

Osteological evidence for paraphyly of the avian order Caprimulgiformes (nightjars and allies)

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Summary

The first phylogenetic analysis of osteological characters in the Caprimulgiformes (nightjars and allies) provides strong evidence that this order is paraphyletic. Well supported is monophyly of a clade comprising Caprimulgidae, Nyctibiidae, Aegothelidae and the traditional Apodiformes (swifts and hummingbirds). Within this clade Nyctibiidae (potoos) and Caprimulgidae (nightjars) on the one hand, and Aegothelidae (owlet-nightjars) and the traditional Apodiformes on the other are sister taxa. Whereas monophyly of Nyctibiidae and Caprimulgidae is in accordance with most previous studies, monophyly of the so far poorly studied Aegothelidae and the traditional Apodiformes has not been suggested by previous authors. The affinities of the Steatornithidae (oilbirds) and Podargidae (frogmouths) cannot be conclusively resolved at present.

Keywords: Phylogeny, Caprimulgiformes, Apodiformes, Aegothelidae, osteology.

Zusammenfassung

Osteologische Hinweise auf Paraphylie der Vogelordnung Caprimulgiformes (Schwalmvögel)

Die erste phylogenetische Analyse der Caprimulgiformes (Schwalmvögel) aufgrund osteologischer Merkmale liefert deutliche Hinweise auf eine Paraphylie dieser Ordnung. Gut gestützt ist die Monophylie eines Taxons, das Caprimulgidae, Nyctibiidae, Aegothelidae und die traditionelle Ordnung Apodiformes (Segler und Kolibris) beinhaltet. Innerhalb dieser Gruppe sind Nyctibiidae (Tagschläfer) und Caprimulgidae (Ziegenmelker) auf der einen Seite, sowie Aegothelidae (Höhlenschwalme) und die traditionellen Apodiformes auf der anderen Seite monophyletisch. Während Monophylie von Nyctibiidae und Caprimulgidae im Einklang mit den meisten bisherigen Untersuchungen steht, wurde eine Monophylie der bisher kaum untersuchten Aegothelidae und der traditionellen Apodiformes noch nicht vorgeschlagen. Die großsystematische Stellung der Steatornithidae (Fettschwalme) und Podargidae (Eulenschwalme) kann zur Zeit nicht überzeugend begründet werden.

Introduction

Virtually all of the currently recognized avian orders were established by anatomists in the

19th and early 20th century, well before the concepts of modern phylogenetic systematics were introduced (Hennig 1950), and some remain very poorly diagnosed. An especially ill-

defined order is the Caprimulgiformes which traditionally includes five recent families: the holarctic Caprimulgidae (nightjars), the neotropic Nyctibiidae (potoos) and Steatornithidae (oilbirds), and the Australasian Aegothelidae (owlet-nightjars) and Podargidae (frogmouths). All are crepuscular or nocturnal birds, and most feed on flying insects (the Steatornithidae are frugivorous). Caprimulgiform birds have a superficially similar external appearance which includes a wide beak with a very large gape, and a soft plumage with cryptic colouration. In their osteology and internal anatomy, however, the members of this order are remarkably different. Monophyly of the Caprimulgiformes has never been convincingly established with derived morphological characters, and the characters usually listed to diagnose this order (e. g. Stresemann 1927–34, Sibley & Ahlquist 1990) are either not present in all taxa, plesiomorphic (e. g., anisodactyl feet, holorrhinal nares, presence of aftershaft), or present in a wide range of other birds (e. g., the pelvic muscle formula, arrangement of the flexor tendons, nude oil gland). Despite this obvious lack of autapomorphic characters, the traditional order Caprimulgiformes was considered monophyletic by all recent and most earlier authors. Among the few exceptions are Huxley (1867) who separated the Podargidae from Nyctibiidae, Caprimulgidae, and Aegothelidae, and Sharpe (1900) who separated Steatornithidae, Podargidae, and Aegothelidae from Nyctibiidae and Caprimulgidae in his linear classification.

The phylogenetic relationships between the caprimulgiform families also are poorly resolved. Most authors based their studies on comparisons with Steatornithidae, Podargidae, and Caprimulgidae, whereas published accounts of the anatomy of Nyctibiidae and Aegothelidae are exceedingly rare. Although only Cracraft (1981) presented a formal phylogenetic hypothesis based on morphological characters, generally Nyctibiidae and Caprimulgidae on the one hand, and Aegothelidae and Podargidae on the other were considered to be

closely related (see Sibley & Ahlquist 1990: pp. 414–418 for a detailed review of the history of classification). Cracraft (1981: 700) noted some morphological characters in order to support this traditional classification. However, the characters he listed as synapomorphies of Aegothelidae and Podargidae are either absent in stem-group Podargidae (“double-notched sternum with long posterior processes”, see Mayr 1999, 2001), incorrect (“anterior iliac blades extremely well developed” – in the podargid genus *Batrachostomus* the alae praeacetabulares ilii are very narrow), or insufficiently defined (“peculiar egg-white protein pattern”). In a recent paper, Cracraft (2001: Fig. 3) considered the systematic position of Aegothelidae and Podargidae to be unresolved.

Wetmore (1960) thought the Steatornithidae to be the sister taxon of all other caprimulgiform birds, which is reflected by their classification into a separate suborder. Cracraft (1981, 2001) assumed that this family is the sister taxon of Nyctibiidae and Caprimulgidae but, again, the characters he listed in order to support monophyly of Steatornithidae, Nyctibiidae, and Caprimulgidae are either not present in all three taxa (contrary to his statement, the caudal margin of the sternum of the Nyctibiidae does not bear a single lateral process but exhibits two pairs of incisions) or plesiomorphic (presence of processus basipterygoidei, see below). Curiously, Cracraft (1988: 354) stated that “the steatornithids are seemingly [...] primitive relative to the other four families”.

Recent molecular phylogenetic studies do not support either monophyly of Caprimulgidae and Nyctibiidae, or monophyly of Podargidae and Aegothelidae. The DNA-DNA hybridization studies of Sibley & Ahlquist (1990) suggested monophyly of the taxon (Caprimulgidae + (Nyctibiidae + Steatornithidae)), with the Aegothelidae as the most basal taxon of recent Caprimulgiformes. A phylogenetic analysis using the mitochondrial cytochrome b gene by Mariaux & Braun (1996) showed the taxon

(Nyctibiidae + (Caprimulgidae + Aegothelidae)) to be monophyletic with the Steatornithidae as the sister taxon of all other Caprimulgiformes. Both studies supported an early branching of the Podargidae (which branch just after the Aegothelidae respectively Steatornithidae in the phylogenies of Sibley & Ahlquist and Mariaux & Braun). An analysis by Johansson et al. (2001) using nuclear DNA sequences did not corroborate monophyly of Steatornithidae, Podargidae, Nyctibiidae, and Caprimulgidae (the Aegothelidae were not included in the analysis). However, the proposed phylogenetic positions of these taxa received only weak statistical support and are thus not discussed in the following.

