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PARTIAL SKELETON OF A BONY-TOOTHED BIRD FROM THE LATE OLIGOCENE/EARLY MIOCENE OF OREGON (USA) AND THE SYSTEMATICS OF NEOGENE PELAGORNITHIDAE

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ABSTRACT—A partial skeleton of a pelagornithid bird found in latest Oligocene or earliest Miocene marine strata in Oregon consists of a pelvis fragment, thoracic vertebrae, and leg bones of a single individual. It is the most completely preserved pelagornithid from the late Oligocene/early Miocene, and one of the few bony-toothed birds from this time period in general. The new fossil is from the Nye Mudstone and shows some previously unknown features that contribute to a better understanding of the osteology of pelagornithids. Because Paleogene and late Neogene pelagornithids differ in several osteological features and the temporally intermediate forms are poorly known, it further bridges a gap in our knowledge of character evolution in pelagornithids. The interrelationships within Pelagornithidae are still poorly resolved, but we detail that a clade of Neogene species, which the Oregon pelagornithid is not part of, can be supported by a derived morphology of the femur. To ease description of Neogene pelagornithids, we synonymize *Palaeochenoides* Shufeldt, 1916 and *Tympanonesiotes* Hopson, 1964 with *Pelagornis* Lartet, 1857, and suggest classification of all Neogene pelagornithids in the latter taxon.

INTRODUCTION

BONY-TOOTHED BIRDS or pelagornithids (Pelagornithidae) were highly specialized soaring birds that lived in marine environments and are characterized by the presence of spikey excrescenses along the tomia of the beak. Pelagornithids had a worldwide distribution and occur in late Paleocene to late Pliocene fossil deposits; some species were among the largest volant birds that ever lived (Olson, 1985; Mayr, 2009; Bourdon, 2011). For a long time these birds were known only from very fragmentary or poorly preserved fossil material, but in recent years new specimens have contributed to a greatly improved understanding of their osteology (Mourer-Chauviré and Geraads, 2008; Bourdon et al., 2010; Mayr and Rubilar-Rogers, 2010; Boessenecker and Smith, 2011; Mayr and Zvonok, 2011, 2012).

North America has a particularly rich fossil record of pelagornithids (Table 1). Some fossils are, however, only briefly mentioned in the literature and others are in dire need of a taxonomic revision. Such a task is not only complicated by the fact that the description of most species is based on very fragmentary material, but also by the unknown exact age of some fossils. In particular this is true for specimens from South Carolina, which were originally considered to be from the early Miocene (Hopson, 1964), but are probably of late Oligocene age (Table 1; Olson, 1985).

That taxonomic uncertainties also surround some of the better represented species is exemplified by "*Osteodontornis*" *orri* Howard, 1957, from the middle and late Miocene of California, the holotype of which is a partial, flattened skeleton on a slab. In the original description, "*O.*" *orri* was not differentiated from *Pelagornis miocaenus* Lartet, 1857, from the early/middle Miocene of Europe. This species was not recognized as being a bony-toothed bird until a few years later (Brodkorb, 1963). *Pelagornis miocaenus* is the first named pelagornithid and, apart from a tentatively referred sternum (Mayr et al., 2008), only known from humeri, which closely correspond with those of "*O.*" *orri*. To disentangle the convoluted taxonomy of pelagornithids, synonymization of *Osteodontornis* Howard, 1957 and *Pelagornis* Lartet, 1857 was proposed (Bourdon et al., 2010; Mayr and Rubilar-Rogers, 2010), and is also assumed here.

The partial skeleton of a large pelagornithid from the late Oligocene/early Miocene Nye Mudstone of Oregon that is described herein is one of the best preserved pelagornithids from North America. Together with the holotype of *Pelagornis orri* and that of *P. chilensis* Mayr and Rubilar-Rogers, 2010, from the late Neogene of Chile, it is also among the few associated pelagornithid remains of a single individual from anywhere in the world. The fossil not only contributes to the insufficiently known osteology of late Paleogene/early Neogene pelagornithids, but also preserves skeletal elements such as the pelvis and pedal phalanges that are poorly known for pelagornithids in general.

GEOLOGICAL SETTING

According to Prothero et al. (2001a) the Nye Mudstone has a thickness of approximately 1500 meters, and based on benthic foraminiferans deposition occurred at depths of 300 to 600 meters in cold water. The pelagornithid fossil was found in a tabular, iron-stained nodule that protruded through both sides of a large block of dark greenish gray, very fine sandy siltstone that had fallen from the beach cliff at a point approximately 65 meters south of the mouth of Moore Creek.

In addition to fish and shark remains (David, 1956; Welton, 1972), vertebrate fossils reported from the Nye Mudstone include a turtle (Brinkman, 2009), the "beach bear" *Kolponomos newportensis* (Tedford et al., 1994), pinnipeds (Berta, 1991), and a sirenian (Domning and Ray, 1986). The only other bird fossil (LACM 129404) from the Nye Mudstone is undescribed and consists of associated fragments of a skull, TABLE *1* —Overview of North American pelagornithid fossils. The letters A and P in the state/province column denote occurrence on the Atlantic or Pacific coast, respectively.

