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SHORT COMMUNICATION

Oldest fossil record of Sulidae from New Zealand

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Abstract

We report the oldest fossil record of Sulidae from New Zealand. Osteological features indicate that a humerus collected from the Hurupi Formation at Whatarangi Bluff (Wairarapa, North Island) belongs to a species more closely related to *Morus* (gannets) than to *Papasula* (Abbott's Booby) or *Sula* (other boobies). The length of the humerus exceeds the species averages of all extant gannet species, and its age pre-dates the estimated divergence of extant *Morus serrator*. The Whatarangi fossil most likely represents an unnamed stem gannet species, and reveals that gannets dispersed to New Zealand at least twice.

Keywords Fossil · Sulidae · Gannet · Zealandia · Micoene

Zusammenfassung

Älteste fossiler Nachweis von Tölpeln aus Neuseeland

Wir berichten über den ersten Fossilnachweis von Tölpeln aus Neuseeland. Osteologische Merkmale deuten darauf hin, dass ein Oberarmknochen aus der Hurupi-Formation bei Whatarangi Bluff (Wairarapa, Nordinsel) zu einer Art gehört, die enger mit *Morus* (Basstölpel) als mit *Papasula* (Abbott-Tölpel) oder *Sula* (andere Tölpel) verwandt ist. Die Länge des Oberarmknochens übertrifft die Durchschnittswerte aller heute lebenden Basstölpelarten, und das Alter des Fossils liegt vor dem geschätzten Auftauchen der heute lebenden *Morus serrator*. Das Whatarangi-Fossil repräsentiert höchstwahrscheinlich eine unbenannte Stammtölpelart und zeigt, dass sich Basstölpel mindestens zweimal nach Neuseeland ausgebreitet haben.

Introduction

Sulidae are renowned for plunge-diving, a feeding strategy in which they dive from altitudes of 10–30 m (in extreme cases up to 100 m) to catch prey near the surface (Carboneras 1992). The family is divided into three genera in most classifications: the large, temperate-adapted gannets (genus *Morus*), the smaller and more tropical-adapted boobies (genus *Sula*), and Abbott's Booby (genus *Papasula*), which today has a breeding range restricted to Christmas Island. Molecular data suggest *Papasula* is the deepest diverging of these three genera (Patterson et al. 2011), whereas morphological data place *Papasula* as sister taxon to *Sula* (Smith 2010). Sulids occur in coastal habitats throughout much of the world, but only two taxa breed in New Zealand today: *Morus serrator* (Australasian Gannet) around the mainland, and *Sula dactylatra tasmani* (Tasman Booby) at the outlying Kermadec Islands (Checklist Committee 2022). *Morus capensis* (Cape Gannet), *Sula leucogaster* (Brown Booby) and *Sula sula* (Red-footed Booby) occur occasionally as vagrants to New Zealand (Checklist Committee 2022). To date, no pre-Holocene sulid fossils have been reported from New Zealand, or from Australasia in general. The oldest published New Zealand records are scattered Holocene remains attributed to *Morus* (Holdaway et al. 2001). Here, we report a Miocene sulid humerus which greatly extends the regional record of the clade.

Systematic paleontology

Suliformes Sharpe, 1891.
Sulidae Reichenbach, 1849.
Morus Vieillot, 1816.

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Morus sp.

Referred specimen

NMNZ S.46065 nearly complete left humerus (Fig. 1).

Locality and horizon

The specimen was collected by Tony Tomlin and the late Lesley Barnes on January 3, 2015 in a gully approximately 2 m below the road edge on the southbound side of the No. 1 culvert at Whatarangi Bluff, Wairarapa, North Island, New Zealand. The fossil was found in situ in an outcrop of mudstone that represents the Hurupi Formation. This fossiliferous unit is dominated by massive marine sandstones and mudstones with pebble-rich horizons (Kamp et al. 2015). The presence of *Globoconella miotumida* and absence of *Globoquadrina dehiscens* together suggest the age of the Hurupi Formation at Whatarangi Bluff spans 6.70–9.03 Ma, corresponding to the regional Tongaporutuan Stage (Late Miocene) (Martin Crundwell, pers. com.).

