PHYLOGENY OF EARLY TERTIARY SWIFTS AND HUMMINGBIRDS (AVES: APODIFORMES)

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ABSTRACT.—The phylogenetic relationships between early Tertiary and extant apodiform birds are only poorly understood, and this study is the first cladistic approach to this problem in which the Trochilidae are included. The analysis supports monophyly of the Lower Oligocene *Jungornis* and extant Trochilidae, as well as monophyly of the Middle Eocene *Scaniacypselus* and extant Apodidae. The "Jungornithidae" sensu Karhu (1999) are shown to be paraphyletic with the Upper Eocene *Argornis* being the sister taxon of the taxon (*Jungornis* + extant Trochilidae). The osteology of *Jungornis* provides a transition between that of the highly derived extant Trochilidae and that of more generalized apodiform birds. An *Argornis*-like apodiform bird from the Middle Eocene of Messel shows a completely unexpected combination of a greatly abbreviated, apodiform humerus with a short and broad wing, and might indicate that the Trochilidae evolved from a short-winged ancestor. *Received 8 April 2002, accepted 26 October 2002.*

RESUMEN.—Las relaciones filogenéticas entre las aves apodiformes del Terciario temprano y las vivientes son sólo pobremente entendidas, y éste es el primer estudio cladístico del problema en el que se incluyen los Trochilidae. El análisis apoya la monofilia de *Jungornis* del Oligoceno bajo y los Trochilidae vivientes, así como la monofilia de *Scaniacypselus* del Eoceno medio y los Apodidae vivientes. Los «Jungornithidae» sensu Karhu (1999) son parafiléticos; *Argornis* del Eoceno superior es el taxón hermano del grupo (*Jungornis* + Trochilidae vivientes). La osteología de *Jungornis* provee una transición entre aquélla altamente derivada de los Trochilidae vivientes, y la más generalizada de las aves apodiformes. Un ave similar a *Argornis* del Eoceno medio de Messel todavía no descrita, presenta una combinación completamente inesperada de un húmero apodiforme muy abreviado con un ala corta y ancha, y podría indicar que los Trochilidae evolucionaron de un ancestro de alas cortas.

THERE IS INCREASING consensus that tree swifts (Hemiprocnidae), true swifts (Apodidae), and hummingbirds (Trochilidae) form a monophyletic clade that is supported by derived anatomical features and most biochemical and molecular analyses (see Johansson et al. 2001, Livezey and Zusi 2001, Mayr 2002). As shown by a recent phylogenetic analysis (Mayr 2002), owlet-nightjars (Aegothelidae) are the sister group of swifts and hummingbirds. Although Apodiformes have a comparatively extensive early Tertiary fossil record, phylogenetic relationships between the fossil and the extant taxa are only insufficiently understood.

One of the earliest swift-like birds described so far is *Eocypselus vincenti* Harrison 1984 from the lower Eocene of England. That species, which is known from a few isolated bones of only a single individual, was classified into a monotypic taxon, Eocypselidae, by Harrison (1984) but included in the Hemiprocnidae by Mourer-Chauviré (1988).

Much better represented by numerous isolated bones are the early Tertiary Aegialornithidae Lydekker 1891, which exhibit a rather generalized overall osteology resembling both extant Hemiprocnidae and—apart from the more abbreviated humerus and tarsometatarsus—extant Aegothelidae. The Aegialornithidae are either considered to be closely related to the Hemiprocnidae (e.g. Harrison 1984; Karhu 1988, 1992; Mlíkovský 2002) or "the last representatives of an old radiation directed toward the realization of the type 'True Swifts'" (Mourer-Chauviré 1988:369).

A few isolated bones from the Upper Eocene to Lower Oligocene deposits of the Quercy were assigned to *Cypselavus gallicus* Gaillard 1908 (Mourer-Chauviré 1978) which is currently recognized as the earliest taxon

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of the Hemiprocnidae (Harrison 1984, Peters 1985, Mourer-Chauviré 1988). The earliest certain members of the Apodidae belong to *Scaniacypselus* Harrison 1984, which includes two species from the Middle Eocene of Denmark and Germany (Harrison 1984, Peters 1985, Mayr and Peters 1999).