Taxon	Age	Formation	State/Province	References
gen. et sp. indet.	early Eocene	Nanjemoy Formation	Virginia (A)	Olson (1999)
? *Dasornis* sp.	middle Eocene	Tepetate Formation	Baja California Sur, Mexico (P)	González-Barba et al. (2002)
gen. et sp. indet.[a]	late Eocene/early Oligocene[b]	Pittsburg Bluff and Keasey Formations	Oregon (P)	Goedert (1989)
"*Tympanonesiotes*" *wetmorei*	?late Oligocene/?late Miocene	?Cooper/Chandler Bridge Formations or unknown "phantom unit"	South Carolina (A)	Hopson (1964), Olson (1985)
"*Palaeochenoides*" *mioceanus*	?late Oligocene	?Cooper or Chandler Bridge Formations	South Carolina (A)	Wetmore (1917), Hopson (1964), Olson (1985)
"*Pseudodontornis*"	?late Oligocene	?Cooper or Chandler Bridge Formations	South Carolina (A)	Hopson (1964), Olson (1985)
gen. et sp. indet.	late Oligocene	Ashley Formation	South Carolina (A)	Olson (1985)
gen. et sp. indet.	early Miocene	Calvert Formation	Delaware (A)	Rasmussen (1998)
LACM 128424	latest Oligocene or early Miocene	Nye Mudstone	Oregon (P)	Olson (1985), this study
Cyphornis magnus	unknown (Eocene to Miocene)	unknown	British Columbia (Vancouver Island) (P)	Wetmore (1928), Olson (1985), Goedert (1989)
gen. et sp. indet.	middle Miocene	Astoria Formation	Oregon (P)	Olson (1985), Goedert (1989), pers. obs. (SAM)
gen. et sp. indet.	middle Miocene	Calvert Formation	Maryland, Virginia (A)	Olson (1984, 1985)
Pelagornis ("*Osteodontornis*") *orri*	middle/late Miocene	Round Mountain Silt, Monterey shale, and others	California (P), Baja California Sur, Mexico (P)	Howard (1957, 1968, 1978, 1984), Howard and White (1962), Stidham (2004), pers. obs. (JLG)
Pelagornis spp.	early Pliocene	Yorktown Formation	North Carolina (A)	Olson and Rasmussen (2001)
Pelagornis sp.	middle/late Pliocene	Purisima Formation	California (P)	Boessenecker and Smith (2011)

[a] The specimen from the Keasey Formation was originally tentatively assigned to *Dasornis* ("*Argillornis*"), but Bourdon et al. (2010, p. 57) detailed that this classification cannot be upheld and that the ulna agrees with that of Neogene Pelagornithidae.

[b] Prothero (2001); Prothero and Hankins (2000, 2001).

humerus, radius and ulna of a small charadriiform. There are also undescribed fossils of odontocete cetaceans in the collections of the LACM and the Smithsonian Institution (Crowley et al., 1999; personal observation, JLG).

Snavely et al. (1976) indicated the age of the Nye Mudstone as "lower Miocene", equivalent to the Saucesian foraminiferal stage, and according to their map the pelagornithid fossil was found stratigraphically near the middle of the Nye Mudstone. A bivalve mollusk, *Vertipecten fucanus* (Dall, 1898), characteristic of the Pillarian molluscan stage (Addicott, 1976), occurs in strata at the pelagornithid locality (Moore, 1963, roughly her localities 184 and 185). Strata of the Clallam Formation in Washington State that yielded the molluscan assemblage used by Addicott (1976) to typify the Pillarian stage were considered by Prothero and Burns (2001) to be latest Oligocene, 23.8 to 24.2 million years (Ma).

Recent magnetostratigraphic work by Prothero et al. (2001a) assigns the Nye Mudstone an age of late Oligocene to early Miocene, or 28 to at least 23 Ma, and Prothero et al. (2001b) show the uppermost part of the Nye Mudstone to be as young as 20 Ma. However, their work was based only on exposures at Newport and Yaquina Bay, and coastal exposures of the Nye Mudstone where the pelagornithid fossil was found were not included. Crowley et al. (1999) called attention to the close similarity of the cetacean assemblages in the Nye Mudstone and Clallam Formation, and Barnes (2006) described a dolphin-like odontocete of the taxon Platanistinae from the Nye Mudstone. A few as yet unpublished derived odontocetes were even found near the top of the underlying Yaquina Formation (personal observation, JLG). Berta (1991) identified the pinniped *Enaliarctos mitchelli* Barnes, 1979, from the Nye Mudstone near the pelagornithid locality. The type locality for *E. mitchelli* is in southern California, in the Pyramid Hill Sand Member of the Jewett Sand, the age of which is 23 to 25 Ma (Scheirer and Magoon, 2007). If indeed from sediments as old as 28 Ma, the odontocetes and pinnipeds from the Nye Mudstone and upper part of the Yaquina Formation would thus be much older than similar ones from anywhere else in the world. Therefore, a reasonable age estimation for the part of the Nye Mudstone that yielded the pelagornithid fossil is probably as young as 23 Ma but no older than 25 Ma (i.e., late Oligocene, Chattian).

SYSTEMATIC PALEONTOLOGY

Osteological terminology follows Baumel and Witmer (1993), if not indicated otherwise. Institutional abbreviations are: LACM, The Natural History Museum of Los Angeles County, U.S.A., Los Angeles, California; MNHN, Museo Nacional de Historia Natural, Santiago de Chile; SMF, Senckenberg Research Institute Frankfurt, Frankfurt am Main, Germany.

PELAGORNITHIDAE Fürbringer, 1888
PELAGORNIS Lartet, 1857

Remarks.—As detailed in the discussion, the taxon *Pelagornis* is used here in a broad sense and includes *Palaeochenoides* Shufeldt, 1916, *Osteodontornis* Howard, 1957, and *Tympanonesiotes* Hopson, 1964.

PELAGORNIS sp.
Figures 1–3

Material.—LACM 128424 (caudalmost four thoracic vertebrae, cranial portion of pelvis, proximal end of left femur, distal end of right femur, right tibiotarsus, right tarsometatarsus, pedal phalanges of right foot); found 22 November 1981 by J. L. and G. H. Goedert.

