Two New Species of *Aegialornis* from France, with Comments on the Ordinal Affinities of the Aegialornithidae

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ABSTRACT

Collections from the upper Eocene–lower Oligocene phosphorite deposits of Quercy, France, include numerous fossil elements attributed to two species of *Aegialornis*. An examination of the humeri in this series disclosed the presence of two unrecgonized species, which are newly described here as *Aegialornis wetmorei* and *A. broweri*. Preliminary study of the other skeletal elements previously assigned to *Aegialornis* indicates that at least some of them are probably referable to the Charadriiformes and the Coraciiformes. The humeri of *Aegialornis* show closer similarity to *Chordeiles* than to any members of the Hemiprocnidae or Apodidae, and, therefore, the Aegialornithidae is removed from the Apodiformes and placed in the Caprimulgiformes near the Caprimulgidae.

Introduction

In the Museum National D'Histoire Naturelle, Paris, and the British Museum (Natural History), are extensive collections of bird fossils from the upper Eocene to lower Oligocene phosphorite deposits of Quercy, France. These include numerous distinctive humeri and some additional material referred to two species in the genus *Aegialornis: A. gallicus* Lydekker and *A. leenhardti* Gaillard. An additional form, *Primapus lacki,* was later described from the lower Eocene London Clay of Britain (Harrison and Walker, 1975). Further study of the Quercy material indicates the presence of two additional species of *Aegialornis*. This genus has been placed in a distinct family, the Aegialornithidae, the taxonomic history of which has been summarized by Harrison (1975). The family was first proposed by Lydekker (1891) who treated it as incertae sedis near the Laridae. The subsequent view of Milne-Edwards (1892) and Gaillard (1908) that *Aegialornis* is more properly included in the Apodiformes has been widely, though seemingly uncritically, accepted. Brodkorb (1971), on the basis of the evidence now presented here, included the Aegialornithidae in the Caprimulgiformes, a placement recently disputed by Harrison (1975). It is the purpose of this paper to review the species of *Aegialornis* and to comment on the possible affinities of the Aegialornithidae.

A wide array of fossil and recent material was examined in this study. Included were the types of *Aegialornis gallicus, A. leenhardti,* and *Tachyornis hirundo,* and much of the additional material referred to these species. Recent skeletons examined included many genera of Caprimulgiformes, particularly *Chordeiles, Caprimulgus,* and *Phalaenoptilus,* and from one to several species of swifts and crested swifts in the genera *Hemiprocne, Cypseloides, Streptoprocne, Apus, Aeronautes, Reinarda, Hirundapus,* and *Chaetura.*

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AEGIALORNITHIDAE Lydekker, 1891

Aegialornis Lydekker, 1891

SYNONYMS.—*Tachyornis* Milne-Edwards, 1892; *Belornis* Milne-Edwards, 1893.

Aegialornis gallicus Lydekker, 1891

FIGURES 1, 4*b*

TYPE-LOCALITY.—Departement de Lot, Bach near Lalbenque, France.

SYNONYM.—*Tachyornis hirundo* Milne-Edwards, 1892. France, Phosphate de Chaux (= Phosphorites du Quercy, fide Gaillard, 1908).

This species is represented by at least 20 humeri: the type-series of 13 and 2 additional specimens in the British Museum, and 5 specimens, including the type of *Tachyornis hirundo,* in the Paris Museum. Referred material includes 2 coracoids, 3 ulnae, 11 carpometacarpi, and 3 proximal phalanges of digit II (BMNH); and 26 tarsometatarsi (PM). As noted by Lydekker (1891) and Harrison and Walker (1975), the humerus is short and stout with a long, prominent, angular deltoid crest; deep ligamental furrow; large, flattened ectepicondylar process; laterally compressed head; broad bicipital surface and bicipital crest; and deep brachial depression. The humeri of *A. gallicus* are

