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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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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). 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; University of California Museum of Paleontology, Berkeley, California, U.S.A.) 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.

Locality and Age—The partial pelagornithid humerus (UCMP 219007) reported herein was collected by RWB 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. 1B). 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. (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 *Patinopecten 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 review) 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 review). A diverse assemblage of 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 review). To that list we now add Pelagornithidae.

SYSTEMATIC PALEONTOLOGY

AVES Linnaeus, 1758

PELAGORNITHIDAE Fürbringer, 1888

PELAGORNIS Lartet 1857*PELAGORNIS* sp.

Material—UCMP 219007, proximal left humerus (Fig. 2).

Diagnosis—Referred to *Pelagornis* based upon the ventral margin of the proximal humerus tapered to a point, tricipital fossa (i.e., apneumatic primary pneumotricipital fossa; Baumel and Witmer 1993:99) located ventrally, rather than posteriorly as in most birds, humeral head anteriorly projected, deltopectoral crest low, distally extended, and bi-lobed, and gigantic size. A proposed autapomorphy of this taxon is the presence of a well-developed pneumatic foramen that extends into the humeral head along the proximal margin of what is likely the secondary pneumotricipital fossa (Fig. 3).

Description—This fossil is a proximal portion of a left humerus with a long, dorsoventrally-compressed shaft (Fig. 2), measuring 385mm as preserved. In addition to large size (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, and is oval in proximal view (Fig. 2F). The humeral head projects distally on the posterior surface, where it has a well-defined convex edge along the border of the secondary pneumotricipital fossa (Fig. 3). It tapers ventrally on both surfaces. 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 bordered ventrally and distally by a fossa of unknown homology. The proximal margin of this fossa is characterized by the presence of a pneumatic foramen that extends into the humeral head, is ventrally floored by finished bone (i.e., not owing to damage), and measures 8 mm across and 4 mm deep (as prepared; Fig. 3). Based upon the position of this fossa and the presence of a pneumatic foramen, we interpret this fossa as the secondary pneumotricipital fossa (Fig. 2C). The presence of this pneumatic foramen has not been noted in other pelagornithid taxa and is therefore proposed as an autapomorphy of this taxon. The secondary pneumotricipital fossa is separated from the large and dorso-distally 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), which also forms the dorsal margin of the tricipital fossa and merges proximally with the ventral tubercle (Fig. 2C, 3). On the posterior surface, the tricipital fossa is elongate, apneumatic, and faces more ventrally than in most birds (Fig. 3).

On the anterior surface, a shallow concavity marks position of the transverse ligament sulcus (Fig. 2A). Both anterior and posterior faces of the shaft are distally convex, and the anterior face is flattened between the deltopectoral crest and proximal end. A shallowly excavated m. pectoralis scar lies adjacent to the deltopectoral crest (Fig. 2B, C). The posterior face is similarly concave adjacent to the deltopectoral crest (Fig. 2A, C). The deltopectoral crest is long (~270% of greatest proximal width), and although damaged along a portion of its dorsal margin, appears to have been very low (i.e., not significantly dorsally or anteriorly projected) like other pelagornithids; the apex of which must have been positioned far from the humeral head (Fig. 2A, C). A prominent protuberance occurs near the ventral margin of the anterior surface of the shaft ventral to the deltopectoral crest, 113mm from the proximal end (Fig. 2A, B, D). This feature is also developed in *Dasornis emuinus*, *Pelagornis chilensis*, *Pelagornis miocaenus*, as well as some pelecanids, diomedeids, and weakly developed in fregatids (Mayr and Smith, 2009; 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*, *Pelagornis longirostris*, *Pelagornis stirtoni*, *Tympanoneisiotes*, 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*, *Pelagornis miocaenus*, and *Pelagornis 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 in their much greater size (Mayr and Rubilar-Rogers, 2010). The new specimen is within the size range of *Pelagornis chilensis*, *Pelagornis miocaena*, and *Pelagornis mauretanicus* (Harrison and Walker, 1976; Mourer-Chauviré and Geraads, 2008; Mayr and Rubilar-Rogers, 2010; Table 2). The proximal humerus fragment of *Pelagornis mauretanicus* (Mourer-Chauviré and Geraads, 2008) differs only slightly from UCMP 219007 in possessing a proximodistally-shallower humeral head. *Pelagornis miocaena* and *Pelagornis 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 prominent protuberance on the anterior surface, and a well-developed fossa on the posterior face distal to the dorsal tubercle and humeral head (also present in *Pelagornis mauretanicus*). UCMP 219007 differs from *Pelagornis chilensis* and *Pelagornis miocaenus* in possessing a much more proximally elevated ventral tubercle which is also posteriorly prominent (rather than ventrally as in *Pelagornis 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, while *Pelagornis chilensis* has a more concave bicipital crest than UCMP 219007 and *Pelagornis miocaenus* (Mayr and Rubilar-Rogers, 2010). Owing to the similar of age and morphology shared by the new specimen and preserved portions of the fragmentary proximal humeri referred to *Pelagornis mauretanicus*, the inability to compare this new material with previously described species of *Pelagornis* known from non-humeral material (e.g., *Pelagornis stirtoni*), and the inferred high mobility of pelagornithids, we refrain from naming a new species and adding to the taxonomic confusion that has characterized Pelagornithidae systematics.