Concerning their higher systematic position most authors considered the Caprimulgiformes to be most closely related either to owls (Strigiformes) or to swifts and hummingbirds (Apodiformes) (see Sibley & Ahlquist 1990). However, morphological similarities between caprimulgiform birds and owls have mainly been found if comparisons were made with Podargidae and Steatornithidae (e. g., Fürbringer 1888, Verheyen 1956), whereas the other families share derived characters with the Apodiformes. Although the DNA-DNA hybridization studies of Sibley & Ahlquist (1990) and Bleiweiss et al. (1994) also resulted in monophyly of the taxon (Caprimulgiformes + Strigiformes), the methodology employed in these studies has repeatedly been criticized (e. g. Houde 1987, Lanyon 1992, Harshman 1994). Moreover, the Fitch tree shown by Sibley & Ahlquist (1990: Fig. 334) which according to Harshman (1994) "should be preferred to the Tapestry [= their more comprehensive trees in Fig. 353–385] in cases of conflict" did not support monophyly of owls and caprimulgiform birds. A phylogenetic analysis using 12S mitochondrial rDNA by Mindell et al. (1997) did not support monophyly of either owls and caprimulgiform birds or caprimulgiform and apodiform birds, whereas an analysis with complete cytochrome b and nearly complete 12S rDNA sequences by Espinosa de los Mon-

teros (2000) did confirm monophyly of Caprimulgiformes and Apodiformes in most of the different trees that were presented (in the analyses of Bleiweiss et al. 1994, Mindell et al. 1997, and Espinosa de los Monteros 2000 only the Caprimulgidae were included).

Further strong evidence for a close relationship between the apodiform and (at least some) caprimulgiform birds comes from the well known osteology of the Aegialornithidae, an Eocene family of basal swifts. The Aegialornithidae (which are considered to be apodiform by virtually all recent authors, e. g. Olson 1985, Peters 1985, Karhu 1988, Mourer-Chauviré 1988a) not only closely resemble the recent Caprimulgidae and Aegothelidae in their osteology (see Olson 1985 and below), but are also very similar to the roughly contemporaneous extinct caprimulgiform family Archaeotrogonidae (Mourer-Chauviré 1980, 1995). On the other hand, there are no derived similarities between early Tertiary owls and contemporaneous caprimulgiform birds, nor derived morphological characters which support monophyly of owls and the traditional order Caprimulgiformes.

I attempted to analyze the exact phylogenetic relationships between apodiform and caprimulgiform birds. The proposed relationships are shown in a cladogram, all nodes of which are supported with derived morphological characters (Fig. 1). Due to the paucity of published information which is available on the anatomy of Aegothelidae and Nyctibiidae, the analysis is largely based on osteological characters

Material and methods

Skeletons of the following caprimulgiform and apodiform taxa – in addition to those of representatives of all other higher avian taxa – were examined in the collections of the Forschungsinstitut Senckenberg and the Museum für Naturkunde, Berlin: Steatornithidae: *Steatornis caripensis*; Podargidae: *Batrachostomus septimus*, *Podargus strigoides*; Aegothelidae: *Aegotheles cristatus*; Nyctibiidae: *Nyctibius*

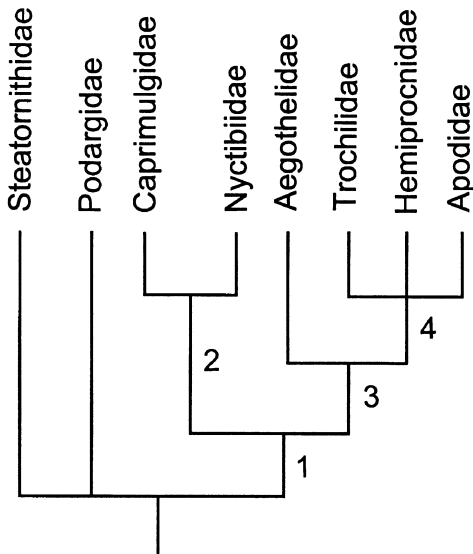


Fig. 1. The proposed phylogeny of caprimulgi-form birds; the nodes are characterized in the text.

Abb. 1. Die vorgestellten Verwandtschaftsbeziehungen caprimulgi-former Vögel; die Verzweigungspunkte sind im Text begründet.

griseus; Caprimulgidae: *Caprimulgus europaeus*, *C. pectoralis*, *C. carolinensis* (only skull), *Chordeiles minor*, *Macrodipteryx vexillarius*; Apodidae: *Apus apus*, *Collocalia salangana*, *C. vanikorensis*; Hemiprocnidae: *Hemiproctne comata*; Trochilidae: *Amazilia versicolor*, *Anthracothonax* sp., *Archilochus colubris*, *Chrysolampis mosquitos*, *Glaucis hirsuta*, *Melanotrochilus fuscus*, *Phaethornis pretrei*, *Thalaurania furcata*, *Trochilus polymus*. Details of the palatal region of *Aeronautes saxatilis* and *Streptoprocne zonaris* (both Apodidae) were studied from the illustrations in Shufeldt (1885) and Cohn (1968).

Anatomical terminology follows Baumel & Witmer (1993) and Vanden Berge & Zweers (1993).

The phylogenetic hypothesis presented in this study (Fig. 1) was tested by a cladistic analysis with the phylogenetic software PAUP, version 3.1 (Swofford 1993), using a data set of 25 anatomical characters (see Appendix 1 for descriptions of characters and Appendix 2 data matrix). The shortest tree was found with the exhaustive search option and the analysis was run with the delayed transformation (DELTRAN) mode, calculation with the ACCTRAN mode did not change the resulting tree topology. The

consistency index (CI), retention index (RI), and re-scaled consistency index (RC) were calculated. The robustness of the tree was tested with a bootstrap analysis. Given the nearly completely unresolved phylogenetic relationships between higher avian taxa, outgroup comparisons in the analysis with PAUP are based on a hypothetical ancestor. Most of the characters used for the analysis could be clearly polarized into derived and primitive states; characters for which this was not possible have been coded as unknown in the outgroup.

