

A new Eocene swift-like bird with a peculiar feathering

GERALD MAYR*

Forschungsinstitut Senckenberg, Division of Ornithology, Senckenberganlage 25, D-60325 Frankfurt/M., Germany

A new taxon of swift-like birds is described from the Middle Eocene of Messel (Germany). It is tentatively assigned to the extinct family Jungornithidae and exhibits a completely unexpected feathering, which contrasts sharply with that of recent swifts. The short and rounded wings clearly show that it was not adapted to gliding, but might have caught its prey by sallying flights from a perch. The tail of the new taxon is very long and the tail feathers are broad and nearly symmetrical. The phylogenetic relationships between the Jungornithidae and other apodiform birds are still not convincingly resolved. The early Oligocene genus *Jungornis* itself shares unique derived characters with hummingbirds which are, however, absent in the Eocene genus *Argornis* and in the new taxon from Messel.

Swifts are classified into two recent families, the Australasian Hemiprocnidae (tree swifts) and the Apodidae (true swifts), which have a worldwide distribution. Both families differ in a number of osteological features, and especially concerning the structure of the wing skeleton, the Hemiprocnidae exhibit a less derived morphology than the Apodidae.

Most recent authors consider the Trochilidae (hummingbirds) to be the closest extant relatives of swifts and both taxa are usually united in a single order Apodiformes (e.g. del Hoyo *et al.* 1999). Monophyly of swifts and hummingbirds is not only supported by derived morphological characters, but also by biochemical and molecular analyses (Kitto & Wilson 1966; Cracraft 1981; Sibley & Ahlquist 1990; Johansson *et al.* 2001; Mayr 2002).

A recent phylogenetic analysis by Mayr (2002) provided strong evidence that the Aegothelidae (owlet-nightjars) are the sister taxon of the Apodiformes.

THE EARLY TERTIARY FOSSIL RECORD OF APODIFORM BIRDS

So far, no pre-Quaternary fossils of hummingbirds are known. However, swifts have a fairly extensive early Tertiary record, and apart from representatives of both recent families, three fossil families of swift-like birds have been identified.

Eocypselus vincenti Harrison 1984 from the Lower Eocene of England represents a tiny swift-like bird that is known from a few skeletal elements only.

Harrison (1984) classified *E. vincenti* in its own family, but Karhu (1988) even doubted its correct assignment to the Apodiformes.

The exact systematic position of the extinct Aegialornithidae Lydekker 1891 has also not yet been convincingly resolved. The family is generally considered to be closely related to the Hemiprocnidae (e.g. Harrison 1984; Karhu 1988, 1992), but this assignment is mainly based on – probably plesiomorphic – overall similarity. Members of the Aegialornithidae are especially abundant in the Upper Eocene fissure fillings of the Quercy, France (Mourer-Chauviré 1988), but Peters (1998) recently described a record of *Aegialornis* from Middle Eocene deposits of the Geiseltal, Germany. Olson (1999) tentatively assigned a tarsometatarsus from the Lower Eocene of North America to the family.

Most authors also classify *Primapus* Harrison & Walker 1975 from the Lower Eocene of England into the Aegialornithidae (e.g. Harrison & Walker 1975; Peters 1985; Karhu 1988; Mourer-Chauviré 1988). Harrison (1984), however, included *Primapus* in the Apodidae.

The genus *Cypselavus* Gaillard 1908 is known from the Upper Eocene and Lower Oligocene of the Quercy, and is generally assigned to the Hemiprocnidae (Harrison 1984; Peters 1985; Mourer-Chauviré 1988).

The earliest certain representatives of the Apodidae belong to the genus *Scaniacypselus* Harrison 1984 which includes two species. *Scaniacypselus wardi* was described by Harrison (1984) from the early Eocene of Denmark and is known from isolated

*Email: Gerald.Mayr@senckenberg.de.

wing elements of a single specimen only. *Scania-cypselus szarskii* (Peters 1985) occurs in the Middle Eocene deposits of Messel, Germany (Peters 1985; Mayr & Peters 1999) and is represented by several articulated skeletons. There is also one specimen in which the feathering is excellently preserved (Mayr & Peters 1999). Like its recent relatives, *S. szarskii* had greatly elongated primaries; the tail was short and hardly forked.

Mlíkovský (1989) described an isolated tibiotarsus from the Quercy as a new species of the recent genus *Cypseloides* (Apodidae), *C. mourerchauvireae*. However, the validity of this new taxon, let alone its assignment to *Cypseloides*, needs further confirmation. At least judging from the illustrations, the bone closely resembles the tibiotarsus of *Aegialornis*, with which it has not been compared in the original description (in size it corresponds to the tibiotarsus of *A. gallicus*; see Mourer-Chauviré 1988).

