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RESEARCH ARTICLE

# Oligocene and Miocene albatross fossils from Washington State (USA) and the evolutionary history of North Pacific Diomedeidae

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## ABSTRACT

Albatross fossils have been collected from the late Oligocene Lincoln Creek Formation and the early/middle Miocene Astoria Formation near the townsite of Knappton, Pacific County, Washington (USA). The albatross from the Lincoln Creek Formation, *Diomedavus knapptonensis*, n. gen. et sp., is smaller than all extant albatrosses and represents the oldest published fossil albatross from the North Pacific Basin. *Diomedavus knapptonensis* is clearly distinguished from extant albatrosses in several osteological features; some are likely plesiomorphic, supporting a phylogenetic position outside the crown group. The unusual shape of the deltopectoral crest of the humerus suggests that *D. knapptonensis* also differed from extant albatrosses in its flight performance. A partial skeleton from the Astoria Formation likely represents another new albatross species; however, it is not named because there is no overlap with the skeletal elements of other fossil Diomedeidae. This species, here informally termed the "Astoria Formation albatross," also identified as a stem group representative of the Diomedeidae, differs from extant species in subtle features of the leg bones. Therefore, stem group albatrosses inhabited the North Pacific Basin before the emergence of the taxon *Phoebastria*, which includes extant North Pacific albatrosses. Cenozoic albatrosses were widely distributed in the Northern Hemisphere and the complex biogeographic history of the Diomedeidae may have been shaped by changes in global marine or atmospheric circulation systems and the loss of safe breeding grounds.

*Keywords:* Astoria Formation, biogeography, *Diomedavus knapptonensis*, n. gen. et sp., evolution, fossil birds, Lincoln Creek Formation

**Fósiles de Albatros del Oligoceno y Mioceno del Estado de Washington (EEUU) e historia evolutiva de Diomedeidae del Pacífico Norte**

## RESUMEN

Los fósiles de albatros han sido colectados de la Formación Lincoln Creek del Oligoceno tardío y de la Formación Astoria de inicios/mediados del Mioceno cerca de la ciudad de Knappton, Condado Pacífico, Estado de Washington (EEUU). El albatros de la Formación Lincoln Creek, *Diomedavus knapptonensis*, n. gen. et sp., es más pequeño que todo los albatros vivientes y representa el fósil publicado más viejo de la Cuenca del Pacífico Norte. *Diomedavus knapptonensis* se distingue claramente de los albatros vivientes en varios rasgos osteológicos; algunos son probablemente plesiomórficos y soportan una posición filogenética afuera del grupo central. La forma inusual de la cresta deltopectoral del húmero sugiere que *D. knapptonensis* se diferenció de los albatros vivientes en su desempeño de vuelo. Un esqueleto parcial de la Formación Astoria también representa una nueva especie de albatros; sin embargo, no es nombrada debido a que no hay superposición con los elementos del esqueleto del otro fósil de Diomedeidae. Esta especie, nombrada aquí informalmente el "albatros de la Formación Astoria", también identificada como un grupo troncal representativo de los Diomedeidae, se diferencia de las especies vivientes en rasgos sutiles de los huesos de las piernas. Por ende, los albatros del grupo troncal habitaron la Cuenca del Pacífico Norte antes del surgimiento del taxón *Phoebastria*, que incluye los albatros vivientes del Pacífico Norte. Los albatros del Cenozoico se distribuyeron ampliamente en el Hemisferio Norte y la compleja historia biogeográfica de Diomedeidae podría haber sido modelada por cambios en los sistemas de circulación marinos o atmosféricos globales y por la pérdida de sitios reproductivos seguros.

*Palabras clave:* aves fósiles, biogeografía, *Diomedavus knapptonensis* n. gen. et sp., evolución, Formación Astoria, Formación Lincoln Creek

## INTRODUCTION

Albatrosses (Diomedeidae) were long split into the taxa *Phoebetria* (sooty albatrosses) and *Diomedea* (all others; e.g., Carboneras 1992); however, analyses of mitochondrial sequence data showed that *Phoebetria* is nested within the extant species and *Diomedea* as traditionally recognized is therefore paraphyletic (Nunn et al. 1996, Chambers et al. 2009). Accordingly, albatrosses are now classified in the 4 taxa *Phoebetria*, *Phoebastria* (North Pacific albatrosses), *Thalassarche* (southern mollymawks), and *Diomedea* (great albatrosses). Although most species of these taxa inhabit the Southern Hemisphere, 3 of the 4 species of *Phoebastria* breed in the North Pacific Basin.

The distribution of the extant species suggests that albatrosses evolved in the Southern Hemisphere, with a later dispersal of the *Phoebastria* lineage to the Northern Hemisphere. The evolutionary and biogeographic history of albatrosses is, however, poorly understood (Olson 1985a, Mayr 2016a) and few fossils have been described from strata predating the Pliocene, the epoch that began 5.3 million years ago (mya).

Fragmentary remains of putative Diomedeidae were reported from middle Eocene (~39–41 mya) marine sediments in Uzbekistan (*Murunkus*; Panteleyev and Nessov 1987) and from late Eocene (~38 mya) strata in Antarctica (*Notoleptos*; Acosta Hospitaleche and Gelfo 2016; a coracoid of a putative loon described by Acosta Hospitaleche and Gelfo 2015: figure 3A is here considered to be from a closely related procellariiform bird). These Eocene fossils are from very small species and, if correctly identified, clearly represent stem group albatrosses (*Murunkus subitus* measured only one-third the size of the extant *Thalassarche melanophris* and with an estimated tarsometatarsus length of 45–50 mm, *Notoleptos giglii* reached about 55–60% the size of *Th. melanophris*). A much larger stem group representative of the Diomedeidae was also reported from early Oligocene (~32–34 mya) rocks in Belgium (Mayr and Smith 2012a). This species, *Tydea septentrionalis*, was of similar size to *Th. melanophris*, but clearly differed from crown group Diomedeidae in plesiomorphic features.

Two species of the taxon *Plotornis*, *P. delfortrii* and *P. graculoides*, were described from the early Miocene (~20–23 mya) of France and Italy, respectively, where albatrosses no longer live (Cheneval 1984, Mayr and Pavia 2014). The smaller size and less well developed processus supracondylaris dorsalis on the distal humerus indicate that *Plotornis* is also a stem group representative of the Diomedeidae. Otherwise, however, the preserved bones of *Plotornis* species are very similar to those of extant albatrosses and certainly these early Miocene species are more closely related to the crown group than are the geologically older taxa *Murunkus*, *Notoleptos*, and *Tydea*.

The fossil record of modern-type albatrosses is restricted to the Neogene period (Miocene and younger) and most of the published material consists of very fragmentary remains, therefore we use quotation marks here to denote uncertainty regarding the generic assignment. "*Diomedea*" *tanakai* from late early Miocene (16.5–17.5 mya) strata in Japan is based on tarsometatarsi and a beak fragment (Davis 2003). A pedal phalanx of an undetermined albatross species of late Miocene age was reported from Argentina (Olson 1984; erroneously considered to be of early Miocene age by Mayr and Smith 2012a) and a late Miocene species from Australia ("*Diomedea*" *thyridata*) is based on a partial beak (Wilkinson 1969). All other Miocene albatross fossils, however, stem from North America.

