

A lithornithid (Aves: Palaeognathae) from the Paleocene (Tiffanian) of southern California

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The proximal end of a bird humerus recovered from the Paleocene Goler Formation of southern California is the oldest Cenozoic record of this clade from the west coast of North America. The fossil is characterized by a relatively large, dorsally-positioned head of the humerus and a subcircular opening to the pneumotricipital fossa, consistent with the Lithornithidae among known North American Paleocene birds, and is similar in size to *Lithornis celetius*. This specimen from the Tiffanian NALMA extends the known geographic range of lithornithids outside of the Rocky Mountains region in the United States. The inferred coastal depositional environment of the Goler Formation is consistent with a broad ecological niche of lithornithids. The age and geographic distribution of lithornithids in North America and Europe suggests these birds dispersed from North America to Europe in the Paleocene or by the early Eocene. During the Paleogene the intercontinental dispersal of lithornithids likely occurred alongside other known bird and mammalian movements that were facilitated by climatic and sea level changes.

Keywords: bird humerus, fossil, Lithornithidae, Goler Formation, Tiffanian, California

INTRODUCTION

The Paleocene is the least well-known epoch of the Cenozoic for the fossil record of birds, and in some ways it is not as well known as many older Cretaceous epochs. Despite new finds and descriptions of Paleocene fossil birds from both Europe and Africa (e.g., Bourdon et al. 2005, Mayr 2007), the record in North America prior to the last ~1 million years of the Paleocene (i.e., the Clarkforkian North American Land Mammal Age) has suffered from a paucity of specimens. Bird fossils from the Tiffanian North American Land Mammal Age (NALMA) (~62–57 Ma) (Gradstein et al. 2012) are rare in North America and restricted to records of the lithornithid, *Lithornis celetius* Houde 1988, from Montana and Wyoming, the owl *Ogygoptynx wetmorei* Rich and Bohaska 1976 from Colorado, the large presbyornithid *Presbyornis isoni* Olson 1994 from Maryland, and a diversity of taxa associated with aquatic habitats from North Dakota mostly represented by single bones and bone fragments, e.g., *Dakotornis cooperi* Erickson 1975, indeterminate graculaids, and other unnamed taxa (Benson 1999, Stidham et al. 2012). The earlier parts of the Paleocene in North America have an even poorer avian fossil record. Thus, the evolutionary history of birds after the mass extinction at the end of the Cretaceous is

largely unknown in North America.

The best known of these Tiffanian avian taxa are the lithornithids. Lithornithidae Houde 1988 is a possibly non-monophyletic grouping of birds from the Paleogene of North America and Europe (Houde 1988, Mayr 2009a, b). They have been placed variously as the sister group to crown group Aves, as allied to Tinamidae Gray 1840, and as the sister group to a monophyletic grouping of the ratite birds (see Mayr 2009a for a review). With those phylogenetic uncertainties, consensus around diagnostic characters for all or part of Lithornithidae is absent. Previous workers have mentioned potential diagnostic characters (Houde 1988, Mayr 2007, 2009a, b), but so far the humerus has not received much scrutiny in this regard.

Recently, the proximal end of a humerus from a lithornithid (cataloged as RAM 15330; RAM—Raymond M. Alf Museum of Paleontology, Claremont, California, USA) was recovered from the Tiffanian part of the Goler Formation of southern California. This specimen extends the known paleogeographic range of lithornithids to the west coast of North America (south and west of their previously known range). Furthermore, this specimen is the first Paleocene and oldest Cenozoic bird from the west coast of the United States, adding new knowledge to the

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diversity of birds during the Paleocene of North America.

