

LATEST PACIFIC BASIN RECORD OF A BONY-TOOTHED BIRD (AVES, PELAGORNITHIDAE) FROM THE PLIOCENE PURISIMA FORMATION OF CALIFORNIA, U.S.A.

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ABSTRACT—Fossils of pelagornithids (bony-toothed birds) have been reported from strata of Paleocene to Pliocene age, and from every continent. The extreme fragility of pelagornithid bones has no doubt contributed to their geographically and temporally sporadic record, and thus it has been difficult to appreciate any long-term phylogenetic trends through geologic time for this group. We report a well-preserved partial humerus of the gigantic bird *Pelagornis* from the late Neogene Purisima Formation of central California. Due to its incompleteness, we refrain from naming a new species. This fossil is fortuitously bracketed by two ash beds, which have been correlated with volcanic rocks at 3.35 ± 0.05 Ma and 2.5 ± 0.2 Ma, indicating a middle to late Pliocene age for this fossil. This fossil extends the record of the pelagornithids in the Northeast Pacific, previously only known up until the early late Miocene (10–12 Ma). This fossil is the latest record of a pelagornithid for the Pacific Basin, and additionally represents the latest reliably dated pelagornithid record worldwide. This record suggests that the pelagornithids survived until the end of the Pliocene, and became extinct during the ocean restructuring and climatic upheavals that caused the demise of many other groups of marine vertebrates at that time.

INTRODUCTION

The extinct Pelagornithidae, also known as pseudodontorns, are often referred to as the ‘bony-toothed’ birds, owing to the tooth-like projections that characterize the beaks of these pelagic birds. Pelagornithid fossil remains are known from every continent and have an age range spanning more than 55 million years from the late Paleocene through the middle Pliocene (Harrison, 1985; Olson, 1985; Mourer-Chauviré and Geraads, 2008, 2010; Mayr, 2009). The systematic position of pelagornithids remains a contentious issue. Recent phylogenetic analysis recovered the pelagornithids as the sister taxon to Anseriformes (e.g., ducks and geese; Bourdon, 2005); however, this hypothesis contrasts with previous authors (Howard, 1957; Harrison and Walker, 1976; Olson, 1985) that considered pelagornithid affinities with Procellariiformes (e.g., albatrosses and petrels) or Pelecaniformes (e.g., pelicans and cormorants). A recent taxonomic revision of the clade resulted in the assignment of all Miocene and Pliocene Pelagornithidae to the taxon *Pelagornis* (Mayr and Rubilar-Rogers, 2010). A recently reported pelagornithid from the Pliocene of Morocco was touted as the youngest known record of the clade, at 2.5 Ma (Mourer-Chauviré and Geraads, 2008). Discovery of a proximal *Pelagornis* humerus (UCMP 219007) from the middle-upper Pliocene (~3.35–2.5 Ma) Purisima Formation (Fig. 1) of northern California represents the youngest record of Pelagornithidae from the Pacific Ocean basin and demonstrates that pelagornithids survived in both the Atlantic and Pacific Oceans until the late Pliocene.

MATERIALS AND METHODS

In the description, the English equivalents of the Latin osteological nomenclature summarized by Baumel and Witmer (1993) are used. With the exception of the terms anterior and posterior

substituted for cranial and caudal, respectively, the terms used for the anatomical orientation of a bird are those used by Clark (1993). Measurements follow those of von den Driesch (1976). All measurements were taken using digital calipers and rounded to the nearest tenth of a millimeter.

Although the Pliocene-Pleistocene boundary was recently revised from 1.806 Ma to 2.588 Ma by inclusion of the late Pliocene Gelasian stage within the early Pleistocene and modification of the Quaternary concept (Gibbard et al., 2009), this change is based on chronostratigraphy and does not reflect the biostratigraphic integrity of the traditionally defined Pleistocene epoch (Aubry et al., 2009). Thus, for the purposes of this paper, the traditional definition as delineated in Gradstein et al. (2004) of the Pliocene-Pleistocene boundary at the 1.806 Ma Gelasian-Calabrian stage boundary is retained along with a threefold division of the Pliocene epoch (lower, middle, and upper, equivalent with the Zanclean, Piacenzian, and Gelasian stages, respectively).