Measurements (in mm): Femur, proximal width, 26.1; distal width, 25.0. Tibiotarsus, length as preserved, 172.7; distal width, 28.1. Tarsometatarsus, maximum length, 111.5; proximal width, 27.2; distal width, 32.2. Longest pedal phalanx, length, 74.7.

Occurrence.—South of Newport, Lincoln County, Oregon, U.S.A.; cliff approximately 65 meters south of the mouth of Moore Creek (N 44°34.305′, W 124°4.186′); Nye Mudstone, late Oligocene/early Miocene (about 23–25 Ma).

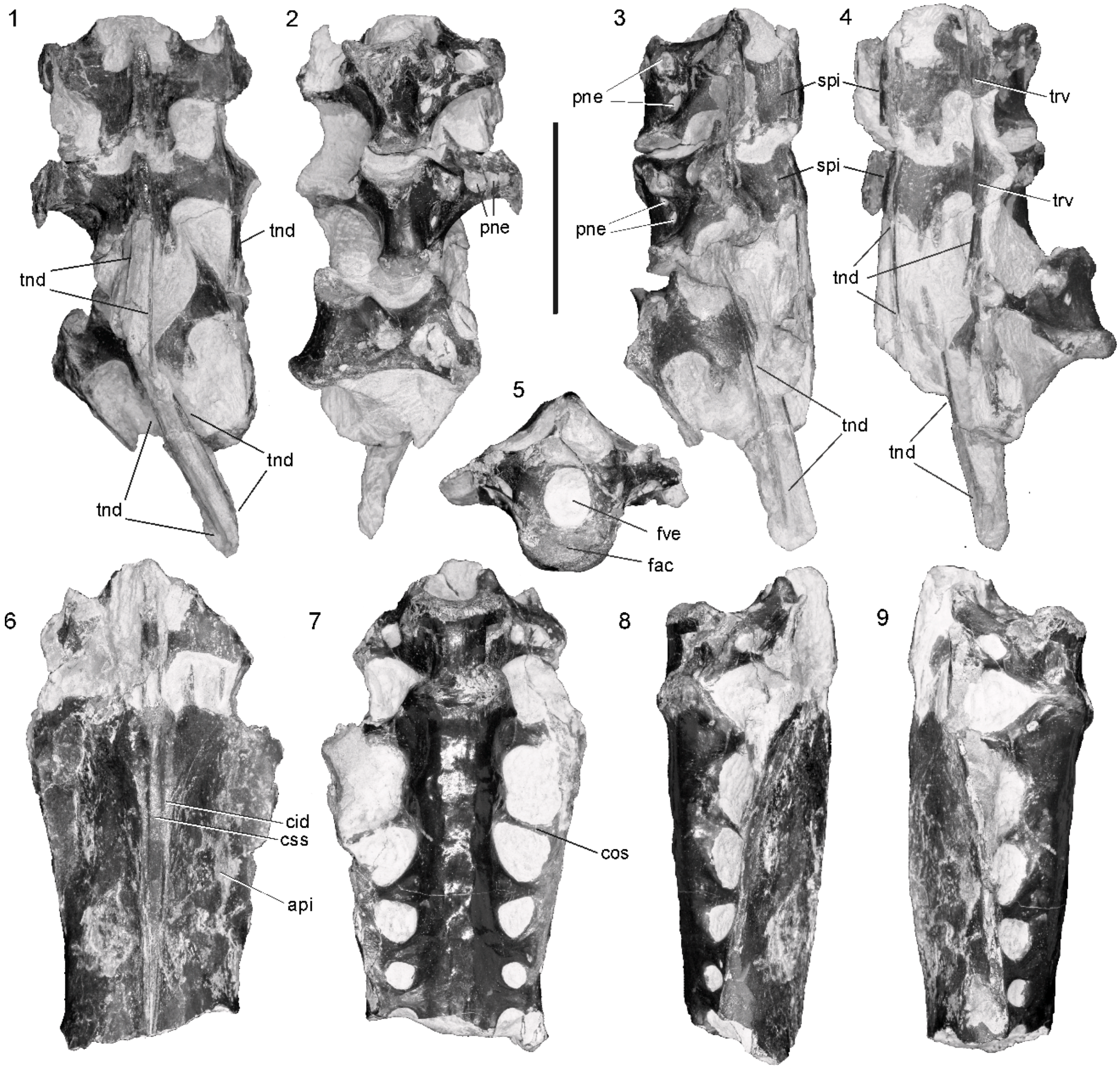

FIGURE *1* —Thoracic vertebrae and pelvis of *Pelagornis* sp. from the late Oligocene/early Miocene Nye Mudstone of Oregon, U.S.A. (LACM 128424). *1–4*, series of three thoracic vertebrae in dorsal, ventral, left and right lateral views, respectively; *5–9*, pelvis and cranialmost thoracic vertebra in cranial, dorsal, ventral, left lateral, and right lateral views, respectively. Abbreviations: api=ala praeacetabularis ilii; cid=crista iliaca dorsalis; cos=narrow processus costalis of synsacrum; css=crista spinosa synsacri; fac=facies articularis caudalis; fve=foramen vertebrale; pne=pneumatic openings; spi=processus spinosus; tnd=ossified tendons; trv=processus transversus. Scale bar=50 mm.