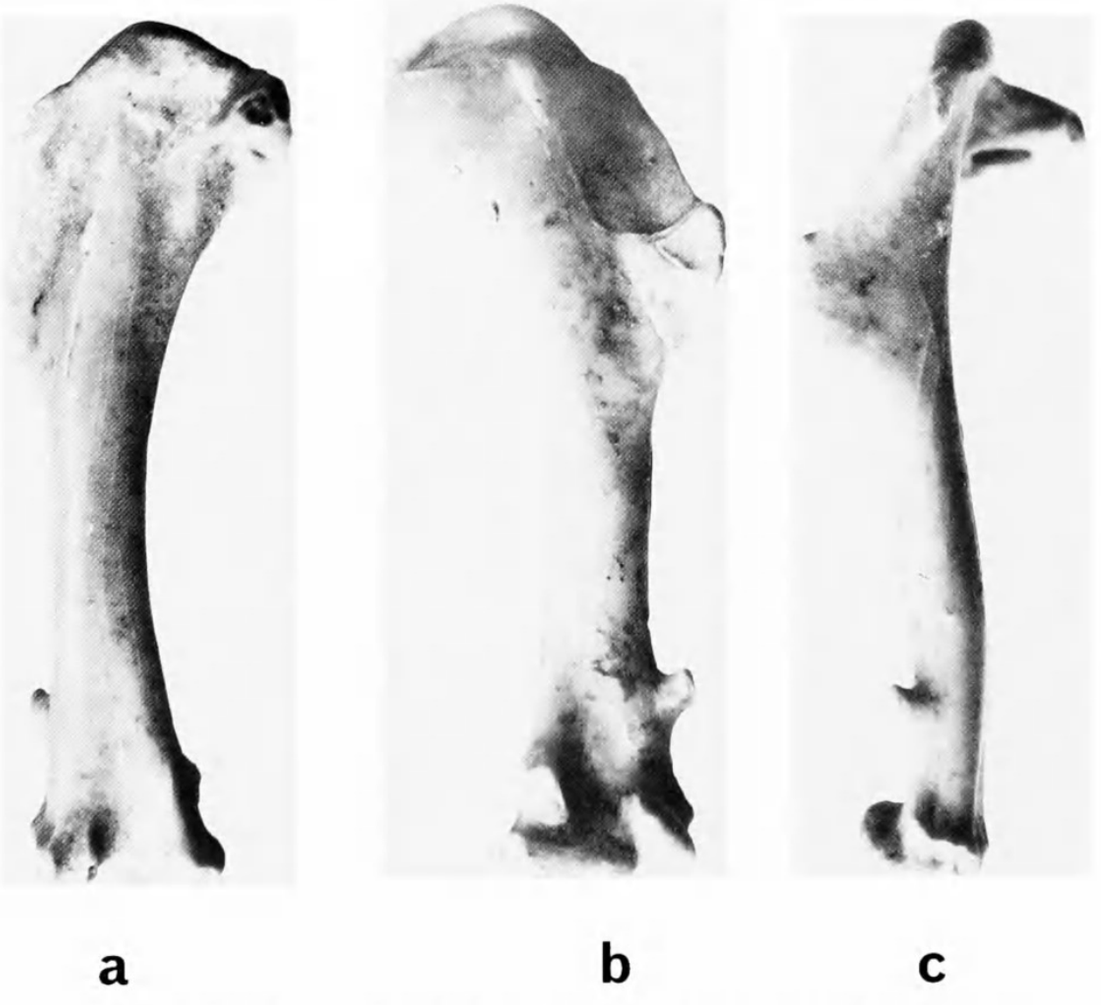

FIGURE 1.—Left humerus of *Aegialornis gallicus: a,* anconal view; *b,* palmar view; *c,* external view. (× 4.)