Institutional Abbreviation—UCMP, University of California Museum of Paleontology, Berkeley, California, U.S.A.

Locality and Age

The partial pelagornithid humerus (UCMP 219007) reported herein was collected by R.W.B. from the upper part of the San Gregorio section of the Purisima Formation, south of Halfmoon Bay in San Mateo County, California (UCMP locality V99846). The San Gregorio section of the Purisima Formation (sensu Powell et al., 2007) refers to exposures of the Purisima Formation that occur west of the San Gregorio Fault in the vicinity of San Gregorio, California (Fig. 1C). The Purisima Formation is late Miocene to late Pliocene in age, interpreted as the result of shallow marine deposition, and is exposed in scattered outcrops west of the San Andreas Fault, in the vicinity of Santa Cruz, Point Año Nuevo, Halfmoon Bay, and Point Reyes (Cummings et al., 1962; Clark et al., 1984; Powell et al., 2007). Five members of the Purisima Formation east of the San Gregorio Fault in the vicinity of Halfmoon Bay were named by Cummings et al.

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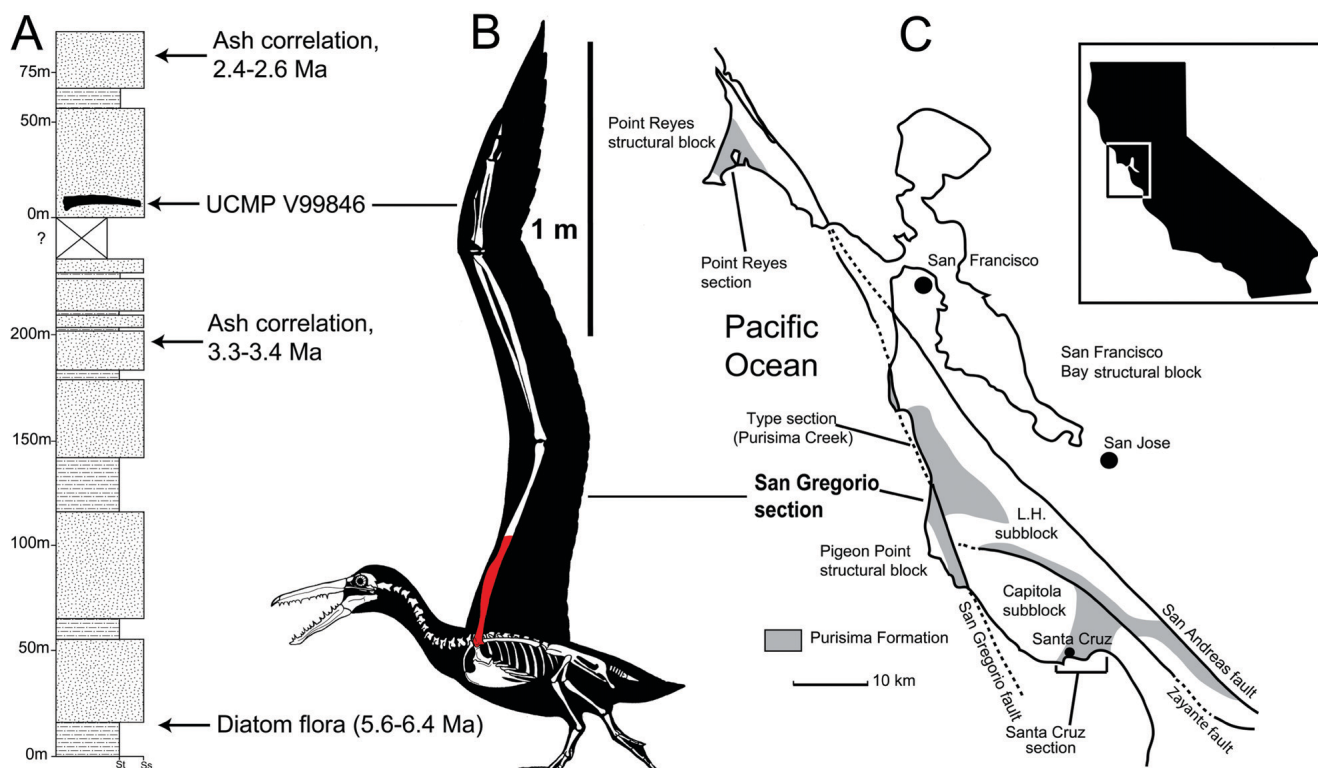


