A Review of the Lower Miocene Swifts (Aves: Apodidae)

Charles T. Collins

ABSTRACT

Three nominal species of swifts have been described from lower Miocene (Aquitanian) deposits of France. Re-examination of these forms, *Cypselus* [=*Apus*] *ignotus* Milne-Edwards, *Collocalia incerta* Milne-Edwards, and *Cypselavus intermedius* Gaillard, indicates that they are attributable to a single species, *ignotus,* referable to the modern genus *Cypseloides.* This provides the first occurrence of the Cypseloidinae in the fossil record and indicates a possible origin in the Old World for this primitive group of swifts, presently restricted to the New World.

Introduction

Up to now, five species of fossil swifts have been described, all coming from Tertiary deposits in France. The present paper is aimed at reviewing the three nominal species from deposits of early Miocene age, with comparisons being made with a much wider array of skeletal material of modern swifts than were available to the original describers of the fossil forms. Recent swifts examined in this study included *Cypseloides rutilus, C. cherriei, C. niger,* and *Streptoprocne zonaris* in the Cypseloidinae; from one to several species in the genera *Apus, Aeronautes, Cypsiurus, Tachornis, Reinarda,* and *Panyptila* in the Apodinae; and *Chaetura, Collocalia,* and *Hirundapus* in the Chaeturinae.

ACKNOWLEDGMENTS.—I thank the Frank M. Chapman Memorial Fund of the American Museum of Natural History for support and I am also indebted to Dr. J. P. Lehman of the Institut de Paléontologie, Museum National D'Histoire Naturelle, Paris, for lending the types of *Cypselus ignotus* and *Collocalia incerta.*

Charles T. Collins, Department of Biology, California State University, Long Beach, California 90840.

Family APODIDAE

Subfamily CYPSELOIDINAE

Cypseloides ignotus (Milne-Edwards, 1871)

Cypselus ignotus Milne-Edwards, 1871:394, pl. 177: figs. 9–13.
Apus ignotus.—Paris, 1912:286.
Collocalia incerta Milne-Edwards, 1871:394, pl. 177: figs. 1–8.
Cypselavus intermedius Gaillard, 1939:42, fig. 20.

From the Aquitanian deposits at St.-Gerand-le-Puy, Departement de Allier, France, Milne-Edwards (1871) described a new species of swift, *Cypselus* [=*Apus*] *ignotus.* This was based on a complete right carpometacarpus and a left ulna with the proximal end badly chipped. When I examined these specimens, a second left ulna, excellently preserved, had somehow been associated with the two syntypes. This is identical to the first ulna and I therefore refer it to the species *ignotus* also. From the same deposits, Milne-Edwards (1871) named a second species of swift, *Collocalia incerta,* based on a single well-preserved left tibiotarsus. This was characterized as being much too small to have come from the same species as the wing elements assigned to *Apus ignotus.* Considerably later, Gaillard (1939) reported a left humerus of a swift from Aquitanian deposits at Chavroches, also in the Departement de Allier, which he described as a new species, *intermedius,* in the

Eocene-Oligocene genus *Cypselavus* (Gaillard, 1908).

I have studied the original material of *Apus ignotus* and *Collocalia incerta* as well as Gaillard's (1939) description and illustrations of *Cypselavus intermedius*. While all these fossils clearly belong to the Apodidae, it is equally apparent that none is referable either to *Apus* or to *Collocalia*.

In size and conformation, the two ulnae of *ignotus* (Figure 1*a*) are very similar to those of some of the smaller species of the genus *Cypseloides*. They lack the well-developed olecranal process found in the subfamilies Apodinae and Chaeturinae. This condition is typical of the Cypseloidinae. The fossil ulnae are slightly longer and stockier than the ulnae of *Cypseloides rutilus* or *C. cherriei,* and the prominence for the anterior articular ligament is more shelf-like. Also, the external cotyla appears slightly more undercut at its palmar edge and the distal ligamental attachment of the carpal tuberosity is less laterally flared.

FIGURE 1.—Bones of *Cypseloides ignotus* (Milne-Edwards): *a*, referred left ulna; *b*, syntype right carpometacarpus; *c*, left tibiotarsus (holotype of *Collocalia incerta*), anterior view; *d*, same, posterior view. (Approximately × 3.5, *c* and *d* at slightly different magnifications.)

The carpometacarpus of swifts shows less marked distinctions between the subfamilies than does the ulna. That of *ignotus* (Figure 1*b*) is somewhat longer and stockier than in *Cypseloides rutilus* or *C. cherriei,* but it does have the more widely flared pollical facet of metacarpal I and the more pronounced tendinal groove on metacarpal II typical of the Cypseloidinae. The fossil also has a broader and more flared tuberosity of metacarpal II, providing a wider articular facet for digit II, which is typical of the two smaller species of *Cypseloides* studied, but not of swifts of other subfamilies.