TABLE 1.—Ranges and means (in parentheses) of measurements (mm) of humeri in *Aegialornis*

Character	*A. leenhardti* $n = 2$	*A. gallicus* $n = 20$	*A. wetmorei* $n = 3$	*A. broweri* $n = 1$
Overall length	29.2–29.8 (29.5)	24.3–27.4 (25.9)	21.8–22.4 (22.0)	19.1
Shaft width	3.7–3.7 (3.7)	2.5–3.3 (3.1)	2.6–2.8 (2.7)	2.3
Shaft depth	2.7–2.8 (2.8)	2.2–2.5 (2.4)	2.0–2.1 (2.1)	1.7
Width of distal end	7.0–7.3 (7.2)	5.6–6.3 (5.9)	4.9–5.0 (5.0)	4.2
Depth of distal end	3.9–4.1 (4.0)	3.6–4.0 (3.7)	3.2–3.4 (3.3)	2.7
Height of ectepicondylar process	5.9–6.1 (6.0)	5.5–6.3 (6.0)	6.1–6.2 (6.2)	4.8
Height of ectepicondylar process as % of total length	20.33	23.04	28.03	25.1

smaller than those of *A. leenhardti* (Table 1), but larger than those of other species of *Aegialornis* or *Primapus*. The referred elements, not all of which appear to be properly assigned to *Aegialornis,* are discussed below.

Aegialornis leenhardti Gaillard, 1908

FIGURES 2, 4*a*

SYNONYM.—Originally proposed as *Aegialornis leehnardti* Gaillard, 1908; spelling emended to *leenhardti* by Brodkorb, 1971:233.

TYPE-LOCALITY.—Phosphorites du Quercy, France.

The holotype right humerus (Musee D'Histoire Naturelle de Montauban) and a previously unrecognized left humerus (PM) agree in being larger than *A. gallicus* and in having a larger and more distally located ectepicondylar process (Table 1). Additional material of this species (not examined in this study) is present in other museum collections (Gaillard, 1908; P. Ballmann, pers. comm.). A left tarsometatarsus from Caylux (Museum de Lyon) figured by Gaillard (1908) appears similar to the numerous tarsometatarsi he referred to *A. gallicus* and which were examined in this study. These specimens are, in my opinion, from an undescribed species possibly belonging in the Coraciiformes.

FIGURE 2.—Holotype right humerus of *Aegialornis leenhardti,* palmar view. (× 4.)

Aegialornis wetmorei, new species

FIGURES 3*a*, 4*c*

HOLOTYPE.—Complete right humerus (PM 15478) from the upper Eocene–lower Oligocene Phosphorites du Quercy, France.

MEASUREMENTS OF HOLOTYPE.—Overall length from head to internal condyle 21.8 mm, width and thickness of shaft at midpoint 2.8 × 2.1 mm, greatest width of distal end 5.0 mm, thickness through internal condyle 3.4 mm, height of proximal edge of ectepicondylar process above distal edge of ectepicondyle 6.3 mm.

PARATYPES.—Two nearly complete left humeri (PM 15479 and 15480) slightly abraded on deltoid crest, bicipital crest, and internal tuberosity; from the same deposits as the type.

ETYMOLOGY.—This species is named after Dr. Alexander Wetmore on the occasion of his ninetieth birthday, in recognition of his many contributions to the field of paleornithology.

DIAGNOSIS AND DESCRIPTION.—These humeri are appreciably smaller and more slender than the smallest humerus of *A. gallicus* (the type of *Tachyornis hirundo*) or that of the still larger species *A. leenhardti*. The ectepicondylar process is less robust than in *A. leenhardti* or *A. gallicus* and is located farther proximally, being well above the proximal edge of the brachial depression, whereas the ectepicondylar process is located at the level of the proximal end of the brachial depression in *A. gallicus* and *A. broweri* and is somewhat more distal in *A. leenhardti* (Table 1).

FIGURE 3.—Holotype right humeri of *Aegialornis*, anconal views: *a*, *A. wetmorei*, new species; *b*, *A. broweri*, new species. (× 4.)

