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The Oldest Record of the Genus *Diomedea*, *Diomedea tanakai* sp. nov. (Procellariiformes: Diomedeidae): an Albatross from the Miocene of Japan

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Abstract Tertiary fossil albatrosses (Family Diomedeidae) are only known from a handful of specimens from America, Australia, Antarctica, Britain, Japan and France. They first appear in the late Eocene of Seymour Island, Antarctica, achieving a Pacific and Atlantic Ocean distribution by the Pliocene. Two tarsometatarsi were collected from an late-Early Miocene horizon at Yanaidani, Aki County, Mie Prefecture, Japan. These specimens represent the first definite fossil evidence for the family Diomedeidae in the North West Pacific and the oldest occurrence of the genus *Diomedea* in the fossil record. These tarsometatarsi of this new species possess some unique osteological characters and, in terms of size, are significantly smaller than those of extinct and extant species. The presence of the Diomedeidae in the fossil avifauna of the North West Pacific further enhances the knowledge of the evolutionary history of this family and seems to suggest that the Albatrosses were derived from a small, near-shore Procellariiform ancestor which adapted (some time in the Oligocene or early Miocene) to an oceanic lifestyle.

Key words: Albatross, *Diomedea*, Diomedeidae, Fossil, Miocene, Japan.

Introduction

At least sixteen species of pre-Quaternary fossil albatrosses are known (see Table 1). In this paper, we report on three new specimens from the Yanaidani District of Aki County, Mie Prefecture, Honshu, Japan. The holotype (NSM PV19388) is a complete right tarsometatarsus and was collected by Mr. Takeshi Tanaka. The second specimen (NSM-PV 19389) is an epoxy resin replica of a distal right tarsometatarsus. The third specimen (CBMPV 412) is a resin cast of a rostral portion of a maxilla (broken both proximally and distally). These specimens were collected from a sandstone horizon within the Mitsugano Member of the Oi Formation, Ichishi Group (late-Early Miocene) at Yanaidani, Misato Village, Aki County, Mie Prefecture (Figure 1). They represent the first pre-Quaternary albatross fossils from the North West Pacific and the oldest occurrence of the genus *Diomedea* in the fossil record.

Terminology: We have followed the anatomical terminology of Howard (1929) and Baumel (1979).

Abbreviations: **BMNH**, The Natural History Museum, London, UK; **CBMPV**, Chiba Natural History Museum and Institute, Chiba, Japan; **LACM**, Natural History Muserum of Los Angeles County, Los Angeles, California, USA; **MFM**, Mizunami Fossil Museum, Gifu, Japan; **MNHN**, Museum National d'Histoire Naturelle, Paris, France; **NMV**, National Museum of Victoria, Melbourne, Australia; **NSM**, National Science Museum, Tokyo, Japan; **SAM**, South African Museum, Cape Town, South Africa; **UCMP**, University of California Museum of Paleontology, Berkeley, California; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.

Table 1. A listing of the known pre-Quaternary fossil albatrosses (Family Diomedeidae).

