# A REVISION OF THE FOSSIL SWIFTS (VERTEBRATA, AVES, SUBORDER APODI), WITH DESCRIPTIONS OF THREE NEW GENERA AND TWO NEW SPECIES

by

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Humeri are available for all fossil swifts, and other forelimb elements for all but one, making osteological comparisons with other fossil and Recent species possible. Six fossil genera are recognized, humeral diagnoses provided for each, two new genera and species being described - *Eocypselus vincenti* of the Early Eocene and *Scaniacypselus wardi* of the Middle Eocene. In addition a new genus *Procypseloides* is erected for *Cypseloides ignotus*, with which *Cypselavus intermedius* is synonymized. Genera are tentatively assigned to families and subfamilies, new taxa being erected for *Eocypselus* and *Primapus*. The morphological divergencies that characterize the Recent major taxa - Hemiprocnidae, Cypseloidinae and Apodinae - are already apparent in the Eocene swifts.

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## SAMENVATTING

Een revisie van de fossiele gierzwaluwen (Vertebrata, Aves, suborde Apodi), met beschrijvingen van drie nieuwe geslachten en twee nieuwe soorten.

Van alle bekende fossiele gierzwaluwen zijn de opperarmbeenderen beschikbaar en andere vleugelelementen voor alle soorten behalve één, hetgeen osteologische vergelijkingen met andere fossiele en recente soorten mogelijk maakt. Er worden zes fossiele geslachten erkend. Voor elk daarvan worden diagnoses gegeven van de opperarmbeenderen. Twee nieuwe soorten en twee nieuwe geslachten worden beschreven, nl. *Eocypselus vincenti* gen. et sp. nov. uit het Vroeg Eoceen en *Scaniacypselus wardi* gen. et sp. nov. uit het Midden Eoceen. Verder wordt *Procypseloides* gen. nov. beschreven voor de soort *Cypseloides ignotus*, waarmede *Cypselavus intermedius* wordt gesyno-nimiseerd. De geslachten worden voorlopig tot families en subfamilies gerekend, waarbij nieuwe taxa worden opgesteld voor *Eocypselus* en *Primapus*. De morphologische divergenties die de belang-rijkste recente taxa (Hemiprocnidae, Cypseloidinae en Apodinae) karakteriseren zijn al duidelijk aanwezig bij de Eocene gierzwaluwen.

## INTRODUCTION

Bird bones are mostly hollow and fragile and unlikely to survive intact in most of the geological strata that provide palaeontological material. Those that are preserved completely tend to be short, stout and solid. The humeri of Apodiformes possess these useful characters. The hummingbirds and swifts that constitute this order have long slender wings. The latter are formed from long feathers attached to a relatively short bony structure on which strong muscular forces are exerted and which has become modified into a series of short, stout bones. The humerus in particular has changed from the elongated and often slender structure present in most birds to a short, squarish bone in the more highly evolved species.

These humeri are usually small, little more than 10-15 mm long, and may easily be overlooked, but tend to persist relatively intact in fossil deposits. A number of early swift-like birds have been described from such specimens, and since it is usually the humerus that is available it is possible to compare these and to establish some degrees of similarity or divergence which may provide possible clues to affinities and evolutionary trends. Of particular importance are the relative length and stoutness of the shaft, length of the crista pectoralis, and the development of the attachment processes of M. extensor metacarpi radialis and M. tensor propatagialis pars brevis.

Several species of fossil swift were identified from deposits in France during the past century. More recently a species was described from the Early Eocene of south-east England. The discovery of another British Early Eocene species differing from the last and of an additional species from the Middle Eocene of Denmark, has made it possible to provide a broader re-examination of these taxa. Both the last two specimens are humeri with a few associated bones of the pectoral girdle, making a more complete comparison possible.

The present paper identifies and defines the taxa available and attempts to indicate their place within the pattern of evolutionary trends. In doing so it has been necessary to describe two new genera and two new species, provide a new genus for an already-described species and a lectotype for another. In the following descriptions and definitions the various forms within the suborder

Apodi are listed by genus, and the family groupings are introduced only within the subsequent discussions. The terminology used is that of the Nomina Anatomica Avium (Baumel, 1979).

## DIAGNOSES AND DESCRIPTIONS

In this section the diagnoses have been primarily based on the humeri which provide reasonably discrete characters for this purpose.

## Order APODIFORMES, hummingbirds and swifts

These are birds having short, stout humeri with a well-developed process of M. extensor metacarpi radialis proximally elevated on the lateral side of the shaft, and a more distal tubercle of M. tensor propatagialis pars brevis often apparent and showing the same tendency to proximal elevation.

Some of the earlier fossil forms show similarities in some characters of the humerus to those of the nightjars (Caprimulgiformes). Collins (1976a) in studying the humeri of the more divergent species of the Eocene/Oligocene genus *Aegialornis* referred them to the Caprimulgiformes, and influenced Brodkorb (1971) in this respect, although this has not been subsequently accepted (Harrison, 1975; Mourer-Chauviré, 1978). Collins cited nightjars of the genus *Chordeiles* as providing evidence of affinity. With the humerus of a very early, generalised species *Eocypselus vincenti* (fig. 1E) now available it is possible to compare the most generalised and most derived forms of swifts with nightjars such as the recent common nighthawk *Chordeiles minor* (fig. 1A).

In general nightjar humeri are larger and more slender than those of swifts. In swift humeri of the more slender type there is a tendency towards a ventral (medial) arching of the whole distal end. One nightjar family, the owlet-frogmouths (Aegothaledidae) show a superficially similar displacement but this is achieved by a distinct medial bend of the shaft, and in most nightjars the proximal head is aligned with the shaft. The caudally-curving arch of the crista bicipitalis and tuberculum ventrale over the pneumotricipital fossa is more distal in the swifts and the bicipital area more caudoventrally curved. The main cranial projection of the crista pectoralis is more distally sited in nightjars. The tuberculum dorsale is small and proximally sited, whereas those of swifts, although variable, are much larger, distally elongated and caudally tilted. The distal end of the humerus is broad in swifts, and even more so in hummingbirds, but in nightjars it is narrower, with a smaller and more deeply defined and proximally placed M. brachialis fossa. In the latter the condylus ventralis is more rounded and the fossa olecrani less deep and more ventrally placed, and in addition the processus flexorius is a simple caudal projection and is not dorsocaudally elongated as in the swifts. Although *Chordeiles* shows papillae for both M. extensor metacarpi radialis and M. tensor propatagialis pars brevis, these are tiny and distally sited on the lateral side near the distal end.

