

## A NEW SPECIES OF AUK (CHARADRIIFORMES, PAN-ALCIDAE) FROM THE MIOCENE OF MEXICO

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**Abstract.** A fossil from the Middle Miocene Rosarito Beach Formation of Baja California represents a previously undescribed, auklet-sized species of wing-propelled diving Pan-Alcidae (Aves, Charadriiformes). This new taxon, *Divisulcus demerei*, is recognized from the presence of a bifurcated scapulothoracic sulcus of the distal end of the humerus, a potentially neomorphic character within Aves. Additionally, the degree of compression of the humeral shaft of this new species is less than that of other pan-alcids. These characters may represent retention of ancestral character states that are associated with the transition to wing-propelled diving from nondiving Charadriiformes. This discovery provides further information regarding paleodiversity in this clade, extends the geographic range of Miocene pan-alcids, and may represent the oldest record of the clade from the Pacific Ocean basin, as previously reported unambiguous records are from Late Miocene or younger deposits (~10–1.6 Ma). Moreover, the age of this new pan-alcid (14–16 Ma) corresponds with the timing of the Middle Miocene climatic optimum, a time for which previous records of Pacific Ocean basin pan-alcids were lacking. Because of the relative incompleteness of the specimen, the systematic position of this new taxon within the Pan-Alcidae from a phylogenetic analysis is not strongly supported. Until additional remains of *D. demerei* are recovered that can provide additional character data, the affinities of this new taxon within the Pan-Alcidae are uncertain.

**Key words:** *Divisulcus demerei*, fossil seabird, neomorph, paleoclimate, paleodiversity, systematics, wing-propelled divers.

### Una Nueva Especie de Alca (Charadriiformes, Pan-Alcidae) del Mioceno de México

**Resumen.** Un fósil de la Formación Playa Rosarito del Mioceno Medio de Baja California representa una especie Pan-Alcidae buceadora propulsada por las alas del tamaño de un alca no descrita previamente (Aves, Charadriiformes). Este nuevo taxón, *Divisulcus demerei*, se reconoce por la presencia de un surco bifurcado escapulothorácico en el extremo distal del húmero, un carácter potencialmente neomórfico dentro de Aves. Adicionalmente, el grado de compresión de la diáfisis humeral de esta nueva especie es menor que la de otros pan-alcidos. Estos caracteres pueden representar la retención del estado de caracteres ancestrales que están asociados con la transición hacia el buceo propulsado por las alas desde Charadriiformes no buceadores. Este descubrimiento brinda nueva información sobre la paleodiversidad de este clado, extiende el rango geográfico de los pan-alcidos del Mioceno y puede representar el registro más viejo del clado de la cuenca del Océano Pacífico, ya que los registros inequívocos previamente reportados son del Mioceno Tardío o de depósitos más jóvenes (~10–1.6 Ma). Más aún, la edad de este nuevo pan-alcido (14–16 Ma) corresponde al momento del óptimo climático del Mioceno Medio, un tiempo para el cual están faltando los registros previos de pan-alcidos de la cuenca del Océano Pacífico. Debido a lo relativamente incompleto del espécimen, la posición sistemática de este nuevo taxón dentro de Pan-Alcidae a partir de un análisis filogenético no cuenta con un sustento fuerte. Hasta que se encuentren restos adicionales de *D. demerei* que puedan brindar datos de caracteres adicionales, las afinidades de este nuevo taxón dentro de Pan-Alcidae son inciertas.

### INTRODUCTION

The Pan-Alcidae are a clade of pelagic charadriiforms characterized by wing-propelled diving and anatomical modifications associated with this derived method of prey pursuit. Extant species comprise 23 species of auks, auklets, murrelets, guillemots, and puffins, restricted to the Northern Hemisphere (del Hoyo et al. 1996). Pan-alcids' ecological

attributes range through planktivorous and piscivorous foraging, solitary and colonial nesting, and differing depths and duration of dives (del Hoyo et al. 1996). Nonetheless, the relatively conserved morphology of pectoral bones that have been modified for wing-propelled diving has greatly facilitated identification of pan-alcid fossils. The fossil record of the Pan-Alcidae is the richest among the Charadriiformes, with approximately 17,000 known specimens representing