Crown group Trochilidae have no early Tertiary fossil record. However, Karhu (1988) described a new apodiform taxon, *Jungornis tesselatus*, from the Lower Oligocene of the Northern Caucasus which agrees with extant Trochilidae in highly characteristic derived features of the humerus (Karhu 1988, 1992). Karhu (1988) classified *J. tesselatus* into a new taxon, Jungornithidae, to which he later (Karhu 1999) assigned the Upper Eocene species *Argornis caucasicus* Karhu 1999. Both *Jungornis* and *Argornis* are known from wing elements of a single individual only, and *A. caucasicus* clearly exhibits a less specialized wing morphology than *J. tesselatus*.

The only phylogenetic analysis of fossil apodiform birds in which the proposed relationships are depicted in some sort of phylogenetic tree is by Harrison (1984) who assumed a major split between a hemiprocnid and an apodid lineage (a recent cladistic analysis of apodiform birds by Dyke [2001] is based on a largely incorrect character matrix [see Mayr 2001] and is thus not discussed in the following). However, whereas Harrison (1984) listed some derived characters to support the apodid lineage, assignment of the taxa *Eocypselus*, *Aegialornis*, and *Cypselavus* to the hemiprocnid lineage was based on plesiomorphic characters ("more generalized humeral structure," "long slender

ulna" with "more generalized proximal end;" see Harrison 1984:172).

Except for Karhu (1988, 1992, 1999), most authors further omitted the Trochilidae from their comparisons, and the present study is the first cladistic approach to the phylogeny of early Tertiary Apodiformes in which hummingbirds are included.

Materials and Methods

Anatomical terminology follows Baumel and Witmer (1993) and Vanden Berge and Zweers (1993), if not indicated otherwise. Comparisons with extant taxa are based on skeletons in the collection of Forschungsinstitut Senckenberg; concerning extant Apodiformes the following species were studied: Aegothelidae: *Aegotheles cristatus*; Hemiprocnidae: *Hemiprocne comata*; Apodidae: *Chaetura vauxi*, *Apus apus*, *Collocalia vanikorensis*, *Co. salangana*; Trochilidae: *Phaethornis pretrei*, *Glaucis hirsuta*, *Amazilia versicolor*, *Archilochus colubris*, *Calypte anna*, *Anthracothorax* sp., and *Chrysolampis mosquitus*. Information on osteology of the Cypseloidinae (Apodidae) is based on illustrations and descriptions in Cohn (1968), Ballmann (1976), and Collins (1976a).

The phylogenetic tree was constructed with the phylogenetic software PAUP (version 3.1; Swofford 1993), using a data set of 27 anatomical characters (see Appendix and Table 1 for character descriptions and data matrix). The only multistate character was coded as "ordered". Unknown characters for particular taxa were coded as "missing". The shortest tree was found with the exhaustive search option, and the analysis was run with the delayed transformation (DELTRAN) mode. The consistency index (CI), retention index (RI), and rescaled consistency index (RC) were calculated. Robustness of the tree was tested with a bootstrap analysis of 1,000 replicates. Extant Podargidae

TABLE 1. Character matrix of 27 morphological characters for fossil and recent apodiform birds (see Appendix for character definitions). Unknown character states are indicated by "?"; polymorphic characters are coded as "01". Podargidae and Aegothelidae were used for outgroup comparisons.

Taxon	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	26	27
Podargidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Aegothelidae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aegialornis	0	0	?	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	?	0	0	?	0	0	?	?
Argornis	0	0	0	?	?	?	1	0	0	1	?	0	0	0	0	0	0	1	1	0	0	0	?	?	?	?	?
Jungornis	1	0	0	0	1	0	1	1	1	2	1	0	1	1	1	0	0	?	1	?	?	?	?	?	?	?	?
Trochilidae	1	0	1	0	1	1	0	1	1	2	1	0	1	1	1	0	1	1	1	0	0	0	0	1	0	0	0
Hemiprocnidae	0	0	1	0	1	1	0	0	0	1	0	0	0	0	0	1	1	0	0	1	0	0	1	1	1	1	1
Scaniacypselus	?	1	?	?	?	?	0	1	1	2	0	1	0	0	0	1	1	0	0	?	1	1	?	?	?	?	1
Apodidae	1	1	1	0	1	1	1	1	1	2	1	1	0	0	0	1	1	01	0	1	1	1	1	1	1	1	1
Eocypselus	0	0	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?