"*Diomedea*" *californica* from middle Miocene rocks in California is represented by a partial tarsometatarsus, a second referred tarsometatarsus, a referred distal humerus, and a tentatively referred distal tibiotarsus (Miller 1962; Howard 1966, 1978). Even more incompletely known is "*Diomedea*" *milleri* of middle Miocene age from California, the holotype of which is the proximal end of an ulna (Howard 1966) as well as a referred fragmentary proximal end of a tarsometatarsus (later designated as the "paratype"; Howard 1972). Fragmentary albatross remains of unnamed species were also found in various late Miocene localities in California (Miller 1935; Howard 1978, 1982).

Albatrosses today only occur as vagrants on the North American Atlantic coast, but a humerus from the middle Miocene Calvert Formation of Maryland documents their presence in the Atlantic Basin by that time (Olson 1985a). Albatrosses are abundant in some Pliocene localities of the North American Atlantic coast, where at least 5 species of the taxon *Phoebastria* coexisted (Olson and Rasmussen 2001). An extinct *Phoebastria* species is also known from Pliocene rocks in England (Dyke et al. 2007). Albatrosses were furthermore described from Pliocene fossil sites in South Africa (Olson 1985b) and the South American Pacific coast (Walsh and Hume 2001, Stucchi and Urbina 2005), and fossils occur in various other Pliocene or Pleistocene localities (Warheit 2002).

The purpose of this report is to describe albatross fossils from marine sediments of the Lincoln Creek and Astoria formations that crop out along the north shore of the Columbia River, east of the townsite of Knappton, Pacific County, Washington, USA. The fossils described herein stem from the late Oligocene upper part of the Lincoln Creek Formation (~26–28 mya; Prothero et al. 2008) and the lower part of the Astoria Formation, considered to be early to early middle Miocene (23–15 mya; Barnes 1987, Prothero et al. 2008). Some of the fossils from the Lincoln Creek Formation were first mentioned by Moore (1984:2). Olson (1985a) commented on unpublished albatross remains from the Astoria Formation near Newport,

Oregon (approximately 215 kilometers south of Knappton), and figured a cranium of a bony-toothed bird (Pelagornithidae) from these localities (Olson 1985a: figure 10). Bird fossils have not been reported previously from the Astoria Formation in Washington and the only avian fossils previously reported from the Lincoln Creek Formation are flightless plotopterids (Goedert and Cornish 2002, Mayr and Goedert 2016). More importantly, the fossils described in the present study are among the most substantial published records of Oligo-Miocene albatrosses and contribute to a better understanding of the evolutionary history of these large marine birds.

## MATERIAL AND METHODS

The fossils are in the collections of the Natural History Museum of Los Angeles County, Los Angeles, California, USA (LACM), the Senckenberg Research Institute, Frankfurt, Germany (SMF), the Smithsonian Institution, United States National Museum, Washington, D.C., USA (USNM), and the Burke Museum of Natural History and Culture, University of Washington, Seattle, Washington, USA (UWBM). All specimens were found in calcareous nodules and were prepared with a dilute solution of formic acid. Anatomical terminology follows Baumel and Witmer (1993).

Skeletons of the following extant species of Diomedeidae were examined in the collection of SMF: *Thalassarche cauta*, *Th. chlororhynchos*, *Th. melanophris*, *Diomedea antipodensis*, *D. epomophora*, *D. exulans*, *Phoebetria fusca*. Comparisons with *Phoebastria* are based on published images of *Ph. nigripes* and *Ph. albatrus* in Matsuoka and Hasegawa (2014) and photos of *Ph. nigripes* in the online Synoptic Skeleton Images database of USNM (http://collections.nmnh.si.edu/search/birds/).

### Systematic Paleontology

Procellariiformes Fürbringer, 1888
Diomedeidae Gray, 1840
*Diomedavus*, n. gen.

**Type species.** *Diomedavus knapptonensis*, n. sp.
**Diagnosis.** Distinguished from crown group Diomedeidae in that apex of crista deltopectoralis of humerus situated farther distally than distal terminus of crista bicipitalis, dorsal portion of facies articularis sternalis of coracoid proportionally longer, and crista lateralis of hypotarsus less prominent. Differs from the early Miocene *Plotornis graculoides* Portis, 1884 in that apex of crista deltopectoralis of humerus situated farther distally than distal terminus of crista bicipitalis and from *P. delfortrii* Milne-Edwards, 1874 (the proximal humerus of which is unknown) in that tarsometatarsus exhibits a partially ossified retinaculum extensorium tarsometatarsi and prox-

imal and distal ends of bone proportionally wider. Distinguished from the early Oligocene *Tydea* Mayr and Smith, 2012a in the proximodistally longer crista bicipitalis, which exhibits a marked cranial bulge (this bulge is absent in *Tydea*). *Diomedavus*, n. gen. is much larger than the middle Eocene *Murunkus* Panteleyev and Nessov, 1987 and the late Eocene *Notoleptos* Acosta Hospitaleche and Gelfo, 2016 and further differs from the latter in the partially ossified retinaculum extensorium tarsometatarsi.

**Etymology.** The taxon name is coined from *Diomedea*, the type genus of Diomedeidae, and avus (Lat.), grandfather.

*Diomedavus knapptonensis*, n. sp.

**Holotype.** LACM 130330: proximal half of left humerus, proximal portion of right carpometacarpus, fragmentary extremitas sternalis of right coracoid, left tarsometatarsus, and cervical vertebra (Figure 1A–M); collected by J. L. Goedert in 1981.

**Referred specimens.** LACM 130331: proximal portion of right humerus and right os carpi radiale (Figure 1N–P); collected at the type locality by J. L. Goedert in 1981. USNM PAL 526218: incomplete right carpometacarpus, distal end of right radius with portion of shaft, distal end of right ulna, and os carpi radiale (Figure 1Q–W); collected at the type locality by J. L. Goedert in 1998. UWBM 109727: partial pelvis (Figure 2); collected near the type locality by J. L. Goedert in 2007.

**Differential diagnosis.** Small albatross that was distinctly smaller than all extant albatross species (tarsometatarsus length 64.0 mm versus 80–122 mm in the extant species; Davis 2003: table 2 and own data for *Phoebetria fusca*). Differs from the species of the taxa *Tydea* and *Plotornis* in the features listed in the differential diagnosis of *Diomedavus*, n. gen. Distinguished from "*Diomedea*" *tanakai* Davis, 2003 in the partially ossified retinaculum extensorium tarsometatarsi. Differs from "*Diomedea*" *californica* Miller, 1962 in the much smaller size (with a distal tarsometatarsus width of 20.6 mm, "*D.*" *californica* is larger than *Th. melanophris,* in which the distal tarsometatarsus measures 17.8 ± 0.7 mm [Davis 2003]). Comparisons with the holotype of "*Diomedea*" *milleri* Howard, 1966, which is a proximal ulna, are not possible. This species may have been of similar size to *Diomedavus knapptonensis*, n. gen. et sp., but because the new late Oligocene species is at least 8 million years older than the middle Miocene "*D.*" *milleri*, we consider a species-level identity unlikely. A tarsometatarsus that was tentatively referred to "*D.*" *milleri* by Howard (1966) differs from *D. knapptonensis*, n. gen. et sp. in that the crista medialis (fdl) of the hypotarsus is proportionally shorter and the lateral foramen vasculare proximale is smaller in plantar view (H. Thomas, personal communication to JLG in 1990).