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at least 28 species (Smith 2011a). Although the majority of pan-alcid fossils are from the Pliocene, Miocene remains of pan-alcids comprise at least 13 species (Smith 2011a). However, Miocene records of the clade from the Pacific Ocean basin are restricted to three species of flightless mancalline auks and a single species each of guillemot, auklet, and murre (Howard 1981, 1982, Smith 2011b, Smith in press). Furthermore, previously described Pacific Ocean basin Miocene pan-alcid fossils are all from the Late Miocene (~6.7–10.0 Ma; i.e., Early and Middle Miocene remains previously undescribed; Howard 1981, 1982, Smith 2011a, in press).

Here I describe the distal end of a humerus from the Middle Miocene (14–16 Ma) Rosarito Beach Formation of Baja California, Mexico (Figs. 1, 2). This fossil represents a new pan-alcid taxon, the earliest record of the clade in the Pacific Ocean basin, and a southward extension of the geographic range of Miocene Pan-Alcidae. The holotype locality of *Divisulcus demerei* is the southernmost Miocene locality known for a pan-alcid fossil. Remains of the substantially younger taxon *Fratercula dowi* from the Pleistocene of Cedros Island, Baja California, represent the southernmost fossil record of the clade worldwide (Guthrie et al.

1999, Smith 2011a; Fig. 1). The Rosarito Beach Formation is bracketed above and below by radiometrically dated basalts; Deméré et al. (1984) interpreted it as the result of deposition in an open marine, subtropical, clear, calm environment on the inner continental shelf. The La Misión Local Fauna of the Los Indios Member of the Rosarito Beach Formation comprises bony and cartilaginous fishes, cetaceans, pinnipeds, sea cows, a desmostylian, a camel, a dog, a turtle, mollusks, siliceous microfossils, and four species of seabirds (Deméré et al. 1984). In addition to the pan-alcid I describe here, Deméré et al. (1984) referred the avian remains to *Puffinus* sp. (shearwaters), *Morus* sp. (gannets), and *Sula* sp. (boobies). The specimen I designate here as the holotype of *D. demerei* had been referred to the Alcidae by Deméré et al. (1984). However, they did not systematically describe, figure, or analyze the fossil phylogenetically. Here, I formally describe this specimen as a new pan-alcid taxon and interpret it in context with recent advances in knowledge of pan-alcid paleodiversity and systematics.

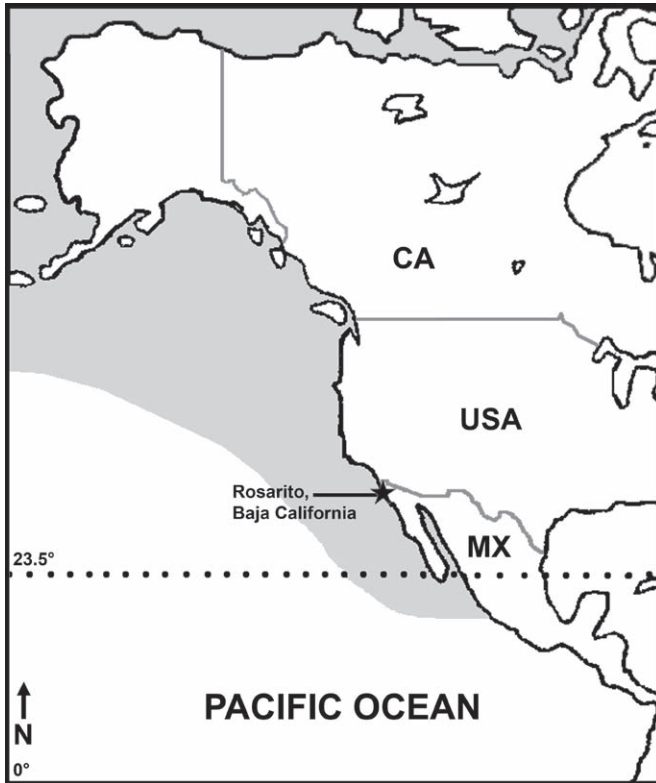


FIGURE 1. Location where the holotype specimen of *Divisulcus demerei* was collected. Gray shading represents the eastern Pacific Ocean range of extant alcids (based on del Hoyo et al. 1996). Abbreviations: CA, Canada; MX, Mexico; USA, United States of America.