Genus	Species	Elements	Age	Stage	Locality	Notes	Reference
?	?	?	Late Eocene	Priabonian	Seymour Island, Antarctica	La Meseta Fm.	Tambussi and Tonni, 1988
Manu	*antiqus*	furcula fragment	Early Oligocene	?	Duntroon, N. Otago, S. Island, New Zealand	Maerewhenua greensand. Doubtful as albatross Olson, 1985	Marples, 1946
Plotornis	cf *delfortrii*	distal humerus	Late Oligocene	Chattian	nr. Stallsville, Dorchester Co., S. Carolina, USA	Chandler Bridge Fm. Specimen identification in Olson 1985b	Sanders et al., 1982 (states bird from Type section of Chandler Bridge Fm.)
Plotornis	*arvernensis*	left tmt [MNHN Av2929], coracoid [FSL 443674?]	Early Miocene	Aquitanian	1 km N of Saint Gérand le Puy, Allier, France	zone MN 2a. Coracoid specimen lost, doubtful as albatross	Cheneval, 1984; Milne-Edwards, 1867-71
Plotornis	cf *delfortrii*	distal humerus	Early–Middle Miocene	Burdigalian –Langhian	Maryland, USA	Calvert Fm.	Olson, 1985b
Diomedea	*milleri*	proximal left ulna [LACM 7319], proximal right tmt, [LACM 16474]	Early–Middle Miocene	Burdigalian –Langhian	Sharktooth Hill Bonebed, Kern County, California, USA	Round Mountain Fm., small size	Howard, 1966
Diomedea	*californica*	distal tbt, distal left tmt [UCMP 61392], distal humerus	Early–Middle Miocene	Burdigalian –Langhian	Sharktooth Hill Bonebed, Kern County, California, USA	Round Mountain Fm., large size in between *D. exulans* and *D. albatrus*	Miller, 1962; Howard, 1966, 1978
Diomedea	*californica*	pedal phalanx [LACM 18271]	Early–Middle Miocene	Burdigalian –Langhian	Laguna Hills, Orange County, California, USA	Monterey Fm, large size in between *D. exulans* and *D. albatrus*	Howard, 1968
Diomedea	sp.	proximal shaft tarsometatarsus [LACM 6906]	Early–Middle Miocene	Burdigalian –Langhian	Laguna Hills, Orange County, California, USA	Monterey Fm, size of *D. nigripes*.	Howard, 1968

Table 1. (Continued).

Genus	Species	Elements	Age	Stage	Locality	Notes	Reference
Diomedea	sp.	Distal left tibiotarsus [LACM 119353]	Early–Middle Miocene	Burdigalian –Langhian	Oceanside, San Diego County, California, USA	San Mateo Fm., size of *D. nigripes*.	Howard, 1982
Diomedea	sp.	?	Early–Middle Miocene	Burdigalian –Langhian	Lomita, Los Angeles County, California, USA	Valmonte Diatomite, size of *D. nigripes*.	Miller, 1935
Plotornis	*delfortrii*	tarsometatarsus and distal humerus	Middle Miocene	?	Léognan, nr Bordeaux, Gironde, France	Molassee de Léognan	Milne-Edwards, 1878
Diomedea	cf *californica*	7 specimens including 3 skulls	Middle Miocene	?	Oregon, USA	Astoria Fm. Not yet described	Olson, 1985b
?	?	left basal phalanax of 4th pedal digit [USNM 336381]	Late Miocene	Tortonian	Punta Ninfas, Valdez Penninsula, Argentina	Larger than D. albtrus	Olson, 1984
Diomedea	*thyridata*	incomplete rostrum [NMV P24172]	Early Pliocene	Zanclean	Beaumaris, Victoria, Australia	Black Rock Sandstone. Size of *D. melanophris*.	Wilkinson, 1969
Diomedea?	at least 4 species	?	Early Pliocene	Zanclean	Lee Creek, N. Carolina, USA	not yet described	Olson, 1985b
Diomedea	sp.	proximal left tarsometatarsus [SAM-PQ L12005]	Pliocene	?	Laanbanweg, SW Cape Province S. Africa	Quartzose Sand member, Varswater Fm. Size of *D. melanophris*.	Olson 1983, 1985b
Diomedea	*anglica*	tibiotarsus	Pliocene	?	Pierce, Polk Co.,Florida, USA	Bone Valley Fm.	Wetmore, 1943
Diomedea	sp.	carpometacarpus	Pliocene	?	Polk Co., Florida	Bone Valley Fm.	Olson, 1985b
Diomedea?	sp.	right femur [MFM 1801]	Late Pliocene	Piacenzian	Misagaya, Shizuoka Prefecture, Japan	Dainichi Sand, Kakegawa Group	Ono, 1980
Diomedea	*anglica*	ulna? proximal right tarsometatarsus, 4 phalanges [BMNH PA 87]	Late Pliocene	Piacenzian	Foxhall, Suffolk, UK	Red Crag Fm.	Lydekker, 1891