Aegialornis broweri, new species

FIGURES 3*b*, 4*d*

HOLOTYPE.—Nearly complete right humerus (PM 15481) from the upper Eocene–lower Oligocene Phosphorites du Quercy, France.

MEASUREMENTS OF HOLOTYPE.—Overall length from head to internal condyle 19.1 mm, width and thickness of shaft at midpoint 2.3 × 1.7 mm, greatest width of distal end 4.3 mm, thickness of distal end through external condyle 2.6 mm, thickness through internal condyle 2.7 mm, height of proximal edge of ectepicondylar process above distal edge of ectepicondyle 4.8 mm.

ETYMOLOGY.—This species is named after Dr. Lincoln P. Brower in recognition of his contributions to other fields of biology and also for instilling in me a way of thinking I have tried to follow throughout my career.

DIAGNOSIS AND DESCRIPTION.—The single known humerus of *A. broweri* differs from *A. leenhardti*, *A. gallicus*, and *A. wetmorei* in being smaller, with a proportionately more slender shaft. The ectepicondylar process is more proximally located than in either *A. leenhardti* or *A. gallicus*, but is not as far proximal as in *A. wetmorei*. The brachial depression is less excavated and the muscle attachments of the proximal end are less well defined than in the other species of the genus. The type shows no signs of immaturity and must therefore pertain to an additional small species of *Aegialornis* in this fauna. The lower Eocene species *Primapus lacki* is still smaller, the humerus being little more than two-thirds the length of that of *A. broweri*.

Discussion

It is perhaps surprising that there should be four

such closely related species of *Aegialornis* (Figure 4) in the same fauna. The differences in the position of the ectepicondylar process in these forms, however, make it unlikely that the apparent species limits are simply breaks in a continuum of one or two highly variable or sexually dimorphic species. *Primapus lacki* from the lower Eocene of Britain differs from the four species of *Aegialornis* in being much smaller and in having a slightly bilobed appearance to the bicipital crest and the entepicondyle projecting distally beyond the internal condyle (Harrison and Walker, 1975). The putative swift, *Cypselavus gallicus* Gaillard, from the upper Eocene–lower Oligocene Phosphorites du Quercy, was not examined in this study, but as noted elsewhere (p. 131, herein), it appears from the published illustrations that it may be a small member of the Aegialornithidae, about the same size as *Primapus lacki*. The earliest known modern swift (Apodidae) is *Cypseloides ignotus* (Milne-Edwards) from the lower Miocene (Aquitanian) of France.

The affinity of the Aegialornithidae to the Apodidae and Hemiprocnidae of the suborder Apodi, has been accepted, largely uncritically, since the early suggestions of Milne-Edwards (1892) and Gaillard (1908). This action has recently been endorsed by Harrison (1975) on the basis of a review of the humeri and other referred elements of *Aegialornis gallicus* and *Primapus lacki*. From my study of the referred material of *A. gallicus* I am convinced that the coracoids, the proximal phalanges of digit 2, and the tarsometatarsi belong to species in the orders Charadriiformes and Coraciiformes, and thus cannot be used to elucidate the ordinal affinities of *Aegialornis*. The similarity of some of these elements to those of the Laridae was noted by Lydekker (1891) in the original description of *Aegialornis*. Until it is possible to restudy all of the referred material, it seems wisest to confine discussion of the possible affinities of *Aegialornis* to characters of the humerus, the type-element in all the species of the Aegialornithidae.