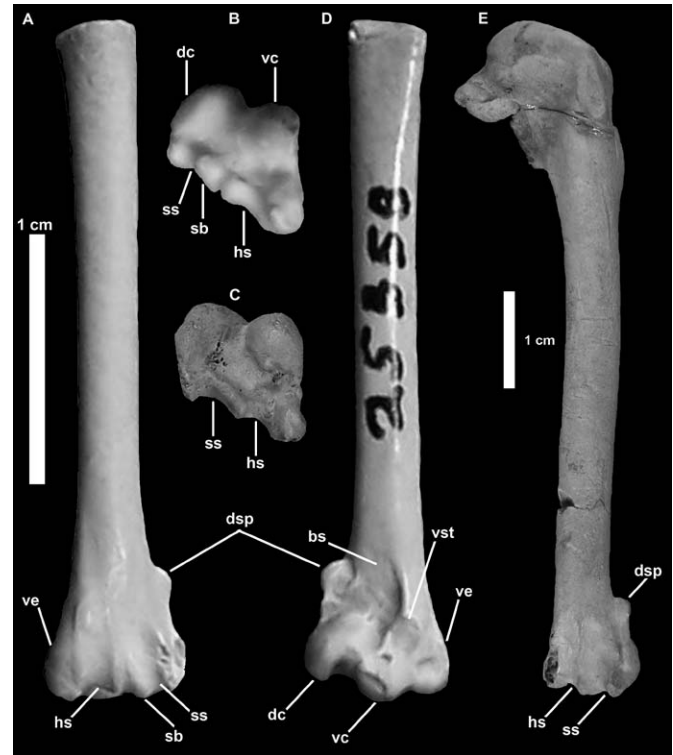


FIGURE 2. Holotype specimen of *Divisulcus demerei* (SDSNH 25358) in posterior (A) distal (B), and anterior (D) views. Holotype specimen of *Pseudocepphus teres* also shown for comparison in distal (C; not to scale for comparison) and posterior (E) views. Anatomical abbreviations: bs, scar for m. brachialis; dsp, dorsal supracondylar process; dc, dorsal condyle; hs, humerotricipital sulcus; sb, scapulotricipital bifurcation; ss, scapulotricipital sulcus; vc, ventral condyle; ve, ventral epicondyle; vst, ventral supracondylar tubercle (modified from Smith 2011a, figure 5.12).

## MATERIALS AND METHODS

Description of anatomical features follows the English equivalents of the Latin osteological nomenclature summarized by Baumel and Witmer (1993). All measurements were taken with digital calipers, rounded to the nearest 0.1 mm, and follow von den Driesch (1976). Ages of geologic time intervals are based on the International Geologic Timescale (Gradstein et al. 2004, Ogg et al. 2008). The term “alcid” refers to the crown clade Alcidae, “pan-alcid” to the clade that includes the Alcidae + Mancallinae (sensu Smith 2011b).