Although some general osteological similarities may justify Collins's (1976a) suggestion that nightjars and swifts have some affinity and possibly a common evolutionary origin later than that of other ordinal taxa, the structures present show sufficient characters to maintain the separation of the taxa involved.
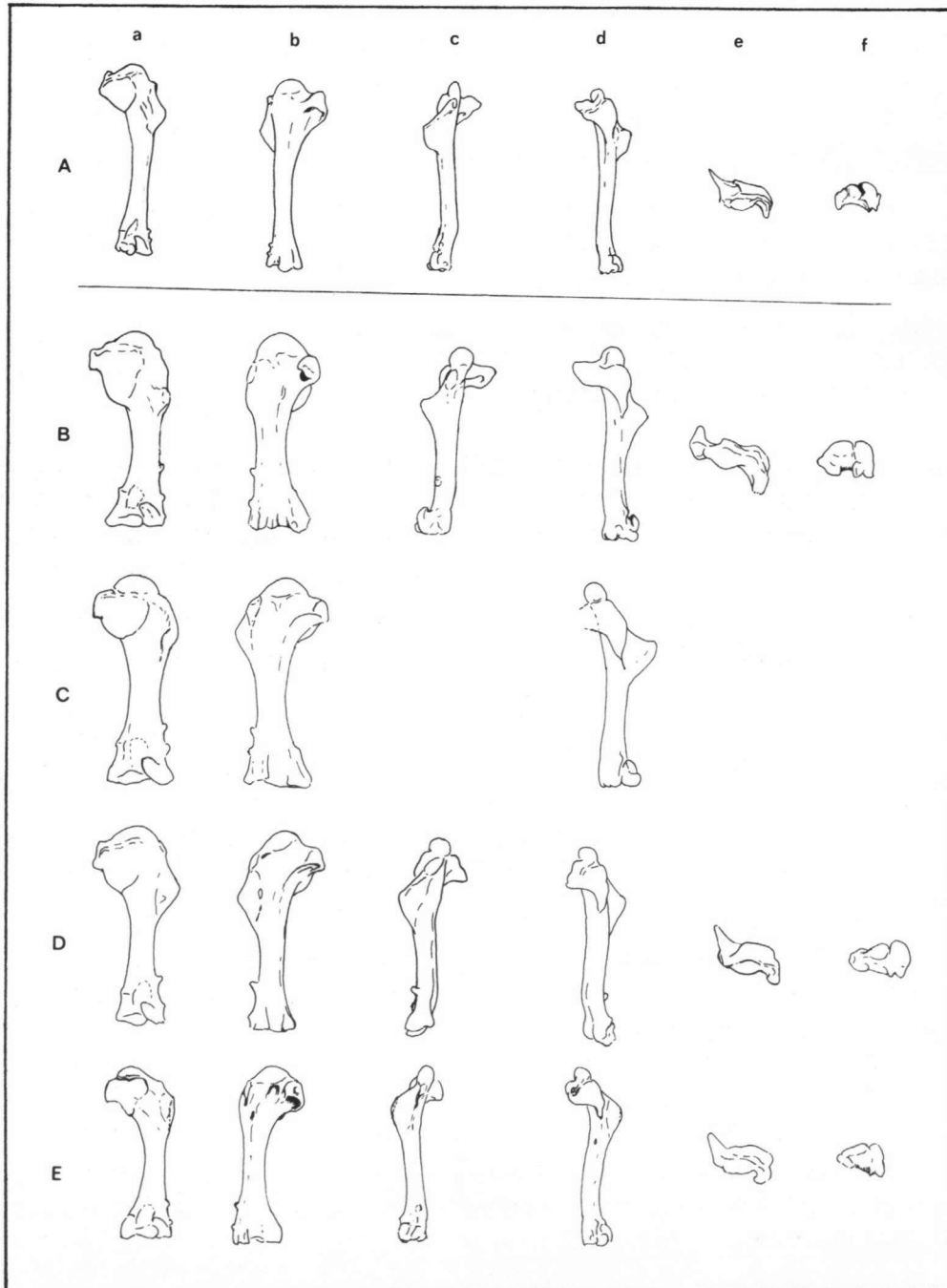
Fig. 1. Left humeri, standardized for comparison.
   The first is a nightjar (Caprimulgiformes), the others are swifts (Apodiformes).
   Views (left to right): a = cranial, b = caudal, c = lateral, d = medial, e = proximal, f = distal.
   A. Common nighthawk, *Chordeiles minor*, Recent; x 2/3.
   B. Lesser treeswift, *Hemiprocne comata*, Recent; x 2.
   C. *Cypselavus gallicus*, Late Eocene/Early Oligocene (after Mourer-Chauviré, 1978); x 2¼.
   D. *Aegialornis gallicus*, Late Eocene/Early Oligocene; x 1.
   E. *Eocypselus vincenti*, Early Eocene, holotype; x 2.

Suborder TROCHILI, hummingbirds

These are small to tiny birds, with the humerus very short and broad, the distal end comparable in width with the proximal end, the shaft forming only about a third of the total length, and a large, broad-ended process of M. extensor metacarpi radialis about halfway along the total length of the bone, or nearer the proximal end.

From their present-day distribution and adaptations it is suspected that the hummingbirds evolved in South America, extending subsequently to Central and North America. Although by extrapolation from the evidence of swift evolution they are likely to have existed as a separate group since Late Cretaceous to Early Tertiary times. There is no fossil evidence available at present to support general hypotheses.

Suborder APODI, swifts

These are mostly small and have short, stout humeri. The distal end of the humerus is broad with a deep fossa olecrani, but much narrower than the proximal end. The shaft forms about two-thirds or a little over half the total length. The process of the M. extensor metacarpi radialis is well-developed, but more variable in size and siting.

There is a gradation from the humeri of tree swifts, Hemiprocnidae (fig. 1B-E), with the M. extensor metacarpi radialis and M. tensor propatagialis brevis processes apparent on the lower half of the length, through the Cypseloidinae (fig. 2B-C) to the Chaeturinae and Apodinae (fig. 2A, 2D, 7) in the true swifts Apodidae in which the shaft becomes progressively and dramatically shorter and stouter, while the M. extensor metacarpi radialis process shifts proximally to end just behind the distal edge of the crista bicipitalis. During these changes other forelimb bones are similarly modified, tending to become short and stout. In particular the ulnae become short, straight and thick (figs. 3-4).

Genera included in this study

Although all the fossil genera are included, only the three key recent genera have been added to provide a basis for comparison, a number of small genera within the subfamilies listed above being omitted.

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Genus Eocypselus gen. nov.
Figs 1E, 3E, 5

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*Etymology* – The name is derived from the original generic name for the swifts, *Cypselus*, here used in its broad sense, and the Latin *eous* (= of the dawn). It is masculine.

*Age* – Early Eocene.

*Diagnosis* – Small, the humerus similar in length to that of the lesser tree swift, *Hemiprocne comata*. Humerus with slender shaft; proximally and ventrally arched, distal end dorsoventrally broad, a little over two-thirds the width of the proximal end, with a marked ventral extension. In distal view, condylus dorsalis caudocranially deep and dorsally flattened. Fossa olecrani deep and rounded.

Distal end of processus flexorus dorsocaudally elongated. In cranial view, fossa M. brachialis broad and large, tuberculum supracondylare ventrale present as a short ridge ventral to the fossa and at a level about halfway along its length. Dorsally a small but prominent rounded papilla of the M. extensor metacarpi radialis process at a level slightly proximal to the fossa M. brachialis, and a smaller tubercle of M. tensor propatagialis pars brevis level with the condylus ventralis. Caput humeri proximodistally deep on the caudal surface but caudocranially narrow. Tuberculum ventrale projects caudally with deep, thin-walled fossa pneumotricipitalis on the distal side, and bears small attachment fossae caudally and dorsally. Small secondary fossa dorsal to this at distal end of incisura capitalis. Well-marked scar of lig. triceps scapularis present on caudal ridge. Crista pectoralis angled sharply towards cranial side. Tuberculum dorsale elongated distally onto narrow caudal ridge of crista. Cranial side of crista pectoralis bordered by broad shallow fossa. Deep sulcus ligamentosus traversus below caput curves caudally towards tuberculum ventrale. Bicipital intumescentum large, caudally curved, with prominent proximal edge; but dorsal edge poorly defined. A narrow, distally-projecting lobe borders shaft, barely apparent in caudal view.

Coracoid slender and straight, long relative to humerus, 90% length of latter. Processus coracoideus prominent, similar in mediolateral width to shaft; elongated, about 26% of total length of bone; and with slight ventral curvature. Sulcus M. supercoracoideus short and rounded. Cotyla scapularis small and laterally sited on dorsal side. Facies articularis humeralis laterally directed. Acrocoracoidal head only slightly arched medially, in medial view aligned with shaft, and cranially peaked. At the sternal end, processus lateralis tapers to small sternal projection. Facies articularis sternalis mainly towards the medial side; deep and dorsoventrally broad.

Radius straight; distal end slightly expanded with a small caudal concavity. Ulna straight and slender. Olecranon low but prominent; towards ventral side and with hollow of sulcus tendineus caudodistally distinct. Cotyla dorsalis ventrocranially elongated, dorsal edge forming projecting flange, with small ridge curving to shaft at cranial end. Cotyla ventralis more distally raised and central, with tuberculum ligamentosus collateralis ventralis well-developed, proximally sited and midway along the ventral edge of the cotyla. A tiny prominence on mid-distal edge of cotyla ventralis, at junction with a poorly-defined linea intermuscularis.

*Type species – Eocypselus vincenti* sp. nov. (monotypic).

## Eocypselus vincenti sp. nov.
### Figs 1E, 3E, 5

*Etymology* – The species is named after Mr S. Vincent who collected and presented this and other specimens.

*Diagnosis* – The only known species of the genus. Characters those of genus.

*Material* – Holotype, associated left humerus, incomplete right humerus, left coracoid, incomplete left ulna, left radius; BMNH A 5429, collected and presented by S. Vincent (his no. 0008977), 1977.

*Occurrence* – Division A, London Clay, Early Eocene (Ypresian); Walton-on-the-Naze, Essex, England.

## Genus Aegialornis Lydekker, 1891
### Figs 1D, 3D

*Age* – Late Eocene/Oligocene.

