorsal, mediodorsal, and ventral faces. As is typical for these elements, the shaft tapers distally. The proximal articular surface is damagedlacking one ventral "corner", either ventromedial or ventrolateral-and obscured by adherent matrix, but seems to be shallowly concave with a dorsal "heel". The adherent matrix conceals the form of the surface. It is not known if the damage occurred before or after burial.

During photography the bone was accidentally broken, revealing that the shaft is hollow, with fairly thick walls (Fig. 1G).

MEASUREMENTS (mm):	
Length	10.9
Maximum height proximal articular face	3.9
Maximum width distal articular face	4.3
Maximum height distal articular face	3.5

IDENTIFICATION

Anatomical

Although the absence of a distinct trochlea at the distal articular surface and the slight development of the distal ligament pits suggests that this element is a metapodial, not a phalanx, the dorsal "heel" (extensor process) above the proximal articular surface indicates that it is actually a phalanx. This process fits a trochlear articular surface not found on carpals or tarsals and so must have articulated with a metapodial.

Poorly developed distal ligamental pits are found in the proximal phalanges of manual digit III of *Allosaurus* (Madsen 1976). Thus, this element may be a proximal phalanx, possibly of manual digit III.

Taxonomic

The forms and differences in form of phalanges in different taxa are generally poorly known, as phalanges are often regarded to be uniform in morphology and taxonomically uninformative. Phalangeal characters are not used in many of the recent phylogenetic studies of non-mammalian tetrapods, such as Benton (1985), Gauthier (1986), Pregill et al. (1986), and Gauthier et al. (1988). However, Sereno (1986) found phalanges (sometimes) useful, suggesting that such characters may be ignored in the absence of detailed knowledge of their taxonomic usefulness, not because they lack such utility altogether. Nevertheless, determining a taxonomic identification from a phalanx is difficult and uncertain.

A brief survey of the descriptive literature reveals that phalanges are often undescribed and uninformatively illustrated—but not always. Indeed, the phalanges of chelonians, plesiomorphic squamatans, and many archosaurs are generally similar in form, but differ in proportions. This form dates back at least to Late Permian times in *Saurosternon* (Carroll 1977, fig. 3), and may well be older. The proportional differences seem to reflect differences in body size as expressed in limb posture. In other words, phalanges from large, heavy animals with graviportal locomotion tend to be stouter and more robust than those of smaller, lighter, cursorial animals: phalanges of large tortoises are stouter than those of iguanids.

However, our survey also showed that some phalanges are characteristic in form, and a few taxa can reliably be identified from phalangeal characters. For example, the distal manual phalanges of *Drepanosaurus*, a plesiomorphic Triassic neodiapsid, are markedly constricted just proximal to the distal articulation and then inflated proximal to this constriction (Renesto 1994, fig. 6–8). The second pedal phalanges of *Phelsuma*, a living gekkonid, have a distal articular region that is broader than the rest of the element, giving them a T-shape in dorsal or ventral view (Russell & Bauer 1990, fig. 1). The distal phalanges of plesiomorphic Triassic turtles (*Proganochelys*) have extensive plate-like horizontal flexor processes projecting back from the ventral edges of the proximal articular faces (Gaffney 1990, fig. 162, 175). Strong flexor processes are retained in some (nonmarine) chelonian lineages to the present (Gaffney 1990; e.g., Gilmore 1934, fig. 7).

So, some unusual phalanges may be taxonomically characteristic, and the unusual form of the Huriwai phalanx, with the distal articular region expanded on one side but not the other, indicates that if more complete material of the same taxon is found (with phalanges), this bone could be referred to it with some confidence.

Considering those tetrapods likely to have been present in New Zealand during the Late Jurassic, the well-finished nature of the proximal articular face (insofar as is visible) suggests that it is not from a frog. Modern frog phalanges in the QM collection have cartilaginous articular faces unlike this in form.

The phalanges of modern lizards in the QM collection, varanids and agamids, have a more strongly developed flexor process beneath the proximal articular surface, a character also found in some Cretaceous lizards (e.g., *Polyglyphanodon* [Gilmore 1942, pl. 25] and *Telmasaurus* [Gilmore 1943, pl. 52]) and in at least some chelonians (cf. Gilmore 1934, fig. 7). This suggests that the Huriwai phalanx is not from a lizard.

Sphenodontians (and at least some primitive lepidosauromorphs) have constricted phalanges, with a markedly broader distal articular region expanded equally on both sides (cf. Carroll 1976, fig. 4 [Noteosuchus]; 1988, fig. 3B [Acerosodontosaurus] and 3C [Sphenodon]; Fraser & Walkden 1984, fig. 14 [Planocephalosaurus]). The distal region expanded only on one side seen here would seem to rule out sphenodontians.

Plesiomorphically, chelonians have strongly constricted phalanges (Gaffney 1990, fig. 162, 175), which are retained in some lineages until the end of the Cretaceous (Whetstone 1978, fig. 15, 18). So it is not from a plesiomorphic chelonian. Many nonmarine chelonian phalanges, including those of modern chelids, have a strong ventral posterior process, giving the phalanges a marked taper, and the distal trochlea seems to be well developed. Thus, turtles seem to be ruled out.

The general form, and particularly the hollow shaft, suggests that the bone derives from an archosaur, probably a dinosaur, as the walls of the bone are proportionately thicker than is usual in pterosaurs, and other archosaurs are not known to have had hollow phalanges. In addition, crocodilian phalanges typically have a shallow excavation on their dorsal surfaces just proximal to the distal trochleae, absent in this bone. Some non-avian theropods have hollow phalanges as do some birds (and even in birds hollow phalanges are thought to be unusual: cf. Perrins 1979, p. 32) and at least one ornithopod (Molnar & Wiffen 1994). So the identification as archosaur, probably theropod, seems most likely on the basis of the evidence available.

DISCUSSION

The size of the bone suggests that it is either from a small form or a juvenile. However, no features used to recognise juvenile bone, such as rough, pitted articular surfaces or a more open texture or grain to the bone surface (Callison & Quimby 1984; Bennett 1993) can be seen here, so it is presumably from an adult of a small form. Just how small the animal was, based on an unidentified phalanx, is uncertain, but the manual phalanges of *Compsognathus* are of similar size (Ostrom 1978).

Theropods (and small ornithopods) are known to have inhabited Late Cretaceous New Zealand, which had cool climatic conditions (Molnar & Wiffen 1994), so the presence of this form during the Jurassic is not unexpected. The abundant paleoflora suggests that the animal lived in a temperate forest, at least partially composed of tree-ferns.

During the Late Jurassic, what is now New Zealand was part of the Pacific coast of what is now Antarctica, so this specimen represents the first Late Jurassic tetrapod from the Antarctic region of Gondwanaland. Other dinosaurian material is known from the Early Jurassic (Hammer & Hickerson 1994) and Late Cretaceous (Gasparini et al. 1987, 1996; Hooker et al. 1991; Olivero et al. 1991), the oldest from the Cretaceous being a Coniacian–Santonian theropod tibia (Molnar et al. 1996). This specimen falls into the gap between the Early Jurassic and the Coniacian–Santonian, and suggests that dinosaurs inhabited New Zealand/ Antarctica throughout the Mesozoic. None of the other specimens represents an animal as small as this, so this is also the smallest known Antarctic Mesozoic tetrapod.

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