Institutional abbreviations: NCSM—North Carolina Museum of Natural Sciences, Raleigh, NC; SDSNH—San Diego Natural History Museum, San Diego, CA; UMMZ—University of Michigan Museum of Zoology, Ann Arbor, MI; USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Comparative material: Cassin’s Auklet (*Ptychoramphus aleuticus*), USNM 491305, 491845, 491846, 557607, 557609; Crested Auklet (*Aethia cristatella*), USNM 223707, 488675, 498282, 561934, 61094; Parakeet Auklet (*A. psittacula*), NCSM 14147, 14804, 18387, 18514, 20177, USNM 12640, 226451; Least Auklet (*A. pusilla*), NCSM 17734, 17736, 17737; USNM 224009, 224010, 498285; Whiskered Auklet (*A. pygmaea*), UMMZ 204592, 224279, 224882, 224883; Dovekie (*Alle alle*), NCSM 18374; USNM 344740, 344748, 499471, 560929; Kittlitz’s Murrelet (*Brachyramphus brevirostris*), USNM 288086; Spectacled Guillemot (*Cephus carbo*), USNM 347755, 347756, 347757; Pigeon Guillemot (*C. columba*), NCSM 18094, 18095, 18096, 18097; Black Guillemot (*C. grylle*), USNM 344759, 344760, 347265, 612213, 612214; Tufted Puffin (*Fratercula cirrhata*), NCSM 17823; Horned Puffin (*F. corniculata*), NCSM 17835; Great Auk (*Pinguinus impennis*), USNM 346387; Craveri’s Murrelet (*Synthliboramphus craveri*), SDSNH 36390, 36391, 37767; Common Murre (*Uria aalge*), NCSM 17822. I also compared SDSNH 25358 to a broad sample of other charadriiforms in the USNM collection and a broad sample of non-charadriiform taxa in the synoptic series at USNM.

## SYSTEMATIC PALEONTOLOGY

AVES Linnaeus, 1758

CHARADRIIFORMES Huxley, 1867

PAN-ALCIDAE Smith, 2011

*Divisulcus demerei*, gen. et sp. nov.

(Fig. 2; Table 1)

*Etymology.* From the Latin for divided groove, the generic name *Divisulcus* reflects the autapomorphic character by which this taxon is diagnosed. The species epithet *demerei* recognizes the many contributions to vertebrate paleontology of Thomas A. Deméré, including previous recognition of the autapomorphy that diagnoses this new taxon. The name is masculine in gender.

TABLE 1. Measurements (after von den Driesch 1976, in mm) of *Divisulcus demerei* and averages of other selected pan-alcids. Abbreviations: Bd, breadth of the distal end; Bp, breadth of proximal end; Dd, distal diagonal; Dip, diagonal of proximal end; Gl, greatest length; Sc, smallest breadth of corpus (shaft). Dashes represent data not available because of damage.

Taxon	<i>n</i>	Bd	Bp	Dd	Dip	Gl	Sc
<i>Ptychoramphus aleuticus</i>	5	7.0	9.4	5.0	9.3	45.1	3.4
<i>Aethia cristatella</i>	5	8.4	11.5	5.9	11.4	52.3	4.1
<i>Aethia psittacula</i>	7	8.7	11.9	6.3	11.3	54.3	4.3
<i>Aethia pusilla</i>	6	5.5	7.7	4.0	7.3	34.9	2.5
<i>Aethia pygmaea</i>	4	5.9	8.1	4.3	7.8	37.9	2.8
<i>Divisulcus demerei</i>	1	5.3	—	4.1	—	—	2.3
<i>Alle alle</i>	5	6.6	9.7	4.6	8.8	41.5	3.2
<i>Cephus columba</i>	4	9.7	15.3	7.6	13.9	66.6	5.1
<i>Synthliboramphus craveri</i>	3	7.1	10.0	4.8	9.6	44.8	3.9

*Holotype.* The holotype specimen is the distal end of a right humerus (SDSNH 25358; Table 1, Fig. 2) collected by D. Baer and J. A. Lillegraven on 2 May 1970 during an expedition of San Diego State University.

*Locality and horizon.* The holotype specimen was collected from the Middle Miocene (~14–16 Ma) Los Indios Member of the Rosarito Beach Formation, located between Tijuana and Rosarito, Baja California, Mexico (Deméré et al. 1984; Fig. 1). Latitude, longitude, and elevation data are on file at SDSNH (locality 3459).

*Diagnosis.* *Divisulcus demerei* is differentiated from all other Pan-Alcidae by having the scapulothoracic sulcus of the distal humerus bifurcated lengthwise (i.e., proximodistally) by a crest (Fig. 2). This character is an autapomorphy of *D. demerei* and is not known in any other avian taxon. Additionally, the humeral shaft is dorsoventrally compressed to a lesser degree than in all other pan-alcids (Fig. 3), and *D. demerei* is smaller than all other known pan-alcids (Table 1).