**Type locality and horizon.** East of Knappton, Pacific County, Washington, USA, LACMVP locality 4510 and
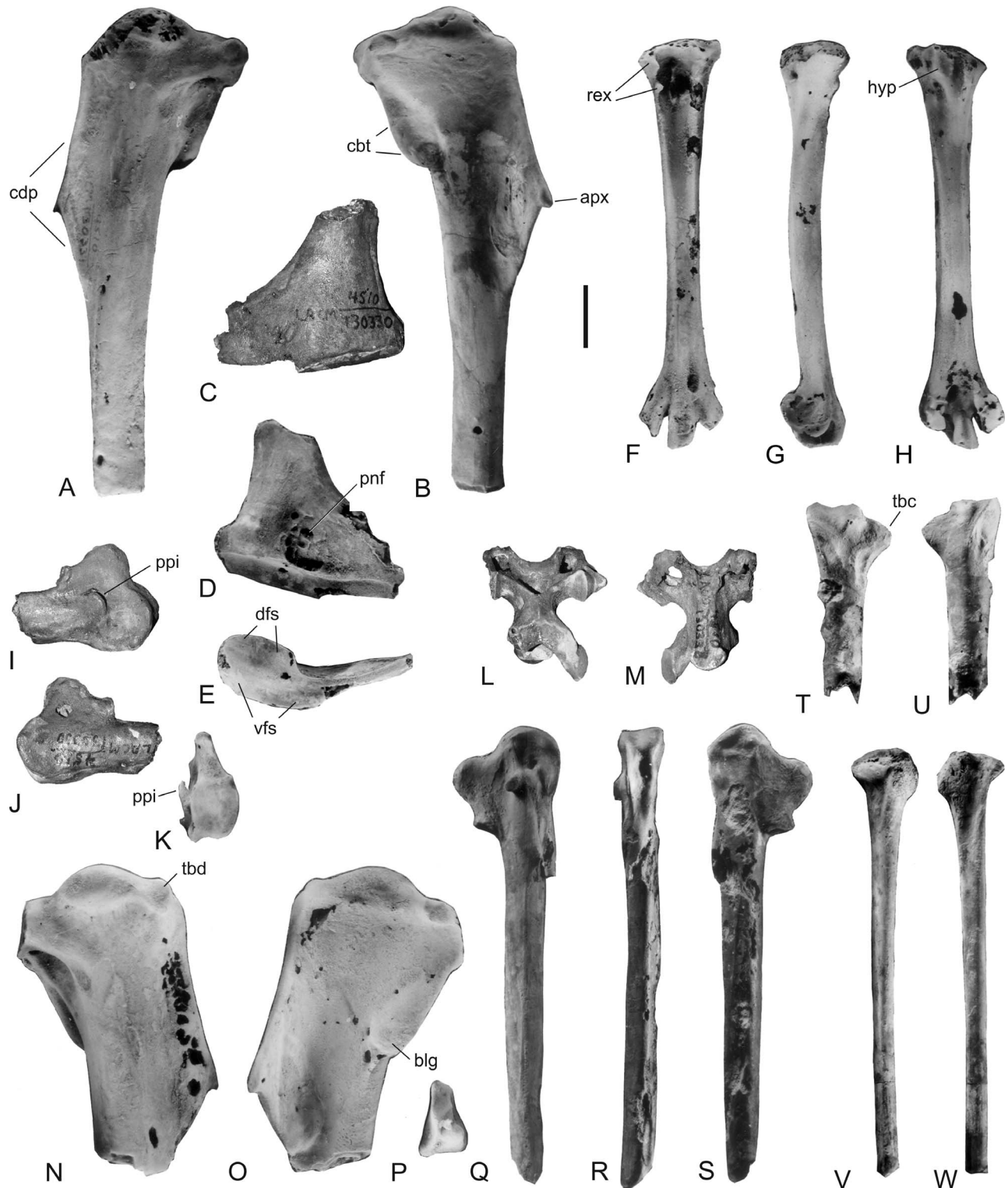
**FIGURE 1.** *Diomedavus knapptonensis*, n. gen. et sp. from the late Oligocene upper part of the Lincoln Creek Formation in Washington (USA). (**A**–**M**) Holotype, LACM 130330; (**N**–**P**) LACM 130331; (**Q**–**W**) USNM PAL 526218. (**A**, **B**) Proximal half of left humerus in (**A**) caudal and (**B**) cranial view. (**C**–**E**) Extremitas sternalis of right coracoid in (**C**) ventral, (**D**) dorsal, and (**E**) sternal view. (**F**–**H**) Left tarsometatarsus in (**F**) dorsal, (**G**) medial, and (**H**) plantar view. (**I**–**K**) Proximal portion of right carpometacarpus in (**I**) ventral, (**J**) dorsal, and (**K**) proximal view. (**L**, **M**) Cervical vertebra in (**L**) dorsal and (**M**) ventral view. (**N**, **O**) Proximal portion of right humerus in (**N**) caudal and (**O**) cranial view. (**P**) Right os carpi radiale. (**Q**–**S**) Incomplete right carpometacarpus in (**Q**) ventral, (**R**)

UWBM locality C2642 on north shore of Columbia River, in the northern part of the bay between Grays Point and Knappton; upper part of Lincoln Creek Formation, late Oligocene (Fierstine 2005, Prothero et al. 2008, Kiel et al. 2013).

**Measurements (in mm).** LACM 130330: Tarsometatarsus, length as preserved, 64.0; proximal width, 13.0; distal width, 12.7. Humerus, length as preserved, 49.6; proximal width (across tuberculum ventrale and tuberculum dorsale), 28.1; craniocaudal width of caput humeri, 7.6; length of crista deltopectoralis, 43.4; length of crista bicipitalis, 30.5. Carpometacarpus, dorsoventral width of trochlea carpalis, 8.2; depth from trochlear rim to tip of processus extensorius, 17.2. Coracoid, dorso-ventral width, 9.4.

LACM 130331: Humerus, length as preserved, 78.4; proximal width (across tuberculum ventrale and tuberculum dorsale), 26.9; craniocaudal width of caput humeri, 6.8; length of crista deltopectoralis, 38.8; length of crista bicipitalis, 28.0.

USNM PAL 526218: Carpometacarpus, length as preserved, 74.6. Ulna, distal width, 14.2.

UWBM 109727: Pelvis, length as preserved, 58.6; width at level of foramen acetabuli, 15.0; width across antitrochanters, ∼26–27; minimum width of preserved praecetabular portion, ∼16.5.

**Etymology.** The species epithet refers to the type locality.

**Description and comparisons.** The specimens belong to at least 3 individuals, which differ somewhat in size, with LACM 130331 being larger than the holotype (Figure 1). *Diomedavus knapptonensis*, n. gen. et sp. was smaller than all extant Diomedeidae, and with a length of 64.0 mm the tarsometatarsus is only slightly shorter than that of *Plotornis graculoides* (∼66 mm; Mayr and Pavia 2014) and "*Diomedea*" *tanakai* (69.8 mm; Davis 2003).