Description.—The specimen includes the four caudalmost thoracic vertebrae, one of which is preserved in articulation with the synsacrum (Fig. 1). Whether this last thoracic vertebra was partially fused with the synsacrum is difficult to ascertain, but we note that such a fusion did not occur in *Pelagornis chilensis* (Mayr and Rubilar-Rogers, 2010). Clearly, the three other thoracic vertebrae are free, i.e., do not form a notarium. There are, however, long ossified tendons along the processus spinosi and the processus transversi, which connected the vertebrae and stabilized the vertebral column (Fig. 1.1–1.4). The caudoventral surfaces of the processus transversi exhibit pneumatic openings that are also found on the vertebral corpora (Fig. 1.2, 1.3; see Mayr and Smith [2010] concerning occurrence of these openings in a middle Eocene pelagornithid). All of the vertebrae are heterocoelous; the facies articularis caudalis of the caudalmost vertebra is dorsoventrally narrow as in Diomedeidae, and the foramen vertebrale is small (Fig. 1.5). In Suloidea (Sulidae, Phalacrocoracidae, and Anhingidae), by contrast, the corpus of the caudalmost thoracic vertebra has an ovate cross-section and opisthocoelous articulation facets. Unlike Diomedeidae the foveae costales are not stalked.

The pelvis of pelagornithids is very poorly known; the only previously published specimen is the very fragmentary cranioventral portion of the synsacrum of the *P. chilensis* holotype (Mayr and Rubilar-Rogers, 2010). In LACM 128424 the cranial third of the pelvis is preserved (Fig. 1.5–1.9) and its overall proportions are similar to those of the pelves of Diomedeidae and some large Anseriformes (*Cygnus* spp.). The shape of the fragment indicates a long and narrow pelvis, and the alae praeacetabulares ilii have similar proportions to those of Diomedeidae and *Cygnus*. Unlike Suloidea, the alae