*Description.* The distal ends of the humeri of Charadriiformes such as *D. demerei* are differentiated from those of the Procellariiformes, including the wing-propelled diving Pelecanoididae, by their less deeply excavated brachial fossa and less dorsally projecting dorsal supracondylar process. *Divisulcus demerei* is referable to Pan-Alcidae on the basis of the dorsoventral compression of the humeral shaft (Fig. 3). As in all pan-alcids other than the Mancallinae, the anterior face of the ventral humeral condyle is flattened (Fig. 2) rather than rounded as in other Charadriiformes. Although the proximal end of the humerus is missing (Fig. 2), the specimen is otherwise well preserved with respect to fine morphological details. The ventral epicondyle is ventrally flared as in the Fraterculinae (Aethiini and Fraterculini; Fig. 4) rather than straight as in some alcids (e.g., *Alca*). The ventral supracondylar tubercle (i.e., anterior articular ligament scar; sensu Howard 1929) is rounded like that of all other Fraterculinae except for an extinct species

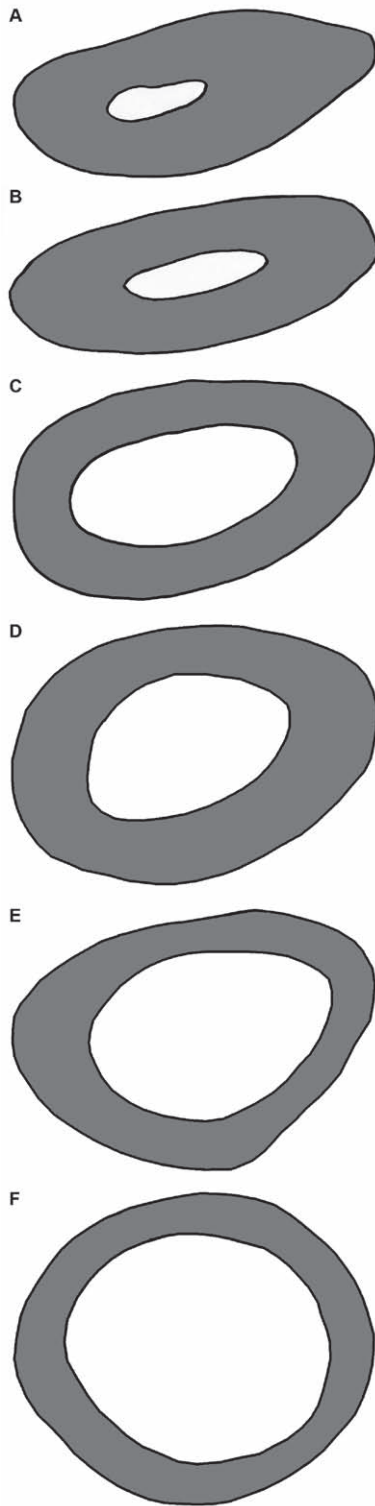


FIGURE 3. Silhouettes of cross-sectional views through the mid-shaft of the humeri of *Divisulcus demerei* (E), flightless alcids (A, *Mancalla vegrandis*; B, *Pinguinus impennis*), extant volant alcids (C, *Alca torda*; D, *Cephus columba*) and the non-wing-propelled-diving sister taxon to the Pan-Alcidae (F, *Stercorarius longicaudus*), showing the range of dorsoventral compression of the shaft. All cross-sections are oriented with the dorsal surface toward the top of the page.