(*Podargus strigoides*) and Aegothelidae (*Aegotheles cristatus*) were used for outgroup comparisons.

RESULTS

The phylogenetic analysis of the character matrix (Table 1) resulted in 10 most-parsimonious trees, the consensus tree of which is shown in Figure 1.

The analysis supported monophyly of a clade including all apodiform taxa except *Eocypselus* and *Aegialornis*. Within that group, two lineages can be distinguished that include swifts and tree-swifts on the one hand, and hummingbirds on the other.

Monophyly of a clade including extant Hemiprocnidae, the fossil *Scaniacypselus*, and extant Apodidae is in concordance with previous phylogenetic hypotheses. Monophyly of the taxon (*Scaniacypselus* + extant Apodidae) received high bootstrap support; derived characters that support monophyly of extant Apodidae to the exclusion of *Scaniacypselus* are the greatly abbreviated proximal pedal phalanges (see figure 4 in Peters 1985 for absence of this feature in *Scaniacypselus szarskii*) and the absence of a well-marked fossa musculi brachialis (that fossa is visible in the type specimen of *S. wardi*).

The analysis further showed that the Jungornithidae sensu Karhu (1999) are paraphyletic and resulted in monophyly of the taxon (*Argornis* + [*Jungornis* + extant Trochilidae]). Sister group relationship between *Argornis* and the taxon (*Jungornis* + extant Trochilidae) is in concordance with the temporal occurrence of the fossil genera, with the Upper Eocene *Argornis* being geologically older than the Lower Oligocene *Jungornis*. Monophyly of *Jungornis* and extant Trochilidae is further supported by the fact that in *Jungornis*, as in extant hummingbirds, the *M. biceps brachii* has a single insertion on the ulna, whereas that muscle inserts on the radius only in extant Apodidae, and on both the ulna and the radius in extant Hemiprocnidae, the fossil *Argornis*, and most other birds (see Karhu 1999). Monophyly of extant Trochilidae to the exclusion of *Jungornis* is supported by numerous derived features including a peculiar morphology of the coracoid in which the processus procoracoideus is connected to the processus acrocoracoideus by an osseous bridge (Fig. 2).
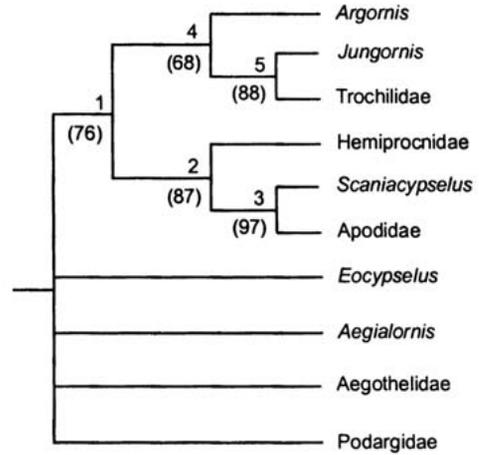

FIG. 1. Strict consensus tree of ten most-parsimonious trees (Length = 41 steps, CI = 0.68, RI = 0.74, RC = 0.51) resulting from a phylogenetic analysis of the character matrix in Table 1. Internal nodes are numbered, bootstrap values of 1,000 replicates are given in parentheses. In all of the resulting trees, the nodes are supported by the following characters (the numbers refer to Table 1; asterisked characters have CI = 1.0): node 1–5*, 10, 24*; node 2–3, 16*, 17, 20*, 23*, 25*, 26*, 27*; node 3–2*, 8, 9, 10, 12*, 21*, 22; node 4–18*, 19*; node 5–1, 8, 9, 10, 11, 13*, 14*, 15*.
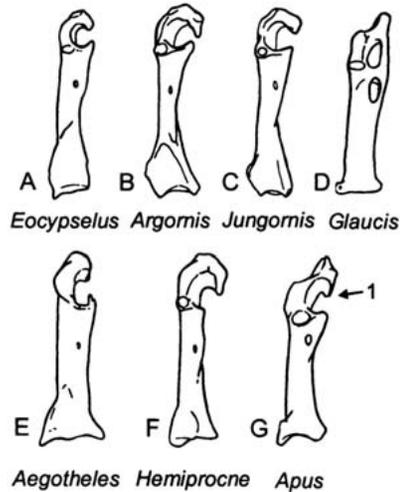