The Goler Formation is a mostly non-marine rock unit that crops out in the northern Mojave Desert of southern California, yielding a diverse record of Paleocene vertebrates, including bony fish, sharks, rays, turtles, lizards, crocodylians, and mammals (Lofgren et al. 2008). The avian humerus fragment (RAM 15330) was collected from the Land of Oz locality (RAM V200001) in Member 4A of the Goler Formation (Fig. 1), and represents the first record of a bird in the formation. The mammalian fauna from Member 4A is correlative to the early-middle Tiffanian NALMA (Lofgren et al. 2008, Albright et al. 2009, Williamson and Lofgren 2014), probably the Ti3 and Ti4a zones (Lofgren et al. 2014). Thus, RAM 15330 is younger than lithornithid specimens from the Bangtail Quarry of Montana that are earliest Tiffanian (Ti1; Houde 1988, Lofgren et al. 2004), and likely slightly older than the probable lithornithid from the Walbeck fissure filling of Germany (Mayr 2007, Smith and Smith 2003, Gradstein et al. 2012). This Goler Formation bird also is likely close in age to the Paleocene fossil birds from North Dakota (e.g., Benson 1999, Stidham et al. 2012), among the oldest Cenozoic birds known in North America. RAM 15330 augments the meager record of Paleocene birds outside of the Rocky Mountain region of western North America and expands avian faunal data for the Tiffanian.

SYSTEMATIC PALEONTOLOGY

PALAEOGNATHAE Pycraft 1900

LITHORNITHIDAE Houde 1988

cf. *LITHORNIS* Owen 1840

Lithornis sp.

(Figs. 2A–D)

Referred specimen—RAM 15330, a proximal end of a right humerus.

Locality and horizon—Locality RAM V200001, Kern County, California (Fig. 1), in Member 4A of the Goler Formation, Tiffanian NALMA, Paleocene (~59–60 Ma; Lofgren et al. 2014). Detailed locality data are on file at RAM and available to qualified investigators upon request.

Description—Osteological terminology here follows Baumel and Witmer (1993), using English equivalents of the Latin terms (e.g., Smith et al. 2013). The specimen preserves the proximal end of the humerus, with some minor fragments missing (Fig. 2). The maximum dorsoventral depth of the specimen, as measured from the deltopectoral crest to the bicapital crest, is 23.9 mm and the craniocaudal depth at the proximal end is 12.0 mm as measured from the cranial edge of the humeral head to the caudal tip of the ventral tubercle. The preserved proximal-distal length

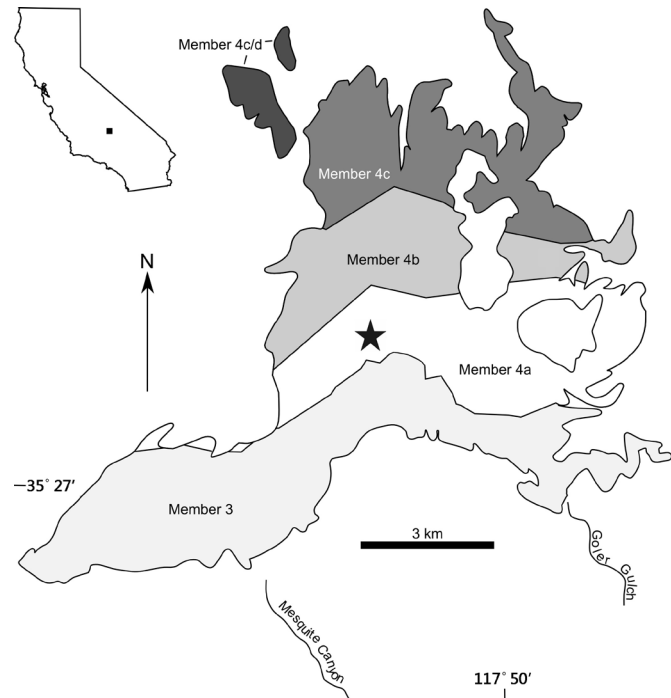


Figure 1. Location of the Goler Formation within California and outcrop map of Member 3 and 4 of the Goler Formation. The position of the Land of Oz locality (RAM locality V200001) that yielded the proximal humerus of a bird is denoted by a star.

of the specimen is 24.4 mm.