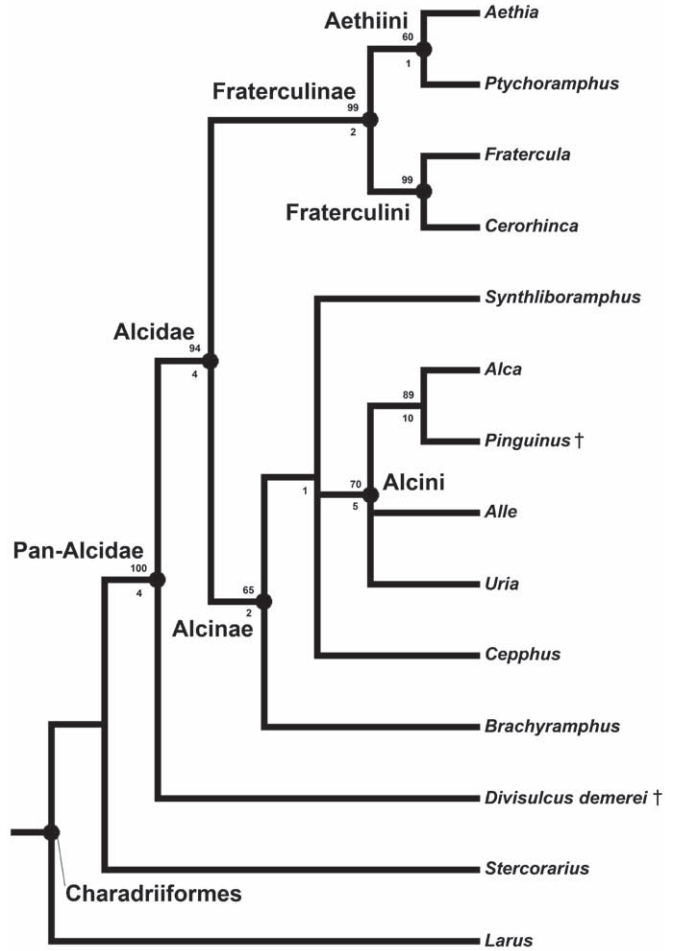


FIGURE 4. Cladogram showing the systematic position recovered for *Divisulcus demerei* (strict consensus of 12 most parsimonious trees). Bootstrap and Bremer values appear above and below nodes, respectively (modified from Smith 2011a, figure 5).

of *Aethia* from the Pliocene of California being described by Smith (in press). As in *Alle alle*, *Pseudocepphus teres* Wijnker and Olson 2009, *Synthliboramphus rineyi* Chandler 1990, and an extinct species of *Aethia* from the Miocene of California being described by Smith (in press) the scapulo- and humero-epitricipital sulcus is broader than the humero-epitricipital sulcus. The degree of dorsoventral compression of the humeral shaft is similar, albeit less than that of *P. teres* and *Cephus* (Fig. 3).

*Remarks.* *Divisulcus demerei* was similar in size to the extant Least Auklet (*Aethia pusilla*). On the basis of available measurement data (Table 1; Smith 2011a, Smith and Clarke 2011), *D. demerei* is the smallest known alcid. SDSNH 25358 was previously described by Deméré et al. (1984) as part of a report on the paleontology of the Rosarito Beach Formation, in which they noted the diagnostic characteristic of *D. demerei*, the bifurcated scapulo- and humero-epitricipital sulcus. However, they refrained from designating the specimen as the holotype

of a new taxon at that time because of a lack of extant comparative material. Furthermore, a survey of the avian synoptic collection at USNM failed to identify any other taxon that possessed a bifurcated scapulothoracic sulcus.

## DISCUSSION

With the exception of the degree of dorsoventral compression of the humeral shaft, which approaches that of *Pseudocepphus teres* and *Cepphus* among the Alcinae (*Alca*, *Pinguinus*, *Alle*, *Miocepphus*, *Uria*, *Brachyramphus*, *Synthliboramphus*, *Pseudocepphus*, *Cepphus*; Fig. 4), *Divisulcus demerei* possesses a combination of characters otherwise shared by auklets and puffins (i.e., Fraterculinae) among pan-alcids (Fig. 3). These characters include a ventrally flared ventral epicondyle, a triangular ventral supracondylar tubercle, and a relatively short and dorsally projected dorsal supracondylar process. The ventrally flared ventral margin of the distal humeral shaft is an apomorphy of the Fraterculinae within the Alcidae but is also characteristic of many other Charadriiformes (e.g., Great Black-backed Gull, *Larus marinus*). The dorsal supracondylar tubercle of many Alcinae is more proximally positioned and less dorsally projected, whereas it is larger and dorsally projected to a much greater degree in many non-alcid charadriiforms (e.g., Long-tailed Jaeger, *Stercorarius longicaudus*).