*Humeral diagnosis* – Large, humerus more than twice the length of that of most other fossil species. Shaft narrow. Crista pectoralis a thin flange, thickened along proximal edge. Incisura capitis broad and shallow. Tuberculum ventrale well-developed and caudally directed, with large fossa pneumotricipitalis in its distal surface. Caput humeri craniocaudally narrow, and tuberculum dorsale articulation distodorsally elongated and mainly dorsal. Sulcus ligamentosus transversus deep, curving distally at ventral end. Intumescentum bicipitalis with poorly-defined dorsal margin, distally broad and rounded, and caudally visible as a rounded flange distal to fossa pneumotricipitalis. Processus M. extensor metacarpi radialis large, rounded and prominent, on cranial margin of dorsal side, a little proximal in position to that of *Eocypselus vincenti*, but tubercle of M. tensor propatagialis pars brevis in similar position to that of latter, level with condylus dorsalis. Fossa M. brachialis large and at centre of cranial surface. Tuberculum supracondylare ventrale large and cranially prominent, at a level halfway along fossa M. brachialis. Epicondylus ventralis not ventrally prominent; condylus ventralis narrow and transverse; condylus dorsalis distally large, cranially and dorsally prominent.

*Type-species* – *Aegialornis gallicus* Lydekker, 1891.

## Aegialornis gallicus Lydekker, 1891
### Figs 1D, 3D

*Material* – The material on which Lydekker based his description included thirteen humeri, three ulnae, eleven metacarpi, three phalanges and two coracoids, from the phosphates of Bach, near Lalbenque, Lot (France); in the collection of the British Museum (Natural History). The right humerus figured by him, BMNH A60, is here selected as the lectotype of the species.

*Comments* – The structure of the humerus is similar in all four species of the genus, but the processus M. extensor metacarpi radialis is more proximally sited in *A. wetmorei* Collins, 1976.

## Genus Cypselavus Gaillard, 1908
### Figs 1C, 3C

*Age* – Late Eocene/Oligocene.

*Humeral diagnosis* – Humerus with shaft narrow, but stouter than those of *Eocypselus* and *Aegialornis*. Crista pectoralis directed cranially, with distal half projecting strongly. Tuberculum dorsale large and distally elongated, on ridge formed by angle of crista and caudal surface. Tuberculum ventrale well-developed, arching caudoventrally, with large fossa pneumotricipitalis. Intumescentum bicipitalis rounded, distally short, with well-defined dorsal margin. Distal end broad, ventral side of shaft curving to a projecting epicondylus ventralis with a proximally raised tuberculum supracondylare ventrale. Processus M. extensor metacarpi radialis prominent and rounded, on dorsal surface, a little more proximally sited than in *Aegialornis*, but a little less than in *Hemiprocne*. Tubercle M. tensor propatagialis pars brevis also more proximal, only a little distal to the process.

*Type species* – *Cypselavus gallicus* Gaillard, 1908 (monotypic).

*Cypselavus gallicus* Gaillard, 1908
Figs 1B, 3B

*Material* – Holotype an imperfect humerus. Further humeri and other bones have been assigned to the species by Mourer-Chauviré (1978).

Genus **Hemiprocne** Nitzsch, 1829
Figs 1B, 3B

*Age* – Recent.

*Humeral diagnosis* – Humerus with shaft narrow. Crista pectoralis directed cranially; distal half projecting, but less than in *Cypselavus*. Tuberculum dorsale rounded but distally elongated, on ridge of crista and caudal surface. Tuberculum ventrale less ventrally arching, strongly deflected caudally and dorsally tilted; with fossa pneumotricipitalis excavating distodorsal surface and having pneumatic foramen at shaft end. Caput humeri broad. Intumescentum bicipitale distally elongated, with elongated edge visible in caudal view. Distal end broad, ventral side of shaft curving to a bluntly-projecting epicondylus ventralis. Fossa olecrani deep. Processus M. extensor metacarpi radialis a little more proximal than that of *Cypselavus*, and in *Hemiprocne comata* much more proximal than in *H. longipennis*; on the dorsal side, towards the cranial edge. Tubercle M. tensor propatagialis pars brevis of *H. comata* more distal than that of *Cypselavus*, but in *H. longipennis* much more proximal and nearer processus.

*Type species* – *Hemiprocne longipennis* Rafinesque, 1802.

Genus **Primapus** Harrison & Walker, 1975
Fig. 2E

*Age* – Early Eocene.

*Emended diagnosis* – Humerus small. Shaft stout, distal end large and slightly deflected cranially; proximal end deflected caudally. Crista pectoralis dorsoventrally stout with cranial and slightly dorsal projection. Proximal edge thick. Tuberculum dorsale distodorsally elongated with facet caudally directed. Incisura capitis broad. Tuberculum ventrale arches ventrocaudally, with deep rounded fossa pneumotricipitalis on distal surface. Intumescentum bicipitale broad, with well-defined dorsal edge; and with rounded distal projection forming a rounded flange in caudal view. Large, peg-like processus M. extensor metacarpi radialis proximodorsally projecting on dorsal side of shaft, at about a quarter of total length from distal end. Shaft distally widening, with epicondylus ventralis projecting ventrally and distally. Condylus dorsalis rounded.

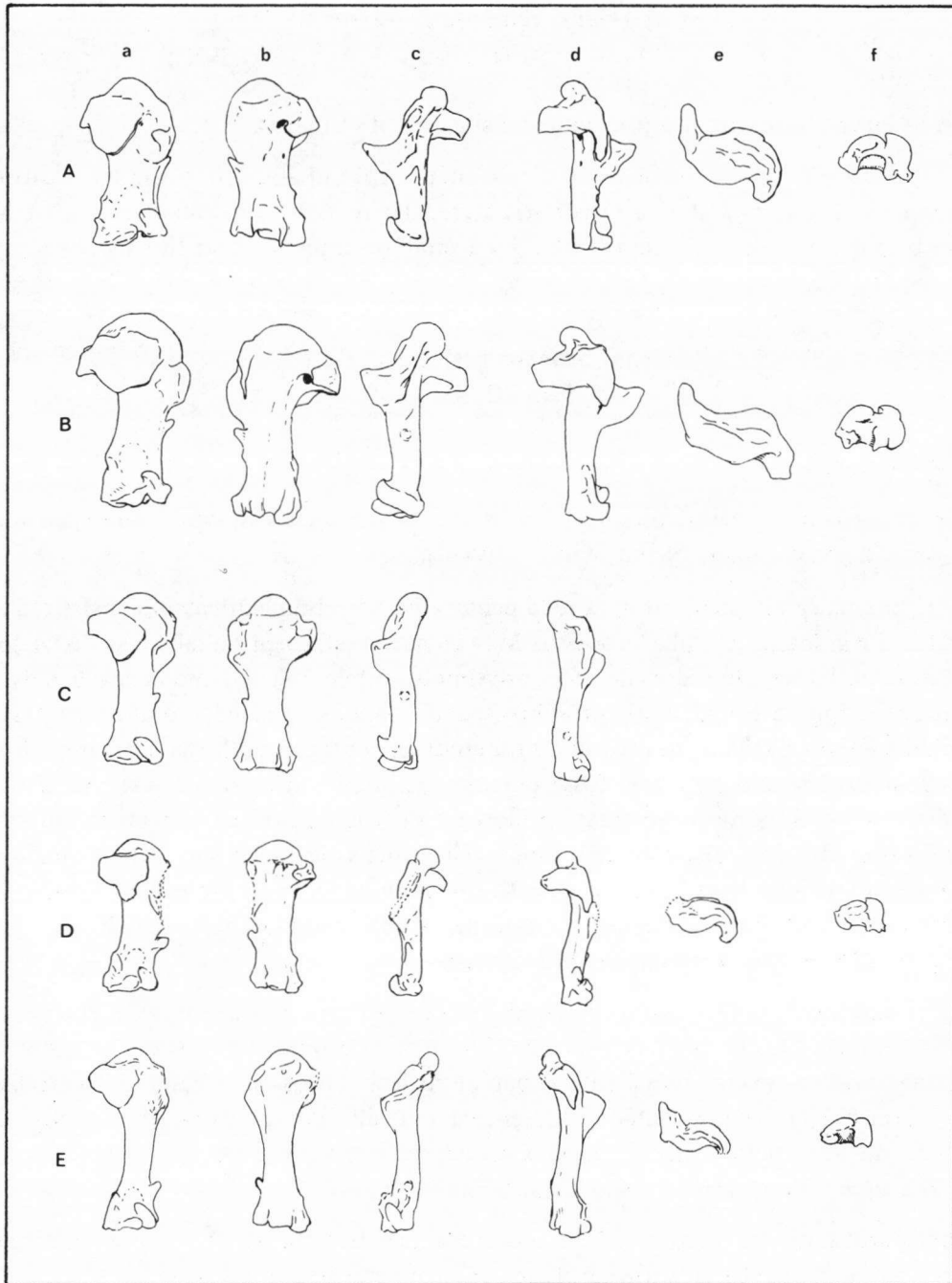*Type species* – *Primapus lacki* Harrison & Walker, 1975 (monotypic).