Systematic Paleontology

Class Aves Linnaeus, 1758

Order Procellariiformes Furbriger, 1888

Family Diomedeidae (Gray, 1840)

Diagnostic characters of Diomedeidae tarsometatarsi: Shallow internal cotyla; relatively small *eminentia intercondylaris*; *hypotarsus* does not form a foramen, and the lateral *hypotarsus* of the calcaneal ridge is broad with a very shallow groove; the medial calcaneal ridge does not expand distally; the distal foramen is medially situated; digit II trochlea expands distally.

Genus *Diomedea* Linnaeus, 1758

Differential diagnoses of tarsometatarsi in the two extant genera of the Diomedeidae:

Diomedea: *Cotyla medialis* medially less expanded; no distinct distal ridge on the *crista medialis hypotarsi*; *crista medialis hypotarsi* high and thick; *crista lateralis hypotarsi* expanded laterally; distinct projection on the *impressiones retinaculi extensorii*; no distinct groove on the medial side of the *crista medialis hypotarsi* (*fossa parahypotarsalis medialis*); indistinct fossa on the medial side of the *eminetia intecondylaris*; deep *fossa infracotylaris dorsalis*; high *tuberositas m. fib. brevis*; two *foramina vascularia proximalia* and no secondary small foramen; *foramen vascular distale* long and distally positioned; no distal secondary *foramen vasculare distale*; distinct groove on the medial side of the base of *trochlea metatarsi tertii*.

Phoebetria: *Cotyla medialis* medially more expanded; distinct ridge on the distal portion of the *crista medialis hypotarsi*; *crista medialis hypotarsi* low and thin; *crista lateralis hypotarsi*

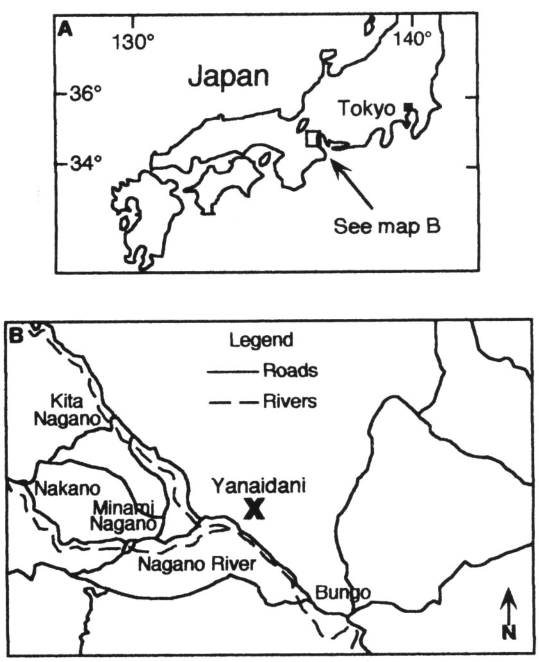


Fig. 1. A, A schematic map of southern Japan with area of enlargement marked by rectangle; B, Schematic map of the type locality of *Diomedea tanakai*. The exact locality is Yanaidani (136°23′E, 34°44′N), Misato Village, Aki County, Mie Prefecture (locality K8 of Shibata, 1970).

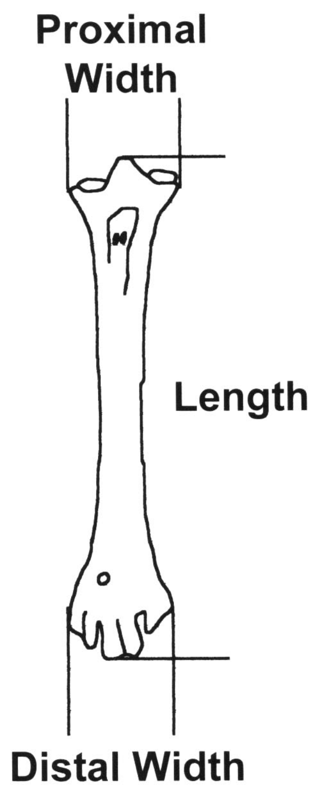


Fig. 2. Generalised drawing shows the location of the measurements made on the extinct and extant species of albatross tarsometatarsi. The data collected is presented in Table 2. All measurements were made in mm.