Results

Analysis with PAUP

Analysis of the data set in Appendix 2 with PAUP 3.1 resulted in six most parsimonious trees (CI = 0.64, RI = 0.74, RC = 0.47). The topology of the strict consensus tree is identical to that shown in Fig. 1, except that the relationships in the clade including Aegothelidae, Hemiprocnidae, Apodidae, and Trochilidae are not resolved. Four trees exhibited the topology shown in Figure 1, in the two other trees the Trochilidae were the sister taxon to a clade including Aegothelidae, Apodidae, and Hemiprocnidae. The 50% majority-rule consensus tree of 200 bootstrapped replicates is shown in Fig. 2.

Monophyly of Caprimulgidae, Nyctibiidae, Aegothelidae, Hemiprocnidae, Apodidae, and Trochilidae (Fig. 1, node 1).

Since monophyly of the traditional Caprimulgiformes has not hitherto been convincingly established with morphological characters (Cracraft 1981, 1988), a sister group relationship between the traditional Caprimulgiformes and Apodiformes is not supported, either.

Although Cracraft (1981: 700) stated that Caprimulgiformes and Apodiformes “are defined as forming a monophyletic lineage by many derived characters, particularly in the skull”, all of the characters he listed as synapomorphies are absent in Steatornithidae and Podargidae (“very short, broad bill with the nasal process of the premaxilla very thin and curved;

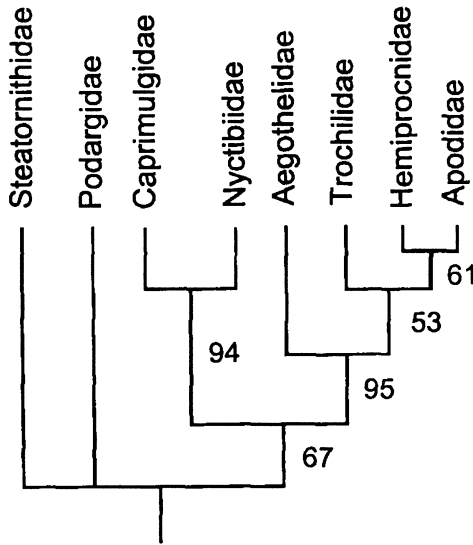


Fig. 2. 50% majority-rule consensus tree of 200 bootstrapped replicates based on a cladistic analysis of the data set in Appendix 2. The numbers indicate the percentage of bootstrapped replicates in which the node was conserved.

Abb. 2. „50% majority-rule“ Konsensus-Stammbaum von 200 Bootstrap-Wiederholungen, basierend auf einer kladistischen Analyse des Datensatzes in Anhang 2. Die Zahlen geben den Prozentsatz der Bootstrap-Wiederholungen an, bei denen der Verzweigungspunkt erhalten blieb.

the external nares very large and extending much the length of the bill; the jugal bars very long, thin, and joined to the premaxilla at the far anterior end of the skull [...]; and the orbital process of the quadrate greatly reduced”). Cracraft (1988) listed four other characters in order to support monophyly of the traditional Caprimulgiformes and Apodiformes (without mentioning those he already suggested in 1981) but again, at least three of these are not present in all taxa (the “very elongated and relatively thin” articular surface of the condylus medialis of the quadrate and the “deep, very long, rectangular-shaped ligamental furrow on humerus” are absent in the Podargidae, and the articular surface of the caput humeri is not “continuous with internal tuberosity [= tuberc-

ulum ventrale] to form ridge between them” in Steatornithidae and Podargidae – I do not know what exactly is meant by the fourth character, “large deep, rounded excavation undercutting the humeral ridge and the ridge to the internal tuberosity”).

Well supported by the following characters, however, is monophyly of a taxon which includes Caprimulgidae, Nyctibiidae, Aegothelidae, Hemiprocridae, Apodidae, and Trochilidae (outgroup comparisons with palaeognathous and basal neognathous birds, e.g. Galliformes and Anseriformes, clearly suggest that these characters are derived within neognathous birds):

(1) *Ossa palatina* with distinct processus rostrales (Fig. 3): These processes are absent in the Nyctibiidae in which the corresponding area of the palatina is, however, strongly modified (Fig. 3D). Distinct processus rostrales otherwise only occur in few other recent birds (see Huxley 1867).

(2) Processus orbitalis of quadratum strongly reduced (Fig. 4): This feature has been listed as synapomorphic for the traditional Caprimulgiformes and Apodiformes by Cracraft (1981), but in Steatornithidae and Podargidae the processus orbitalis is well developed. Contrary to the statement in Cracraft (1981), this process is however not completely lost in the Caprimulgidae (Bühler 1970: Fig. 5). With very few exceptions (see Elzanowski et al. 2000), the processus orbitalis is well developed in other recent birds, including swallows (Passeriformes, Hirundinidae), which have a similar bill shape to the above-listed taxa.

(3) Condylus caudalis of quadratum reduced (Fig. 4): Concerning the Caprimulgidae, this feature was already noted by Bühler (1970). The condylus caudalis otherwise is reduced in only very few recent birds (see Elzanowski et al. 2000).

(4) Beak very wide with narial openings large and reaching almost to the tip of the beak; distal part of rami mandibulae very narrow: owing to the predominantly nectarivorous diet of the Trochilidae, their beak is greatly

elongated; unlike other nectarivorous birds with a similar bill shape (e. g. the passeriform Nectariniidae), however, the narial openings are very long in hummingbirds, too.

(5) Fossa dorsalis of the phalanx proximalis digiti majoris divided into two depressions by an oblique bulge: owing to the highly derived morphology of the corresponding phalanx, this feature cannot be clearly discerned in recent Trochilidae. In Caprimulgidae, Aegothelidae, and basal swifts (e. g. Mourer-Chauviré 1988a, Karhu 1999) the phalanx is further bifenes-

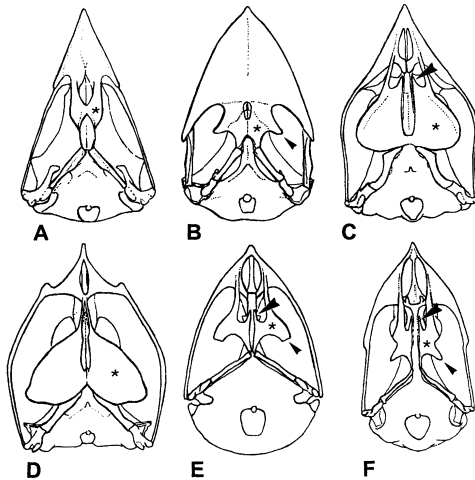


Fig. 3. Ventral view of caprimulgiform and apodiiform skulls in comparison (slightly schematic). A, *Steatornis caripensis* (Steatornithidae); B, *Podargus strigoides* (Podargidae); C, *Chordeiles minor* (Caprimulgidae); D, *Nyctibius griseus* (Nyctibiidae); E, *Aegotheles cristatus* (Aegothelidae); F, *Apus apus* (Apodidae). The large arrow indicates the processus rostralis, the small arrow points to the angulus caudolateralis; the asterisk marks the left os palatinum. Not to scale.