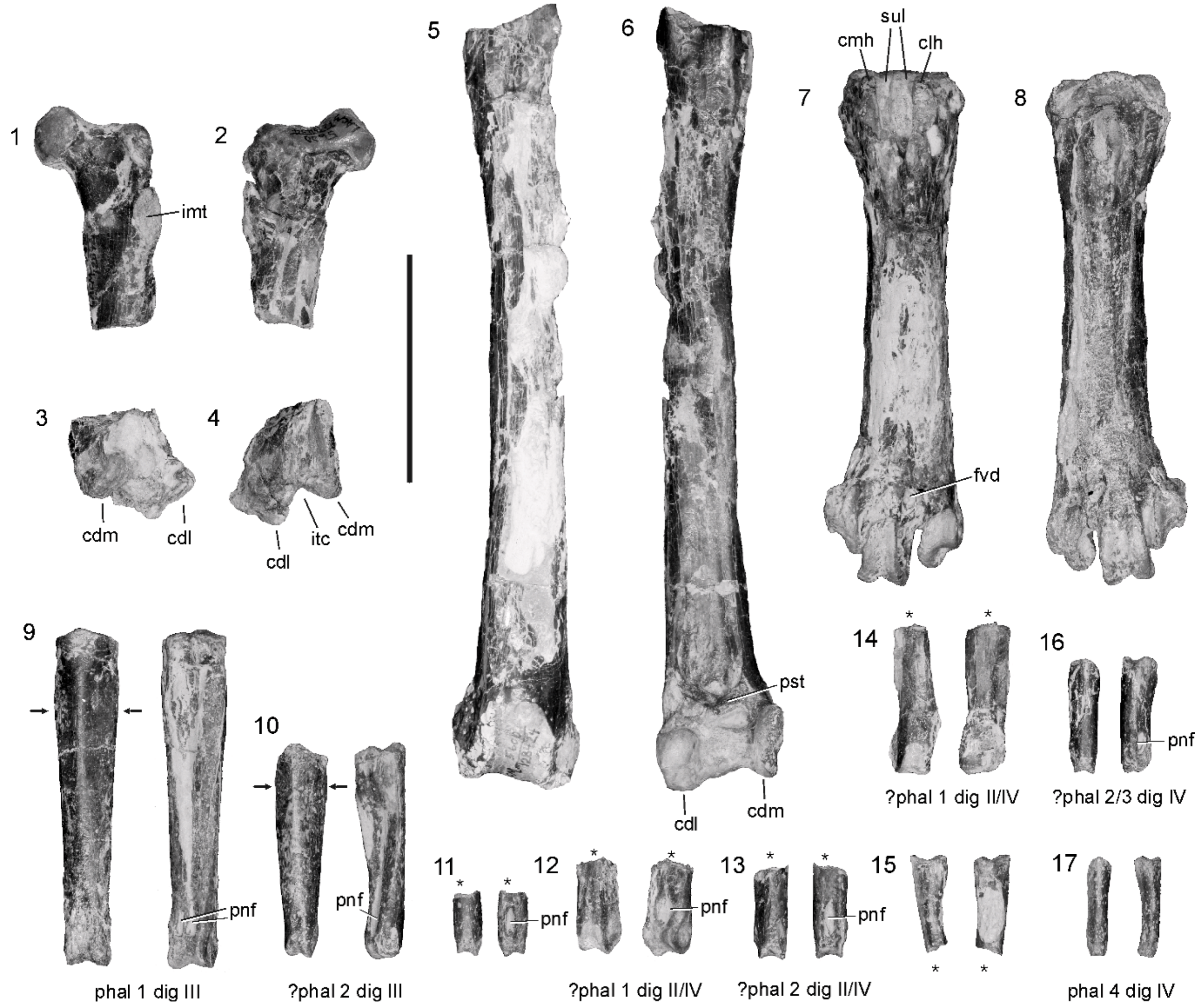

FIGURE 2—Leg bones and pedal phalanges of *Pelagornis* sp. from the late Oligocene/early Miocene Nye Mudstone of Oregon, U.S.A. (LACM 128424). *1*, *2*, proximal end of left femur in cranial and caudal views, respectively; *3*, *4*, distal end of right femur in caudomedial and cranial views, respectively; *5*, *6*, right tibiotarsus in caudal and cranial views, respectively; *7*, *8*, right tarsometatarsus in plantar and dorsal views, respectively; *9*–*17*, pedal phalanges in dorsal (left image, except *15*, which shows the lateral side) and ventral/ventrolateral view (right image). The phalanges are oriented with the distal ends pointing downwards; the asterisks indicate broken ends. The small arrows in *9* and *10* point to the widened portion of the phalanges. Abbreviations: cdl=condylus lateralis; cdm=condylus medialis; clh=crista lateralis hypotarsi; cmh=crista medialis hypotarsi; fvd=foramen vasculare distale; imt=impressiones musculares trochanteris; pnf=?pneumatic fossa on plantar surface of distal end of pedal phalanges; itc=sulcus intercondylaris; pst=pons supratendineus; sul=hypotarsal sulci. Scale bar=50 mm.

praeacetabulares ilii are not oriented in a markedly horizontal plane (this feature was considered an apomorphy of "pelecaniform" birds by Cracraft [1985]). The cristae iliacae dorsales are fused with the crista spinosa of the synsacrum, so that there was a closed canalis iliosynsacralis as in Diomedeidae. The cranial portion of the synsacrum is not as narrow and dorsoventrally deep as in Suloidea. The size of the ovate intervertebral openings defined by the processus costales (transverse struts) decreases caudally, whereas this size difference is less marked in Diomedeidae. Further unlike the latter, the processus costales of the penultimate synsacral vertebra are much narrower than those of the caudally following ones (Fig. 1.7).

Of the femur only the proximal and distal ends are preserved (note that these are not from the same bone, i.e., the proximal end is from the left side and the distal end from the right side). The proximal end resembles the proximal femur of *P. chilensis*, and as in the latter and other pelagornithids (Mourer-Chauviré and Geraads, 2008; Mayr and Zvonok, 2012) the area of the impressiones musculares trochanteris on the craniolateral surface forms a marked embossment. The sulcus intercondylaris on the distal end of the bone is, however, at least as deep as in "*Palaeochenoides*" *mioceanus* (Fig. 3.2), whereas it is much shallower in *P. chilensis* (Fig. 3.3). The lateral portion of the distal end is damaged, and whether or not there was a sulcus on the trochlea fibularis (see discussion and Fig. 3.1–3.3) cannot be discerned.

The tibiotarsus of LACM 128424 also corresponds well with that of *P. chilensis* in its overall proportions. As in the latter, the condylus lateralis is proximodistally lower than the narrow condylus medialis, of which the medial portion is slightly damaged in LACM 128424. Also as in *P. chilensis* and other Pelagornithidae, there is a tubercle distolateral of the pons