Only the base of the deltopectoral crest is preserved, and the base is relatively thick (up to 2.7 mm as preserved) (Fig. 2D, E). The area ventral to the deltopectoral crest is nearly flat all the way to the ventral edge of the bone. The only convex area on the cranial surface is at the proximodorsal corner, where the humeral head is located (Fig. 2). The proximal and ventral edges of the bone are moderately abraded, with small missing bone fragments. The humeral head is large, bulbous, and shifted mostly dorsal to the dorsoventral midpoint of the bone. The dorsal tubercle is damaged, but does not appear to have been very large or very distinct from the dorsal end of the humeral head (Fig. 2C–E). The proximodistal transition from the humeral head to the shaft on the caudal surface is smooth (i.e. no distinct lip as in many crown group birds) (Fig. 2C). Approximately the dorsal half of the shaft on the caudal surface is convex (Fig. 2C). The capital incision is a wide “U,” but it does not make a notch in the proximal outline of the bone (i.e., it is on the caudal face only, unlike the state in *Paracathartes* Harrison 1979, and some species of *Lithornis*; see Houde 1998, figs. 15 and 16).

The ventral tubercle is large and bulbous (Fig. 2A, D), but its ventral side and the adjacent ventral rim of the

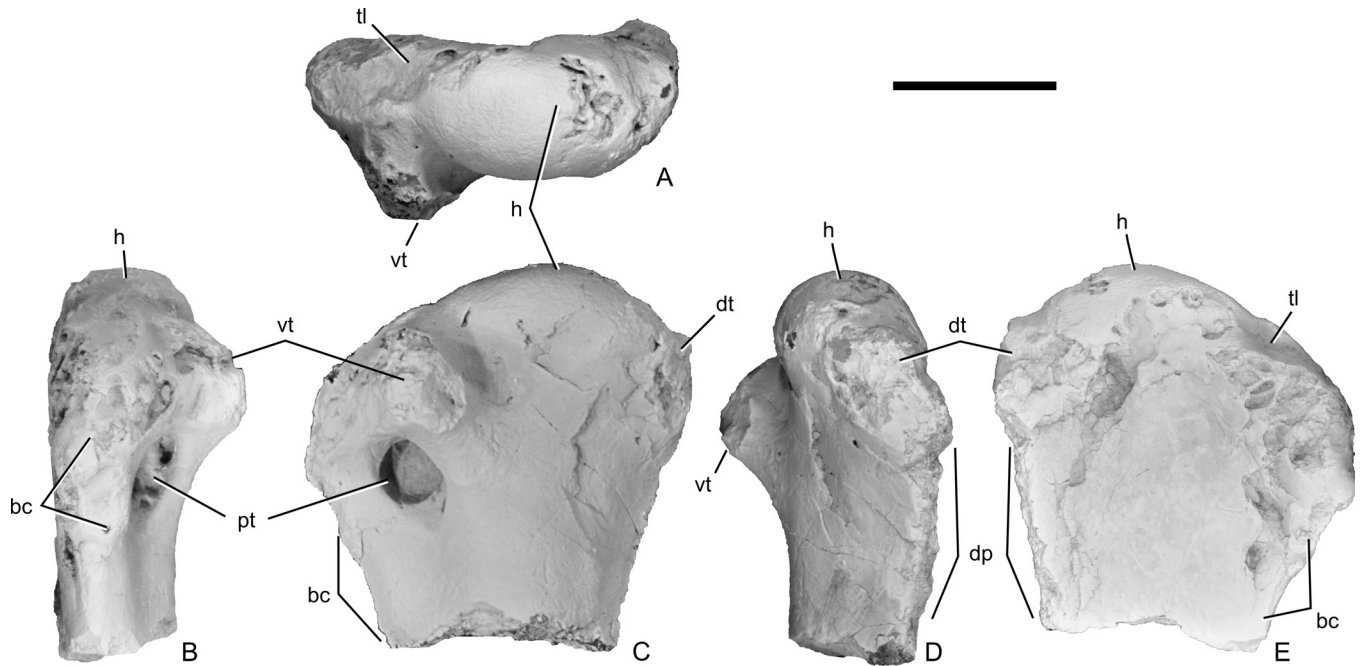


Figure 2. Lithornithid proximal humerus (RAM 15330). Scale bar = 1 cm. **A.** Proximal view. **B.** Ventral view. **C.** Caudal view. **D.** Dorsal view. **E.** Cranial view. Abbreviations: bc, bicipital crest; dp, deltopectoral crest; dt, dorsal tubercle; h, head; pt, pneumotricipital fossa; tl, transverse ligamental groove; vt, ventral tubercle.