The original allocation of *Aegialornis* to a fam-

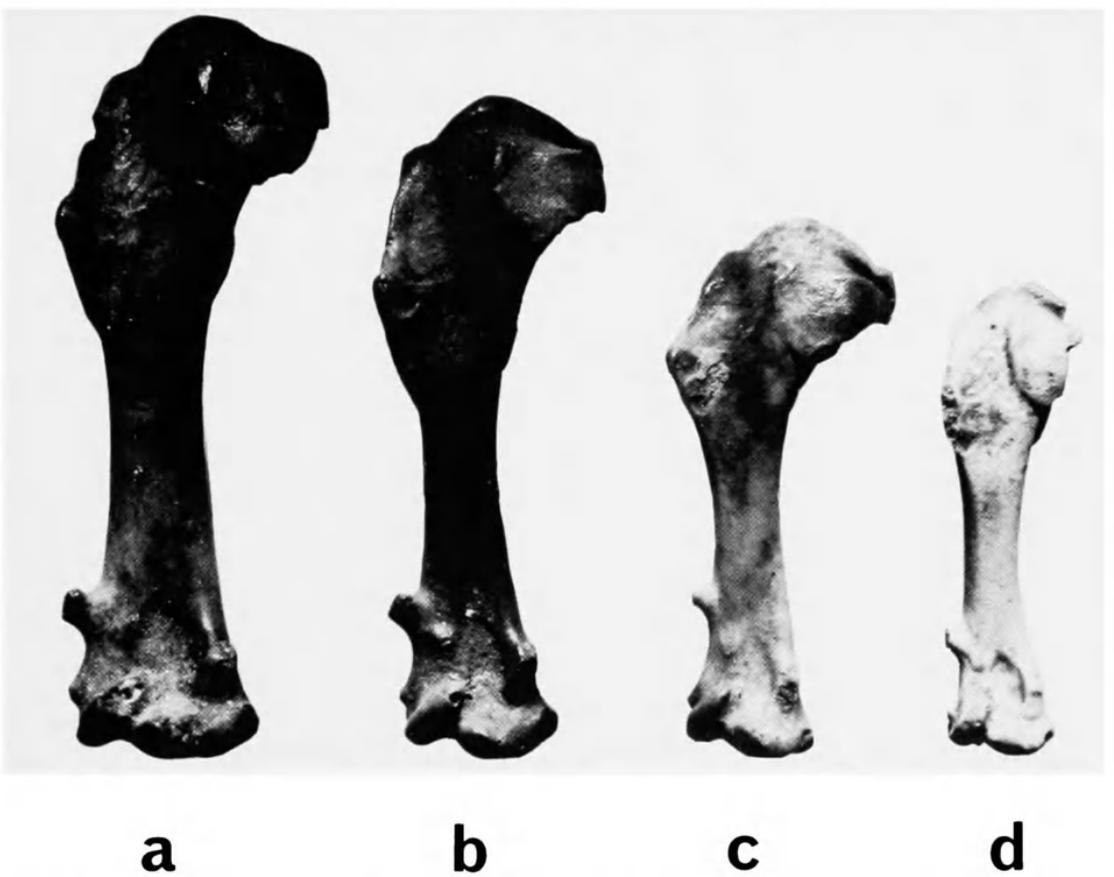

FIGURE 4.—Size comparison of palmar views of right humeri of the four species of *Aegialornis: a, A. leenhardti,* holotype; *b, A. gallicus;* c, *A. wetmorei,* new species, holotype; *d, A. broweri,* new species, holotype. (× 3.)

ily within the Apodi seems to have been based principally on the superficial resemblance of the short and stout humeri to those of the Hemiprocnidae and Apodidae. Harrison (1975) also cites the prominent ectepicondylar process, shorter and more abruptly projecting deltoid crest, less proximally deflected internal tuberosity, and the presence of the distinct flange on the bicipital crest as characteristics shared with the Apodi. Although there are some definite similarities between the humeri of *Aegialornis* and those of the Apodi, particularly *Hemiprocne,* I feel there is a greater resemblance between *Aegialornis* and some members of the Caprimulgidae, particularly *Chordeiles* and related genera (the Chordeilidae of Oberholser, 1914).