Abb. 3. Ventralansicht des Schädels caprimulgiformer und apodiiformer Vögel im Vergleich (leicht schematisch). A, *Steatornis caripensis* (Steatornithidae); B, *Podargus strigoides* (Podargidae); C, *Chordeiles minor* (Caprimulgidae); D, *Nyctibius griseus* (Nyctibiidae); E, *Aegotheles cristatus* (Aegothelidae); F, *Apus apus* (Apodidae). Der große Pfeil markiert den Processus rostralis, der kleine Pfeil zeigt auf den Angulus caudolateralis; das Sternchen kennzeichnet das linke Os palatinum. Nicht im gleichen Maßstab.

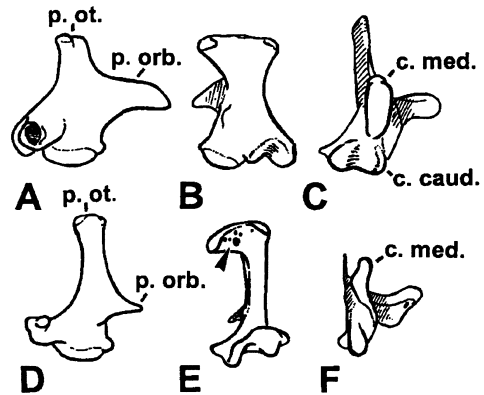


Fig. 4. Right quadrate of *Steatornis caripensis* (Steatornithidae; A, B, C) and *Aegotheles cristatus* (Aegothelidae; D, E, F) in comparison. A, D: lateral view; B, E: caudal view; C, F: ventral view. The arrow indicates the pneumatic foramina on the caudal surface of the processus oticus in *Aegotheles*. Abbreviations: p. ot. – processus oticus; p. orb. – processus orbitalis; c. caud. – condylus caudalis; c. med. – condylus medialis. Not to scale.

Abb. 4. Rechtes Quadratum von *Steatornis caripensis* (Steatornithidae; A, B, C) und *Aegotheles cristatus* (Aegothelidae; D, E, F) im Vergleich. A, D: Lateralansicht; B, E: Caudalansicht; C, F: Ventralansicht. Der Pfeil zeigt auf die pneumatischen Foramina auf der caudalen Fläche des Processus oticus in *Aegotheles*. Abkürzungen: p. ot. – Processus oticus; p. orb. – Processus orbitalis; c. caud. – Condylus caudalis; c. med. – Condylus medialis. Nicht im gleichen Maßstab.

trated. Unquestionably, this, too, is a derived feature which has apparently been secondarily lost in recent swifts (Olson 1985). In the Nyctibiidae the corresponding part of the phalanx is covered by a very thin osseous sheet, in the Trochilidae there is a single fenestra.

In its composition, this clade is identical to the “Cypselomorphae” of Huxley (1867), who was virtually the only author to make osteological comparisons with both Aegothelidae and Nyctibiidae (though Huxley’s study was restricted to the palatal region).

The earliest fossil record of the Podargidae is *Masillapodargus* from the Middle Eocene of Messel (Mayr 1999, 2001). This taxon shares the characteristic large and massive bill with

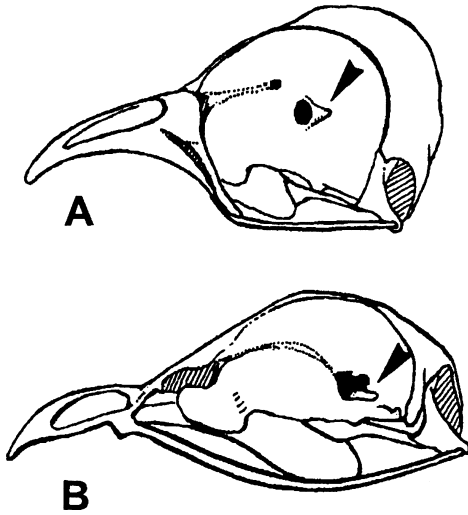


Fig. 5. Lateral view of skull of A, *Chordeiles minor* (Caprimulgidae) and B, *Nyctibius griseus* (Nyctibiidae) in comparison (slightly schematic). The arrow indicates the cone-like bony protrusion which is synapomorphic for Caprimulgidae and Nyctibiidae. Not to scale.

Abb. 5. Lateralansicht des Schädels von A, *Chordeiles minor* (Caprimulgidae) und B, *Nyctibius griseus* (Nyctibiidae) im Vergleich (leicht schematisch). Der Pfeil zeigt auf den zapfenförmigen knöchernen Vorsprung, der synapomorph für Caprimulgidae und Nyctibiidae ist. Nicht im gleichen Maßstab.

its recent relatives. An articulated skeleton from the early Eocene of North America was described as a new taxon of the Steatornithidae by Olson (1987), but the systematic position of this bird is controversial (Mayr 2001, Mayr & Daniels in press).

Monophyly of Nyctibiidae and Caprimulgidae (Fig. 1, node 2)

Osteological evidence strongly supports monophyly of the clade (Nyctibiidae + Caprimulgidae). The following characters are unquestionably derived and, apart from character 3, unique among recent birds:

(1) Cone-like bony protrusion at the caudal margin of the foramen nervi optici (Fig. 5):

This is a unique and highly characteristic feature which is only found in Nyctibiidae and Caprimulgidae, and which to the best of my knowledge has not been mentioned in the literature so far. Its functional significance is unknown.

(2) Ossa palatina extremely widened (Fig. 3C, D): In no other avian taxon are the ossa palatina widened to such a degree as in Nyctibiidae and Caprimulgidae.

(3) Processus paroccipitales strongly protruding ventrally.

(4) Mandible with intraramal joint and caudal half of rami mandibulae greatly widened and dorso-ventrally flattened (see Bühler 1970 for a detailed description of this feature in the Caprimulgidae). The combination of these features is unique to Nyctibiidae and Caprimulgidae.