Among the Charadriiformes, dorsoventral compression of the humeral shaft is an apomorphy of the Pan-Alcidae (Smith 2011a). However, the degree of compression varies considerably among the pan-alcid clades (Fig. 3). In *D. demerei* the degree of compression is reminiscent of albeite less than that seen in *Cepphus* (Fig. 3). The range of shaft compression among extant alcids is relatively small (i.e., differences between *Cepphus* and other alcids). However, when *Divisulcus*, *Pinguinus*, and the Mancallinae are considered, it is apparent that the range of pan-alcids' shaft compression was much greater in the past. *D. demerei* fits along a potential morphocline of shaft compression (Fig. 3), and the possibility that the shaft morphology of *D. demerei* represents retention of an ancestral state should be considered.

Like *D. demerei*, *Pseudocepphus teres* is characterized by a humeral shaft less dorsoventrally compressed than that of extant Alcidae (Wijnker and Olson 2009). Although that species is known exclusively from the Atlantic Ocean basin (Wijnker and Olson 2009), the Middle–Late Miocene (8–14 Ma) age range of that taxon may overlap with that of *D. demerei* (14–16 Ma). Wijnker and Olson (2009) considered the affinities of *P. teres* to be with the Alcini (i.e., *Alca*, *Pinguinus*, *Alle*, *Uria*, and *Miocepphus*; Smith and Clarke 2011; Fig. 4). But a phylogenetic analysis suggests it may be more closely related to other Alcinae (e.g., *Cepphus*; Smith 2011a), though this inference is not strongly supported. Although it is an intriguing possibility, there is currently not enough data to conclude that *Divisulcus* and *Pseudocepphus* are representatives of a

previously unrecognized clade of Miocene pan-alcids that were characterized in part by a degree of dorsoventral shaft compression less than that of extant alcids.

The bifurcated scapulothoracic sulcus that characterizes *D. demerei* is not present in any other charadriiform or any other avian taxon I have surveyed. Therefore, the functional significance of this characteristic and its potential correlation with ecological or ethological attributes remain uncertain. However, like those of penguins, the pectoral limbs of alcids have undergone extensive morphological changes associated with the transition to wing-propelled diving (i.e., changes in relative proportions, bone density, and osteological characteristics; Livezey 1988, 1989, Habib and Ruff 2008, Ksepka and Clarke 2010). In contrast to other Charadriiformes, in the Pan-Alcidae the relative widths of the tricipital sulci are variable (Smith 2011a), and the tricipital crest that separates the scapulothoracic and humerotricipital sulci has been lost in some penguins (Ksepka and Clarke 2010). The bifurcated scapulothoracic sulcus of *D. demerei* may represent retention of a morphological feature that is characteristic of a stage in the transition to wing-propelled diving, a characteristic that is not retained by more derived members of the clade.

There are no fossil records of the volant ancestors of penguins or of transitional lineages leading to the wing-propelled diving penguins or pan-alcids (Smith 2011a, Ksepka and Clarke 2010). Therefore, the morphological characters associated with the early reorganization of pectoral tissues are unknown for these clades. Thus the unique morphological characteristics of *D. demerei* may provide new insights into the evolution of wing-propelled diving. The earliest fossil penguins (i.e., stem-lineage penguins) from the Paleocene (~61 Ma) possess morphological characteristics consistent with wing-propelled diving (Ksepka and Clarke 2010). Likewise, the earliest fossil of the Pan-Alcidae from the Late Eocene (35 Ma) has the dorsoventrally compressed humeral shaft characteristic of more derived members of the clade (Chandler and Parmley 2002). However, given the antiquity of the penguin lineage in comparison to the more recently diverged pan-alcid lineage (split with the Stercorariidae estimated at ~38 Ma by Smith 2011a), it follows that probability of identifying transitional pan-alcid forms should be higher. Furthermore, the lesser degree of shaft compression of *D. demerei* fits with predictions of the morphology of nondiving ancestors of pan-alcids and penguins (Livezey 1988, 1989, Ksepka and Clarke 2010). However, given the approximately 20-Ma gap between the age of *D. demerei* and the age of the oldest known pan-alcid fossil, an alternative hypothesis that cannot be ruled out is that *D. demerei* had abandoned or was in the process of abandoning wing-propelled diving in favor of some other method of foraging or locomotion.