FIGURE 1. Locality information for *Pelagornis* sp. (UCMP 219007). **A**, stratigraphic column for the San Gregorio section of the Purisima Formation showing stratigraphic position of UCMP locality V99846; **B**, reconstruction of *Pelagornis* sp. with preserved portion of humerus shaded (modified with permission by R. W. Boessenecker from the reconstruction of *P. chilensis* by C. Anzuers in Mayr and Rubilar-Rogers, 2010); **C**, map of the San Francisco Bay area showing Purisima Formation exposures. **Abbreviations:** slt, siltstone; ss, sandstone. (Figure appears in color online.).

(1962); they are, from oldest to youngest, the Tahana Member (upper Miocene), Pomponio Member (lower Pliocene), San Gregorio Member (middle Pliocene), Lobitos Member (middle Pliocene), and the Tunitas Member (middle Pliocene; Powell et al., 2007). Molluscan biostratigraphy and lithologic correlations led Cummings et al. (1962) to map the San Gregorio section as belonging to the Tahana Member, which is entirely late Miocene in age. However, ash correlations reported by Sarna-Wojcicki et al. (1991) and Powell et al. (2007), in combination with the occurrence of the Pliocene bivalve *Patiniopecten healyi*, suggested to Powell et al. (2007) that the San Gregorio section is much younger and should not be mapped as the Tahana Member. Age correlations of two ashes, which fortuitously bracket UCMP locality V99846, were reported by Powell et al. (2007; Fig. 1A). A zone of disseminated tephra and pumice clasts occurs stratigraphically below the locality, and is correlative with the ~3.3–3.4 Ma Putah Tuff (Powell et al., 2007). A second ash was correlated with the 2.5 ± 0.2 Ma Ishi Tuff (Powell et al., 2007).

The rich vertebrate fossil assemblage was utilized by Boessenecker (in press) to evaluate the age of this locality. Vertebrate fossils from the upper and middle sections of the San Gregorio section indicated a middle to late Pliocene age based on comparisons with other California fossil assemblages, and shark teeth in concert with a 5.6–6.4 Ma diatom flora (reported by Powell et al., 2007; Fig. 1A) suggested a late Miocene to earliest Pliocene age for the base of the San Gregorio section (Boessenecker, in press). A diverse assemblage of 27 vertebrate taxa including sharks, bony fish, birds, and marine mammals (pinnipeds, toothed whales, and baleen whales) have been previously documented from the San Gregorio section of the Purisima Formation (Table 1; Boessenecker, in press). To that list we now add *Pelagornithidae*.

TABLE 1. Vertebrate fossil assemblage of the San Gregorio section of the Purisima Formation. Modified from Boessenecker (in press); additions to assemblage in bold.

Chondrichthyes
<i>Carcharodon carcharias</i>
<i>Carcharodon</i> sp.
<i>Cetorhinus maximus</i>
cf. <i>Hexanchus</i>
<i>Isurus oxyrinchus</i>
<i>Pristiophorus</i> sp.
<i>Raja</i> sp., cf. <i>R. binoculata</i>
<i>Squatina</i> sp.
cf. <i>Sphyrna</i>
Osteichthyes
<i>Paralichthys</i> sp.
<i>Thunnus</i> sp.
Aves
<i>Mancalla diegensis</i>
<i>Morus</i> sp.
<i>Pelagornis</i> sp.
Mammalia
Pinnipedia
Otariidae indet.
cf. <i>Dusignathus</i>
Odontoceti
<i>Parapontoporia</i> sp., cf. <i>P. sternbergi</i>
Phocoenidae sp. 1
Phocoenidae sp. 2
Globicephalinae indet.
Odontoceti indet.
Mysticeti
Balaenidae sp. indet. 1
Balaenidae sp. indet. 2
Balaenopteridae n. sp.
Balaenopteridae indet.
<i>Herpetocetus bramblei</i>
<i>Herpetocetus</i> sp.