expanded caudally; no distinct expansion of the *impressiones retinaculi extensorii*; distinct groove on the medial side of the *crista medialis hypotarsi* (*fossa parahypotarsalis medialis*); distinct fossa on the medial side of the *eminentia intercondylaris*; shallow *fossa infracotylaris dorsalis*; low *tuberositas m. fib. brevis*; two *foramina vascularia proximalia* and two secondary small foramina; proximally positioned *foramen vasculare distale*; a distal secondary *foramen vasculare distale*; no groove on the medial side of the base of *trochlea metatarsi tertii*.

Diomedea tanakai, sp. nov.

(Figs. 3, 4)

Diagnosis: Genus as above, species as for description (below).

Etymology: From the surname of discoverer of the holotype, Mr. Takeshi Tanaka.

Holotype: An almost complete (lacking distal articular surfaces of trochlea II and IV) right tarsometatarsus, NSM-PV 19388 (Figure 3).

Referred specimens: A resin cast of a distal right tarsometatarsus (lacking distal articular surfaces of trochlea II and IV), NSM-PV 19389 (Figure 3). A resin cast of a rostral portion of a maxilla (broken both proximally and distally), CBMPV 412 (Figure 4).

Type Locality: All specimens were collected at Yanaidani (136°23′E, 34°44′N), Misato Village, Aki County, Mie Prefecture (locality K8 of Shibata, 1970) (Figure 1).

Horizon and age: Both specimens were collected from a sandstone horizon within the Mitsugano Member of the Oi Formation, Ichishi Group (Shibata, 1967; Yoshida, 1991). This formation is considered to be late-Early Miocene in age (ca. 16.5–17.5 Ma; Yoshida, 1991) and represents circa-littoral (50–200 m) and archi-benthal (200–1000 m) sediments (Shibata, 1970).

Measurements: See Fig. 2 for measurement locations and Table 2 for comparison against modern species. The holotype is 69.8 mm long and has a proximal width of 14.5 mm and a distal width of 13.9 mm. The referred tarsometatarsus has a distal width of 14.7 mm.

Description: The holotype specimen curves caudally and lacks canals in the *hypotarsus*. The *hypotarsus* is narrow in proximal width and cranio-caudally robust. The caudal margin of the proximal cotylae is shallowly concave. There is a shallow and broad groove between the internal and external cotylae. The internal cotyla expands medially. The external cotyla expands laterally. The anterior face of the shaft is depressed below the level of the proximal cotylae. There are two main covering calcaneal ridges that are narrow in the hypotarsal area posteriorly above the proximal foramina, and the medial calcaneal ridge is thin and large. The lateral calcaneal ridge is lower and broad. The attachment of the external ligament is indistinct. The proximal foramina and the attachment for *tibialis anticus* muscle are placed intermediately. There is a vestigial metatarsal facet for digit I. The trochleae of digit II and IV are broken at their caudal ends. The trochlea for digit III is longer laterally than medially. The anterior groove of the trochlea for digit III is deep in its proximal half. The posterior intermetatarsal groove is very shallow. The distal foramen is situated slightly proximally. The distal portion of the caudal surface of the distal foramen is deeply excavated. The shaft is square in cross section. The distal trochlea are broadened mediolaterally. The attachment of the external ligament is robust. The inner extensor groove is not very shallow. The inner intertrochlear notch is higher than the external intertrochlear notch.