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* and indeterminate pelagornithids from the lower-middle Oligocene Pittsburg Bluff Formation and the lower Oligocene Keasey Formation (Goedert, 1989), and *Pelagornis* sp. from the middle Miocene Astoria Formation (Ray, 1977; Olson, 1985). *Pelagornis orri* was reported from unidentified Miocene diatomites from the Los Angeles basin by Howard (1957) and Howard and Warter (1957), and subsequently also reported from the upper Miocene Monterey Formation by Domning (1978) and the Middle Miocene Sharktooth Hill bonebed by Stidham (2004). The sole record from Baja California 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 meters. Wingspan incorporating the length of primary feathers ranges from 4.3 meters (40cm long primaries preserved in *Pelagornis orri*; Howard, 1957) to 5.37 meters (scaled from estimates based on *Diomedea* primary length; Mayr and Rubilar-Rogers, 2010). While slightly smaller than *Pelagornis chilensis*, UCMP 219007 represents a truly gigantic bird, and one of the largest volant birds ever reported.

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., 2006; Fig. 1a). Although purportedly younger *Pelagornis* remains were reported by Mourer-Chauviré and Geraads (2008, 2010), the 2.5Ma age assigned to those remains is based upon biochronology of the admittedly sparse Pliocene North African mammalian fossil record, and although 2.5 Ma is certainly a minimum age for the Ahl Oughlam locality in Morocco (Geraads, 2001), it is not clear what the maximum age may be. Compared with the biostratigraphically dated *Pelagornis mauretanicus*, the more precise dating of UCMP-219007 makes it the youngest reliably dated pelagornithid fossil worldwide. Although an Upper Pliocene pelagornithid specimen was reported by Ono et al., (1985), this isolated femur has not been figured in publication, and the systematic affinities of this specimen remain somewhat uncertain (Matsuoka et al., 2003).

The final emergence of the Panamanian Isthmus and the closure of the Central America Seaway at ~2.7 Ma resulted a severe drop in sea-level (~45m) and the establishment of the modern profile of the California ocean-current system (Hyrenbach and Viet, 2003; Bartoli et al., 2005). By ~2.5Ma 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). 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). However, it is puzzling that such a long-lived, cosmopolitan, and presumably adaptable taxon such as the Pelagornithidae did not survive this climatic upheaval.

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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**, map of the San Francisco Bay area showing Purisima Formation exposures; **C**, reconstruction of *Pelagornis* sp. with preserved portion of humerus shaded (modified by R.W. Boessenecker from reconstruction of *Pelagornis chilensis* by C. Anzures which appeared in Mayr and Rubilar-Rodgers, 2010). **Abbreviations:** slt, siltstone; ss, sandstone. [planned for page width]

FIGURE 2. Left humerus (UCMP 219007) of *Pelagornis* sp. **A**, anterior view; **B**, ventral view; **C**, posterior view; **D**, dorsal view; **E**, UCMP 219007 with an outline reconstruction based on *Pelagornis chilensis*; **F**, proximal view; **G**, distal view showing cross section. **Anatomical Abbreviations**—bc, bicipital crest; cd, dorsal crest; ci, capital incisure; dc, deltopectoral crest; dt, dorsal tubercle; h, humeral head; pf2, secondary pneumotricipital fossa; pt, protuberance; tf, tricipital fossa; vt, ventral tubercle. [planned for page width]

FIGURE 3. Drawing of the proximal portion of UCMP 219007 in posterior view; cross-hatching indicates damaged areas (drawing by R.W. Boessenecker). **Anatomical Abbreviation—pfo**, pneumatic foramen. [planned for column width]