Fig. 2.  Left humeri, standardized for comparison.

Typical swifts.

Views (left to right): a = cranial, b = caudal, c = lateral, d = medial, e = proximal, f = distal.

A. Common swift, *Apus apus*, Recent; x 2.

B. Black swift, *Cypseloides niger*, Recent; x 2.

C. *Procypseloides ignotus* (previously *Cypselavus intermedius*), Late Oligocene/Early Miocene; x 2¼.

D. *Scaniacypselus wardi*, Middle Eocene, holotype; x 2.

E. *Primapus lacki*, Early Eocene, holotype; x 2.

## Primapus lacki Harrison & Walker, 1975
## Fig. 2E

*Material* – A holotype humerus and paratypical distal end of humerus.

*Comments* – Although the processus M. extensor metacarpi radialis is in a similar position on the shaft to those of *Aegialornis* it is a larger structure. There is no obvious tubercle of M. tensor propatagialis pars brevis unless it is represented by a small prominence near the distal end.

## Genus Scaniacypselus gen. nov.
## Figs 2D, 4D, 6

*Age* – Middle Eocene.

*Etymology* – The name is based on the Latin name of the region in which the type species was found, and the old generic name of the swifts, *Cypselus*.

*Diagnosis* – Humerus small, shaft stout. Crista pectoralis extending halfway along shaft, and basally thick in width. Prominent, peg-like processus M. extensor metacarpi radialis just distal to the end of crista pectoralis. Tuberculum dorsale facet proximodistally elongated and caudodistally directed. Intumescentum bicipitale broad, with prominent and abrupt dorsal edge and narrow distal lobe. Crista bicipitalis curves caudally to projecting tuberculum ventralae with two attachment pits on its flattened caudal surface and a narrow fossa pneumotricipitalis on its distal side. As in *Eocypselus vincenti* there is a small, shallow secondary hollow on the caudal surface, ventral to the tuberculum ventrale projection and just distal to the caput. The sulcus ligamentosus transversus is deep and narrow, and the caput stout. Distal end broad, with epicondylus ventralis projecting distally. Condylus ventralis transverse and narrow, condylus dorsalis stout, caudocranially thick and proximally curved, the craniodorsal edge forming an abrupt ridge.

Ulna short and stout, longer and more slender than in Recent Apodinae, with the proximal end more cranially curved. Olecranon very short and blunt, with proximal sulcus tendineus well-marked and the cotylae with a strong cranial tilt. Tuberculum ligamentosum collateralis ventralis projects cranially to form a deep hollow distal to the cotyla ventralis. At the distal end, condylus dorsalis projects more distally than other structures, condylus ventralis does not have well-developed projection, and tuberculum carpale is short and blunt.

Carpometacarpus similar to that of Recent Apodinae but the shaft of os metacarpale majus tends to taper towards distal end, showing strong anteroposterior compression.

*Type species* – *Scaniacypselus wardi* sp. nov. (monotypic).

## Scaniacypselus wardi sp. nov.
## Figs 2D, 4D, 6

*Etymology* – The species is named after David J. Ward, who collected and presented the specimen.

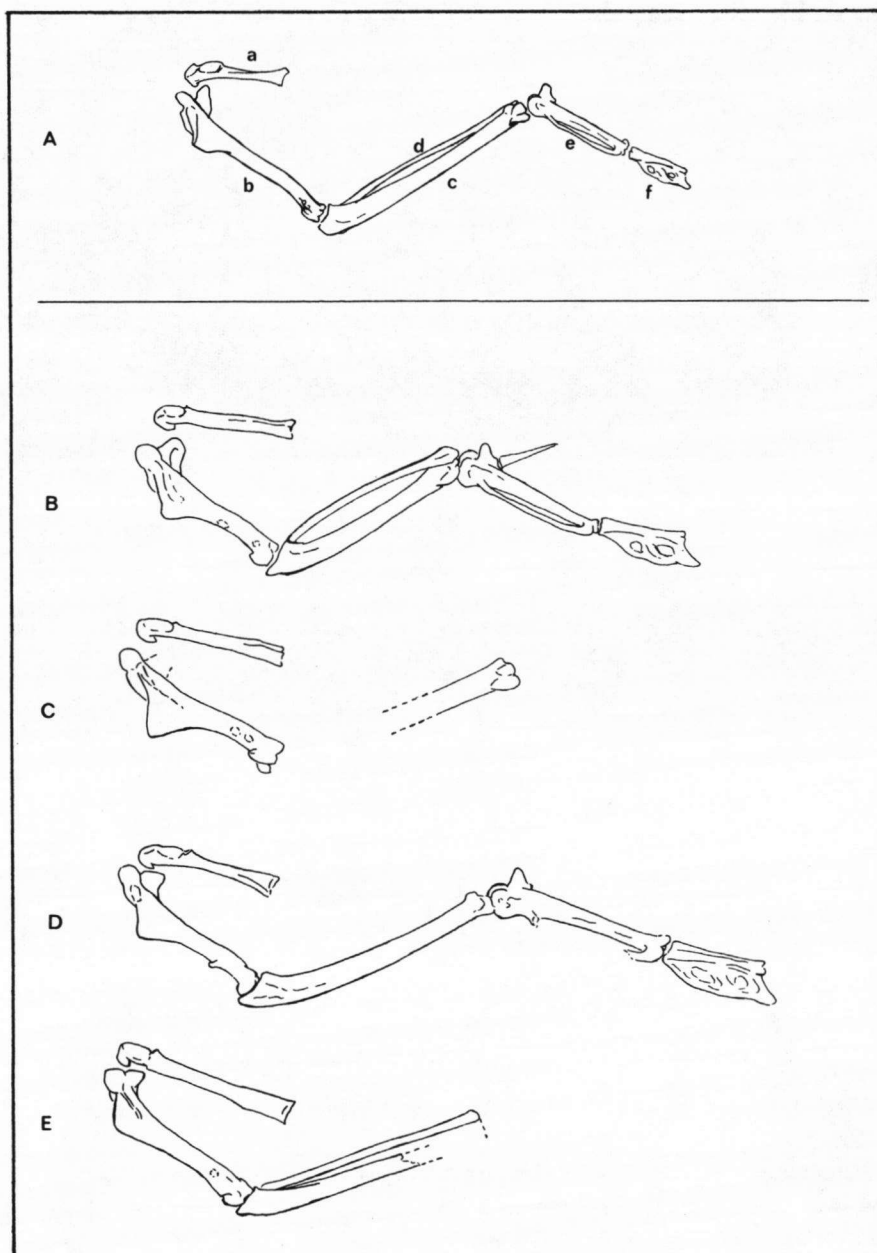*Diagnosis* – The only known species of its genus. Characters those of the genus.

Fig. 3. Bones of left wing, standardized for comparison, not as articulated.
The first is a nightjar (Caprimulgiformes), the others are swifts (Apodiformes).
Bones: a = coracoid, b = humerus, c = ulna, d = radius, e = carpometacarpus, f = metacarpal.
A. Common nighthawk, *Chordeiles minor*, Recent; appr. x 2/3.
B. Lesser treeswift, *Hemiprocne comata*, Recent; appr. x 5/3.
C. *Cypselavus gallicus*, Late Eocene/Early Oligocene (after Mourer-Chauviré, 1978); appr. x 2.
D. *Aegialornis gallicus*, Late Eocene/Early Oligocene; appr. x 5/6.
E. *Eocypselus vincenti*, Early Eocene, holotype; x 2.

*Material* – Holotype: associated left humerus, left ulna, left carpometacarpus and alular phalanx, BMNH A5430; collected and presented by Mr D. J. Ward, April 1981.