FIG. 2. Left coracoid of apodiform birds in comparison. (A) *Eocypselus vincenti* (Eocypselidae, Lower Eocene); (B) *Argornis caucasicus* (Upper Eocene, after Karhu 1999); (C), *Jungornis tesselatus* (Jungornithidae, Lower Oligocene, after Karhu 1999); (D) *Glaucis hirsuta* (Trochilidae, recent); (E) *Aegotheles cristatus* (Aegothelidae, recent); (F) *Hemiprocne comata* (Hemiprocnidae, recent); (G) *Apus apus* (Apodidae, recent). (1) Extremitas omalis; all figures slightly schematic and not to scale.

Discussion

As already noted by Karhu (1999), the fossil record of apodiform birds is in agreement with monophyly of swifts and hummingbirds. Monophyly of the taxon (*Jungornis* + Trochilidae) is supported by unique derived characters, and the osteology of *Jungornis* provides a transition between the highly derived morphology of extant Trochilidae and that of a more generalized apodiform bird (Figs. 2 and 3).

The nectarivorous hummingbirds evolved a derived mode of hovering flight that allows them to remain virtually motionless in front of flowers. Probably as an adaptation to their unique way of locomotion, extant Trochilidae have unusually short wings (Rayner 1988) that differ from the long and pointed wings of swifts.

The feathering of either *Argornis* or *Jungornis* is unknown, but there is a specimen (Fig. 4) of an apodiform bird from the Middle Eocene of Messel, Germany, which is osteologically very similar to *Argornis* and in which the wing and tail feathers are excellently preserved (Mayr 2003). As in *Argornis*, the robust humerus is strongly abbreviated and bears a poorly developed processus musculi extensor metacarpi radialis which is much more protruding in other apodiform taxa with a similarly abbreviated humerus (i.e. *Jungornis*, extant Trochilidae, and the Apodidae; see Fig. 3). The Messel apodiform further exhibits the diagnostic characters that support monophyly of the taxon (*Argornis* + [*Jungornis* + extant Trochilidae]) (see Fig. 1). Most unusual and completely unexpected is the combination of a short and stout humerus with a short and broad wing, the tip of which is completely preserved in the specimen. If it is a stem group representative of the Trochilidae, the Messel apodiform might indicate that strongly elongated wings indeed are synapomorphic for the taxon (Hemiprocnidae + Apodidae) and that the Trochilidae evolved from a rather short-winged ancestor.

It has been assumed that hummingbirds evolved from insectivorous ancestors (e.g. Cohn 1968) and underlying the phylogeny in Figure 1, a "swift-like" or "aegothelid" beak almost certainly was present in the last common ancestor of the Apodiformes and is thus plesiomorphic for the taxon (*Jungornis* +Trochilidae). Hovering
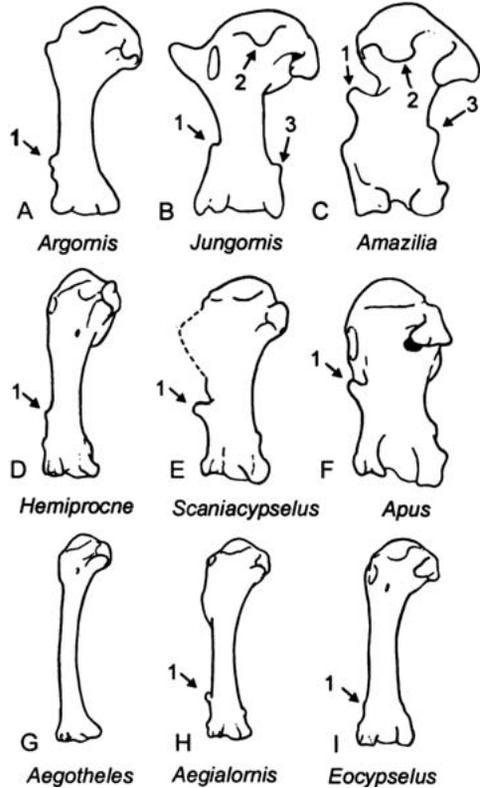