Comparison: The holotype and referred tarsometatarsus specimens were compared with the tarsometatarsi of the following extant albatrosses: *Diomedea albatrus* (Short-Tailed Albatross); *Diomedea nigripes* (Black Footed Albatross); and *Phoebetria fusca* (Sooty Albatross) and the following extinct forms *Plotornis delfortrii*; *Diomedea californica*; *Diomedea milleri*; *Diomedea anglica*.

The specimens of the above species are all larger than *D. tanakai* (Table 2). Of the above species, only *D. milleri* resembles *D. tanakai* in osteological characteristics.

D. milleri is represented by the proximal end of a left ulna (LACM 7319; holotype) and a proximal fragment of a right tarsometatarsus (LACM 16474), both specimens from the Middle Miocene of Kern County, California (Howard, 1966). Comparison with *D. milleri* (LACM 16474) indicates the following differences between the tarsometatarsi in *D. tanakai*: the anterior face of the shaft is depressed below the proximal cotylae, and the proximal foramina and attachment for the *tibialis anticus* muscle is more proximally placed than in *D. milleri*. These differences combined with the difference in size are sufficient to support a different specific diagnosis.

The referred rostral portion of the maxilla can only be loosely referred to the new species — however by comparison against all modern maxilla and known fossil maxilla (Figure 4) it is apparent that it is different to any known species. As this maxilla is found in the same locality as the new species and the new species is the only albatross from this locality it is prudent, for the moment, to refer the specimen to *D. tanakai* until more material is discovered.

Discussion

Coues (1866) and Wilkinson (1969) adopted the idea of grouping *Diomedea* species. They identified two groups of *Diomedea*: the *Diomedea melanophris* group and the *Diomedea exulans* group.

The *Diomedea melanophris* group includes *D. melanophris*, *D. cauta* (including all 3 subspecies), *D. chrysostoma*, *D. chlororhynchos*, *D. bulleri* and *D. irrorata*.

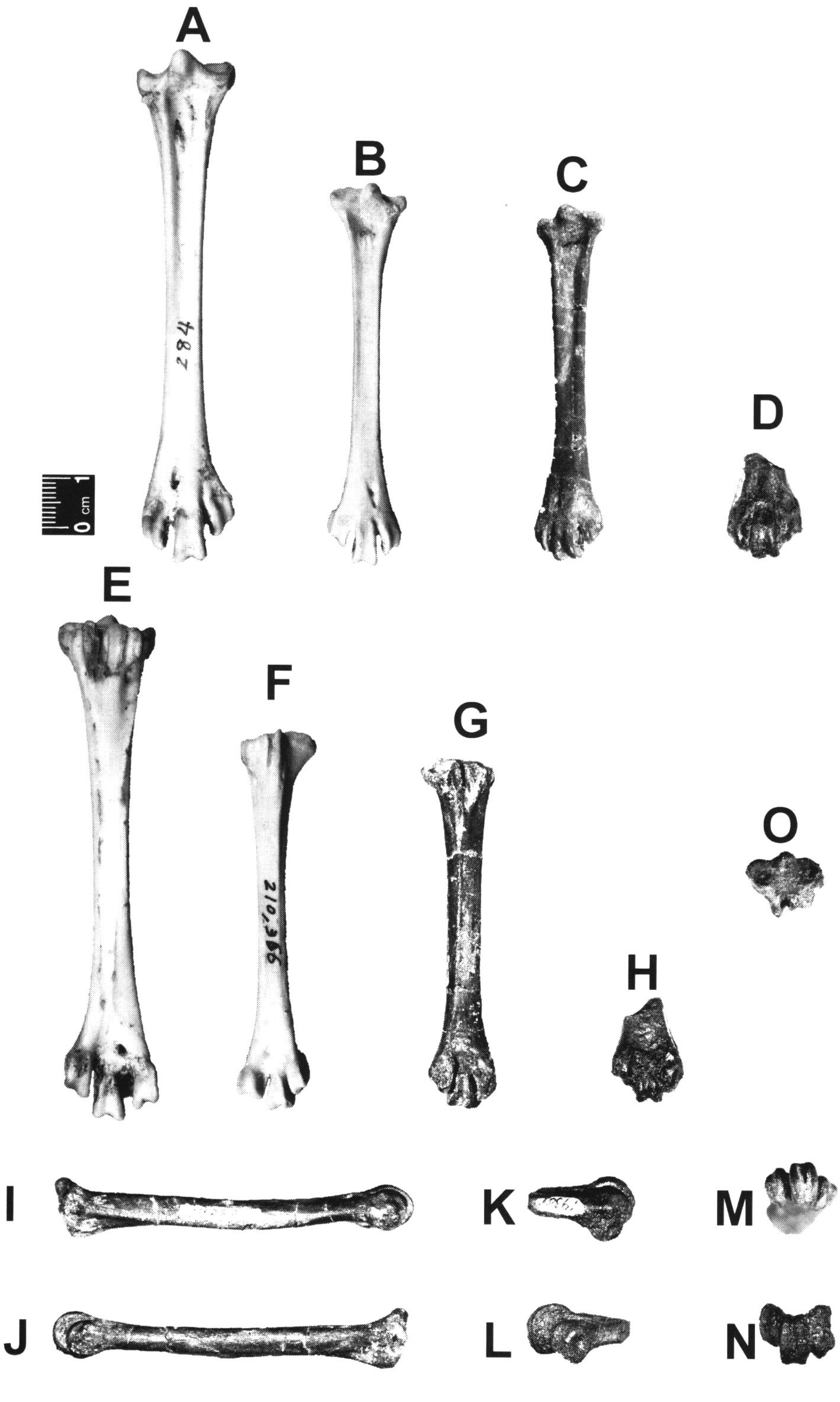
The *Diomedea exulans* group includes *D. exulans*, *D. epomophora*, *D. immutabilis*, *D. albatrus* and *D. nigripes*. *Diomedea amsterdamensis* is so poorly known — it may not be a species at all as it is only known from long-range visual observations — that classification into these groups is impossible.