pneumotricipital fossa are damaged (Fig. 2B, C). The opening of the pneumotricipital fossa is nearly circular in outline and has a thick rim. The fossa has a maximum depth of 4 mm proximally, and a distinct foramen extends proximally from the dorsal edge of the fossa. The area distal to the pneumotricipital fossa is nearly flat, resulting in a triangular cross-section for the preserved distal end. The humeral head is craniocaudally wide. A slight concavity occurs on the dorsal end of the proximal face, near the dorsal tubercle. The transverse ligamental groove is relatively wide and only slightly concave (Fig. 2A, E). It is located ventral to the humeral head, on the proximal (not cranial) face of the humerus, extending from the ventral edge of the humeral head to at least the vicinity of the broken ventral edge of the bone. The groove may have extended farther ventrally, but this cannot be determined due to breakage. No muscle scars are visible on the bone.

Comparisons—RAM 15330 exhibits a relatively large humeral head that is dorsally positioned and has a subcircular opening to the pneumotricipital fossa, much like a foramen opening into a pneumatic pocket. Those characters, along with its overall morphology, agree with lithornithids and differ from other known Paleocene taxa such as presbyornithids, colliiforms, and “graculavid” shorebirds. These non-lithornithids have a very different pneumotricipital fossa that lacks a subcircular foramen opening with a thick rim (instead possessing a wider distal

opening or aperture, or just a concave area on the bone) as well as a more gracile morphology that contrasts with the inflated proximal end of the humerus in *Lithornis* (see Benson 1999, Houde and Olson 1992). Note that the inflated state may be plesiomorphic for crown group birds, because similar morphologies occur in crown group galliforms. However, that character’s distribution could be convergent. Despite that character distribution, the particular morphology of the pneumotricipital fossa opening in RAM 15330 differs from that illustrated in *Paracathartes* (Houde 1988, fig. 17D). Overall, the morphology of the Goler fossil is entirely consistent with that known in species of *Lithornis* and differs from all other known Paleocene avian taxa in North America. Thus, we tentatively refer the specimen to *Lithornis*.

Prior to the description of RAM 15330, the only known North American lithornithid specimens from the Tiffanian were individuals assigned to *Lithornis celetius* from the Fort Union Formation in Montana and the Polecat Bench Formation in Wyoming (Houde 1988). The illustrations of *Lithornis celetius* Houde 1988 lack scale bars and are designated as being published at natural size. However, the size of the illustrations does not match measurements of the specimens provided by Houde (1988). For example, the length of humerus USNM 336535 is 112.7 mm (Houde 1988, table 10), but the length of USNM 336535 measured from its illustration (Houde 1988, fig. 16) is 135.6

mm (approximately 17% longer). Similarly, the length of humerus USNM 336534 is 78.2 mm (Houde 1988, table 10), but the length measured from the illustration (Houde 1988, fig. 17) is 93.5 mm (an error of about 16%). Compensating for that difference and using Houde's (1988) published measurements, RAM 15330 is quite close in size to *Lithornis celetius*.

Although the overall morphology of RAM 15330 is similar to that of *Lithornis celetius*, the capital incision in *Lithornis celetius* (and other lithornithids) reaches the proximal end of the bone, forming a notch in the proximal outline of the bone adjacent to the humeral head (Houde 1988, fig. 15A). That character is absent in RAM 15330. This difference could be attributable to individual variation, but the issue cannot be resolved with the limited number of specimens. The Bangtail Quarry specimens of *Lithornis celetius* are older than the Goler Formation specimen. However, Houde's (1988) referred specimen of *Lithornis celetius* (Yale Peabody Museum YPM VPPU 020510, formerly part of the Princeton University collection) is from Cedar Point Quarry in the Polecat Formation, within the Ti3 zone (Secord et al. 2006) and penecontemporaneous with the Goler Formation. Although it is tempting to refer RAM 15330 to *Lithornis celetius*, we refrain from assigning the Goler Formation specimen to any species level taxon in light of the lack of definitive morphological characters and the geographical separation of the two Tiffanian occurrences.