(5) Caudal end of mandible unusually small, with very short cotyla lateralis and stout processus medialis (see Bühler 1970: Fig. 15). This feature is unique to Nyctibiidae and Caprimulgidae.

Cracraft (1981) further listed a "reduction in the length of the dentary relative to the post-dentary bones" as a synapomorphy of the clade (Caprimulgidae + Nyctibiidae).

Stem-group members of the Nyctibiidae are known from the Middle Eocene of Messel (Mayr 2001). However, owing to the flattening of the bones, interpretation of the structure of the mandible in the fossil specimens is difficult. Mayr (1999) assumed that the Eocene forms had a less specialized mandible than recent Nyctibiidae but a definitive assessment is only possible with better preserved specimens. Other early Tertiary Nyctibiidae have been found in the Upper Eocene to Upper Oligocene deposits of the Quercy, France (Mourer-Chauviré 1989), and the fossils reveal that the neotropical distribution of recent potoos is relictual. The split between Nyctibiidae and Caprimulgidae must have occurred before the early Eocene, although the Paleogene record of the Caprimulgidae still is very scanty (Mourer-Chauviré 1988b, Olson 1999).

Monophyly of Aegothelidae, Hemiprocnidae, Apodidae, and Trochilidae (Fig. 1, node 3)

With respect to their anatomy, the Aegothelidae are probably one of the least studied avian families which, owing to the scarcity of adequate material in museum collections, is usually omitted from studies of caprimulgiform relationships (e. g. Shufeldt 1885, Clark 1901, Wetmore 1919, Lowe 1939, Verheyen 1956). As far as I know, the bony palate of *Aegothales* is illustrated for the first time in the present study (Fig. 3E).

In his pioneering studies of the avian palate, Huxley (1867: 469) already noted that “*Aegothales* approaches the Swifts more nearly than *Caprimulgus* does in the form of its palatine bones, and in the absence of basipterygoid processes”. However, despite the striking similarity in skull morphology (which was also recognized by Cohn 1968), so far no author has considered the possibility that the Aegothelidae are more closely related to swifts than to the other caprimulgiform birds. Obviously this was largely due to the fact that owl-nightjars differ distinctly from swifts in external appearance and some features of the postcranial skeleton, i. e. the proportions of wing and leg bones and the presence of deep incisions in the sternum. However, since the corresponding features of apodiform birds (i. e. greatly abbreviated humeri and ulnae, short legs, and complete reduction of incisions in the caudal margin of the sternum) are unquestionably derived, their absence in the Aegothelidae does not constitute evidence against monophyly of owl-nightjars, swifts, and hummingbirds.

I did not find any derived characters shared by Aegothelidae and the taxon (Nyctibiidae + Caprimulgidae) that are not also present in the Apodiformes. On the other hand, monophyly of Aegothelidae, Hemiprocnidae, Apodidae, and Trochilidae is supported by the following characters (outgroup comparisons with palaeognathous and basal neognathous birds, e. g. Galliformes and Anseriformes, clearly suggest that

these characters are derived within neognathous birds):

(1) Os palatinum with greatly protruding angulus caudolateralis (Fig. 3, “transpalatine process” of Lowe 1939): In the Trochilidae the angulus caudolateralis is only poorly developed but bears a long cartilaginous extension (Lowe 1939: pl. 4, Fig. 1A). A greatly protruding angulus caudolateralis only otherwise occurs in a very few recent birds (including Passeriformes, see Huxley 1867). It is also present in the Podargidae, which, however, lack most other features characterising nodes 1 and 3 of Figure 1.

(2) Processus basipterygoidei reduced: Processus basipterygoidei are present in palaeognathous and basal neognathous birds (e. g. Galliformes, Anseriformes), and their absence is generally considered to be derived within neognathous birds (e. g. Ericson 1997). Although these processes have been reduced independently in a number of recent birds, among the Caprimulgiformes they are only reduced in Aegothelidae and Podargidae (in the podargid genus *Batrachostomus* vestigial remains of these processes still are present).

(3) Pneumatic foramina on the caudal surface of the processus oticus (Fig. 4E): This feature was listed by Cracraft (1981) as a synapomorphy of the taxon (Apodi + Trochili) but is also well developed in the Aegothelidae, of which the entire quadratum is very similar to that of swifts and hummingbirds. In all other members of the traditional Caprimulgiformes, as well as in most other recent avian taxa (see Elzanowski et al. 2000), there are no pneumatic foramina on the caudal surface of the processus oticus.

(4) Coracoid, extremitas omalis hooked and processus lateralis greatly reduced (Fig. 6): Unlike in all other caprimulgiform birds but like in all recent and fossil swifts, the extremitas omalis of the coracoid is hooked in the Aegothelidae, and the processus lateralis is greatly reduced. This condition is unquestionably derived within neognathous birds. The hooked extremitas omalis is absent in the Tro-

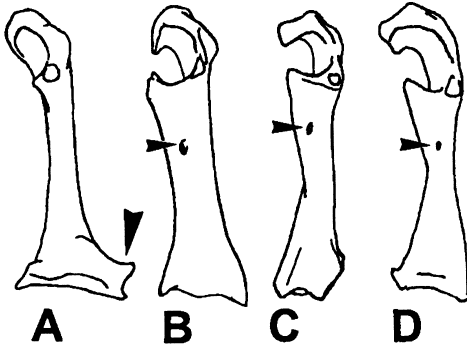


Fig. 6. Right coracoid of A, *Steatornis caripensis* (Steatornithidae); B, *Aegotheles cristatus* (Aegothelidae); and the extinct apodiform taxa C, *Jungornis tessellatus* (Jungornithidae; after Karhu 1999) and D, *Aegialornis gallicus* (Aegialornithidae; after Mourer-Chauviré 1988a) in comparison. The large arrow points to the processus lateralis, the small arrow indicates the foramen nervi supracoracoidei. Not to scale.