*Occurrence* – Bed R6, Røsnaes Clay, Middle Eocene. Ølst, Jutland, Denmark.
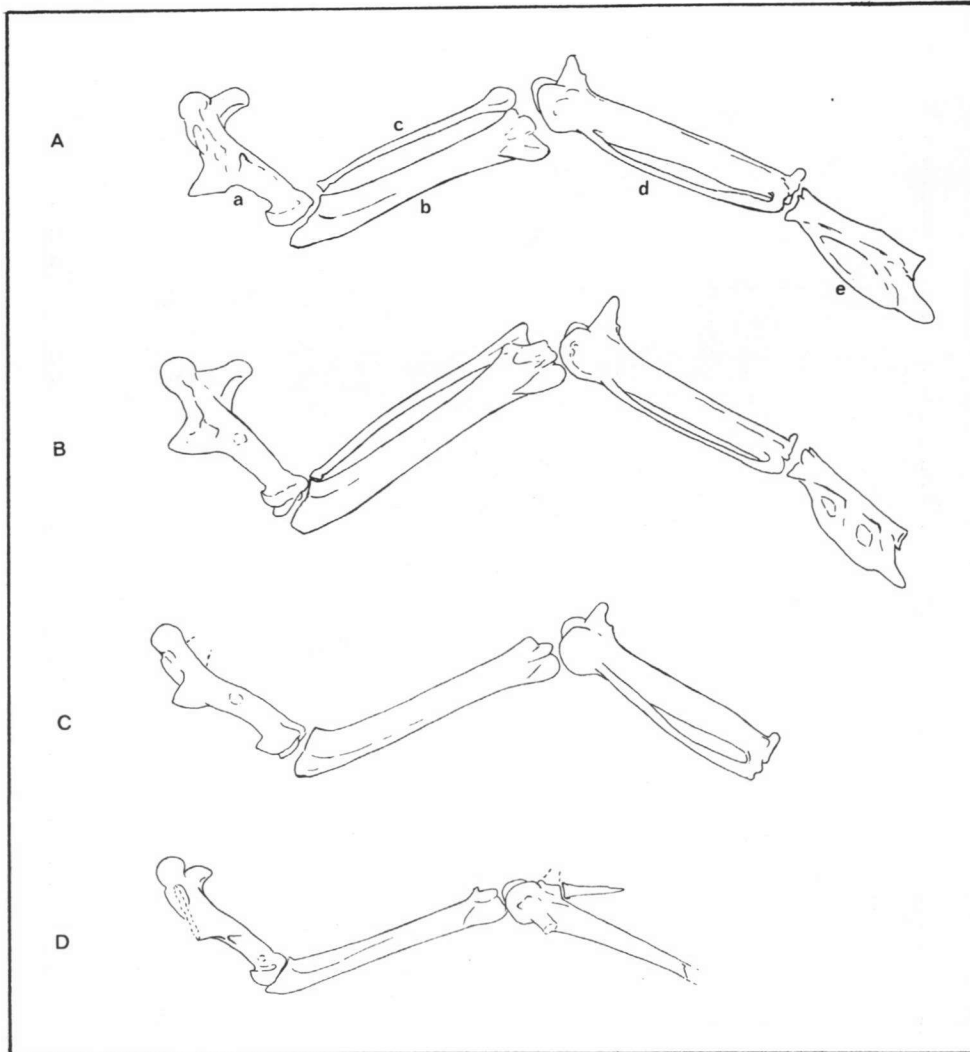
Fig. 4. Bones of left wing, standardized for comparison, not as articulated.
Typical swifts.
Bones: a = humerus, b = ulna, c = radius, d = carpometacarpus, e = metacarpal.
A. Common swift, *Apus apus*, Recent; appr. x 1 5/6.
B. Black swift, *Cypseloides minor*, Recent; appr. x 1 5/6.
C. *Procypseloides ignotus* (combining *Cypselavus intermedius*, humerus, *Apus ignota*, ulna and carpometa-carpus; after Collins, 1976), Late Oligocene/Early Miocene; x 2¼.
D. *Scaniacypselus wardi*, Middle Eocene, holotype; x 2.

## Genus Procypseloides gen. nov.
### Figs 2C, 4C

*Age* – Early Miocene.

*Etymology* – The generic name refers to the fact that the specimens assigned here were shown by Collins (1976) to be closest to the Recent genus *Cypseloides* but appear to show a reasonable degree of differentiation attributable to the earlier origin.

*Diagnosis* – Small swift with carpometacarpus similar to Recent *Cypseloides* species but larger and stouter. Os metacarpale minus more notched at distal end. Processus extensorius less prominent. Ulna short and stout. Tuberculum ligamentosus collateralis ventralis well-developed and ventrally prominent, with well-marked depressus M. brachialis; more similar to that of *Scaniacypselus*. Distal end with well-developed condylus ventralis.

*Humeral diagnosis* – (based on specimen previously the type of *Cypselavus intermedius*). Shaft straight and moderately stout. Distal end wide and proximal head large. Processus M. extensor metacarpi radialis projects dorsally on the shaft more than halfway from distal end but with distinct gap before the distal end of crista pectoralis. Tubercle of M. tensor propatagialis pars brevis not apparent. Small ventral projection of tuberculum supracondylare ventrale occurs more than one-third of the length of shaft from distal end. Intumescentum bicipitale broad, tapering to distal lobe, with well-defined dorsal edges. It narrows towards a medially-projecting crista bicipitalis and tuber-culum ventrale, with little evidence of caudal curvature and a poorly developed fossa pneumo-tricipitalis. Caput thick, short and rounded. Crista pectoralis blunt and cranially-projecting, with thickened proximal edge. Tuberculum dorsale rounded and proximocaudally directed. Processus flexorius of epicondylus ventralis only slightly prominent distally. Condylus dorsalis narrow and elongated, projecting abruptly at proximal end. Condylus ventralis narrow and transverse.

*Type species – Procypseloides ignotus* (Milne-Edwards, 1871).

## Procypseloides ignotus (Milne-Edwards, 1871)
### Figs 2C, 4C

*Synonyms – Cypselus ignotus* Milne-Edwards, 1871; *Collocalia incerta* Milne-Edwards, 1871; *Cypselavus intermedius* Gaillard, 1938; *Cypseloides ignotus* Collins, 1976.

*Material* – A new generic name is provided here for *Cypseloides ignotus* of Collins (1976b). The original species *Cypselus ignotus* Milne-Edwards, 1871 was described from a carpometacarpus and an ulna from the Aquitainian deposits of Allier, France. From the same deposits a cave-swift, *Collocalia incerta* Milne-Edwards, 1871, was described from a tibiotarsus, and another swift, *Cypselavus intermedius* Gaillard, 1938, from a humerus. The last was assigned to an already described genus of fossil swifts, *Cypselavus* Gaillard, 1908.

Collins (1976b) decided that all three were referable to a single species. On the characters of the carpometacarpus, ulna and tibiotarsus he regarded it as similar to the New World swifts of the genus *Cypseloides* and assigned it to that genus. In view of the differences now apparent I have created a new genus for it.

The material is a syntypical right carpometacarpus and a left ulna, previously syntypes of *Cypselus ignotus* Milne-Edwards, 1871, at the Institut de Paléontologie, Museum Nationale d'Histoire Naturelle, Paris. Tentatively referred specimens are a left ulna, and a left tibiotarsus previously the holotype of *Collocalia incerta* Milne-Edwards, 1871, both at the above museum; and a left humerus, previously the holotype of *Cypselavus intermedius* Gaillard, 1938, in the Museum of the Faculté des Sciences de Lyon.

## Genus Cypseloides Streubel, 1848
### Figs 2B, 4B

*Age* – Recent.

– Shaft straight and stout, dorsoventrally broad. Processus M. extensor metacarpi radialis prominent, projecting dorsally only a little distal to the distal end of the crista pectoralis. A slight prominence of the M. tensor propatagialis pars brevis occurs only a little distal to it. Ridge of tuberculum supracondylare ventrale prominent on the ventral side of the shaft. Crista pectoralis proximodistally narrow and prominent, tapering a little towards the proximal edge; and dorso-ventrally stout. It projects cranially, the caudal angle with the shaft marked by a distally-tapering ridge. Caput thick, and ventrally elongated. Intumescentum bicipitale large and broad but not distally prominent, and with dorsodistal edge well-defined. Crista bicipitalis curves caudally to a very prominent tuberculum dorsale, undercut distally with an elongated fossa pneumotricipitalis with a caudally-visible foramen towards the ventral side. Distal end only a little broader than shaft, with a dorsally-projecting epicondylus dorsalis. Fossa olecrani deep and narrow; caudal surface of the dorsal side width with a distinct sulcus M. scopulotricipitalis. Condylus dorsalis stout, with the articulating surface abruptly bordered by distinct ridges.