The humerus (Figure 1) differs from the humeri of crown group Diomedeidae and the early Miocene *Plotornis graculoides* in that the apex of the crista deltopectoralis is situated farther distally than the distal margin of the crista bicipitalis (Figure 3A–D). The crista bicipitalis is more elongated than in crown group Diomedeidae; as in the latter, it forms a marked cranial bulge that is absent in the early Oligocene *Tydea septentrionalis*. The crus dorsale fossae on the caudal surface of the proximal humerus is better developed than in extant albatrosses (Figure 3A, B)
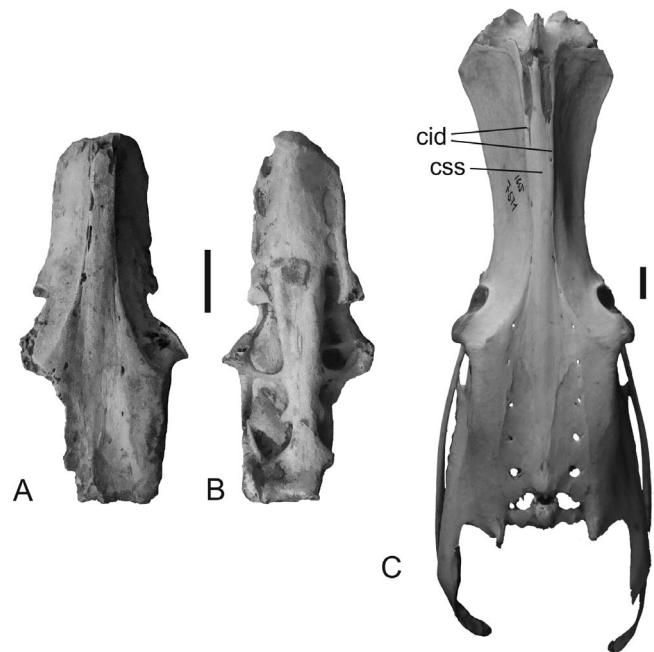


**FIGURE 2.** *Diomedavus knapptonensis*, n. gen. et sp. from the late Oligocene upper part of the Lincoln Creek Formation in Washington (USA). (**A**, **B**) Partial pelvis (UWBM 109727) in (**A**) dorsal and (**B**) ventral view, in comparison to (**C**) the pelvis of *Diomedea antipodensis*. Anatomical abbreviations: cid = crista iliaca dorsalis; css = crista spinosa synsacri. Scale bars equal 10 mm.

and the tuberculum dorsale, also on the caudal surface of the humerus, is somewhat larger.

In contrast to the unusual humerus morphology, the preserved portions of the distal wing elements of *D. knapptonensis* correspond to those of extant albatrosses. This is true for the distal end of the ulna (Figure 1T, U), which exhibits a wide tuberculum carpale, and for the distal end of the radius (Figure 1V, W). The carpometacarpus (Figure 1I–K, Q–S) likewise closely resembles that of modern albatrosses and as in extant Diomedeidae, the tip of the processus pisiformis is turned cranially to form a deeply concave slide for the tendon of musculus flexor digitorum profundus (Figure 1K).

*Diomedavus knapptonensis* differs from crown group Diomedeidae in the extremitas sternalis of the coracoid, where the boss formed by the dorsal portion of the facies articularis sternalis is mediolaterally longer than in extant Diomedeidae (Figure 3H–L). As in extant albatrosses,

←
caudal, and (**S**) dorsal view. (**T**, **U**) Distal end of right ulna in (**T**) ventral and (**U**) dorsal view. (**V**, **W**) Distal section of right radius in (**V**) ventral and (**W**) dorsal view. Anatomical abbreviations: apx = apex of crista deltopectoralis; blg = cranial bulge of crista bicipitalis; cbt = crista bicipitalis; cdp = crista deltopectoralis; dfs = dorsal portion of facies articularis sternalis; hyp = hypotarsus; pnf = pneumatic foramina in impressio musculi sternocoracoidei; ppi = processus pisiformis; rex = partially ossified retinaculum extensorium tarsometatarsi; tbc = tuberculum carpale; tbd = tuberculum dorsale; vfs = ventral portion of facies articularis sternalis. All specimens except those in **C**, **I**, **J**, **L**, and **M** were coated with ammonium chloride. Scale bar equals 10 mm.
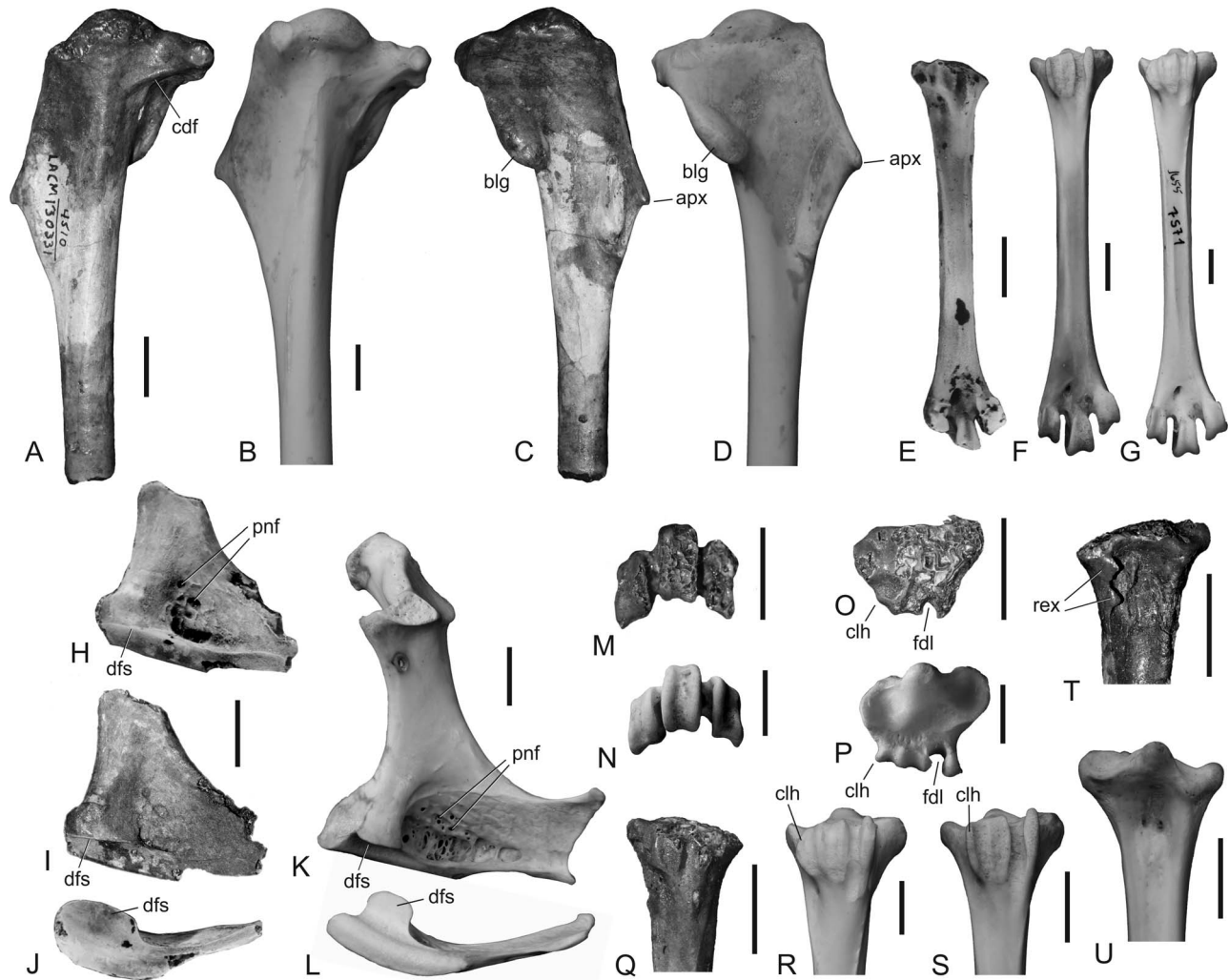
**FIGURE 3.** Selected bones of *Diomedavus knapptonensis*, n. gen. et sp. from the late Oligocene upper part of the Lincoln Creek Formation in Washington (USA) in comparison to extant Diomedeidae. (**A, C**) Proximal half of left humerus (holotype, LACM 130330) in (**A**) caudal and (**C**) cranial view, in comparison to (**B, D**) the proximal left humerus of *Thalassarche melanophris* in the same views. (**E**) Left tarsometatarsus of *D. knapptonensis* (holotype) in plantar view in comparison to the tarsometatarsi of (**F**) *Th. melanophris* and (**G**) *Diomedea antipodensis*. (**H–J**) Extremitas sternalis of right coracoid of *D. knapptonensis* (holotype) in (**H, I**) dorsal (**H**: coated with ammonium chloride, **I**: uncoated) and (**J**) sternal view in comparison to the coracoid of (**K, L**) *Th. melanophris* in (**K**) dorsal and (**L**) sternal view. (**M**) Distal end of left tarsometatarsus of *D. knapptonensis* (holotype) in distal view in comparison to (**N**) *Th. melanophris*. (**O**) Proximal end of left tarsometatarsus of *D. knapptonensis* (holotype) in proximal view in comparison to (**P**) *D. antipodensis*. (**Q**) Proximal end of left tarsometatarsus of *D. knapptonensis* (holotype) in plantar view in comparison to (**R**) *D. antipodensis* and (**S**) *Th. melanophris*. (**T**) Proximal end of left tarsometatarsus of *D. knapptonensis* (holotype) in dorsal view in comparison to (**U**) *Th. melanophris*. Anatomical abbreviations: apx = apex of crista deltopectoralis; blg = cranial bulge of crista bicipitalis; cdf = crus dorsale fossae; clh = crista lateralis hypotarsi; dfs = dorsal portion of facies articularis sternalis; fdl = hypotarsal sulcus for tendon of musculus flexor digitorum longus; pnf = pneumatic foramina in impressio musculi sternocoracoidei; rex = partially ossified retinaculum extensorium tarsometatarsi. Specimens in **H**, **J**, and **E** were coated with ammonium chloride. Scale bars equal 10 mm.