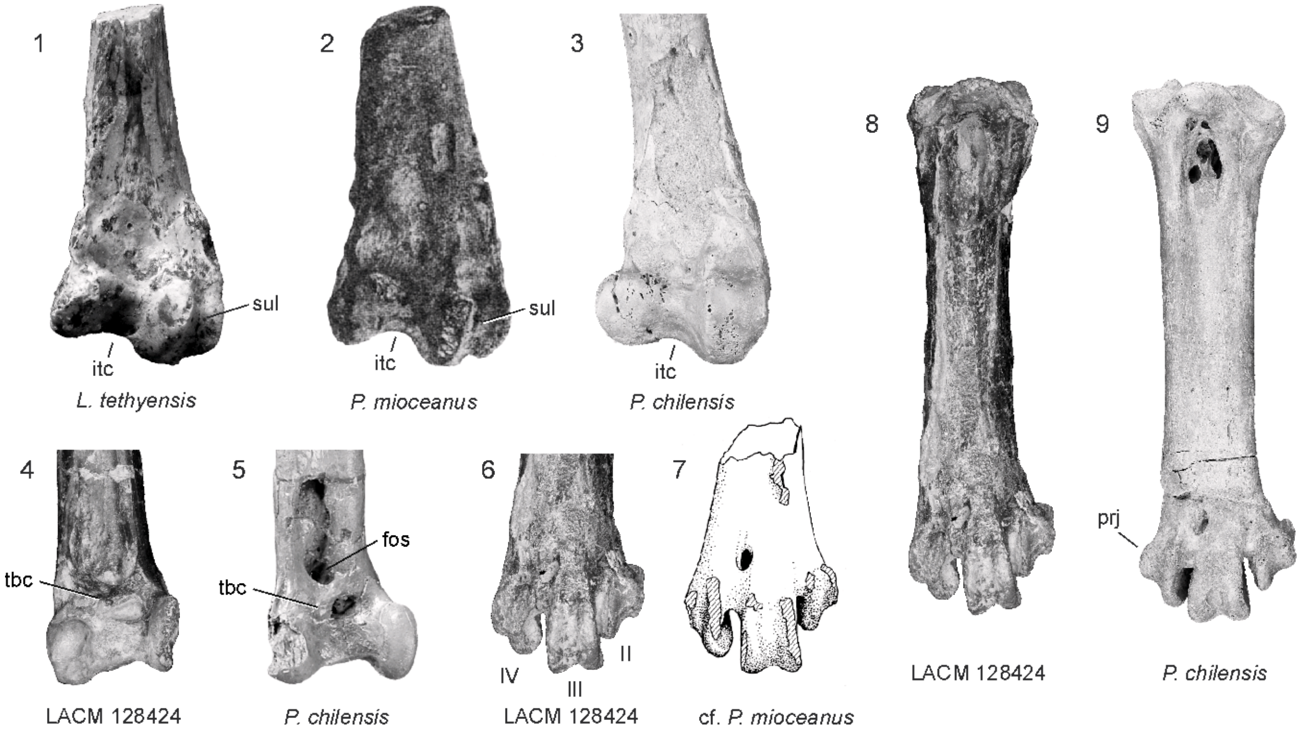

FIGURE *3*—Femur, tibiotarsus, and tarsometatarsus of pelagornithid species in comparison. *1–3*, distal end right femur: *1*, *Lutetodontopteryx tethyensis* from the middle Eocene of Ukraine (SMF Av 576); *2*, *Pelagornis* ("*Palaeochenoides*") *mioceanus* from the ?late Oligocene of South Carolina (holotype, from Wetmore, 1917); *3*, *Pelagornis chilensis* from the late Miocene of Chile (holotype, MNHN SGO.PV 1061; left side, reversed to facilitate comparisons); *4*, *5*, distal end of right tibiotarsus: *4*, *Pelagornis* sp. from the late Oligocene/early Miocene Nye Mudstone of Oregon, U.S.A.; *5*, *P. chilensis* (MNHN SGO.PV 1061); *6*, *7*, distal end of tarsometatarsus: *6*, *Pelagornis* sp. from the Nye Mudstone; *7*, cf. *Pelagornis* ("*Palaeochenoides*") *mioceanus* from the ?late Oligocene of South Carolina (left side, reversed to facilitate comparisons; from Hopson, 1964); *8*, *9*, right tarsometatarsus: *8*, *Pelagornis* sp. from the Nye Mudstone; *9*, *P. chilensis* (MNHN SGO.PV 1061). In *6* the tarsometatarsal trochleae are numbered. Abbreviations: fos=fossa extensoria; itc=sulcus intercondylaris; prj=projection of lateral portion of trochlea metatarsi IV; sul=sulcus of trochlea fibularis; tbc=tubercle next to pons supratendineus. Not to scale.

supratendineus (Fig. 3.4). The sulcus extensorius is wide as in other Pelagornithidae, but unlike *P. chilensis* (Fig. 3.5) and an unnamed pelagornithid from the late Miocene/early Pliocene of Australia (Fitzgerald et al., 2012, fig. 3A), LACM 128424 lacks a marked and deeply excavated fossa extensoria (sensu Fitzgerald et al., 2012).

The tarsometatarsus of LACM 128424 closely resembles a tarsometatarsus from the ?late Oligocene of South Carolina, which was tentatively referred to "*Palaeochenoides*" *mioceanus* by Hopson (1964). The Oregon specimen is, however, slightly smaller (distal width 30.5 versus 34.7; Hopson, 1964), and the trochlea metatarsi II is proportionally somewhat larger and reaches farther distally (Fig. 3.6, 3.7). The tarsometatarsus of LACM 128424 is much smaller than that of *Cyphornis magnus* Cope, 1894 (proximal width 27.2 mm versus 36.7 mm; Wetmore, 1928), but larger than the tarsometatarsus of "*Tympanonesiotes*" *wetmorei* (distal width 30.5 versus ~24.5; Hopson, 1964). Detailed comparisons with the poorly preserved, similar-sized (see discussion) tarsometatarsus of *P. orri* are not possible, but the bone differs from the tarsometatarsus of *P. chilensis* in that the trochlea metatarsi III is narrower and the lateral portion of the trochlea metatarsi IV less laterally projected (Fig. 3.8, 3.9). The hypotarsus exhibits two sulci (Fig. 2.7), which are separated by a narrow crista intermedia; whether there were also enclosed canals as in *P. chilensis* is not clearly discernible in the specimen.

Nine pedal phalanges, or parts thereof, are preserved in LACM 128424, none of which is an ungual phalanx. The identity of some of these (Fig. 2.9–2.17) can be tentatively determined by comparison with the pedal phalanges of the *P. orri* holotype (Howard, 1957). At least the two proximal phalanges of the third toe exhibit an unusual morphology in that they are very wide in their proximal portion and in that the shaft has a peculiar "bloated" appearance (Fig. 2.9, 2.10). On the plantar surface of the distal end of the phalanges there is a marked fossa, which may have contained pneumatic openings and is bipartite in the case of the longest phalanx. An unusual flattening of the pedal phalanges also occurs in the middle Eocene *Lutetodontopteryx* (Mayr and Zvonok, 2011, p. 1351). The second and third toes of the *P. orri* holotype also have very wide pedal phalanges, which went, however, unnoticed by Howard (1957).

DISCUSSION

Olson (1985, p. 198) first mentioned pelagornithid fossils from the Nye Mudstone that are in the collection of the Smithsonian Institution and considered these to be "almost certainly referable to the same genus as the California birds" (="*Osteodontornis*" sensu Olson, 1985). Then, Bourdon et al. (2010, fig. 26I) figured the tarsometatarsus of LACM 128424 and likewise referred it to *Osteodontornis*, which is here considered to be a junior synonym of *Pelagornis* (see introduction).

In the dimensions of its leg bones (tarsometatarsus length 111.5 versus 114.3 mm; Howard, 1957), the Oregon pelagornithid corresponds with *Pelagornis* ("*Osteodontornis*") *orri* and the similar-sized (according to humerus dimensions; Mayr and Rubilar, 2010, tab. 2) *P. miocaenus*. Further osteological comparisons of the new fossil with these latter two species are however not possible, because the corresponding skeletal elements are either poorly preserved (*P. orri*) or altogether unknown (*P. miocaenus*).