As noted by Milne-Edwards (1871) the tibiotarsus of *Collocalia incerta* (Figure 1*c,d*) is indeed more delicate than would be expected for any member of the Apodinae or Chaeturinae of the size of *Apus ignotus*. However, the tibiotarsus in the Cypseloidinae is proportionately more slender than in the other subfamilies of swifts, particularly the Apodinae. There is, in fact, a very close agreement in overall size and morphology between the type of *Collocalia incerta* and Recent specimens of *Cypseloides rutilus*. The posterior intercondylar groove of *incerta* is not deeply excavated as it is in members of the Apodinae and Chaeturinae, including *Apus* and *Collocalia*. The proximal portion of the shaft is straight, as in *Cypseloides,* and not distinctly bent laterally as typical of many other swifts. The fossil element is slightly smaller and stockier than in *C. rutilus* (*C. cherriei* has a much longer tibiotarsus than *C. rutilus* in spite of its having wing elements similar in size to both *C. rutilus* and *A. ignotus*), and the internal ligamental prominence is less developed but more excavated under the lip of the rotular crest.

The wing elements of *ignotus* are clearly those of a small swift belonging to the genus *Cypseloides*. The tibiotarsus of *incerta* similarly shows affinities to *Cypseloides* particularly to *C. rutilus*. Contrary to Milne-Edwards (1871), it is entirely probable that these fossils, which are from the same locality and horizon, come from the same species. This species should now be known as *Cypseloides ignotus* (Milne-Edwards) with *incerta* becoming a junior synonym, *ignotus* being chosen on the basis of line priority.

In the referred ulna of *Cypseloides ignotus,* the

maximum length is 17.9 mm, distal width 3.2 mm, proximal width 3.7 mm, and shaft width 1.6 mm. No accurate length could be determined for the chipped ulna in which the distal width is 3.2 mm, proximal width 3.7 mm, and shaft width 1.8 mm. The single carpometacarpus measures 16.4 mm in total length, proximal height 5.2 mm, proximal width 2.35 mm, and distal width 3.95 mm. The tibiotarsus has a total length of 21.1 mm, width across condyles 2.2 mm, width across proximal articular surfaces 2.5 mm, and shaft dimensions of 0.9 × 1.0 mm at the narrowest point and 1.0 × 1.5 mm at the middle of the fibular crest.

The type-humerus of *Cypselavus intermedius* Gaillard (1939) was not examined in this study, but from the original figures it appears to have the distinctively longer and narrow proportions characteristic of the species of *Cypseloides*. As was noted by Lowe (1939:324), the ectepicondylar process of *intermedius* is much more distally positioned than in any of the modern forms of the Apodinae or Chaeturinae but is only slightly more distal than in *Cypseloides,* a genus that was not compared by earlier workers. The measurements of the type of *C. intermedius* as given by Gaillard (1939:43) are: total length 11 mm, proximal width 4.5 mm, distal width 3 mm. Thus, this specimen agrees closely in size with specimens of modern *Cypseloides rutilus* and *C. cherriei,* and it would therefore also be of the same approximate size as *C. ignotus*. The type of *Cypselavus intermedius* comes from the same horizon and from a locality close to that of *Cypseloides ignotus*. Since it also appears to belong to the genus *Cypseloides* and is of the same size as *C. ignotus,* I feel that *Cypselavus intermedius* should also be synonymized with *Cypseloides ignotus*. As a result, the genus *Cypselavus* Gaillard is reduced to a single species, *C. gallicus,* from the upper Eocene or lower Oligocene (Phosphorites du Quercy) of France; the genus *Collocalia* is deleted from the fossil record; and the earliest fossil possibly attributable to *Apus* now becomes *Apus gaillardi* (Ennouchi) from the upper middle Miocene (Tortonian) of France (Brodkorb, 1971).

Although the specimens of *Cypselavus gallicus* and *Apus gaillardi* were not examined in this study, the published illustrations are sufficient to determine that neither species shows any similarities to *Cypseloides ignotus* or the modern Cypseloidinae. In fact, *Cypselavus gallicus* shows a distinctly closer resemblance to the Aegialornithidae, the humerus agreeing in size with the newly described small aegialornithid *Primapus lacki,* from the lower Eocene of Britain (Harrison and Walker, 1975). In the published illustrations (Gaillard, 1908), the humerus of *Cypselavus gallicus* appears to lack the prominant ectepicondylar process seen in the Aegialornithidae, but this could well be the result of damage. The illustrations of the humerus of *Apus gaillardi* (Ennouchi, 1930) show it to have the general proportions of the modern Apodidae and Chaeturinae. This species, and an additional swift from the upper Miocene of Italy, are currently under review elsewhere (P. Ballmann, pers. comm.).

The Cypseloidinae (see Brooke, 1970:14–15 for use of this term) appears to be the most primitive subfamily of the Apodidae. It is therefore not unexpected that an extinct species of *Cypseloides* be among the earliest known swifts. Like the vultures of the family Cathartidae [= Vulturidae], the modern species of Cypseloidinae are confined to the New World; but also like the Cathartidae (Cracraft and Rich, 1972), they can now be shown to have had a past distribution and possible origin in the Old World. Further elucidation of the origin and evolution of the Apodidae will have to await a review of additional modern forms and the remaining fossil swifts, as well as the swift-like members of the Aegialornithidae (see Harrison and Walker, 1975; Harrison, 1975, Collins, pp. 121–127, herein).

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