DISCUSSION

Lithornithids are known exclusively from North America and Europe during the Paleocene and Eocene. This disjunction in lithornithid distribution must have arisen through dispersal during the early Cenozoic, but the direction and timing of their intercontinental movements are unknown. However, only a limited number of scenarios are possible given the known fossil record. Those hypotheses are dispersal in the Paleocene or Eocene and dispersal to or from North America and Europe.

The distribution of lithornithid species during the Paleogene in Europe and North America is shown in Table 1. The oldest unequivocal lithornithid material from North America is *Lithornis celetius* from Bangtail Quarry in the Fort Union Formation of Montana, associated with a Ti1 fauna and correlated approximately to the early Selandian of Europe (Houde 1988, Lofgren et al. 2004, Gradstein et al. 2012). The Bangtail Quarry occurrence is older than the age estimate for the oldest probable European lithornithid, *Fissuravis* Mayr 2007 from Walbeck, a site near the Selandian-Thonetian Boundary (Smith and Smith 2003,

Mayr 2007). Hope (2002) described a scapula from sediments near the Cretaceous-Paleocene Boundary in New Jersey as a possible lithornithid, but that specimen requires further study to verify its exact phylogenetic placement (Mayr 2009a). Even without that older record, the oldest lithornithid fossils are from North America. Other than the probable lithornithid *Fissuravis*, there are no known Paleocene records of European lithornithids, and that group's next oldest European records are from the Eocene (Houde 1988, Mayr 2009a). Furthermore, lithornithids have not been reported in the late Paleocene of France (i.e. a gap in the Paleocene), even though many avian taxa are known from Cernay and Mont du Berru (e.g., Mourer-Chauviré 1995, Martin 1992, Mayr 2009a). Thus, the hypothesis that the initial dispersal of lithornithids was from North America to Europe is supported by the occurrence of the oldest lithornithids in North America. Constraining the timing of initial intercontinental dispersal is more problematic. If *Fissuravis* is indeed a lithornithid, then the disjunct distribution was present in the Paleocene (Tiffanian or Selandian). If it is not a lithornithid, then the intercontinental dispersal may not have happened until the beginning of the Eocene, when the next oldest records of lithornithids in Europe occur (Houde 1988, Mayr 2009a).

Birds were not the only clades that moved among Northern Hemisphere continents in the Paleocene. Relatively few mammal taxa are shared between North America and Europe during the Tiffanian, whereas more mammalian, turtle, and plant taxa are shared between those continents in the early Eocene (Bowen et al. 2002, Wing et al. 2005, McInerney and Wing 2011). Based on the stage of evolution, the mammalian assemblage from the Walbeck fissure fill site in Germany may be a temporal equivalent of the early Tiffanian mammalian assemblages from North America, including the Land of Oz locality in the Goler Formation (Savage and Russell 1983, Lofgren et al. 2004). Shared taxa between these continents in the Paleocene include the plesiadapiforms *Plesiadapis* Gervais 1877 (known from throughout the Tiffanian) and *Saxonella* Russell 1964 (known only from Ti3 faunas; Russell 1964, Fox 1984, Gingerich 1976, Lofgren et al. 2004). *Plesiadapis walbeckensis* Russell 1964 from the Walbeck assemblage is interpreted to be comparable to a taxon intermediate between the North American species, *Plesiadapis anceps* Simpson 1936 and *Plesiadapis rex* Gidley 1923 (Gingerich 1976). Thus, the European occurrence of *Plesiadapis walbeckensis* likely would correlate approximately to the Ti2 or Ti3 zones. Given that correlation, the occurrence of *Fissuravis* in Europe coincides with some initial intercontinental dispersal among mammals (from North America to Europe).

Table 1. Stratigraphic and Geographic Distribution of Lithornithid Taxa and the potential lithornithid *Fissuravis*.