SYSTEMATIC PALEONTOLOGY

AVES Linnaeus, 1758
PELAGORNITHIDAE Fürbringer, 1888
PELAGORNIS Lartet, 1857
PELAGORNIS sp.

Material—UCMP 219007, proximal left humerus (Fig. 2).
Identification—Referred to *Pelagornis* based upon the ventral margin of the proximal humerus tapered to a point; ventral tricipital fossa oriented ventrally, rather than posteriorly as in most birds; humeral head anteriorly projected; deltopectoral crest low, distally extended; and overall gigantic size. A proposed autapomorphy of the taxon that includes this specimen is the presence of a well-developed pneumatic foramen that extends into the humeral head ventral to the dorsal tubercle along the proximal margin of a sulcus we interpret as the dorsal pneumotricipital fossa (Fig. 3).

Description—This fossil is a proximal portion of a left humerus with a long, dorsoventrally compressed shaft (Fig. 2), measuring 385 mm as preserved. In addition to large size (Figs. 1B, 2, Table 2), UCMP 219007 exhibits several characteristics typical of pelagornithid humeri, such as an anteriorly protruding humeral head, distal elongation of the dorsal tubercle, proximodistally elongate tricipital fossa (considered synapomorphies of the Odontopterygiformes by Bourdon, 2005), an anteroposteriorly compressed proximal end, a distally positioned and elongate deltopectoral crest, and a prominent protuberance on the anterior surface of the humeral shaft (Fig. 2).

The humeral head projects anterior to the bicipital surface, is oval in proximal view (Fig. 2F), projects distally on the posterior surface, where it has a well-defined convex edge along the border of the dorsal pneumotricipital fossa (Fig. 3), and it tapers ventrally anteriorly and posteriorly. The dorsal and ventral tubercles are proximally elevated to the level of the humeral head, so that the proximal margin appears flattened in anterior and posterior views (Fig. 2A, C). The ventral tubercle is strongly developed and widely separated from the humeral head by a narrow ridge flanked posteriorly by the capital incisure. The ventral tubercle projects ventrally and posteriorly in proximal aspect, and it projects farther posteriorly than the humeral head or dorsal tubercle (Fig. 2E). The dorsal tubercle is sub-triangular in posterior view and prominent. From the sulcus immediately ventral to the dorsal tubercle, a pneumatic foramen extends into the humeral head, and measures 8 mm across and 4 mm deep (as prepared; Fig. 3). Based upon its position and the presence of a pneumatic foramen, we interpret this fossa as the dorsal pneumotricipital fossa (Fig. 2C). The presence of this pneumatic foramen has not been noted in other pelagornithid taxa and it may indicate that this specimen derives from an undescribed taxon. The dorsal pneumotricipital fossa is separated from the large and dorsodistally extended capital incisure (Fig. 2C). The ventral margin of the capital incisure is clearly defined by the dorsal crest (*crus dorsale fossae*; Baumel and Witmer, 1993:99). On the posterior surface, the tricipital fossa is elongate, apneumatic, and faces more ventrally than in most birds (Fig. 3).

On the anterior surface, the transverse ligament sulcus is shallow (Fig. 2A), the area between the deltopectoral crest and prox-

imal end is flattened, and the m. pectoralis scar adjacent to the deltopectoral crest is shallow (Fig. 2B, C). The posterior face is also concave adjacent to the deltopectoral crest (Fig. 2A, C). The deltopectoral crest is long (~270% of greatest proximal width), and although damaged along a section of its dorsal margin, the preserved portions are very low (i.e., not significantly dorsally or anteriorly projected; Fig. 2A, C). The apex (i.e., the most dorsally extended point) of the deltopectoral crest was positioned far from the humeral head (Fig. 2A, C). A distinct protuberance occurs ventral to the deltopectoral crest on the anterior facies near the shaft ventral margin, 113 mm from the proximal end (Fig. 2A, B, D). This feature is also developed in *Dasornis emuinus*, *Pelagornis chilensis*, and *P. miocaenus*, and is potentially homologous with a similar feature in pelecaniforms, albatrosses, and frigatebirds (Mayr and Smith, 2010; Mayr and Rubilar-Rogers, 2010), but was not scored by Bourdon (2005), who recovered the Odontopterygiformes as the sister taxon to Anseriformes. The posterior face of the shaft is strongly convex leading to the proximal end. As in other pelagornithids, the bone is extremely thin-walled, with compacta measuring 1–2 mm thick at the broken distal end and <1 mm thick at the proximal end (Fig. 2F).