Description

The humerus is nearly complete, save for some erosion of the cranial part of the head and the tuberculum ventrale proximally, and the loss of the condylus dorsalis and adjacent part of the shaft distally. The shaft is preserved in four separate segments. This breakage allows the cross-section to be observed and confirms that the bone wall is extremely thin as in extant sulids. Despite a small portion of the shaft having been lost, the length exceeds the species average for all three extant *Morus* species (Table 1).

The fossa pneumotricipitalis is shallow, with multiple small foramina penetrating the bone wall within the fossa.

Fig. 1 Left humerus of the Whatarangi gannet (NMNZ S.46065) in (**a**) caudal and (**c**) cranial views with extant *Morus serrator* (Australasian Gannet: NMNZ OR.27481) in (**b**) caudal and (**d**) cranial views for comparison. Close-up cranial views of the proximal and distal ends of the humerus in (**e, h**) the Whatarangi gannet, (**f**, **i**) *Morus serrator,* and (**g**, **j**) *Sula dactylatra* (Masked Booby: NMNZ OR.27613). Abbreviations: *fb* fossa m. brachialis, *fo* fossa olecrani, *gr* groove-like depression, *ld* insertion of m. latissimus dorsi, *tps* tubercle for insertion of m. pectoralis superficialis, *tsv* tuberculum supracondylare ventrale. Arrow indicates distal extension of the caput humeri into the sulcus transversus, which is outlined with dashed lines. Scale applies to (**a**)–(**d**), other images not to scale

Table 1 Measurements (mm) from NMNZ S.46065 and modern gannets

	NMNZ S.46065	*Morus serrator*	*Morus capensis*	*Morus bassanus*
Humerus length (species mean)	~230.0	210.3	214.5	226.1
Humerus length (min/max)	n/a	202.0–221.0 ($n=26$)	198.4–223.4 ($n=9$)	216.6–232.7 ($n=14$)

Because the broken edges do not align perfectly, at least a small amount of the shaft is missing NMNZ S.46065, so the measurement represents a minimum. Values for *M. serrator* and *M. bassanus* were taken directly from NMNZ and USNM specimens, values for *M. capensis* were taken from Dabee (2013)

In caudal view, the sulcus transversus is modestly developed as in *Morus* and *Papasula*, whereas in *Sula* it is deeper and more rectangular (Warheit 1990). Also as in *Morus*, the articular surface of the caput humeri forms a distal projection at the margin of the sulcus, whereas the boundary between the articular surface and the sulcus is straight in *Sula* (Fig. 1e–g) and *Papasula* (see Hume 2023: Fig. 5). The crista deltopectoralis is very weakly projected, and near its distal end a tubercle for insertion of m. pectoralis superficialis is developed. This tubercle has a relatively smooth border as in *Morus* and *Papasula*, whereas it is more raised with a groove-like depression at its margin in *Sula* (see Warheit 1990; Smith 2010) (Fig. 1e, f). A linear scar for the insertion of the cranial head of m. latissimus dorsi extends more than one-third the length of the shaft.

At the distal end of the humerus, the fossa m. brachialis is very wide and extends far proximally (Fig. 1h), and the fossa olecrani is deeply excavated and bowl-shaped (Fig. 1a). No foramina are visible in the latter fossa, matching the condition in *Morus*. Extant species of *Sula* show a varying number of pneumatic foramina within the fossa olecrani, concentrated along the lateral wall. The tuberculum supracondylare ventrale is oriented cranially as in extant *Morus*, whereas it is canted dorsally in extant *Sula* and ventrally in *Papasula* (see Warheit 1990; Smith 2010). In ventral view, the profile of the tuberculum supracondylare ventrale is flat as in extant *Morus* and *Papasula*, whereas it is convex in extant *Sula*.