The *D. melanophris* group includes the majority of the smaller albatrosses and is virtually confined to the Southern Hemisphere. Within this group, two sub-groups are recognized although these are not sharply differentiated and need not concern us further.

The *D. exulans* group includes the largest albatrosses and also all of the species with a North Pacific distribution. Wilkinson (1969) noted that this group was closely allied with the other extant albatross genus, *Phoebetria*. *Diomedea tanakai* can be placed within this *D. exulans* plus *Phoebetria* group (based on osteological characters of its tarsometatarsi: e.g. location and number of the calcaneal ridges, position of the distal foramen, curvature and cross section of the shaft, location of the *tibialis anticus* tubercle, angle of the intertrochlear notches etc.).

Wilkinson (1969) stated that *D. thyridata* indicated that the *D. melanophris* group had evolved by the Miocene and that the *D. exulans* group also has a fossil record back to this period (based on his placement of *D. californica* in this group). He also noted that *D. californica* had affinities with *Macronectes* (the giant petrels — family Procellariidae), *D. nigripes* and the 'primitive'

Fig. 3. Photographs of the Holotype and Referred tarsometatarsus of *Diomedea tanaka*, sp. nov., compared with recent tarsometatarsi from *Diomedea albatrus* and *Phoebetria fusca*. Scale bar is 10 mm. A, B, C, D are ventral views, A=*Diomedea albatrus*, B=*Phoebetria fusca*, C=*Diomedea tanaka* sp. nov. Holotype NSM-PV 19388, D=*Diomedea tanaka*, sp. nov., referred specimen NSM-PV 19389; E, F, G, H are dorsal views, E=*Diomedea albatrus*, F=*Phoebetria fusca*, G=*Diomedea tanaka*, sp. nov., Holotype NSM-PV 19388, H=*Diomedea tanaka*, sp. nov., referred specimen NSM-PV 19389; I and K are medial views, I=*Diomedea tanaka*, sp. nov., Holotype NSM-PV 19388, K=*Diomedea tanaka*, sp. nov., referred specimen NSM-PV 19389; J and L are lateral views, J=*Diomedea tanaka*, sp. nov., Holotype NSM-PV 19388, L=*Diomedea tanaka*, sp. nov., referred specimen NSM-PV 19389; M and N are distal views, M=*Diomedea tanaka*, sp. nov., Holotype NSM-PV 19388, N=*Diomedea tanaka*, sp. nov., referred specimen NSM-PV 19389; O=proximal view of *Diomedea tanaka*, sp. nov., Holotype NSM-PV 19388.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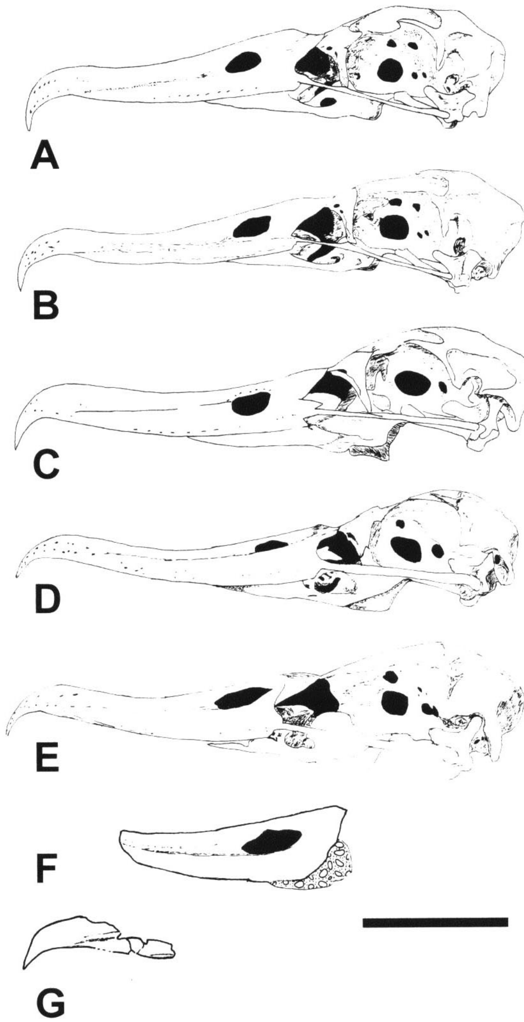

Fig. 4. Drawings of extant albatross skulls (A–E) and fossil maxilla (F & G) to compare with the tentatively referred maxilla of *Diomedea tanaka*, sp. nov. Scale Bar is 50 mm. A=*Diomedea immutabilis*; B=*Diomedea nigripes*; C=*Diomedea albatrus*; D=*Diomedea chlororhynchos*; E=*Diomedea melanophris*; F=*Diomedea thyridata*, from the Lower Pliocene (Zanclean) Black Rock Sandstone of Beaumaris, Victoria, Australia (NMV P24172); G=*Diomedea tanaka*, sp. nov., referred specimen (CBMPV 412)

Phoebetria. This led him to suggest that the *D. exulans* group is closer to the ancestry of the albatrosses and that the *D. melanophris* group may have evolved from them.

As *Diomedea tanakai* can be placed within the *D. exulans* group and it is the oldest record for the genus it may support Wilkinson's (1969) view for the 'primitive' state of this group. In addition to this *D. tanakai* is similar to *D. milleri* (the oldest member of the *D. melanophris* group), which adds further support to the evolutionary phylogeny suggested by Wilkinson (1969).

The *D. exulans* group has many synapomorphies with the Procellariidae (Olson 1985b) and these characters appear to be pleisomorphic in *D. tanakai*, *D. nigripes*, *Phoebetria* and the Procellariidae (Wilkinson, 1969). This data tends to support Olson's (1985b) view that the Diomedeidae evolved from a near shore Procellariiform ancestor.