Remarks—Comparisons with *Odontopteryx*, *Cyphornis*, *Gigantornis*, *Pelagornis orri*, *P. longirostris*, *P. stirtoni*, *Tymppanoneisotes*, and *Paleochenoides* are not possible because none of those taxa are known from well-preserved proximal humeri. Humeri have been reported for cf. *Macrodonopteryx oweni*, *Dasornis emuinus*, *Pelagornis chilensis*, *P. miocaenus*, and *P. mauretanicus*, and are thus comparable with UCMP 219007. *Dasornis emuinus* humeri are of similar size to UCMP 219007, and also exhibit a protuberance on the anterior surface. Aside from *Dasornis emuinus*, UCMP 219007 and other *Pelagornis* spp. can be differentiated from all other Paleogene pelagornithids by their much greater size (Mayr and Rubilar-Rogers, 2010). The new specimen is within the size range of *Pelagornis chilensis*, *P. miocaenus*, and *P. mauretanicus* (Harrison and Walker, 1976; Mourer-Chauviré and Geraads, 2008; Mayr and Rubilar-Rogers, 2010; Table 2). The proximal humerus fragment of *P. mauretanicus* differs only slightly from UCMP 219007 in possessing a proximodistally shallower humeral head (Mourer-Chauviré and Geraads, 2008). *Pelagornis miocaenus* and *P. chilensis* are similar to UCMP 219007 in possessing a relatively straight shaft, distally positioned deltopectoral crest, concave bicipital crest, a proximally prominent ventral tubercle, a distinct protuberance on the anterior surface, and a well-developed fossa on the posterior face ventral to the dorsal tubercle that excavates the humeral head (also present in *Pelagornis mauretanicus*). UCMP 219007 differs from *Pelagornis chilensis* and *P. miocaenus* in possessing a much more proximally elevated ventral tubercle, which is also posteriorly prominent (rather than ventrally as in *P. chilensis*). *Pelagornis miocaenus* has a dorsoventrally shallower proximal humerus with a less proximally elevated dorsal tubercle, and a less concave bicipital crest than UCMP 219007, whereas *P. chilensis* has a more concave bicipital crest than UCMP 219007 and *P. miocaenus* (Mayr and Rubilar-Rogers, 2010). Owing to the similar age and morphology of the new specimen and the preserved portions of the fragmentary proximal humeri referred to *P. mauretanicus*, the incomparable nature of some species of

TABLE 2. Measurements and wingspan estimates of *Pelagornis* spp.

Measurement	UCMP 219007	<i>Pelagornis miocaenus</i>	<i>Pelagornis chilensis</i>
Greatest proximal width	71.1 mm	59.3/61.5 mm	80.6 mm
Humeral length	723 mm (e)	591/710 mm	821 mm
Estimated skeletal wingspan	3.925 m	3.257/3.395 m	4.450 m

Wingspan estimates for UCMP 219007 and *Pelagornis miocaenus* are based on the ratio of proximal width to skeletal wingspan reported for *Pelagornis chilensis* (Mayr and Rubilar-Rogers, 2010). (e) denotes estimation.

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FIGURE 2. Left humerus (UCMP 219007) of *Pelagornis* sp. **A**, anterior view; **B**, ventral view; **C**, posterior view; **D**, dorsal view; **E**, outline reconstruction based on *Pelagornis chilensis*; **F**, proximal view; **G**, distal view showing cross-section. **Abbreviations:** **bc**, bicipital crest; **cd**, dorsal crest; **ci**, capital incisure; **dc**, deltopectoral crest; **dt**, dorsal tubercle; **h**, humeral head; **pf2**, dorsal pneumaticipital fossa; **pt**, protuberance; **tf**, tricipital fossa; **vt**, ventral tubercle. (Figure appears in color online.).