*Type species* – *Cypseloides fumigatus* (Streubel, 1848).

## Genus Apus Scopoli, 1777
### Figs 2A, 4A, 7

*Age* – Miocene to Recent.

*Humeral diagnosis* – Shaft straight and very stout, dorsoventrally almost as broad as distal end of bone. Shaft length to distal end of crista pectoralis only about half the total length of humerus. Processus M. extensor metacarpi radialis proximally sited, just distal to distal edge of crista pecto-ralis, tapering, and with proximal edge basally caudal to crista edge. Prominence for M. tensor propatagialis pars brevis not apparent. Crista pectoralis cranially prominent and proximodistally narrow, tapering to proximal edge. Proximal edge of crista thick, forming dorsal ridge back to dorsocaudal edge. Tuberculum dorsale rounded and dorsally sited. Intumescentum bicipitale broad and distally elongated, with distinct distodorsal edge. Crista bicipitalis curves strongly to caudal tuberculum ventrale projection, making the proximal head of the bone dorsoventrally narrower than in other species. Fossa pneumotricipitalis on distodorsal side of caudal projection of tuberculum ventrale, with foramen visible internally towards dorsal side. Caput humeri dorsoventrally short and caudally tilted. Two attachment prominences apparent on the ventrocranial edge towards the distal end. Epicondylus ventralis distally prominent. Fossa olecrani broad and deep. Condylus ventralis narrow and transverse, comdylus dorsalis short.

*Type species* – *Apus apus* (Linnaeus, 1758).

## FAMILIES AND SUBFAMILIES

The suborder Apodi at present consists of two Recent families, the treeswifts or crested swifts, Hemiprocnidae, and the typical swifts, Apodidae; although Brodkorb (1971) has treated the former

as a subfamily of the latter. The Apodidae may be subdivided into the New World swifts, Cypseloidinae, and typical swifts, Apodinae; the latter often divided further to recognise the spine-tailed swifts, Chaeturinae, as an additional taxon.

In studying forelimb bones there is little difficulty in recognising the Hemiprocnidae. The humerus has a relatively long and slender shaft with prominences for both M. extensor metacarpi radialis and M. tensor propatagialis pars brevis apparent towards the distal end of the bone. The crista pectoralis is thin. The ulna is slender and distinctly longer than the carpometacarpus, the latter with the os metacarpale majus tapering towards the distal end.

The Apodidae have a short, stout humerus with a thick shaft. The prominence for M. tensor attachment is sometimes apparently absent. The process for M. extensor is large, well-developed and shows a progressively proximal shift on the shaft. The crista pectoralis is stout, with a thickened proximal edge. The ulna is short and stout, only a little longer than the carpometacarpus, and the latter does not show the pronounced distal taper.

Within the Apodidae the Cypseloidinae can be separated as having humeri with the distal end and shaft occupying more than half the total length, and a distinct gap on the shaft between the distal edge of the crista pectoralis and the M. extensor process. A small attachment point of the M. tensor is present on the shaft a little distal to the last.

The Apodinae have humeri with the distal end and shaft a little less than half the total length and the M. extensor process at the distal edge of the crista pectoralis. *Apus apus* shows no obvious evidence of the presence of an M. tensor propatagialis pars brevis attachment, but on two specimens of *Apus melba* (Linnaeus, 1758) which were examined there is a tiny projection on the shaft aligned with the distal end of the base of the M. extensor process and about halfway between the latter and the epicondylus dorsalis. A specimen of *Apus aequatorialis* (von Müller, 1851) shows a similar tiny prominence, slightly more proximal in position.

The Chaeturinae are difficult to separate from the Apodinae on the basis of the humerus. According to Zuzi & Bentz (1982) there is a minute projection of the M. tensor attachment on the base of the M. extensor process on the humerus of *Hirundapus caudacutus* (Latham, 1801). There appears to be no evidence of this on the humerus of *Chaetura pelagica* (Linnaeus, 1758) which is almost indistinguishable in proportions from that of *Apus apus*. The humerus may not be a useful character for separation in this instance, but in *C. pelagica* the ulna is very short, only 80-83% of the length of the carpometacarpus, compared with 90-99% in *Apus* species. If the character is consistent it would appear useful in separating the two subfamilies osteologically and suggest that, at least in the structure of the forelimb, the Chaeturinae may be further derived than the Apodinae.

The longer, more slender forelimb bones appear to be a primitive, more generalised character of the Apodiformes, comparable with those of such orders as the Caprimulgiformes (fig. 3). The earliest fossil swift *Eocypselus* shows this character well, and in this group, in a sequence of increasingly short and stout structures the arrangement would appear to be *Eocypselus*-Hemiprocnidae-Cypseloidinae-Apodinae-Chaeturinae.

However, the other fossil forms do not fit into this sequence between *Eocypselus* and *Hemiprocne*. The forelimb characters typical of the subfamilies of the Apodidae are already apparent in some of the earlier fossil swifts, and to integrate them will produce a more complex arrangement. The known fossil species show characters which have justified their separation in discrete taxa,
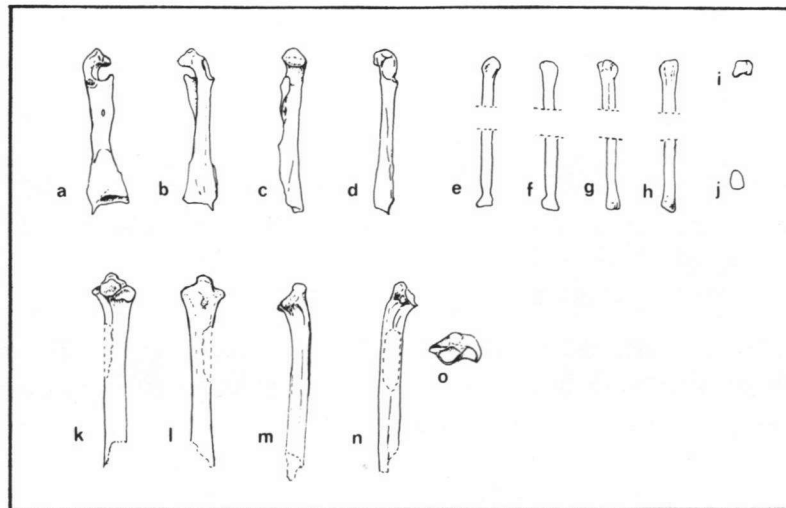
Fig. 5. *Eocypselus vincenti* sp. nov., holotype; x 2.
   Left coracoid: a = dorsal, b = ventral, c = medial, d = lateral.
   Left radius (distal end at top): e = (interosseous) caudal, f = cranial, g = dorsal, h = ventral, i = distal, j = proximal.
   Left ulna: k = cranial, l = caudal, m = proximal.

and without a full array of intervening forms it is impossible to be wholly certain of affinities. However, in order to comprehend and discuss the group as a whole it is useful to fit these earlier forms into the currently accepted taxonomic framework based on Recent species, and in doing this to use such shared characters as are available.

There are three fossil swift genera that have the slender humerus typical of the Hemiprocnidae, and may have some affinity with the latter. *Eocypselus vincenti* of the Early Eocene has the more generalized humeral structure, long and slender (fig. 1E) with a more generalized proximal end, the tuberculum ventrale projecting only a short way caudally. It has a long coracoid (fig. 3E). In a broad classification this might be assigned to the Hemiprocnidae but the degree of difference and its early and generalized structure could justify keeping it separate. It is therefore assigned to the Eocypselidae *fam. nov.*, at present the earliest known swift family, its characters those of the type genus and species *Eocypselus vincenti*.

Four *Aegialornis* species have been described from the Late Eocene/Early Oligocene (Collins, 1976a). The humeri (fig. 1D) resemble those of *Eocypselus* in some respects, and in others bear some resemblance to those of nightjars Caprimulgidae, as Collins pointed out. They differ from most other swifts in the large size, and although the coracoid is relatively short and comparable with that of the Hemiprocnidae they retain a long slender ulna, suggesting that they may have retained a more generalized mode of flight (fig. 3D). I believe them to be members of this general hemiprocnid group, but the degree of specialisation that they show suggests a divergence which may justify the retention of the family Aegialornithidae Lydekker, 1891.