Fig. 3. Caudal surface of left humeri of apodiform birds in comparison. (A) *Argornis caucasicus* (Upper Eocene, after fig. 2f in Karhu 1999); (B) *Jungornis tesselatus* (Jungornithidae, Lower Oligocene, after fig. 2c in Karhu 1992, fig. 2r in Karhu 1999; the specimen is somewhat flattened and the crista deltopectoralis originally might have protruded more cranially); (C) *Amazilia versicolor* (Trochilidae, recent); (D) *Hemiprocne comata* (Hemiprocnidae, recent); (E) *Scaniacypselus wardi* (Apodidae, Middle Eocene); (F) *Apus apus* (Apodidae, recent); (G) *Aegotheles cristatus* (Aegothelidae, recent); (H) *Aegialornis gallicus* (Aegialornithidae, Upper Eocene, after fig. 1a in Collins 1976b), *Eocypselus vincenti* (Eocypselidae, Lower Eocene). (1) Processus musculi extensor metacarpi radialis; (2) distal protrusion on caput humeri; (3) tuberculum musculi pronator superficialis. All figures slightly schematic and not to scale.

ability of hummingbirds might have primarily evolved as an adaptation for gleaning insects from the underside of leaves (Cohn 1968) or around flowers and was a preadaptation for the highly derived nectarivory of extant Trochilidae (Mayr and Manegold 2002).

FIG. 4. *Argornis*-like fossil apodiform bird from the Middle Eocene of Messel (Hessisches Landesmuseum, Darmstadt, Germany, collection number HLMD Be 163) described and discussed in detail in Mayr (2003; fig. 8); scale bar equals 10 mm.

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APPENDIX. Character descriptions.

1. Coracoid, facies articularis sternalis greatly widened dorso-ventrally, greatest dorso-ventral width at least half of greatest medio-lateral width: absent (0), present (1).

2. Coracoid, processus acrocoracoideus long, distance from center of facies articularis scapularis to tip of processus acrocoracoideus measuring about one third of entire length of coracoid, and tip of processus acrocoracoideus reaching much farther medially than medial margin of shaft: absent (0), present (1). Concerning *Scaniacypselus*, this feature is visible in *S. szarskii* (see figure 4 in Peters 1985).

3. Furcula, extremitas omalis with long and slender processus acromialis and distinct, laterally protruding facies articularis acrocoracoidea: absent (0), present (1).

4. Sternum, cranially protruding, bifurcated spina externa: absent (0), present (1).

5. Sternum, sulci/facies articulares coracoidei: concave (0), saddle-shaped or slightly convex (1).

6. Sternum, facies articulares coracoidei contacting the rostrum sterni: absent (0), present (1). See Karhu (1988) for condition of this feature in *Jungornis* and Mourer-Chauviré (1988) for *Aegialornis*.

7. Humerus, crista deltopectoralis proximo-distally narrow, strongly protruding and tapering: absent (0), present (1).

8. Humerus, processus musculi extensor metacarpi radialis (Fig. 3; terminology after Zusi and Bentz 1982) strongly developed and protruding: present (0), absent (1).

9. Humerus, processus musculi extensor metacarpi radialis shifted proximally, situated in proximal two thirds of the bone: present (0), absent (1).

10. Humerus, ratio length of bone: width of shaft in midsection: not as follows (0), <7.0 (1), <5.0 (2). This character, which indicates the relative squatness of the bone, has been coded as "ordered".

11. Humerus, well marked fossa musculi brachialis: present (0), absent (1).

12. Humerus, intumescentia humeri strongly raised with abrupt and steeply sloping dorsal margin: absent (0), present (1). Concerning *Scaniacypselus*, this feature is visible in *S. wardi*.

13. Humerus, caput humeri bearing a distinct distal protrusion: absent (0), present (1). This feature only occurs within *Jungornis* and extant Trochilidae (Fig. 3) and allows "extreme supination of the adducted humerus during hovering flight" (Karhu 1999:215).