LACM 128424 is older than *P. miocaenus*, which occurs in deposits from the early and middle Miocene (20–11 Ma; Mourer-Chauviré and Geraads, 2008, p. 175). Brodkorb (1963) and Olson (1985) assumed that *P. orri* is of late Miocene age, but Howard (1957) noted that the holotype is from the Relizian local stage, in which case it would have an age of 17–16 Ma (early/middle Miocene, i.e., Burdigalian; Prothero, 2001); *P. orri* remains from the middle Miocene of the Sharktooth Hill bone bed in California date back 15.2–16.0 Ma (Stidham, 2004). In any case, the Oregon pelagornithid is older than the known *P. orri* remains.

In size, morphology, and age, LACM 128424 agrees well with a tarsometatarsus from the ?late Oligocene of South Carolina, which was tentatively referred to "*Palaeochenoides*" *mioceanus* by Hopson (1964), and from which the new fossil is only distinguished by a somewhat larger and farther distally reaching trochlea metatarsi II (see Fig. 3.6, 3.7 and description). With a distal width of 40 mm (Shufeldt, 1916), the holotype femur of *P. mioceanus* is distinctly larger than that of LACM 128424, but some pelagornithid species are known to have covered a very large size range (Bourdon et al., 2010). The Isthmus of Panama had not yet formed in the late Oligocene/early Miocene (e.g., Lunt et al., 2008), and we consider it very possible, if not likely, that the Oregon pelagornithid is most closely related to the roughly contemporaneous pelagornithids from the Atlantic coast of South Carolina. This differs from the opinion of Olson (1985, p. 199) who indicated that North American Pacific Coast pelagornithids are "generically distinct from those known from the Miocene of the Atlantic", but did not detail how exactly these birds differ and which fossils were compared.

Cyphornis magnus from an unknown horizon (late Eocene to Miocene; Olson, 1985; Goedert, 1989) of Vancouver Island is based on a poorly preserved proximal tarsometatarsus, and "*Tympanonesiotes*" *wetmorei* Hopson, 1964, from the Oligocene or Miocene (Olson, 1985) of South Carolina is known from a reworked and very fragmentary distal tarsometatarsus. As detailed above, both species differ from the Oregon pelagornithid in size, but the material otherwise does not allow for meaningful comparisons.

Neither *Palaeochenoides* Shufeldt, 1916, nor *Tympanonesiotes* Hopson, 1964 and *Cyphornis* Cope, 1894 have so far been differentiated from *Pelagornis* Lartet, 1857. Even if the exact age of *C. magnus* were known, taxonomic conclusions are hardly possible for the holotype bone fragment; it may be closely related to either the very large Eocene pelagornithids (e.g., Goedert, 1989) or to some of the Neogene species. To ease further studies, we suggest, however, to synonymize *Palaeochenoides* and *Tympanonesiotes* with *Pelagornis*, which has taxonomic priority over the former two taxa (note that this results in the species names *P. mioceanus* Shufeldt, 1916 and *P. miocaenus* Lartet, 1857 being distinguished only by the sequence of the central vowels). Taking into consideration the taxonomic details discussed above, it is in this broad sense that we refer the Oregon pelagornithid LACM 128424 to the taxon *Pelagornis*.

The interrelationships of pelagornithid species are poorly resolved, but at least two clades can now be recognized (Fig. 4). As detailed by Bourdon et al. (2010), plesiomorphic characters clearly distinguish the early Eocene *Dasornis* species from all later pelagornithids. In addition to a very short olecranon of the ulna, all post-early Eocene pelagornithid species exhibit a derived humerus morphology, in which the ventral portion of the proximal end is very narrow proximodistally and the tuberculum dorsale strongly proximally projected. This *Pelagornis*-type humerus morphology is already known from the middle Eocene *Lutetodontopteryx* and *Gigantornis* (Bourdon and Capetta, 2012; Mayr and Zvonok, 2012) and is also present in late Eocene/early Oligocene pelagornithids from Oregon (Goedert, 1989; Bourdon et al., 2010).