*Cypselavus gallicus* of the Late Eocene/Early Oligocene is perhaps most like *Hemiprocne* species in its humerus (fig. 1C). On present evidence it seems reasonable to assign it to the Hemiprocnidae Oberholser, 1906 and to leave the question of a possible separate subtaxon open to subsequent opinion.
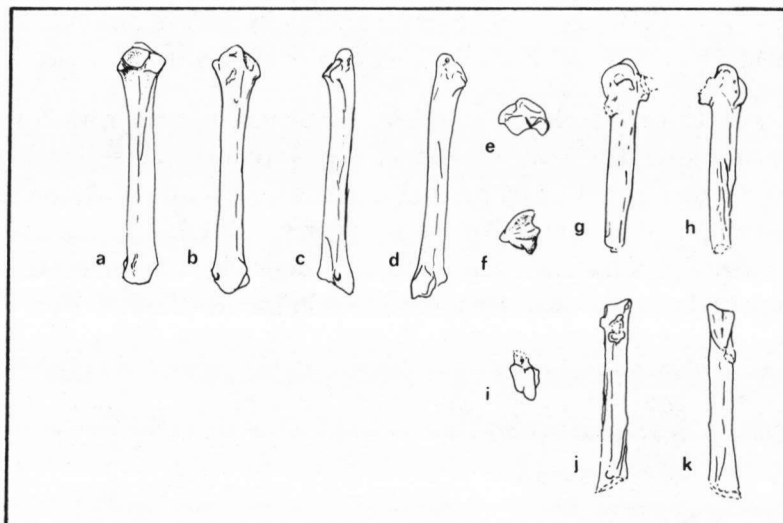
Fig. 6. *Scaniacypselus wardi* sp. nov., holotype; x 2.
    Left ulna: a = cranial, b = caudal, c = dorsal, d = ventral, e = proximal, f = distal.
    Left carpometacarpus: g = ventral, h = dorsal, i = proximal, j = cranial, k = caudal.
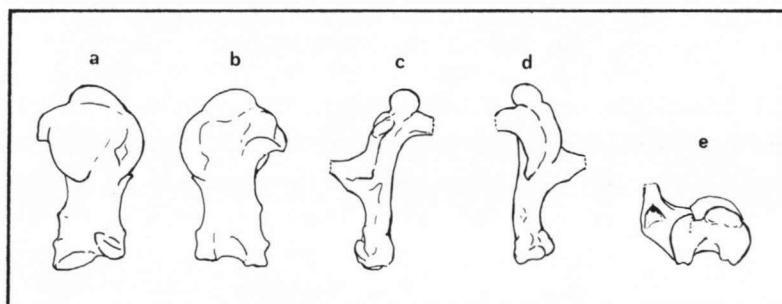


Fig. 7. *Apus gaillardi* (after Ennouchi, 1930); x 2¼.
    Left humerus: a = cranial, b = caudal, c = lateral, d = medial, e = distal.

The arrangement used here is a conservative one, retaining existing taxa at family level and of necessity adding to these. It might be thought to retain too many major taxa and in view of the diversity apparent within the Apodidae an alternative treatment would be to include *Eocypselus* and *Aegialornis* in subfamilies within the Hemiprocnidae.

The remaining fossil swifts show the stouter, shorter humeri and straighter stout ulnae more typical of the Apodidae. *Primapus lacki* of the Early Eocene is known only from the humerus (fig. 2E). It might be regarded as a borderline species since it was originally assigned to the Hemiprocnidae, but with a greater range of comparative material available is transferred to the Apodidae. Although an Early Eocene species it shows a slightly stouter shaft and a larger process for the M. extensor metacarpi radialis. The tuberculum ventrale projection is of the more generalized, shorter type, but the crista pectoralis is stout and cranially directed. At this earlier period the specimen has already diverged from the hemiprocnid type and shows the characters later present in more derived form in the Apodidae. I think it bears a similar relationship to later apodid forms, to that of *Eocypselus* to the hemiprocnid forms, and in similar fashion it is separated by its more

generalized character. I think it merits a separate subfamily within the Apodidae – Primapinae *subfam. nov.* –, its characters those of the type genus and species *Primapus lacki.*

*Scaniacypselus wardi* of the Middle Eocene is of particular interest in that it shows some more highly derived characters regarded as diagnostic of the Apodinae. These include the stout, short humerus, with the distal end of the crista pectoralis occurring about halfway along the length of it, and with the well-developed M. extensor process at the crest's distal edge (fig. 2D). In spite of some less developed osteological characters, such as the more slender ulna and carpometacarpus (fig. 4D), its affinities may be best expressed by including it in the Apodinae as the earliest form within that subfamily.

The gap between this and Recent species within the subfamily is partly bridged by an early *Apus* species, *A. gaillardi* Ennouchi, 1930 (fig. 7) from the Late Miocene of Grive-Saint-Alben in France. This already shows on its humerus the characters typical of that highly-derived genus.

*Procypseloides ignotus* of the Late Oligocene/Early Miocene is of later occurrence than *Scaniacypselus wardi* but shows (fig. 4C) the more generalized longer and more slender humerus shaft, and M. extensor process more separated from the distal edge of the crista pectoralis, which characterize the Cypseloidinae. Most specimens are damaged to some degree and it is not possible to be certain of the original extent to which the tuberculum ventrale projected caudally. It may have been poorly developed. However, in its critical characters the humerus is most similar to that of *Cypseloides* and its closest affinity would appear to be with the Cypseloidinae.

Following these proposals the apparent relationships of the fossil forms based mainly on the structure of the humerus is shown in figure 8. Although the lines connecting forms are conjectural the divergence to produce the array of forms recognized in Recent species appears to have occurred at an early period, in the Eocene, and subsequently the various lines of development seem to be co-extant.

From what has been suggested the taxonomy of the fossil genera would be as follows:

| either | or |
|---|---|
| EOCYPSELIDAE fam. nov. | HEMIPROCNIDAE Oberholser, 1906 |
| *Eocypselus* gen. nov. | Eocypselinae subfam. nov. |
| AEGIALORNITHIDAE Lydekker, 1891 | *Eocypselus* gen. nov. |
| *Aegialornis* Lydekker, 1891 | Aegialornithinae subfam. nov. |
| HEMIPROCNIDAE Oberholser, 1906 | *Aegialornis* Lydekker, 1891 |
| *Cypselavus* Gaillard, 1908 | Hemiprocninae (Oberholser, 1906) |
| | *Cypselavus* Gaillard, 1908 |

APODIDAE (Hartert, 1897)
    Primapinae subfam. nov.
        *Primapus* Harrison & Walker, 1975
    Cypseloidinae Brooke, 1970
        *Procypseloides* gen. nov.
    Apodinae Hartert, 1897
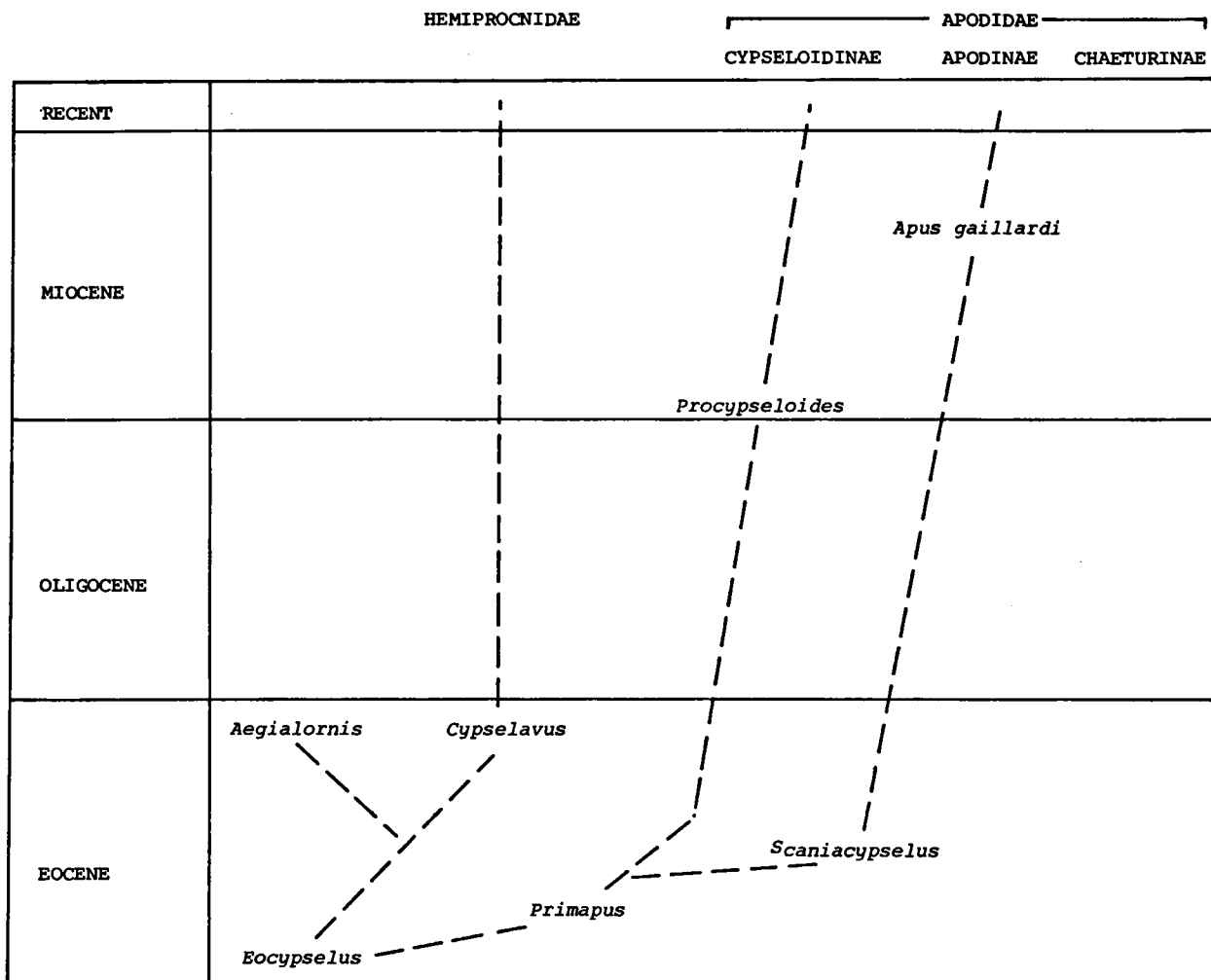        *Scaniacypselus* gen. nov.