Abb. 6. Rechtes Coracoid von A, *Steatornis caripensis* (Steatornithidae); B, *Aegotheles cristatus* (Aegothelidae); und den ausgestorbenen apodiformen Taxa C, *Jungornis tessellatus* (Jungornithidae; nach Karhu 1999) und D, *Aegialornis gallicus* (Aegialornithidae; nach Mourer-Chauviré 1988a) im Vergleich. Der große Pfeil zeigt auf den Processus lateralis, der kleine Pfeil markiert das Foramen nervi supracoracoidei. Nicht im gleichen Maßstab.

chilidae, but owing to their peculiar mode of flight, hummingbirds exhibit a very specialised extremities omalis of the coracoid, in which the processus acrocoracoideus is fused with the processus procoracoideus. The coracoid of the Aegothelidae further corresponds with that of swifts and hummingbirds in that a foramen nervi supracoracoidei is present (see Fig. 6). This has not to my knowledge been noted by previous authors – Fürbringer (1888: 1342), for example, lists the absence of this foramen as a diagnostic feature of the Caprimulgiformes. Although among “higher landbirds” (sensu Olson 1985) a foramen nervi supracoracoidei otherwise only occurs in owls, its presence might be plesiomorphic within recent birds. The coracoid of the Aegothelidae is especially similar to that of basal Apodiformes

of the extinct family Jungornithidae (Fig. 6B, C).

(5) Cruciform origin of musculus splenius capitis: Burton (1971) first recognized that Aegothelidae, swifts and hummingbirds share a cruciform origin of musculus splenius capitis. This muscle arises from the neural spine of the second cervical vertebra, and in Aegothelidae, swifts, and hummingbirds “the fibres of the muscle take their origin on the opposite side of the midline from that on which they insert” (Burton 1971: 19). Although a tendency towards this feature is found in very few other avian taxa (though none of the other Caprimulgiformes, see Burton 1971), the exaggerated condition which is accompanied by a modified neural spine of the second cervical vertebra is unique to the three above-mentioned taxa. Judging from the shape of the neural spine of the second vertebra, this feature is absent in the Nyctibiidae (which is the only caprimulgiform family that was not investigated by Burton 1971). Cracraft (1981) listed this feature as synapomorphy of the Apodiformes.

(6) Absence of caeca: like recent Hemiprocnidae, Apodidae, and Trochilidae, *Aegotheles* completely lacks caeca, which are very well developed in all other caprimulgiform birds (Beddard 1886, Lowe 1939). Caeca have been reduced independently in a number of recent birds, but their absence in the Aegothelidae is so much the more of phylogenetic significance since Caprimulgidae, Nyctibiidae, Aegothelidae, and swifts have a similar insectivorous diet.

In their postcranial osteology, the Aegothelidae compare well to basal swifts of the extinct family Aegialornithidae (e.g. sternum with slightly bifurcated spina externa, morphology of carpometacarpus, proximal end of the ulna, tibiotarsus, and hypotarsus, Fig. 7). Differences between Aegothelidae and Aegialornithidae mainly concern the much more abbreviated humerus and ulna of the Aegialornithidae (a derived character of swifts, see below) and the more elongated legs of recent Aegothelidae (a derived character of owl-nightjars which

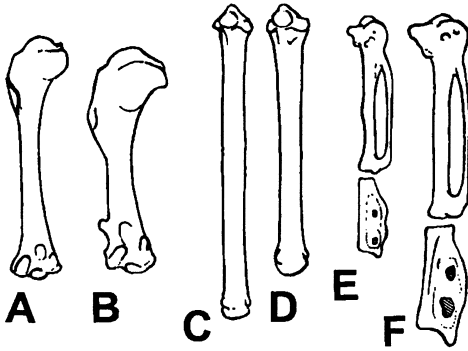


Fig. 7. Wing bones of *Aegotheles cristatus* (Aegothelidae; A, C, E) and *Aegialornis gallicus* (Aegialornithidae; B, D, F, after Collins 1976 and Mourer-Chauviré 1988a) in comparison. A, B: right humerus; C, D: left ulna; E, F, right carpometacarpus and phalanx proximalis digiti majoris. All bones are shown in the same magnification.

Abb. 7. Flügelknochen von *Aegotheles cristatus* (Aegothelidae; A, C, E) und *Aegialornis gallicus* (Aegialornithidae; B, D, F, nach Collins 1976 und Mourer-Chauviré 1988a) im Vergleich. A, B: rechter Humerus; C, D: linke Ulna; E, F, rechter Carpo-metacarpus und Phalanx proximalis digiti majoris. Alle Knochen in derselben Vergrößerung.

might be related to their fairly terrestrial way of living). Unlike that of the Aegothelidae, the humerus of the Aegialornithidae also exhibits a large processus supracondylaris, which is, however, only poorly developed in other apodiform taxa (e.g. Hemiprocnidae and Jungornithidae).

Although the sternum of the Aegothelidae is similar to that of the Hemiprocnidae in its proportions, it differs from that of all recent apodiform birds in the presence of four large fenestrae in its caudal margin (Fig. 8). Whether the connection of the caudal ends of the trabeculae by an osseous bridge is an early stage of the complete reduction of incisions found in swifts and hummingbirds, cannot be said at present.

Contrary to previous statements (e.g. Serventy 1985, Sibley & Ahlquist 1990, Holyoak 1999), the palate of the Aegothelidae is not desmognathous as is that of Podargidae and

Steatornithidae (i.e. vomer greatly reduced or completely absent, and processus maxillopalatini fused along their midline) but aegithognathous as in swifts (i.e. vomer well developed and with truncate rostral end), as already noted by Huxley (1867). Although Lowe (1939: 330) considered the palate of the Trochilidae to be aegithognathous, too, the condition in hummingbirds is less clear; generally they are thought to be schizognathous (i.e. tip of vomer pointed). Depending on the author, the palate of Caprimulgidae and Nyctibiidae also is classified either as aegithognathous or schizognathous (see Bühler 1970).

Kitto & Wilson (1966) reported a unique form of the enzyme malate dehydrogenase which is shared by swifts and hummingbirds. Unfortunately, these authors did not include any caprimulgiform taxon in their study, and it would certainly be interesting to find out whether this feature is also present in the Aegothelidae. There is also very little published material on the myology and visceral anatomy of the Aegothelidae. Like apodiform birds, the Aegothelidae lack a propatagial slip of musculus biceps brachii which is present in the Caprimulgidae (this slip is, however, also absent in Podargidae and Steatornithidae, see Beddard

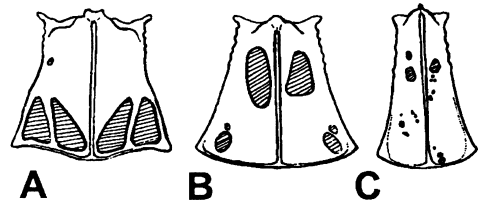


Fig. 8. Sternum of A, *Aegotheles cristatus* (Aegothelidae); B, *Hemiproctne comata* (Hemiprocnidae); and C, *Apus apus* (Apodidae) in comparison. Note the additional and irregular perforations in the corpus sterni of Hemiprocnidae and Apodidae. Not to scale.