Taxon	Age	Locality	Reference
<i>Fissuravis weigelti</i>	middle Paleocene	Walbeck, Germany	Mayr 2007
<i>Lithornis celetius</i>	middle Paleocene	Wyoming, USA	Houde 1988
<i>Lithornis hookeri</i>	early Eocene	London Clay, U.K.	Houde 1988
<i>Lithornis nasi</i>	early Eocene	London Clay, U.K. Wyoming, USA	Houde 1988
<i>Lithornis plebius</i>	late Paleocene	Wyoming, USA	Houde 1988
<i>Lithornis promiscuus</i>	late Paleocene	Wyoming, USA	Houde 1988
<i>Lithornis vulturinus</i>	early Eocene	London Clay, U.K. Denmark	Houde 1988 Leonard et al. 2005
<i>Lithornis</i> sp.	middle Eocene	Messel, Germany	Mayr 2009b
cf. <i>Lithornis</i> sp.	middle Paleocene	California, USA	This paper
Lithornithidae indet.	middle Eocene	Wyoming, USA	Houde 1988
<i>Paracathartes howardae</i>	early Eocene	Wyoming, USA	Houde 1988
<i>Pseudocrypturus cercanaxius</i>	early Eocene	Wyoming, USA London Clay, U.K.	Houde 1988

Even though lithornithids were volant, climatic and environmental changes likely would have aided their intercontinental movements. Sea level lows that occurred during the earlier part of the Tiffanian, the late Paleocene, and the Early Eocene, may have facilitated the movement of terrestrial organisms between North America and Europe, supported by the temporal co-occurrence of these sea level changes and increased mammalian faunal similarity (Woodburne and Swisher 1995). The unequivocal occurrence of lithornithids in Europe after the Paleocene-Eocene Boundary could indicate that lithornithids dispersed penecontemporaneous to mammals, and that their movements may have been facilitated by the same environmental (climatic warming) or geographic mechanism (lowered sea level) that allowed or aided the biogeographic changes among other tetrapods.

Known species of lithornithids occupied the ground, and their ecology was at least somewhat similar to extant tinamous with their omnivorous diet. Lithornithids are thought to have foraged in leaf litter by probing with their slender bills (Houde 1988). Their occurrence outside of the Wyoming/Montana region within North America is not unexpected because habitats suitable for them likely occurred across the continent. Many mammalian taxa are shared between the Goler Formation and faunas in many of the states where the Rocky Mountains occur today (Lofgren et al. 2008). Thus, the presence of a lithornithid

in southern California adds to those biogeographic links with at least the northern parts of the western interior (i.e., Montana and Wyoming). Despite those shared vertebrate taxa, there is significant Goler Formation endemism among mammals and turtles derived, at least partly, from the potential topographic barriers around the Goler Basin (Lofgren et al. 2008, 2014). Therefore, it is possible that this new specimen represents a species different from the contemporaneous *Lithornis celetius*, and one that was limited to the Goler Basin. However, only additional material will help resolve that species' level identification.

The geology and fossils of the Goler Formation suggest a forested near-coastal depositional environment, corroborated by shark and ray teeth in the highest part of the formation and significant accumulations of petrified wood in Member 4A and Member 4B (Lofgren et al. 2008). The occurrence of lithornithids in a North American coastal environment is not unexpected, because that clade also is known from nodules in Denmark's marine Fur Formation (Leonard et al. 2005, Dyke and Lindow 2009). Furthermore, Kristoffersen (1999) advocated for a coastal habitat for Danish lithornithids. At a minimum, those individual Danish birds also occurred in a coastal setting similar to where the Goler Formation bird was deposited. These environments suggest that lithornithids had a relatively broad niche extending from mountainous interior basins to coastlines.