Pelagornis that have been described from non-humeral material (e.g., *P. stirtoni*), and the inferred high mobility of pelagornithids, we refrain from naming a new species.

DISCUSSION

This new discovery adds to the diversity of pelagornithids known from the northeastern Pacific Ocean Basin and provides evidence that pelagornithids survived until the latest Pliocene.

Previous records of pelagornithids from the northeast Pacific include occurrences from British Columbia, Oregon, California, and Baja California. Cope (1894) reported *Cyphornis magnus* (of unknown age: Goedert, 1989) from British Columbia. Records from Oregon include aff. *Dasornis* (originally reported as aff. *Argillornis*, which was synonymized with *Dasornis* by Mayr, 2008) and indeterminate pelagornithids from the lower-middle Oligocene Pittsburg Bluff Formation and the lower Oligocene Keasey Formation (Goedert, 1989), and *Pelagornis* sp. from

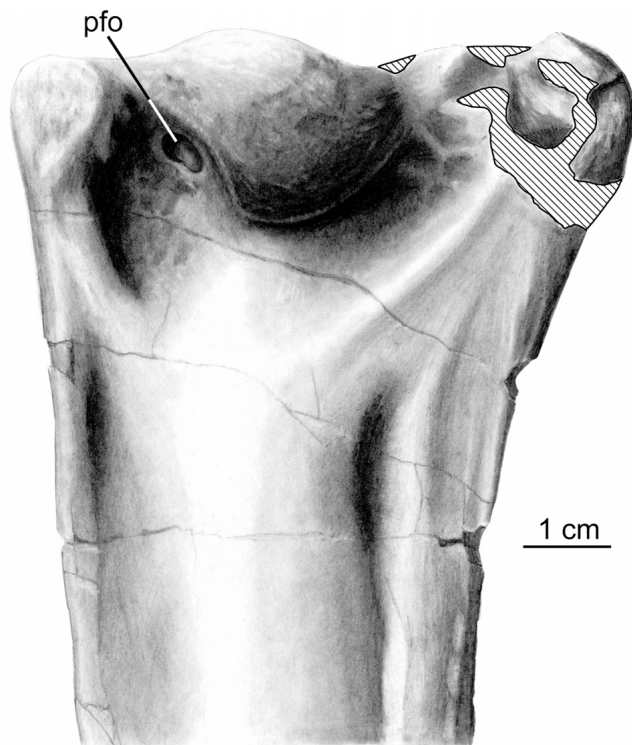


FIGURE 3. Drawing of the proximal portion of UCMP 219007 in posterior view; cross-hatching indicates damaged areas (drawing by R. W. Boessenecker). **Abbreviation:** pfo, pneumatic foramen.

the middle Miocene Astoria Formation (Ray, 1977; Olson, 1985). *Pelagornis orri* (formerly *Osteodontornis*, which was synonymized with *Pelagornis* by Mayr and Rubilar-Rogers, 2010) was reported from unidentified Miocene diatomites from the Los Angeles basin by Howard (1957) and Howard and White (1962), and subsequently also reported from the upper Miocene Monterey Formation (Domning, 1978) and the middle Miocene Sharktooth Hill bonebed (Stidham, 2004). The sole record from Baja California (Mexico) is cf. *Odontopteryx* from the lower-middle Eocene Tepetate Formation (González-Barba et al., 2002).

The ratio of the greatest proximal width and skeletal wingspan reported for *Pelagornis chilensis* by Mayr and Rubilar-Rogers (2010) allowed estimation of the wingspan of UCMP 219007 (Table 2) at 3.9 m. Wingspan incorporating the length of primary feathers ranges from 4.3 m (40 cm long primaries preserved in *P. orri*; Howard, 1957) to 5.37 m (scaled from estimates based on *Diomedea* primary length; Mayr and Rubilar-Rogers, 2010). Although slightly smaller than *P. chilensis*, UCMP 219007 represents a truly gigantic bird (Fig. 1B), and one of the largest volant birds ever reported.