Regardless of the potential implications of this new taxon with respect to the evolution of wing-propelled diving, *D. demerei* represents the earliest record of the Pan-Alcidae

from the eastern Pacific Ocean basin and may represent the earliest record of the clade for the entire Pacific Ocean basin. *Divisulcus demerei* is potentially superseded in age by pan-alcid remains from the Oligocene of northern Japan (Ono and Hasegawa 1991). Those fossils consist of two fragmentary, isolated, and potentially taxonomically indeterminate specimens from the Iwaki Formation. Given the increase in character data generated from recently described pan-alcid remains (Smith et al. 2007, Wijnker and Olson 2009, Smith 2011a, b, in press, Smith and Clarke 2011), those Oligocene specimens should be re-evaluated to determine if their taxonomic status can be established unambiguously.

The Middle Miocene age of *D. demerei* (14–16 Ma) corresponds with the Middle Miocene Climatic Optimum (~11–16 Ma). You et al. (2009) estimated sea surface temperatures at this time were ~3 °C higher than today's, near the levels predicted to result from global warming in the next century. Because warmer sea surface temperature has been correlated with reduced reproductive success of planktivorous alcids (Kitaysky and Golubova 2000), the cooling since the Middle Miocene Climatic Optimum may offer an explanation for the faunal turnover among Miocene and Pliocene alcids. The fossil record provides evidence that alcids were successful, potentially dominant seabirds through the Late Miocene and Early Pliocene (Wijnker and Olson 2009, Smith et al. 2007, Smith 2011b, in press, Smith and Clarke 2011) when sea temperatures were cooler than during the Middle Miocene Climatic Optimum. However, there are few examples of alcid species that span this period (Smith 2011a), so apparently the Miocene–Pliocene boundary represents a faunal turnover for alcids similar to that documented for the Pliocene–Pleistocene climatic transition (Smith 2011a). The fossil record of pan-alcids before and during the Middle Miocene Climatic Optimum is currently too sparse for any detailed conclusions about how species richness may have differed at that time. The question of whether the absence of *D. demerei* from Late Miocene deposits represents its extinction or is an artifact of sampling will be answered only through additional collection of fossils from Middle and Late Miocene deposits.

A previous phylogenetic analysis identified *D. demerei* as the sister taxon to the Alcidae (Smith 2011a; Fig. 4). Those results are intriguing because *D. demerei* would represent the second record of a stem-lineage alcid, after the flightless lineage the Mancallinae, from the Miocene of the Pacific Ocean basin. However, the holotype of *D. demerei* could be scored for only 20 of the 353 morphological characters included in that analysis (i.e., 94% missing data). Although the phylogenetic analysis places *D. demerei* in the Pan-Alcidae, its hypothesized systematic position is not strongly supported. Moreover, the large percentage of missing data and the combination of character states otherwise known exclusively in the Fraterculinae or Alcinae (e.g., *Cephus*) may be responsible for *D. demerei* appearing as the sister of all other Alcidae in

that analysis (Fig. 4). Until additional remains of *D. demerei* that can provide further character data are recovered, this new taxon is best considered Pan-Alcidae incertae sedis.

Because *D. demerei* represents an increase in Miocene avifaunal diversity, a southward extension of the range of Miocene Pan-Alcidae, and an extension of the age of records of the Pan-Alcidae for the eastern Pacific, further study of this taxon and its associated fauna may have implications for the interpretation of faunal dynamics associated with the Middle Miocene Climatic Optimum. Furthermore, in the absence of more informative fossils, the new character data this diminutive taxon provide may be important for the study of the evolution of wing-propelled diving. The Rosarito Beach Formation and other Middle Miocene marine deposits should be targeted for recovery of additional remains of this intriguing new taxon.

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