Abb. 8. Sternum von A, *Aegotheles cristatus* (Aegothelidae); B, *Hemiproctne comata* (Hemiprocnidae); und C, *Apus apus* (Apodidae) im Vergleich. Beachte die zusätzlichen unregelmäßigen Perforationen im Corpus sterni von Hemiprocnidae und Apodidae. Nicht im gleichen Maßstab.

1886, Lowe 1939). Aegothelidae and apodiform birds further lack the *musculus fibularis longus* (this muscle is also absent in the *Steatornithidae* but present in *Caprimulgidae* and *Podargidae*, see Beddard 1886, Zusi & Bentz 1984). Apodiform birds are characterized by a large number of additional derived non-osteological characters (e. g. Fürbringer 1888, Lowe 1939, Karhu 1999) and future dissections of spirit specimens of the *Aegothelidae*, which are not available to me, will have to show whether some of these features are also present in owl-nightjars. However, it has to be emphasized that the absence of derived apodiform features in the *Aegothelidae* does not refute the phylogeny proposed herein. Paraphyly of the taxon including *Aegothelidae*, *Apodidae*, *Hemiprocnidae*, and *Trochilidae* could only be shown by finding derived characters which more convincingly assign the *Aegothelidae* to some other avian taxon.

The traditional idea of a closer relationship between *Aegothelidae* and *Podargidae* might have been influenced by the fact that the rufous morphs of some *Aegothelidae* (e. g. *Aegothales insignis* and *A. tatei*) have a similar plumage pattern to the rufous morphs of *Podargidae* of the genus *Batrachostomus*. However, no plumage feature is consistently present in all members of *Aegothelidae* and *Podargidae*, and it seems more likely that the grey plumage, which is present in all species, is primitive within the *Aegothelidae*.

Although recent *Aegothelidae* and *Podargidae* have a similar geographical distribution, the fossil record shows that at least the *Podargidae* were also present in the Eocene of Europe (Mourer-Chauviré 1989, Mayr 1999, 2001).

The earliest certain record of the *Aegothelidae* is an incomplete articulated skeleton from the Middle Miocene of Australia (Rich & McEvey 1977). However, since there is a fairly extensive fossil record of swifts from Eocene deposits, the *Aegothelidae* too must have branched off well before the early Eocene.

Monophyly of *Apodidae*, *Hemiprocnidae*, and *Trochilidae* (Fig. 1, node 4)

Except for Cohn (1968), who proposed a closer relationship to the *Passeriformes*, recent authors have considered hummingbirds to be the closest extant relatives of swifts (e. g., Cracraft 1981, 1988, Sibley & Ahlquist 1990). Monophyly of swifts and hummingbirds is supported by a large number of derived myological features (e. g., Lowe 1939, Zusi & Bentz 1984, Cracraft 1988, Karhu 1999), biochemical and molecular analyses (Kitto & Wilson 1966, Sibley & Ahlquist 1990, Bleiweiss et al. 1994, Johansson et al. 2001) and, among other features (see Cracraft 1988), by the following derived osteological characters:

- (1) Proximo-dorsal part of narial openings covered by an osseous sheet.
- (2) *Facies articularis coracoideus* weakly saddle-shaped or convex (no sulcus as in other birds), see Karhu (1999: 209).
- (3) Incisions in the caudal margin of the sternum reduced.
- (4) Humerus and ulna strongly abbreviated and hand greatly elongated.

Further evidence for monophyly of the traditional *Apodiformes* comes from recently described fossils from the early Tertiary of the Caucasus which show a mosaic of apodid and trochilid characters (Karhu 1988, 1992, 1999).

Although the *Trochilidae* lack some of the features which diagnose nodes 1 and 3 of Figure 1, in each case the corresponding part of the skeleton shows a highly apomorphic morphology (beak, *extremitas omalis* of coracoid, *phalanx proximalis digiti majoris*).

I did not investigate the exact phylogenetic relationships between the traditional apodiform taxa. Most authors have assumed monophyly of *Hemiprocnidae* (tree swifts) and *Apodidae* (true swifts), but Karhu (1988: 87, 1992: 383) considered a sister group relationship between *Apodidae* and *Trochilidae* (hummingbirds).

Conclusion

Whereas paraphyly of the Caprimulgiformes has already been suggested by a small number of earlier authors (see Sibley & Ahlquist 1990), the phylogeny presented in this study differs from all previous classifications in the proposed sister group relationship between Aegothelidae and Apodiformes. Monophyly of Aegothelidae and Apodiformes is strongly supported by 11 derived morphological characters. Most authors who have questioned a close relationship between caprimulgiform and apodiform birds have considered the latter to be closely related to the Passeriformes (perching birds) (e. g. Shufeldt 1885, Lowe 1939). However, the few derived osteological characters which were listed by Lowe (1939) in order to support monophyly of Apodiformes and Passeriformes are also present in the Aegothelidae (e. g. aegithognathous palate, strongly protruding angulus caudolateralis ["transpalatine process"]), and Aegothelidae and Apodiformes further correspond in some derived features in which the latter differ from the Passeriformes (e. g. absence of caeca).

Apart from the relative position of the Aegothelidae, the topology of the cladogram in Fig. 1 is identical to that presented by Mariaux & Braun (1996) in their study of the mitochondrial cytochrome b gene (see introduction). Unfortunately, however, these authors did not include the Apodiformes in their analysis. Although the phylogeny of Sibley & Ahlquist (1990) differs from that proposed in this study, in their figures 96, 106, and 107 the melting curve of *Aegothales* is closer to that of the Apodiformes than are the melting curves of the other caprimulgiform birds.

The phylogenetic relationships proposed in this study seem to suggest that the Apodiformes evolved from nocturnal or crepuscular ancestors, since this assumption is more parsimonious than a four-fold independent origin of nocturnal activity (in Steatornithidae, Podargidae, Nyctibiidae/Caprimulgidae, and Aegothelidae). However, it has to be emphasized that I

did not find derived characters which support monophyly of all taxa included in the analysis. The phylogenetic position of Steatornithidae and Podargidae can be settled only by the inclusion of a large number of other avian taxa, which is beyond the scope of this study. As assumed by previous authors, these birds might be more closely related to owls than to the caprimulgid/aegothelid/apodid lineage. If this were the case, a nocturnal way of living would have arisen only twice independently in Aegothelidae and Nyctibiidae/Caprimulgidae (if one does not accept nocturnal ancestors for the Apodiformes).