Other Pliocene records include fragmentary pelagornithid bones from the lower and middle Pliocene of North Carolina, Morocco, Peru, New Zealand, and Japan. The only other Pliocene record from North America includes two indeterminate species of *Pelagornis* from the lower Pliocene Yorktown Formation of North Carolina (Olson and Rasmussen, 2001). *Pelagornis mauretanicus* was described from the middle-late Pliocene (~2.5 Ma) of Morocco (Mourer-Chauviré and Geraads, 2008). A partial skeleton in a concretion including a partial cranium was described as *Pseudodontornis stirtoni* (recombined as *Pelagornis stirtoni* by Mayr and Rubilar-Rogers, 2010) by Howard and Warter (1969), which was collected as 'float' on a New Zealand Beach, probably lower Pliocene, but possibly as old as lower

Miocene. A fragmentary humerus and radius of an unidentified pelagornithid were reported from the middle Pliocene of New Zealand (McKee, 1985). A fragmentary humerus from the lower Pliocene of Japan was reported by Ono et al. (1985). Lastly, a middle Pliocene pelagornithid femur was reported by Ono (1980), although the systematic affinities of this specimen remain somewhat uncertain (Matsuoka et al., 2003).

The specimen of *Pelagornis* reported herein (UCMP 219007) is bracketed by two ash correlation dates that tightly constrain the age of this specimen to 3.35–2.5 Ma (Powell et al., 2007; Fig. 1A). The middle Pliocene records from New Zealand and Japan overlap with the age of this specimen, although none are bracketed (or associated) with precise absolute dates.

Although possibly younger *Pelagornis* remains were reported by Mourer-Chauviré and Geraads (2008, 2010), the 2.5 Ma age assigned to those remains is based upon biochronology of the admittedly sparse Pliocene North African mammalian fossil record. Furthermore, although 2.5 Ma is certainly a minimum age for the Ahl Oughlam locality in Morocco (Geraads, 2001), a maximum age was not given by those authors. Compared with the uncertain biostratigraphic date of *Pelagornis mauretanicus*, and other older fossils from the early and middle Pliocene, the more precise dating of UCMP 219007 makes it the youngest reliably dated pelagornithid fossil worldwide.

The final emergence of the Panamanian Isthmus and the closure of the Central America Seaway at ~2.7 Ma resulted in a marked drop in sea level (~45 m) and the establishment of the modern profile of the California ocean-current system (Hyrenbach and Viet, 2003; Bartoli et al., 2005). By ~2.5 Ma the modern climate regime was in place, involving small (i.e., meter scale) fluctuations in sea level associated with late Pliocene and Pleistocene glacial cycles (Bartoli et al., 2005). The apparent response of seabirds to these climate-related changes in the environment was a significant decrease in diversity and changes in geographic distribution (Warheit, 1992; Olson and Rasmussen, 2001; Mayr and Rubilar-Rogers, 2010). The extinction of the pelagornithids, an avian clade with a temporal span of more than 55 million years and a worldwide geographic distribution, speaks to the severity of the end-Pliocene climatic upheaval, which has a documented record of effects on other forms of marine life (Domning, 2001; Fordyce et al., 2002; Deméré et al., 2003; Fitzgerald, 2005). Indeed, the number of lower and middle Pliocene pelagornithid fossils from the Pacific and Atlantic basins, in addition to the specimen reported herein, suggests their extinction occurred during the upper Pliocene. However, it is puzzling that such a long-lived, cosmopolitan, and presumably adaptable taxon such as the Pelagornithidae did not survive this climatic upheaval. It is important to note that the upper Pliocene and Pleistocene are characterized by rare marine strata with even rarer marine vertebrate fossil-bearing localities, likely a result of lower sea levels (relative to the lower Pliocene and Miocene). This pattern may be due to preservational bias and the general rarity of Pleistocene marine vertebrate assemblages (Boessenecker, 2011), and pelagornithids may have survived longer than the middle Pliocene.

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