14. Humerus, tuberculum musculi pronator superficialis (terminology after Karhu 1988) strongly ventrally protruding: absent (0), present (1). This tubercle only occurs within *Jungornis* and extant Trochilidae (Fig. 3); in the latter it is situated farther proximally.

15. Humerus, dorsal margin of distal end with sharp crest distal to processus musculi extensor metacarpi radialis: absent (0), present (1).

16. Humerus, tuberculum supracondylare ventrale elongated and narrow: absent (0), present (1).

17. Ulna, ratio width of shaft in midsection: maximum length of bone <12: absent (0), present (1). This character indicates the relative squatness of the ulna. Only about the proximal half of the ulna of *Eocypselus* is known, but the bone is much more slender than the ulna of most other apodiform birds. The ulnae of *Argornis* and *Jungornis* are badly crushed and thus probably appear wider than they actually were; the ratios have been calculated using the preserved width of the bone and thus have been underestimated at best.

18. Ulna, olecranon: short and blunt (0), elongated and narrow (1) (Fig. A1). Concerning *Scaniacypselus*, this feature is visible in *S. wardi*. Within Apodidae, the development of this feature is variable, whereas the olecranon is elongated and narrow in *Apus*, it is short and blunt in *Collocalia* and Cypseloidinae (Collins 1976a).

19. Ulna, cotyla ventralis with weakly pronounced ventro-proximal edge: absent (0), present (1). This character was listed by Karhu (1999) as one of the main features distinguishing the "Jungornithidae" from the nontrochilid Apodiformes. Concerning *Scaniacypselus*, it is visible in *S. wardi*.

20. Radius, distal end with marked tubercle on ventral side of shaft, opposite to tuberculum carpale of ulna: absent (0), present (1).

21. Carpometacarpus greatly elongated, ~1.5× longer than coracoid: absent (0), present (1). Concerning *Scaniacypselus*, this feature is visible in *S. szarskii* (see Peters 1985).

22. Phalanx proximalis digiti majoris: bifenestrated (0), both fenestrae closed by thin osseous sheet (1). Concerning *Scaniacypselus*, this feature is visible in *S. szarskii* (see Peters 1985).

23. Phalanx proximalis digiti majoris, distal part of caudal margin with sulcus for tendon of *M. interosseus ventralis*: absent (0), present (1).

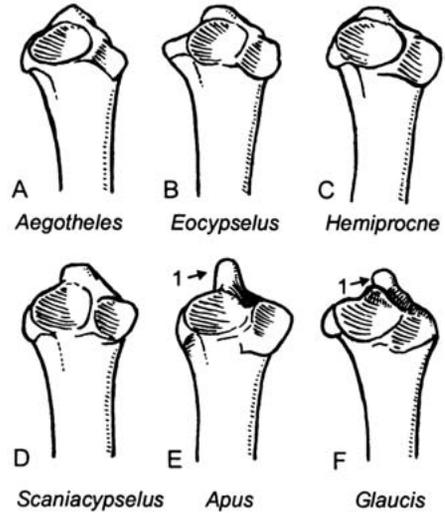**24**. Tibiotarsus, cristae cnemiales poorly developed: absent (0), present (1).

Fig. A1. Proximal end of left ulna of apodiform birds in comparison. (A) *Aegotheles cristatus* (Aegothelidae, recent); (B) *Eocypselus vincenti* (Eocypselidae, Lower Eocene); (C) *Hemiprocne comata* (Hemiprocnidae, recent); (D) *Scaniacypselus wardi* (Apodidae, Middle Eocene); (E) *Apus apus* (Apodidae, recent); (F) *Glaucis hirsuta* (Trochilidae, recent). (1) Olecranon; all figures slightly schematic and not to scale.

25. Tarsometatarsus, deep sulcus on dorsal surface, proximal to foramen vasculare distale: absent (0), present (1).

26. Salivary glands greatly enlarged, owing to the fact that saliva is used in nest construction: absent (0), present (1) (e.g. Stresemann 1927–1934, Sibley and Ahlquist 1990).

27. Outermost primaries greatly elongated, measuring at least 2.5× the length of the longest secondaries: absent (0), present (1). Concerning *Scaniacypselus*, this feature is visible in *S. szarskii* (see figure 2 in Mayr and Peters 1999).