there are pneumatic foramina in the impressio musculi sternocoracoidei on the dorsal surface of the bone.

The partial pelvis agrees well with the pelvis of extant Diomedeidae (Figure 2). As in the latter, but unlike in other procellariiform birds, the ilia are fused with the synsacrum. The crista spinosi synsacri forms a broad bulge and the cristae iliacae dorsales are therefore widely spaced. Among the extant albatrosses examined by us, a similar condition only occurs in *Diomedea antipodensis* and *D. exulans*, whereas the cristae iliacae dorsales are more closely adjoined in *D. epomophora*, *Thalassarche* spp., *Phoebetria fusca*, and *Phoebastria nigripes*.

Olson and Rasmussen (2001) noted that the tarsometatarsi of *Phoebastria* and *Diomedea* are more elongated than that of *Thalassarche*, and a slender tarsometatarsus is also characteristic for *Phoebetria*. In its proportions, the tarsometatarsus of *D. knapptonensis* corresponds with that of *Thalassarche* (Figures 1F–H, 3E–G), and an equally stout tarsometatarsus is also found in the two *Plotornis* species and in "*Diomedea*" *tanakai*. A distinctive feature of the new species is the presence of 2 distinct projections on the medial side of the dorsal surface of the proximal end (Figure 3T), which represent a partially ossified retinaculum extensorium tarsometatarsi. A similar structure is unknown from other fossil or extant albatross species, in which the corresponding area (that is, the medial impressio retinaculi extensorii) is essentially flat. The hypotarsus is damaged and part of the crista medialis (fdl) is broken (terminology of hypotarsal crests follows Mayr 2016b). The largely intact lateral portion of the hypotarsus is of similar proximodistal length to that of *Diomedea* and *Phoebastria*, whereas it is proportionally longer in *Thalassarche* (Figure 3Q–S). Unlike in extant albatrosses, the crista lateralis (fhl) is very low and does not form a prominent ridge, which is especially evident in proximal view of the bone (Figure 3O, P). On the distal end, the distolateral portion of the trochlea metatarsi III and the distal half of the trochlea metatarsi IV are broken. The lateral rim of the trochlea metatarsi II is likewise damaged but appears to have been less developed than in crown group Diomedeidae.

Diomedeidae, gen. et sp. indet.
("Astoria Formation albatross")

**Referred specimen.** SMF Av 644: partial skeleton consisting of the upper beak, partial mandibles, 4 vertebrae (atlas, axis, third vertebra, and the 17th presacral vertebra), proximal portion of left phalanx proximalis digiti majoris, right femur, proximal portion of left tibiotarsus, distal portion of left ulna, and a few bone fragments (including the dorsal extremity of a rib and the distal end of the ?left radius); the upper beak, mandible, and distal ulna are still in association and partially embedded in a block of paraffin wax, in which they were molded for acid preparation; collected in several separate pieces of a broken sandstone nodule by J. L. and G. H. Goedert in 2004.

**Locality and horizon.** East of Knappton, Pacific County, Washington, USA, from toe of mudslide east of LACM localities LACMVP 4584 and LACMIP 5864 (Prothero et al. 2008: figure 2); Astoria Formation, early or early middle Miocene (Barnes 1987, Prothero et al. 2008).

**Measurements (in mm).** Upper beak, total length from preserved caudal end to tip, 104.1. Femur, length, 75.5; proximal width, 15.9; distal width as preserved, 16.1. Tibiotarsus, total length as preserved, 78.1.

**Remarks.** The Astoria Formation albatross is somewhat smaller than the extant *Thalassarche melanophris*. It is therefore distinctly larger than *Diomedavus knapptonensis* n. gen. et sp., the 2 species of *Plotornis* (*P. delfortrii* and *P. graculoides*), as well as "*Diomedea*" *tanakai* and "*D*." *milleri*. It differs from "*Diomedea*" *californica* Miller, 1962 in its smaller size, with the latter species being distinctly larger than *Th. melanophris*. Owing to a lack of overlap of skeletal elements, comparisons with the early Oligocene *Tydea septentrionalis* are not possible.

The Astoria Formation albatross is distinguished from all crown group Diomedeidae in that the crista cnemialis cranialis of the tibiotarsus is craniocaudally wider. However, we refrain from a definitive taxonomic assignment, because no meaningful comparisons are possible with critical fossil taxa. In particular, there exists little or no overlap with the known skeletal elements of *D. knapptonensis*, *Plotornis* spp., "*D*." *tanakai*, and "*D*." *milleri*. Although we are confident that the fossils from the Astoria Formation likely belong to a new species, a well-founded assignment to *Diomedavus*, *Plotornis*, or a new genus-level taxon is not possible and we introduce the informal term "Astoria Formation albatross" for this fossil species.

**Description and comparisons.** The upper beak exhibits characteristic procellariiform features, such as a deeply hooked tip and a marked furrow distal of the nostril (Figure 4). Typical for albatrosses are the laterally facing nostrils, which are more dorsally oriented in giant petrels (*Macronectes*) and other Procellariidae. Although the beak is fractured in its rostral third and the 2 halves are somewhat displaced, no intermediate section appears to be missing. In its proportions, it resembles the beak of *Phoebastria nigripes*, with the beaks of *Phoebetria*, *Thalassarche*, and *Diomedea* being proportionally longer and less deep (Figure 4D–G). The culmen, however, appears to be less concave than in extant albatrosses and its proximal part does not form a marked dorsal bulge (Figure 4); in cross section it is broadly U-shaped as in *Phoebastria* and *Diomedea* (the culmen of *Thalassarche* is mediolaterally narrower; Matsuoka and Hasegawa 2014). The nostril is large and has well-defined margins, whereas its margins form irregular bony excrescences in extant albatrosses; the smooth margin of the nostril was also noted by Olson (1985a) for unpublished albatross skulls from the Astoria Formation of Oregon. The mandible lacks the caudal part and the preserved portions correspond with the mandible of extant albatrosses.