In *Aegialornis* the head is deflected anconally and the distal end is directed palmarly. This condition, somewhat accentuated by the longer shaft, is also found in *Chordeiles.* The humerus is notably straight in *Hemiprocne* and the primative swifts of the subfamily Cypseloidinae; only a slight anconal deflection of the head is present in the Apodinae and Chaeturinae. The deep ligamental furrow in *Aegialornis* and *Chordeiles* extends well out onto the internal tuberosity, where it curves to approach the distal margin. In the Apodi the ligamental furrow is shorter and straighter, ending near the proximal base of the internal tuberosity. In *Chordeiles* the internal tuberosity is deflected slightly more proximally at the tip than in *Aegialornis,* and the pnenumatic fossa is more exposed. In the Apodi the internal tuberosity projects laterally or is deflected distally and bears little resemblance to that of *Aegialornis.* A distinct similarity exists between *Aegialornis* and *Chordeiles* in the thickened median crest and broadly excavated capital groove proximal to it. A slight projecting flange on the bicipital crest of *Aegialornis* can also be noted in some specimens of *Chordeiles.* Although this flange is usually much more highly developed in *Aegialornis,* considerable variation is shown in the specimens examined in this study, with some individuals showing only slight development of this feature. The shape of the deltoid crest is very similar in *Chordeiles* and *Aegialornis* and lacks the more abrupt taper and concave proximal edge of the Apodi. The deltoid crest is appreciably different in other genera of the Caprimulgidae (e.g., *Caprimulgus* and *Phalaenoptilus*), which have a more flattened lateral edge and a longer, more gradual slope to the distal edge. Thus, only some of the genera of Caprimulgidae have the "longer and more smoothly rounded" profile of the deltoid crest incorrectly attributed to the entire family by Harrison (1975).

The distal end of the humerus shows many similarities between *Aegialornis, Hemiprocne,* and to a lesser extent *Streptoprocne,* in the flared external tricipital groove and medially expanded entepicondyle. *Aegialornis* and *Chordeiles* are alike in having a broader and more protruding attachment for the anterior articular ligament and a deeper intercondylar groove. A large peglike ectepicondylar process, the single most distinctive characteristic of the humeri of swifts and *Aegialornis,* is accompanied by a distinct, raised lateral muscle scar at its base in *Aegialornis* which is lacking in the Apodi. A small ectepicondylar process and associated muscle scar is also present in *Chordeiles* and, as noted by Harrison (1975), in *Podager.* In the Apodi the ectepicondylar process is never as thickened as in *Aegialornis* and is always substantially more proximally located. In some of the Apodi there is also a secondary process located distal to the ectepicondylar process. This is particularly well developed in the Hemiprocnidae and Cypseloidinae but completely absent in *Aegialornis.* Within the Caprimulgidae there is considerable difference in the appearance of the distal portion of the humerus, as well as in the development of the ectepicondylar process. A strong resemblance to *Aegialornis* can be found in *Chordeiles* and related genera, but not in *Caprimulgus, Phalaenoptilus,* and *Eurostopodus.*

Although the Aegialornithidae show some similarities to the Hemiprocnidae, I feel that the majority of the characters of the humeri indicate a closer relationship with the *Chordeiles* group of the Caprimulgidae. I therefore place the Aegialornithidae as a family within the Caprimulgiformes, possibly allied to the Caprimulgidae.

With the tentative removal of *Cypselavus gallicus* from the Apodidae to the Aegialornithidae, the earliest fossil swifts appear in the lower and middle Miocene deposits of France (p. 131, herein). There is thus no longer any evidence to support the earlier notion that the Apodidae and Aegialornithidae were contemporaneous during the late Eocene or early Oligocene. Therefore, the possi-

bility exists that the Aegialornithidae are representatives of a caprimulgiform lineage that later gave rise to the swifts and crested swifts. Although a close relationship between the Caprimulgiformes and the Apodi is not supported by presently available biochemical information (Sibley and Ahlquist, 1972), neither does this information provide any conclusive evidence of the affinities of swifts to other groups. A caprimulgiform-apodiform relationship should be reviewed further when additional fossil elements are found that can definitely be assigned to the Aegialornithidae.

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