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LITERATURE CITED

- Albright, L.B., III, D.L. Lofgren and M.C. McKenna. 2009. Magnetostratigraphy, mammalian biostratigraphy, and refined age assessment of the Goler Formation (Paleocene), California. Pgs. 259–277 in L.B. Albright III (ed.), *Papers on Geology, Paleontology, and Biostratigraphy in Honor of Michael O. Woodburne. Museum of Northern Arizona Bulletin* 65.
- Baumel, J.J., and L. Witmer. 1993. Osteologica. Pgs. 45–132 in J.J. Baumel, A.S. King, J.E. Breazile, H.E. Evans, and J.C. Vanden Berge (eds.), *Handbook of avian anatomy: Nomina Anatomica Avium, Second Edition. Bulletin of the Nuttall Ornithological Club* 23.
- Benson, R.D. 1999. *Presbyornis isoni* and other Late Paleocene birds from North Dakota. *Smithsonian Contributions to Paleobiology* 89:253–259.
- Bourdon, E., B. Bouya and M. Iarochene. 2005. Earliest African neornithine bird: A new species of Prophaethontidae (Aves) from the Paleocene of Morocco. *Journal of Vertebrate Paleontology* 25:157–170.
- Bowen, G.J., W.C. Clyde, P.L. Koch, S. Ting, J. Alroy, T. Tsubamoto, Y. Wang and Y. Wang. 2002. Mammalian dispersal at the Paleocene/Eocene Boundary. *Science* 295:2062–2065.
- Dyke, G., and B. Lindow. 2009. Taphonomy and abundance of birds from the Lower Eocene Fur Formation of Denmark. *Geological Journal* 44:365–373.
- Erickson, B.R. 1975. *Dakotornis cooperi*, a new Paleocene bird from North Dakota. *Scientific Publications of the Science Museum of Minnesota* 7(3):1–19.
- Fox, R.C. 1984. First North American record of the Paleocene primate *Saxonella*. *Journal of Paleontology* 58:892–894.
- Gervais, P. 1877. Énumération de quelques ossements d'animaux vertébrés recueillis aus environs de Reims par M. Lemoine. *Journal de Zoologie (Paris)* 6:74–79.
- Gidley, J.W. 1923. Paleocene primates of the Fort Union, with discussion of relationships of Eocene primates. *Proceedings of the United States National Museum* 63:1–38.
- Gingerich, P.D. 1976. Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). *University of Michigan Papers in Paleontology* 15:1–141.
- Gradstein, F.M., J.G. Ogg, M.D. Schmitz and G.M. Ogg. 2012. *The Geologic Time Scale, Volume 2*. Elsevier, Boston. Pgs. 437–1144.
- Gray, G.R. 1840. A list of the genera of birds: With their synonyms and an indication of the typical species of each genus. R. and J.E. Taylor, London. 404 Pgs.
- Harrison, C.J.O. 1979. A new cathartid vulture from the lower Eocene of Wyoming. *Tertiary Research Special Paper* 5:7–10.
- Hope, S. 2002. The Mesozoic radiation of Neornithes. Pgs. 339–388 in L.M. Chiappe and L.M. Witmer (eds.), *Mesozoic birds. Above the heads of dinosaurs*. University of California Press, Berkeley.
- Houde, P.W. 1988. Paleognathous birds from the early Tertiary of the Northern Hemisphere. *Publications of the Nuttall Ornithological Club* 22:1–148.
- Houde, P.W., and S. Olson. 1992. A radiation of coly-like birds from the Eocene of North America (Aves: Sandcoleiformes New Order). Pgs. 137–160 in K.E. Campbell (ed.), *Papers in Avian Paleontology honoring Pierce Brodkorb. Natural History Museum of Los Angeles County, Science Series* 36.
- Kristoffersen, A.V. 1999. Lithornithid birds (Aves, Palaeognathae) from the Lower Palaeogene of Denmark. *Geologie en Mijnbouw* 78:375–381.
- Leonard, L., G.J. Dyke and M. van Tuinen. 2005. A new specimen of the fossil paleognath *Lithornis* from the lower Eocene of Denmark. *American Museum Novitates* 3941:1–11.
- Lofgren, D.L., J.G. Honey, M.C. McKenna, R.L. Zondervan and E.E. Smith. 2008. Paleocene primates from the Goler Formation of the Mojave Desert in California. *Natural History Museum of Los Angeles County, Science Series* 41:11–28.
- Lofgren, D.L., M. McKenna, J. Honey, R. Nydam, C. Wheaton, B. Yokote, L. Henn, W. Hanlon, S. Manning and C. McGee. 2014. New records of eutherian mammals from the Goler Formation (Tiffanian, Paleocene) of California and their biostratigraphic and paleobiogeographic implications. *American Museum Novitates* 3797:1–57.
- Lofgren, D.L., J.A. Lillegraven, W.A. Clemens, P.D. Gingerich and T.E. Williamson. 2004. Paleocene biochronology: The Puercan through Clarkforkian Land Mammal Ages. Pgs. 43–105 in M.O. Woodburne (ed.), *Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology*. Columbia University Press, New York.
- Martin, L.D. 1992. The status of the Late Paleocene birds *Gastornis* and *Remiornis*. Pgs. 97–108 in K.E. Campbell (ed.), *Papers in Avian Paleontology honoring Pierce Brodkorb. Natural History Museum of Los Angeles County, Science Series* 36.
- Mayr, G. 2007. The birds from the Paleocene fissure filling of Walbeck (Germany). *Journal of Vertebrate Paleontology* 27:394–408.
- Mayr, G. 2009a. *Paleogene Fossil Birds*. Springer-Verlag, Berlin. 262 Pgs.
- Mayr, G. 2009b. Towards the complete bird—the skull of the Middle Eocene lithornithid (Aves, Lithornithidae). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 79:169–173.