Atlas and axis are preserved in articulation, with the third cervical vertebra being closely associated (Figure 5A, B). As in extant Diomedeidae (Figure 5D–F), the atlas exhibits a dorsally open incisura fossae. The axis also resembles that of modern albatrosses in proportions, but bears a rudimentary processus costalis, which we only
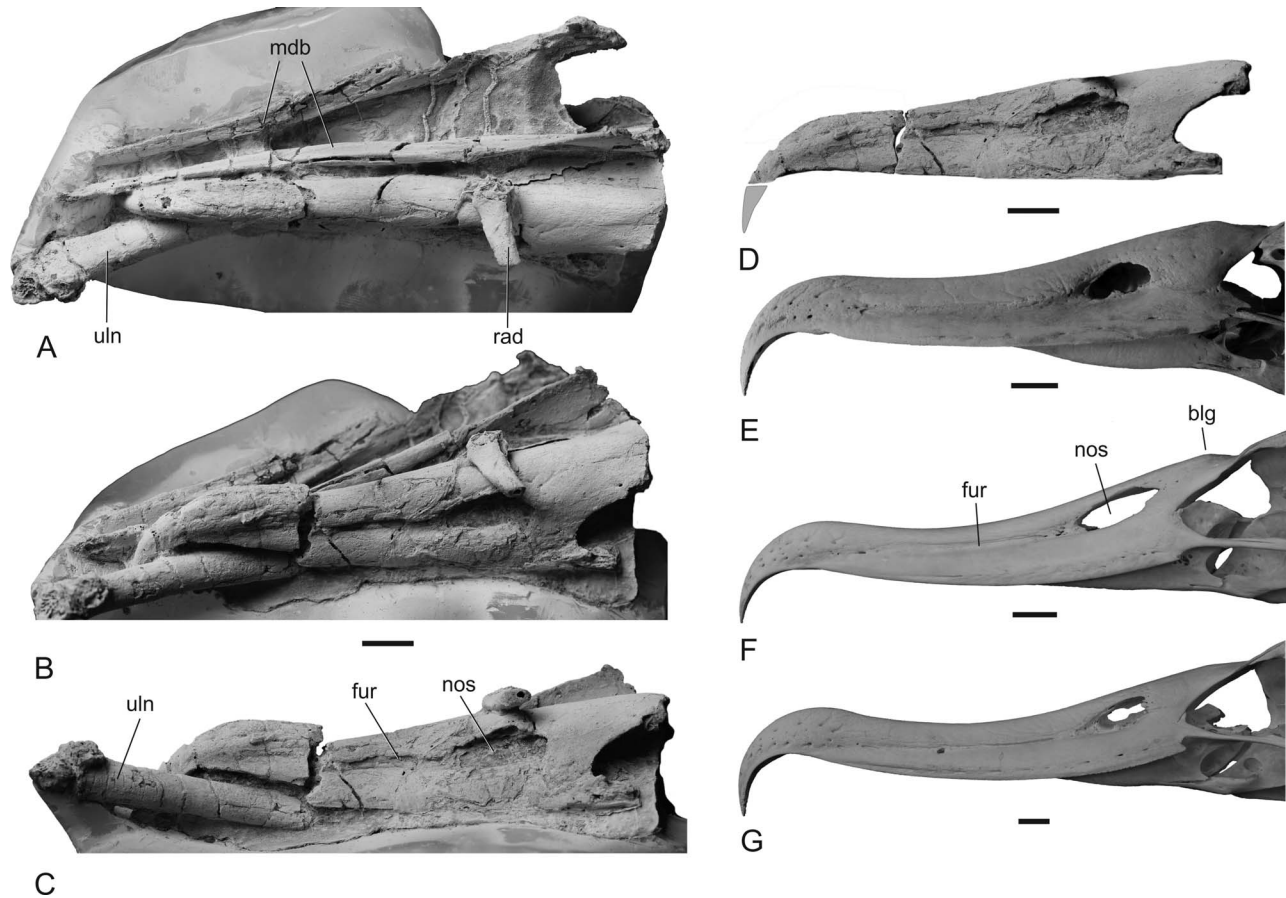
**FIGURE 4.** Diomedeidae, gen. et sp. indet. ("Astoria Formation albatross"; SMF Av 644) from the early or early middle Miocene Astoria Formation of Washington (USA). Upper beak with mandible and associated wing bones in (**A**) dorsal, (**B**) dorsolateral, and (**C**) lateral view. (**D**) Upper beak in lateral view, with matrix and surrounding bones digitally removed, the two broken parts digitally reassembled, and the approximate course of the tip outlined. Beaks of (**E**) *Phoebastria nigripes* (image from the online Synoptic Skeleton Images database of USNM), (**F**) *Thalassarche melanophris*, and (**G**) *Diomedea antipodensis*. Note that the fossil specimen is partially embedded in a block of paraffin wax, in which it was molded for acid preparation. Anatomical abbreviations: blg = dorsal bulge at base of upper beak; fur = furrow along upper beak; mdb = mandible; nos = nostril; rad = distal end of ?left radius; uln = distal portion of left ulna. Fossils were coated with ammonium chloride. Scale bars equal 10 mm.

observed in *Thalassarche cauta* among the examined extant species (no vertebrae of *Phoebastria* were available for comparison). On the third vertebra, the fossa for reception of the processus ventralis of the axis (fovea cranioventralis) is better developed than in *Phoebetria*, *Thalassarche*, and *Diomedea*.

Presence of very short processus ventrolaterales in the cranioventral portion of the corpus vertebrae identifies the thoracic vertebra (Figure 5G–I) as the 17th presacral vertebra (these processes are absent on the 18th–20th presacral vertebrae of albatrosses and are particularly well developed on the 17th vertebra of *Phoebetria*). The lateral surface of the corpus exhibits a centrally positioned pneumatic foramen; such an opening is absent on the caudalmost thoracic vertebrae of *Phoebetria* and less centrally positioned in *Diomedea* and