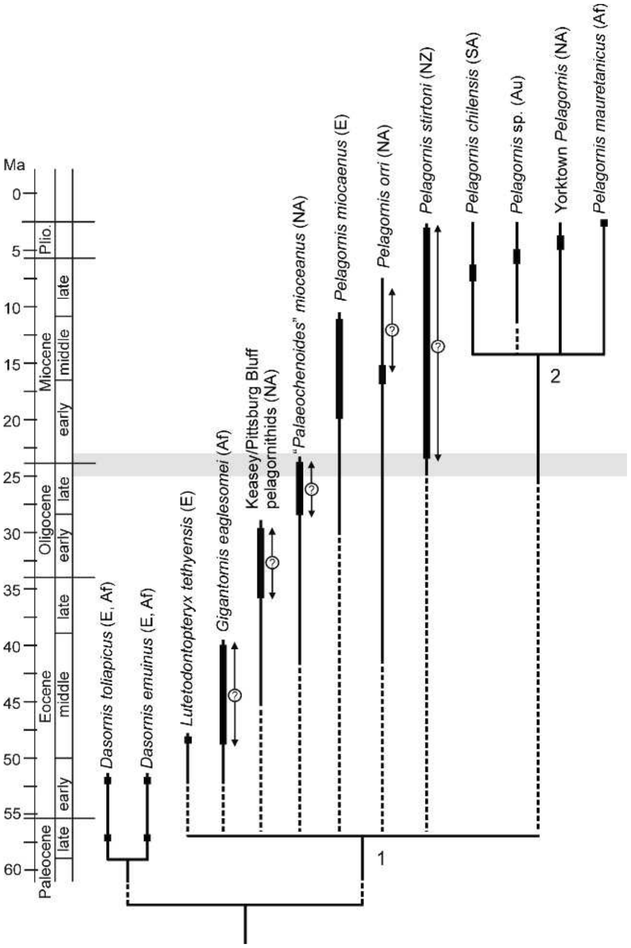

FIGURE *4* —Temporal distribution and phylogenetic affinities of selected pelagornithid species. The two internal nodes are supported by the following derived features (see text for further details). *1*, humerus with ventral portion of proximal end narrow and tuberculum dorsale strongly projected; ulna with very short olecranon; *2*, femur, trochlea fibularis without sulcus (unknown for the Australian pelagornithid reported by Fitzgerald et al., 2012, the tibiotarsus of which does, however, closely resemble that of *Pelagornis chilensis*). The temporal distribution is indicated by black squares/bars. A question mark indicates that a bar does not reflect a temporal range but an uncertain age. The area shaded in gray indicates the age range of the Nye Mudstone pelagornithid described in the present study. Geographic occurrences are given in parentheses: Af=Africa; Au=Australia; E=Europe; NA=North America; NZ=New Zealand; SA=South America.

In the late Neogene *P. chilensis* and *P. mauretanicus* Mourer-Chauviré and Geraads, 2008, as well as a pelagornithid from the Yorktown Formation, the femur further exhibits an unusual derived morphology in that the trochlea fibularis lacks a sulcus (Fig. 3.3; Mayr and Rubilar-Rogers, 2010). This sulcus is plesiomorphic for neornithine birds and well developed in Eocene pelagornithids and *Pelagornis* ("*Palaeochenoides*") *mioceanus* (Fig. 3.1, 3.2; Bourdon et al., 2010; Mayr and Zvonok, 2012). A well-developed sulcus is also present in *P. stirtoni* (Howard and Warter, 1969) from New Zealand, of which the exact age is unknown; this species was originally assigned to the taxon "*Pseudodontornis*", but Mayr and Rubilar-Rogers (2010) argued for an inclusion in *Pelagornis*.

The trochlea fibularis of the femur of LACM 128424 is too poorly preserved to establish presence or absence of a sulcus, but a sulcus is present on the femur of the presumably coeval and closely related *P. mioceanus*, which suggests a position of these late Oligocene/early Miocene pelagornithids outside of a clade that includes *P. chilensis*, *P. mauretanicu*s, and the Pliocene North American pelagornithids. The tibiotarsus of LACM 128424 is further distinguished from that of *P. chilensis* and an undetermined pelagornithid from the late Miocene/early Pliocene of Australia (Fitzgerald et al., 2012) in that it lacks a deeply excavated fossa extensoria (Fig. 3.5).

We are aware of the fact that in addition to differences in the above femur and tibiotarsus features, further morphological diversity existed in late Paleogene and Neogene pelagornithids. For example, a mandible fragment from the ?late Oligocene of South Carolina, which was assigned to "*Pseudodontornis*" by Hopson (1964) but is likely to have come from the same species as the tarsometatarsus fragment he tentatively assigned to "*Palaeochenoides*" *mioceanus*, is distinguished from the mandible of *Pelagornis orri* in the pattern of arrangement of the pseudoteeth (differences in pseudotooth pattern were also discussed by Matsuoka [1998, 2003] and Stidham [2004]). This osteological distinctness of late Oligocene/early Miocene and late Neogene pelagornithids may indicate the existence of well-separated clades that deserve ranking as different "genera". Because the beak and leg bones are, however, unknown for *Pelagornis miocaenus,* it would be impossible to attribute any of these clades to the taxon *Pelagornis*, which impedes a well-founded taxonomic revision. In the current state of our knowledge, and until more data on the osteology and interrelationships of the various species are available, the benefits of a simplified taxonomy, i.e., use of the taxon *Pelagornis* for a broadly defined clade including all Neogene pelagornithid species, outweigh the detriments of a nomenclatural loss of phylogenetic information.

Pelagornithids have long been associated with either procellariiform or "pelecaniform" birds (e.g., Olson, 1985; Olson and Rasmussen, 2001), but Bourdon (2005, 2011) suggested that they are the sister taxon of Anseriformes. A position outside Neoaves also resulted from an analysis of Mayr (2011), who detailed that plesiomorphic features do, however, not support a classification of pelagornithids within crown group Galloanseres. The new remains described in the present study do not contribute to an ultimate phylogenetic placement of pelagornithids, but exhibit characters of the pelvis (absence of horizontally oriented alae praeacetabulares ilii) and thoracic vertebrae (which are hetero- instead of opisthocoelous) that conflict with a close relationship to the "pelecaniform" Suloidea as proposed by Olson and Rasmussen (2001).

LACM 128424 also informs about the previously poorly known morphology of the feet of pelagornithids, and the curious widening of some of the phalanges is unparalleled by other birds. Widened pedal phalanges occur in some Procellariiformes, which use their immersed feet as a brake (Mayr et al., 2002). In these birds the phalanges are, however, more flattened, especially with regard to their distal sections, and flattening also involves the ungual phalanges, which in pelagornithids have the usual shape (as evidenced by the *P. orri* holotype; see Howard, 1957, figs. 7, 8). The highly aerial pelagornithids, whose Neogene representatives were probably not capable of sustained flapping flight (Olson, 1985), may have also used their feet to assist in flight maneuvers just above sea surface level. However, because pelagornithids had unusually small legs compared to the size of their wing and pectoral girdle (e.g., Mayr and Rubilar-Rogers, 2010), the peculiar morphology of their toes could as well have just contributed to bipedal stance on land.

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