Acknowledgements

I thank Andrzej Elzanowski (University of Wrocław, Poland), Stefan Peters (Forschungsinstitut Senckenberg), and Cécile Mourer-Chauviré (Université Claude Bernard, Lyon) for critical comments which improved the manuscript.

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Appendix 1. Description of characters.

1. Skull, processus basiptygoidei: present (0), absent (1). Processus basiptygoidei are present in palaeognathous and basal neognathous birds (e. g. Galliformes, Anseriformes), and their occurrence is generally considered to be plesiomorphic within neognathous birds (e. g. Ericson 1997).
2. Ossa palatina with greatly protruding angulus caudolateralis: absent (0), present (1). Outgroup comparisons with basal neognathous birds clearly suggest that a greatly protruding angulus caudolateralis is derived (this feature only occurs in a very few recent avian taxa).
3. Ossa palatina: not greatly enlarged (0), greatly enlarged (1). Greatly enlarged ossa palatina (to the degree as shown in Fig. 3) are unquestionably derived within neognathous birds and among their extant representatives only found in Nyctibiidae and Caprimulgidae.
4. Ossa palatina with long and slender processus rostrales: absent (0), present (1). Outgroup comparisons with basal neognathous birds suggest that long and slender processus rostrales are derived (this feature only occurs in a very few recent avian taxa).
5. Cone-like bony protrusion at caudal margin of foramen nervi optici: (0) absent, (1) present. This is a unique feature among neognathous birds which is only found in Nyctibiidae and Caprimulgidae.
6. Beak very wide, with narial openings large and reaching almost to the tip of the beak: absent (0), present (1). Outgroup comparisons with palaeognathous and basal neognathous birds suggest that a very wide beak and greatly elongated narial openings are derived.
7. Processus paroccipitales greatly protruding ventrally: absent (0), present (1). Outgroup comparisons with basal neognathous birds suggest that greatly protruding processus paroccipitales are derived.
8. Processus orbitalis of quadratum: not greatly reduced (0), greatly reduced (1). A greatly reduced processus orbitalis is clearly derived within neognathous birds (Elzanowski et al. 2000).
9. Condylus caudalis of quadratum reduced: absent (0), present (1). A reduced condylus caudalis is clearly derived within neognathous birds (Elzanowski et al. 2000).
10. Caudal surface of processus oticus of quadratum with pneumatic foramina: absent (0), present (1). This feature is very rarely found in other neognathous birds and certainly derived within that taxon (Elzanowski et al. 2000).
11. Distal part of rami mandibulae very narrow: absent (0), present (1). Outgroup comparisons with basal neognathous birds suggest that very narrow rami mandibulae are derived.
12. Proximal end of mandible unusually small, with very short cotyla lateralis and stout processus medialis: absent (0), present (1). This feature is unique to Nyctibiidae and Caprimulgidae and certainly derived within neognathous birds.
13. Mandible with intraramal joint and caudal half of rami mandibulae greatly widened and dorso-ventrally flattened: absent (0), present (1). The combination of these features is unique to Nyctibiidae and Caprimulgidae.
14. Caudal margin of sternum: with four notches (0), with two notches or without notches (1). The presence of a four-notched sternum is generally considered to be primitive within recent birds (e. g. Olson 1987).
15. Facies articularis coracoideus weakly saddle-shaped or convex: absent (0), present (1). This feature is unique to swifts and hummingbirds; all other recent birds possess a sulcus articularis coracoideus (Karhu 1999).
16. Coracoid, extremitas omalis: not hooked (0), hooked (1). Outgroup comparisons with basal neognathous birds suggest that a hooked extremitas omalis is derived.
17. Coracoid, processus procoracoideus: (0) well developed, (1) greatly reduced. The polarity of this feature is unknown.
18. Coracoid, foramen nervi supracoracoidei: present (0), absent (1). The polarity of this feature is unknown.
19. Coracoid, processus lateralis: not greatly reduced (0), greatly reduced (1). A greatly reduced processus lateralis is certainly derived within recent birds.
20. Humerus greatly abbreviated (measuring less than 1.5 times the length of the coracoid), and ulna stout and short (measuring less than twice the length of the coracoid): absent (0), present (1). A greatly abbreviated humerus and ulna are unquestionably derived within recent birds, and otherwise only occur in swallows (Hirundinidae, Passeriformes).
21. Fossa dorsalis of phalanx proximalis digiti majoris divided into two depressions by an oblique bulge: absent (0), present (1). Outgroup comparisons with basal neognathous birds suggest that the presence of this feature is derived.

22. Phalanx proximalis digiti majoris, well-developed processus internus indicis (terminology after Stegmann 1963): absent (0), present (1). A well developed processus internus indicis is absent in palaeognathous and basal neognathous birds and certainly derived within recent birds (see Stegmann 1963).
23. Tarsometatarsus extremely stout and abbreviated (less than half as long as carpometacarpus): absent (0), present (1). An extremely stout and abbreviated tarsometatarsus (to the degree as found in Nyctibiidae and Steatornithidae) is unquestionably derived within neognathous birds.
24. Caeca: well developed (0), absent (1). Outgroup comparison with other tetrapods suggests that the presence of caeca is plesiomorphic within recent birds.
25. Musculus splenius capitis: without cruciform origin (0), with cruciform origin (1). The cruciform origin is a derived feature which is only found in a very few recent birds (see Burton 1971).

Appendix 2. Data matrix of 25 morphological characters for caprimulgiform and apodiform birds (see Appendix 1. for definitions of characters). 0 = absent; 1 = present; ? = unknown states of characters.

	characteristics																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0
Aegothelidae	1	1	0	1	0	1	0	1	1	1	1	0	0	0	0	1	0	0	1	0	1	0	0	1	1
Nyctibiidae	0	0	1	0	1	1	1	1	1	0	1	1	1	0	0	0	1	1	0	0	1	1	1	0	0
Steatornithidae	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	1	0	0
Caprimulgidae	0	0	1	1	1	1	1	1	1	0	1	1	1	1	0	0	1	1	0	0	1	1	0	0	0
Podargidae	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
Apodidae	1	1	0	1	0	1	0	1	1	1	1	0	0	1	1	1	1	0	1	1	1	1	0	1	1
Hemiprocnidae	1	1	0	1	0	1	0	1	1	1	1	0	0	1	1	1	1	0	1	1	1	1	0	1	1
Trochilidae	1	0	0	1	0	0	0	1	1	1	0	0	0	1	1	0	0	0	1	1	?	1	0	1	1