Discussion

The deeply excavated and bowl-shaped fossa olecrani is a clear synapomorphy that supports placement of the Whatarangi fossil within Sulidae. Additional features support assignment to *Morus*. We identify the distal extension of the smooth, finished bone of the head into the sulcus transversus (Fig. 1e, f) as a new synapomorphy of *Morus*. Two other features are consistent with assignment of the fossil to *Morus*, but have ambiguous distributions. A deep rectangular sulcus transversus is present in *Sula* as well as in Phalacrocoracidae and Anhingidae, which together form the sister taxon to Sulidae (Smith 2010). The shallow sulcus transversus observed in the fossil may thus represent a synapomorphy of *Morus* that arose convergently in *Papasula*, or may alternatively have been present in the common ancestor of crown Sulidae and have been lost in *Sula*. The Whatarangi fossil closely resembles *Morus* in that the tuberculum supracondylare ventrale is oriented cranially. The primitive condition for Sulidae is unclear, as Anhingidae shares the cranially canted condition present in *Morus*, whereas *Papasula* and Phalacrocoracidae show a ventrally canted condition, and *Sula* shows a dorsally canted orientation. Overall, available morphological observations support inclusion of the Whatarangi fossil within a clade including the three extant *Morus* species, but are insufficient to resolve whether the fossil is more closely related to any of the extant species or sister taxon to all three.

Although there is no strong morphological evidence for the stem versus crown status of the Whatarangi gannet, the age of the fossil favors a stem placement. Patterson et al. (2011) estimated an age of approximately 2.5 Ma (0.0–9.2 Ma 95% HPD interval) for the split between *Morus bassanus* and other gannets, and only 0.5 Ma (0.0–4.1 Ma 95% HPD interval) for the split between *Morus serrator* and *Morus capensis*. If these dates are accurate, the Whatarangi gannet would be too old to represent the sister taxon of extant Australasian *Morus serrator*, though it would fall inside the upper range of ages bounding the gannet crown clade.

The taxonomy of fossil sulids is plagued by highly incomplete holotypes and in dire need of revision. At present, six Late Miocene Pacific species of *Morus* are recognized (Stucchi 2003). The humerus of the Peruvian species *Morus peruvianus* remains unknown, precluding comparisons. All five of the remaining species are known from California. Humerus length (HL) indicates that *Morus willetti* (HL = 156 mm) and *Morus media* (HL = 180 mm) are both much smaller than the Whatarangi gannet (HL = ~230 mm). In turn, *Morus magnus* (HL = ~280 mm, extrapolated from distal width) is substantially larger. *Morus lompocanus* (HL = 245 mm) and *Morus stocktoni* (HL = ~264 mm) fall within the potential range of sizes expected for the species represented by the Whatarangi gannet, assuming intraspecific size variation mirrored extant gannet species and the NZ fossil was at the lower end of the range. Unfortunately, no meaningful comparisons can be made due to damage to the proximal and distal ends of the holotype humeri of these species. Given the wide geographical ranges of several modern sulid species, it is within the realm of possibility that the Whatarangi gannet represents a cross-Pacific occurrence of *Morus lompocanus* or *Morus stocktoni*, though we consider this unlikely.

The Whatarangi gannet exceeds the average size of even the largest extant gannet species, *Morus bassanus* (Northern Gannet). Large size conveys more extensive plunge-diving capabilities to modern gannets, which typically reach greater depths than boobies and practice more vertical dives from higher dropping points (Carboneras 1992). The Northern Gannet can reach depths of up to 10 m from the impulse of their plunge dive alone, from which point they can continue further using their wings to propel themselves (Carboneras 1992). Given its size and position within crown Sulidae, similar diving capabilities can be inferred for the Whatarangi gannet.

The Whatarangi gannet adds another taxon to the Miocene marine avifauna of New Zealand, which, while still emerging, appears to have included many of the major clades that inhabit the region today (e.g., penguins, procellariiforms, sulids). Aside from abundant and diverse penguins, the Neogene marine avifauna of New Zealand now includes albatrosses, *Pelecanoides*, *Procellaria* and *Macronectes* petrels, and shearwaters (e.g. Tennyson and Mannering 2018; Mayr and Tennyson 2020; Tennyson and Salvador 2023). Given that the fossil described here represents a single occurrence, it is not possible to make wider-ranging conclusions about the deep history of sulids in New Zealand. Nonetheless, the fossil does provide a minimum Late Miocene age for the dispersal of gannets into the region. Given that molecular dates suggest *Morus serrator* diverged from *Morus capensis* less than one million years ago, the Whatarangi gannet also provides evidence that at least one ancient lineage of Sulidae arrived in New Zealand prior to Australasian gannets.

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