Fig. 8. Conjectural relationships of known fossil swifts, based on trends of increased specialisation of structure relative to time.

## MEASUREMENTS

In order to compare the species involved the bones used have been converted to comparable sizes in the figures. The actual measurements are given in tables 1 and 2. Not all the comparative dimensions are available and where it seemed reasonable to do so some measurements have been calculated from photographs or figures of specimens not immediately available. These calculations are placed in parentheses in the tables.

In addition to those provided in the tables, measurements of associated material other than humeri included as part of the holotypes of the two new species described here are given below (in mm).

| | A | B | C | D | E | F | G | H | I | J |
|---|---|---|---|---|---|---|---|---|---|---|
| *Eocypselus vincenti* | 11.9 | 2.5 | 6.6 | 3.3 | 4.4 | 1.4 | 2.2 | 2.3 | 1.8 | 1.1 |
| *Aegialornis gallicus* | 27.7 | 6.5 | 14.7 | 6.6 | (10.4) | 3.2 | (5.3) | 4.7 | 3.7 | 2.4 |
| *Aegialornis wetmorei* | 22.0 | 6.5 | (13.3) | 5.0 | (9.6) | 2.7 | -- | -- | -- | 2.1 |
| *Cypselavus gallicus* | 12.7-13.6 | (3.3-3.7) | (6.8-7.0) | 3.7-4.0 | 4.8-5.0 | 1.6-2.0 | -- | (2.9) | -- | (1.3) |
| *Hemiprocne comata* | 13.4 | 4.0 | 6.9 | 3.8 | 5.5 | 2.0 | 3.3 | 2.3 | 2.3 | 1.2 |
| *Primapus lacki* | 12.4 | 2.7 | 6.8 | 3.4 | 5.4 | 1.9 | -- | 2.8 | 2.1 | 1.6 |
| *Scaniacypselus wardi* | 10.7 | 3.5 | 3.8 | 3.3 | -- | 2.3 | -- | -- | 2.2 | 1.2 |
| *Procypseloides ignotus* | 11.5 | (3.8) | (5.3) | (3.7) | (5.7) | (2.4) | -- | (2.6) | (2.0) | (1.5) |
| *Cypseloides niger* | 13.4 | 5.8 | 7.2 | 4.6 | 7.7 | 3.0 | 4.7 | 4.6 | 3.1 | 1.6 |
| *Apus gaillardi* | (10.8) | (4.6) | (4.4) | (4.3) | (6.5) | (3.1) | -- | -- | (2.5) | (1.5) |
| *Apus apus* | 11.9 | 5.8 | 5.3 | 4.9 | 6.8 | 3.3 | 4.5 | 4.3 | 2.7 | 1.7 |
| *Chaetura pelagica* | 9.4 | 3.5 | 3.6 | 3.9 | 6.1 | 2.8 | 4.0 | 3.8 | 2.4 | 1.3 |

Table 1. Measurements of humeri (mm).

Key to measurements: A = total length, B = distal end to M. extensor process, C = distal end to distal edge of crista pectoralis, D = distal width, E = proximal width, F = width at narrowest part of shaft, G = craniocaudal thickness at tuberculum ventrale, H = craniocaudal thickness at projection of crista pectoralis, I = craniocaudal thickness at condylus dorsalis, J = thickness at narrowest part of shaft. Figures in parentheses are estimated from photographs or other data.

| | A | B | C | D | E | F | G |
|---|---|---|---|---|---|---|---|
| *Eocypselus vincenti* | 10.7 | 11.9 | (c. 16.5) | -- | 1.2 | 1.1 | -- |
| *Aegialornis gallicus* | 17.3 | 27.7 | c. 35 | 23.9-24.7 | 2.5 | 2.8 | 2.1-2.5 |
| *Cypselavus gallicus* | 10.1 | 12.7-13.6 | -- | -- | (1.3) | (1.4) | -- |
| *Hemiprocne comata* | 11.3 | 13.4 | 16.4 | 12.4 | 1.3 | 1.4 | 1.3 |
| *Scaniacypselus wardi* | -- | 10.7 | 16.2 | (c. 14.5) | 1.5 | 1.5 | 1.3 |
| *Procypseloides ignotus* | -- | 11.5 | 17.5 | 16.4 | 1.5 | (1.3) | (1.8) |
| *Cypseloides niger* | -- | 13.4 | 20.0 | 17.4 | 2.0 | 2.1 | 2.4 |
| *Apus apus* | 14.2 | 11.9 | 18.3 | 20.0 | 2.0 | 2.0 | 2.1 |
| *Chaetura pelagica* | 12.0 | 9.4 | 13.4 | 16.2 | 1.5 | 1.5 | 1.7 |

Table 2. Measurements of main forelimb bones (mm).

Key to measurements: Length of -- A = coracoid, B = humerus, C = ulna, D = carpometacarpus. Thickness about mid-shaft of -- E = humerus, F = ulna, G = os metacarpale majus of carpometacarpus.

Figures in parentheses: ulna length of *Eocypselus* calculated from radius, ulna of *Aegialornus* and carpometacarpus of *Scaniacypselus* calculated from incomplete bones by extrapolation, others calculated from figures or photographs.

*Eocypselus vincenti* sp. nov., holotype BMNH A5429.

Humerus: see table 1.

Coracoid: length 10.7; facies sternalis to processus coracoideus 8.9, length and width of processus 3.2 X 1.3; width and greatest thickness of facies articularis sternalis 2.1 X 0.7; width and greatest thickness of acrocoracoid 1.9 X 1.3.

Radius: length 15.3; greatest width at proximal end 1.1, at distal end 0.9.

Ulna: length of specimen (incomplete) 12.5; dorsoventral width of proximal end 2.6; diametre of cotyla dorsalis 1.2; dorsoventral width of cotyla ventralis 0.7.

*Scaniacypselus wardi* sp. nov., holotype BMNH A5430.

Humerus: see table 1.

Ulna: length 16.2; dorsoventral width of proximal end 3.0, of distal end 2.3; craniocaudal thickness of proximal end 2.0, of distal end 2.4; thickness of mid-shaft 1.5, width and thickness of cotyla dorsalis 1.9 X 1.5, of cotyla ventralis 1.1 X 1.3.

Carpometacarpus: length of specimen (incomplete) 2.8; dorsal width of trochlea 2.3, ventral width 1.5; dorsoventral thickness at proximal end of trochlea 1.5; width and dorsoventral thickness of shaft of os metacarpale majus at proximal end 1.6 X 1.3, at distal end 1.1 X 1.6 mm.

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