- McInerney, F.A., and S.L. Wing. 2011. The Paleocene-Eocene Thermal Maximum: A perturbation of carbon cycle, climate, and biosphere with implications for the future. *Annual Review of Earth and Planetary Sciences* 39:489–516.
- Mourer-Chauviré, C. 1995. A large owl from the Palaeocene of France. *Palaeontology* 37:339–348.
- Olson, S.L. 1994. A giant *Presbyornis* (Aves: Anseriformes) and other birds from the Paleocene Aquia Formation of Maryland and Virginia. *Proceedings of the Biological Society of Washington* 107:429–435.
- Owen, R. 1840. Description of the remains of a mammal, a bird, and a serpent from the London Clay. *Proceedings of the Geological Society of London* 3:162–166.
- Pycraft, W.P. 1900. On the monophyly and phylogeny of the Palaeognathae (Ratitae and Crypturi) and Neognathae (Carinatae). *Transactions of the Zoological Society of London* 15:149–290.
- Rich, P.V., and D.J. Bohaska. 1976. The world's oldest owl: A new strigiform from the Paleocene of southwestern Colorado. *Smithsonian Contributions to Paleobiology* 27:87–93.
- Russell, D.E. 1964. Les Mammifères Paleocène d'Europe. *Memoires Museum National d'Historire Naturelle, Serie C* 13:1–324.
- Savage, D.E., and D.E. Russell. 1983. Mammalian paleofaunas of the world. Addison-Wesley Publishing Co., Reading, MA. 432 Pgs.
- Secord, R., P.D. Gingerich, M.E. Smith, W.C. Clyde, P. Wilf and B.S. Singer. 2006. Geochronology and mammalian biostratigraphy of middle and upper Paleocene continental strata, Bighorn Basin, Wyoming. *American Journal of Science* 306:211–245.
- Simpson, G.G. 1936. A new fauna from the Fort Union of Montana. *American Museum Novitates* 873:1–27.
- Smith, N.D., L. Grande and J.A. Clarke. 2013. A new species of Threskiornithidae-like bird (Aves, Ciconiiformes) from the Green River Formation (Eocene) of Wyoming. *Journal of Vertebrate Paleontology* 33:363–381.
- Smith, T., and R. Smith. 2003. Terrestrial mammals as biostratigraphic indicators in upper Paleocene–lower Eocene marine deposits of the southern North Sea Basin. Pgs. 513–520 in S.L. Wing, P.D. Gingerich, B. Schmitz, and E. Thomas (eds.), Causes and Consequences of Globally Warm Climates in the Early Paleogene. *Geological Society of America Special Paper* 369.
- Stidham, T.A., J. Hoganson and J. Person. 2012. New Middle Paleocene (Tiffanian NALMA) birds from North Dakota. *Journal of Vertebrate Paleontology* (Program and Abstracts supplement) 33:179.
- Williamson, T.E., and D.L. Lofgren. 2014. Late Paleocene (Tiffanian) metatherians from the Goler Formation, California. *Journal of Vertebrate Paleontology* 34:477–482.
- Wing, S.L., G.J. Harrington, F.A. Smith, J.I. Bloch, D.M. Boyer and K.H. Freeman. 2005. Transient floral change and rapid global warming at the Paleocene-Eocene Boundary. *Science* 310:993–996.
- Woodburne, M.O., and C.C. Swisher III. 1995. Land mammal high-resolution geochronology, overland dispersals, sea level, climate, and vicariance. Geochronology Time Scales and Global Stratigraphic Correlation. *SEPM Special Publication* 54:335–364.