*Thalassarche* (in the latter, the foramen is bipartite in most of the studied specimens of *Th. melanophris* and in *Th. cauta*, but not in the single skeleton of *Th. chlororhynchus* available to us). The fossil differs from the 17th presacral vertebra of crown group Diomedeidae (Figure 5J–L) in that the fovea costalis is less laterally prominent (Figure 5G, J) and the dorsal portion of the rim of the facies articularis cranialis is more strongly projecting. As in extant Diomedeidae, there is a pneumatic foramen at the base of the cranial surface of the processus transversus, but in the fossil such an opening is absent from the base of the caudal surface of this process (Figure 5I, L; in extant Diomedeidae, the caudal surface bears a pneumatic foramen in *Thalassarche*, whereas this opening is absent in the 17th presacral vertebra of *Phoebetria* and *Diomedea*).
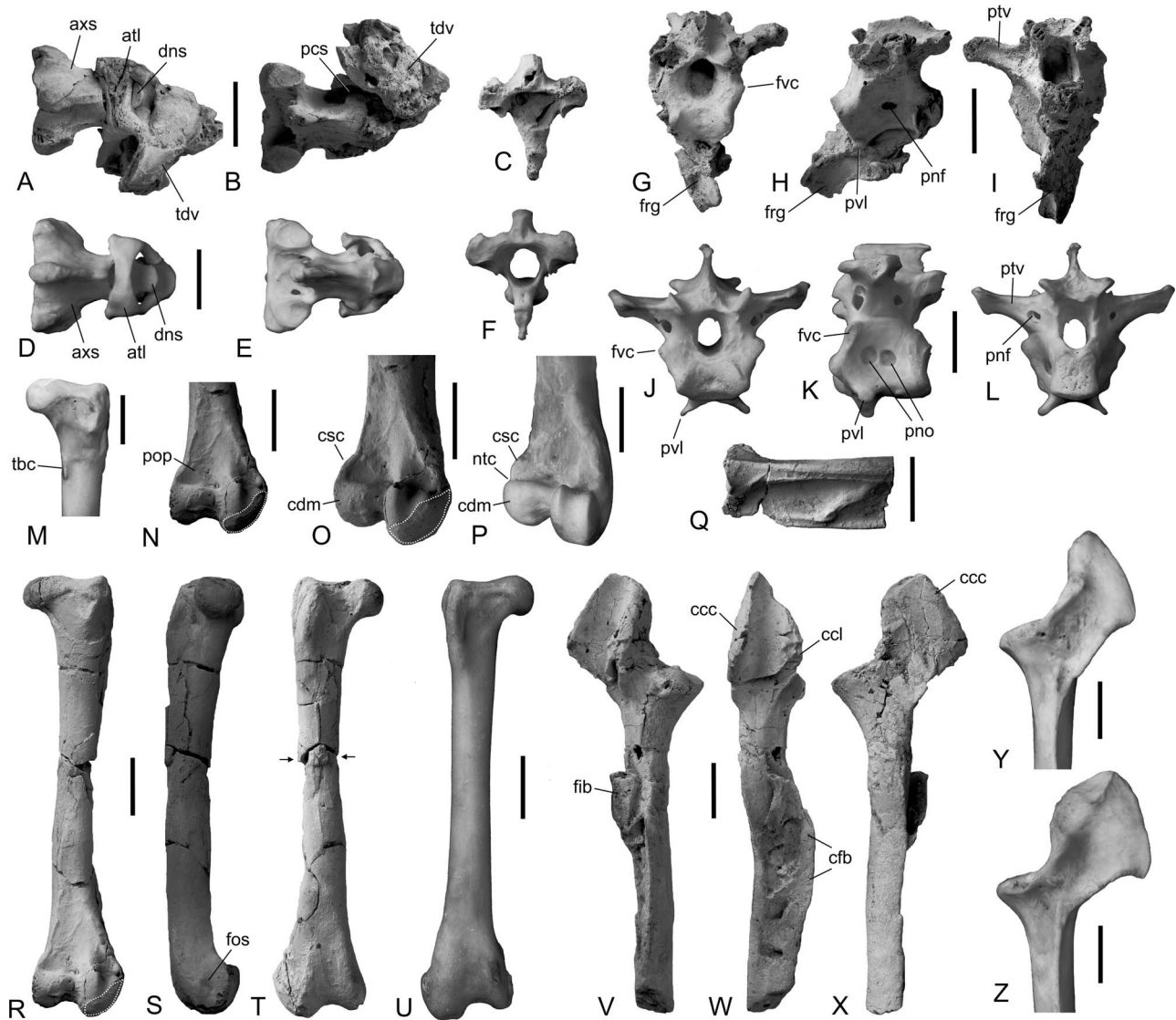
**FIGURE 5.** Diomedeidae, gen. et sp. indet. ("Astoria Formation albatross"; SMF Av 644) from the early or early middle Miocene Astoria Formation of Washington (USA). (**A**, **B**) Atlas, axis, and third vertebra in (**A**) dorsal and (**B**) ventral view. (**C**) Axis in caudal view (matrix and adhering bones digitally removed). (**D–F**) Atlas and axis of *Thalassarche melanophris* in the same views as before. (**G–I**) 17th presacral vertebra in (**G**) cranial, (**H**) left lateral, and (**I**) caudal view. (**J–L**) 17th presacral vertebra of *Th. melanophris*, in the same views as before. (**M**) Proximal end of the right femur of *Diomeda antipodensis* in caudal view. Distal end of the right femur (caudal view) of the Astoria Formation albatross in (**N**) caudal and (**O**) caudolateral view (the dotted lines indicate a restored part of the condylus lateralis), in comparison to (**P**) the distal femur of *D. antipodensis* (caudolateral view). (**Q**) Proximal portion of left phalanx proximalis digiti majoris in ventral view. (**R–T**) Right femur in (**R**) caudal, (**S**) medial, and (**T**) cranial view (the dotted line in **R** indicates a restored part of the condylus lateralis, the arrows in **T** denote the breakage, where the two halves of the bones were connected for the figure). (**U**) Right femur (cranial view) of *T. melanophris*. (**V–X**) Proximal end of left tibiotarsus in (**V**) lateral, (**W**) cranial, and (**X**) medial view, in comparison to the proximal tibiotarsus of (**Y**) *Th. melanophris* and (**Z**) *Macronectes halli* (Procellariidae). Anatomical abbreviations: atl = atlas; axs = axis; ccc = crista cnemialis cranialis; ccl = crista cnemialis lateralis; cdm = condylus medialis; cfb = crista fibularis; csc = crista supracondylaris; dns = dens of axis; fib = fibula; fos = fossa on condylus medialis; frg = unidentified bone fragment; fvc = fovea costalis; ntc = notch between crista supracondylaris and condylus medialis; pcs = processus costalis; pnf = pneumatic foramen; pop = fossa poplitea; pvl = processus ventrolateralis; tbc = tubercle on proximal end of femur; tdv = third cervical vertebra. Fossil specimens were coated with ammonium chloride. Scale bars equal 10 mm.

The fragmentary wing phalanx (Figure 5Q; phalanx proximalis digiti majoris) closely resembles the corresponding bone of crown group Diomedeidae.

The femur is preserved in 2 portions. The bone was already fractured in situ and its 2 halves were left separate, because only a very small contact zone between both ends exists (Figure 5R–T). The bone corresponds well with the femur of crown group Diomedeidae, but a few subtle differences can be observed. On the proximal end, there is no distinct tubercle on the caudomedial surface of the shaft (Figure 5M, R). In medial view, the distal end differs from the femur of crown group Diomedeidae in that the crista supracondylaris medialis merges smoothly into the condylus medialis, whereas there is a small notch between this crest and the condylus medialis in extant albatrosses (Figure 5O, P). The well developed fossa poplitea is laterally bordered by a distinct bulge and bears a pit-like fossa as in *Phoebetria* and *Phoebastria*, whereas the fossa poplitea is essentially flat in *Thalassarche* and *Diomedea*. There is further a pit-like fossa on the medial surface of the condylus medialis (Figure 5S), which is shallower in *Phoebetria* and barely developed in *Thalassarche* and *Diomedea*. The sulcus intercondylaris is moderately developed as in *Phoebetria* and *Diomedea*, with this sulcus being deeper in *Thalassarche*.

The tibiotarsus (Figure 5V–X) exhibits a deformed, sigmoidally curved shaft (Figure 5W), which is either due to a pathological condition or an artifact of the fossilization process. The crista cnemialis cranialis is well developed as in crown group Diomedeidae and other procellariiform birds. Although the very tip of this crest may be broken, the preserved part of its proximal portion is craniocaudally wider than in all extant albatrosses, which—based on outgroup comparison with the Procellariidae (Figure 5Z)—probably represents a plesiomorphic feature for the Diomedeidae (see Discussion). A large transverse cleft on the cranial surface of the proximal tibiotarsus is a preservational artifact and the apex of the crista cnemialis lateralis is broken. The crista fibularis is unusually prominent, but it is uncertain whether this is a real feature or represents a taphonomic artifact.