Conclusions

Surprisingly the fossil record of the Diomedeidae is poor considering their accumulation of populations along coastal regions, especially on margins with active sedimentary basins. However enough comparative material is available to allow generic and specific diagnosis to be made on isolated, discrete and often fragmentary fossil material. *Diomedea tanakai*, sp. nov., is the earliest record of the genus *Diomedea* and as such indicates that the albatrosses had obtained a Pacific wide distribution by the late-Early Miocene and also by this time had adapted to a fully oceanic lifestyle (as suggested by the palaeoenvironmental reconstruction of the Ichishi Formation).

Diomedea tanakai, sp. nov., is also the smallest known representative of the genus and as such seems to supports Olson's (1985b) view that the albatrosses evolved from a small, near-shore Procellariiform ancestor and also Wilkinson's (1969) view that the *D. exulans* group (plus *Phoebetria*) are more basal member in relation to the *D. melanophris* group. However until a complete rigorous phylogenetic analysis of the skeletal characters of the Procellariiforms is undertaken in conjunction with molecular studies of the extant members of the order, the evolutionary

Table 2. Statistics of Extant Albatross Tarsometatarsus.

Tarsometatarsus For Statistics	Length mm	Proximal mm	Distal mm	Tarsometatarsus Statistics For	Length mm	Proximal mm	Distal mm
Diomedea exulans				*D. chlororhynchus*			
Mean	120.56	24.42	23.96	Mean	80.08	15.88	16.4
Standard Error	1.41	0.42	0.26	Standard Error	0.89	0.36	0.82
Standard Deviation	3.15	0.94	0.59	Standard Deviation	1.77	0.71	1.64
Range	7.9	2.3	1.6	Range	3.7	1.6	3.5
Number of specimens	5	5	5	Number of specimens	4	4	4
D. bulleri				*D. melanophrys*			
Mean	84.67	16.67	16.33	Mean	85.89	18.17	17.8
Standard Error	1.44	0.55	0.59	Standard Error	0.58	0.36	0.26
Standard Deviation	2.49	0.95	1.03	Standard Deviation	1.53	0.95	0.68
Range	4.5	1.9	2	Range	4.5	2.4	2
Number of specimens	3	3	3	Number of specimens	7	7	7
D. irrorata				*D. chrysostoma*			
Mean	102.5	19	17.96	Mean	85.96	17.34	17.21
Standard Error	1.26	0.259	0.3	Standard Error	0.9	0.16	0.21
Standard Deviation	2.81	0.57	0.78	Standard Deviation	3.13	0.57	0.73
Range	7.4	1.2	1.9	Range	11.2	1.8	2.7
Number of specimens	5	5	5	Number of specimens	12	12	12
D. immutabilis				*D. albatrus*			
Mean	88.67	15.9	15.18	Mean	100.11	19.19	18.39
Standard Error	0.63	0.11	0.1	Standard Error	0.86	0.33	0.34
Standard Deviation	3.15	0.54	0.49	Standard Deviation	2.72	1.03	1.09
Range	11.8	1.9	2.2	Range	9.4	2.9	3.1
Number of specimens	25	25	25	Number of specimens	10	10	10
D. nigripes				*D. epomophora*			
Mean	94.72	17.06	15.97	Mean	122.66	23.5	23.09
Standard Error	0.56	0.13	0.16	Standard Error	1.38	0.26	0.37
Standard Deviation	2.88	0.67	0.82	Standard Deviation	5.15	0.97	1.37
Range	12.2	2.3	2.7	Range	18.1	3.9	5.3
Number of specimens	26	26	26	Number of specimens	14	14	14
D. cauta				*Phoebetria palpebrata*			
Mean	90.03	19.08	18.62	Mean	84.9	16.3	16.45
Standard Error	0.9	0.59	0.59	Standard Error	0.9	0.2	0.45
Standard Deviation	4.12	2.72	2.72	Standard Deviation	1.27	0.28	0.64
Range	16	14.8	14.7	Range	1.8	0.4	0.9
Number of specimens	21	21	21	Number of specimens	2	2	2

pathways within this order will remain unclear.

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