A long bone situated beneath the skull proved difficult to identify and is here considered to be the distal portion of the left ulna (Figure 4). The morphology of this bone is obscured by the fact that bone fragments are attached to the distal articular surface and the tuberculum carpale (which therefore appears larger than it was). A more proximal portion of the shaft is exposed on the underside of the specimen next to the mandibular rami; the intermediate section of the bone is still hidden in matrix.

## DISCUSSION

*Diomedavus knapptonensis*, n. gen et sp. from the late Oligocene upper part of the Lincoln Creek Formation is the oldest published fossil albatross from the North Pacific Basin. Derived features shared by the new species and extant albatrosses include the cranial bulge formed by the crista bicipitalis of the humerus, the presence of pneumatic openings in the impressio musculi sternocoracoidei of the coracoid, the fusion of the ilia with the synsacrum, and the absence of a sulcus for the tendon of musculus flexor hallucis longus in the hypotarsus. *Diomedavus knapptonensis* is smaller than all extant albatrosses, from which it is also clearly distinguished in morphological features, notably the shape of the crista deltopectoralis, the long dorsal portion of the facies articularis sternalis of the coracoid, and the less prominent crista lateralis of the hypotarsus (Figure 3 and description).

The distally displaced apex of the deltopectoral crest indicates that *D. knapptonensis* differed from extant albatrosses in features of the pectoral musculature, which likely indicate that the flight performance of this Oligocene species differed from that of extant albatrosses. This is also suggested by the morphology of the sternal extremity of the coracoid, but the incompletely known osteology of the new species does not allow well-founded considerations on details of its flight technique. Regarding the shape of the crista deltopectoralis, *D. knapptonensis* also differs from the Procellariidae and other extant procellariiform birds, as well as from the early Oligocene procellariiform Diomedeoididae (Mayr and Smith 2012b), and it is possible that the unusual morphology of the proximal end of the humerus is an autapomorphic character of the new species.

Based on outgroup comparisons with non-diomedeid procellariiforms, at least the coracoid and hypotarsus characters of *D. knapptonensis* are, however, likely to be plesiomorphic, and we therefore conclude that *D. knapptonensis* is a stem group representative of the Diomedeidae. Whether *Diomedavus*, n. gen. or *Plotornis* is more closely related to crown group Diomedeidae cannot be definitely said, because some skeletal characters (e.g., the extremitas sternalis of the coracoid and details of the hypotarsus morphology) are unknown or poorly known for *Plotornis*, and because it is uncertain whether the peculiar shape of the crista deltopectoralis of *Diomedavus* is plesiomorphic for albatrosses or represents an autapomorphy of the new taxon. Although we consider it likely that *Diomedavus* is phylogenetically more distant from extant albatrosses than is *Plotornis*, more data on the osteology of fossil Diomedeidae are needed for firm phylogenetic conclusions.

A position outside the crown group also needs to be considered for early and middle Miocene albatrosses with a smaller body size than crown group Diomedeidae. Davis (2003) hypothesized that the early Miocene "*D.*" *tanakai* is more closely related to *Phoebetria*, *Phoebastria*, and *Diomedea* than to *Thalassarche*, thereby suggesting a position of this species within crown group Diomedeidae.

However, his conclusion was merely based on overall similarity and conflicts with the fact that *Thalassarche* was recovered as the sister taxon of *Phoebetria* in molecular analyses (Nunn et al. 1996, Chambers et al. 2009). Instead, the small size of "*D.*" *tanakai* suggests that this early Miocene species represents a stem group albatross. Although Davis (2003:43) noted that he compared "*D.*" *tanakai* with the somewhat older early Miocene *Plotornis delfortrii*, the single difference he mentioned is a purportedly smaller size of the Japanese species. With a length of 69.8 mm (Davis 2003), the tarsometatarsus of "*D.*" *tanakai* is, however, only slightly shorter than that of *Plotornis delfortrii*, which measures 70.5 mm (Milne-Edwards 1874). Morphologically, the bones also appear to be similar, but restudy of the original material is requisite for a reconsideration of possible affinities between "*D.*" *tanakai* and the taxon *Plotornis*.

In size and morphology, the bones of the early/middle Miocene Astoria Formation albatross are closer to those of extant albatrosses. Unfortunately, critical skeletal elements, such as the humerus and tarsometatarsus, are missing, and a lack of overlap with skeletal elements known from other fossil albatrosses impedes a taxonomic assignment of the Astoria Formation albatross and prevents an assessment of its phylogenetic affinities. The fossil exhibits the characteristic bill shape of albatrosses, with laterally facing nostrils (see description), but it is clearly distinguished from crown group Diomedeidae in the craniocaudally wider crista cnemialis cranialis of the tibiotarsus (Figure 5X, Y). Outgroup comparisons with other Procellariiformes (Figure 5Z) suggest that a wide crista cnemialis cranialis is a plesiomorphic feature, which argues for a position of the Astoria Formation albatross outside crown group Diomedeidae. Such is also supported by the less extensively ossified margins of the nostrils of the fossil species and the subtle differences in the morphology of the distal end of the femur (see description). The cnemial crests of the tibiotarsus serve for the attachment of the shank musculature; the functional significance of these differences in hindlimb morphology is unknown, but the resemblance of the tibiotarsus to that of the Procellariidae may indicate that the Astoria Formation albatross was better capable of terrestrial locomotion than its extant relatives, which seldom walk on land.

The fossil record documents that part of the early evolution of albatrosses took place in the Northern Hemisphere. Stem group Diomedeidae are now known from the North Pacific (*Diomedavus knapptonensis*, "*Diomedea*" *tanakai*, and the Astoria Formation albatross), the North Atlantic (*Plotornis delfortrii*), and the Mediterranean Sea (*P. graculoides*). These fossils document that albatrosses had a wide distribution in the Northern Hemisphere in late Oligocene and early Miocene time, and the confinement of most albatross diversity to the Southern Hemisphere is likely to have happened in the late Neogene.

Stem group albatrosses occurred in the North Pacific Basin before the emergence of *Phoebastria*, but exactly when representatives of the latter lineage first appeared in the North Pacific is difficult to assess. Olson and Rasmussen (2001) considered it possible that the large middle Miocene "*D.*" *californica* is an ancestor of the likewise large-sized, extinct Northern Hemisphere *Phoebastria anglica*, fossils of which were found in Pliocene rocks of England and the North American Atlantic coast (Olson and Rasmussen 2001, Dyke et al. 2007). However, an assignment of "*D.*" *californica* to *Phoebastria* still has to be firmly established and the recognition of a fairly large-sized stem group albatross in the Miocene Astoria Formation puts a caveat on this hypothesis.

Albatrosses not only depend on persisting wind systems for their aerial locomotion, but also forage in nutrient-rich surface waters resulting from marine upwelling. The biogeography of these birds is therefore likely to have been shaped by changes in global marine or atmospheric circulation systems, and a loss of safe breeding grounds may have also limited their distribution in the Northern Hemisphere. Currently, our knowledge of the fossil record of albatrosses is too patchy for far-reaching hypotheses, but once an improved understanding of albatross evolution exists, future research will have to set it in context with paleogeographic events that may have impacted marine and atmospheric circulation systems, such as the late Cenozoic formation of the Panamanian Isthmus, which affected the thermohaline circulation in the Atlantic Ocean (Haug and Tiedemann 1998).

## ACKNOWLEDGMENTS

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