Other fossil Apodidae are known from Miocene deposits and were assigned to the Cypseloidinae (Collins 1976) and Apodinae (Ballmann 1976). Only the latter assignment, however, was supported by derived characters, and the similarity of lower Miocene swifts to the Cypseloidinae might well be plesiomorphic.

Among the most enigmatic taxa of swift-like birds are the members of the extinct family Jungornithidae. The first species assigned to this family was *Jungornis tesselatus* Karhu 1988 from the Lower Oligocene of the Northern Caucasus (Karhu 1988). Karhu (1988, 1992) noted several derived features in which *Jungornis* differs from recent swifts and corresponds with hummingbirds. Recently, Karhu (1999) described a second species of the Jungornithidae, *Argornis caucasicus*, from the Upper Eocene of the Northern Caucasus, which exhibits a less specialized wing morphology than *J. tesselatus*. Both *Jungornis* and *Argornis* are known only from wing elements of single specimens. An isolated coracoid from the Upper Eocene of the Quercy, which was assigned to *Cypselavus gallicus* by Mourer-Chauviré (1978), was described by Karhu (1988) as a new species of the Jungornithidae, *Palescyvus escampensis* (see Discussion below).

I herein describe a new apodiform bird from the Middle Eocene (~49 million years ago) deposits of Messel (Hessen, Germany), which closely resembles *Argornis caucasicus* in skeletal morphology. In the new taxon the feathering is excellently preserved and strikingly different from that of recent swifts. It reveals that there was a high diversity among apodiform birds in the early Tertiary, and that the

evolution of apodiform birds is more complicated than previously thought.

A survey of the fossil avifauna of Messel was given by Mayr (2000), and general information on the site can be found in Schaal and Ziegler (1988) and Mayr (2001).

MATERIAL AND METHODS

Dimensions are given in millimetres and refer to the greatest length along the longitudinal axis of the bone. For claws, the distance between the tuberculum extensorium and the apex phalangis was measured. The phalanges of the toes are numbered from the proximal to the distal, thus dI p2 means the distal (second) phalanx of the first toe. The wing area was measured following Pennycuick (1985, p. 223). If not indicated otherwise, the anatomical terminology follows Baumel and Witmer (1993). The fossil specimens are deposited in the Hessisches Landesmuseum (HLMD), Darmstadt, Germany.

SYSTEMATIC PALAEOLOGY

Apodiformes Peters 1940

?Jungornithidae (*sensu* Karhu 1999)

An assignment of the new taxon to the Apodiformes is supported by the following characters, which I consider to be derived within neognathous birds: beak wide and very short, with a pointed tip and long narial openings; extremitas omalis of coracoid hooked; processus lateralis of coracoid strongly reduced; humerus greatly abbreviated and with large, ventrally protruding proximal end; manus longer than humerus; phalanx proximalis digiti majoris with distinct processus internus indicis; distal end of tibiotarsus with small condyli and wide incisura intercondylaris. A presumably plesiomorphic feature shared with recent Apodiformes is the presence of a foramen nervi supracoracoidei, which is absent in most other 'higher' landbirds.

In overall morphology, the new taxon from Messel is very similar to *Argornis*; it shares the following combination of characters with this genus and with *Jungornis*: (1) humerus with very large and tapering crista deltopectoralis; (2) processus supracondylaris dorsalis (humerus) very small; (3) ventro-proximal edge of cotyla ventralis (ulna) weakly pronounced and tuberculum ligamenti collateralis ventralis very large; (4) facies articulares coracoidei (sternum) widely separated; (5) processus lateralis of coracoid protruding beyond the level of the angulus lateralis.

Character (1) is derived within Apodiformes and only found in Jungornithidae (*sensu* Karhu 1999) and Apodidae. Character (3), presumably, is also derived and shared by Jungornithidae and Trochilidae. Characters (2), (4) and (5) are probably plesiomorphic but distinguish Jungornithidae from Apodidae and Trochilidae. Owing to preservation, other diagnostic characters of the Jungornithidae which were listed by Karhu (1999) are not clearly visible in the new specimen. Although the Jungornithidae (*sensu* Karhu 1999) exhibit a very characteristic morphology, monophyly of *Argornis* and *Jungornis* has not been established with unique derived characters so far; for this reason the classification of the new taxon from Messel is tentative (see Discussion).

Parargornis, gen. nov.

DIAGNOSIS

Parargornis gen. nov. includes very small birds which are characterized by: humerus similar in proportions to that of *Argornis*, with weakly developed and distally situated processus supracondylaris dorsalis; carpometacarpus slightly shorter than humerus; phalanx proximalis digiti majoris not fenestrated; legs long; tarsometatarsus with large and medially protruding trochlea metatarsi II; claw of hallux straight and longer than those of three anterior toes; wings very short and rounded; tail long with nearly symmetrical rectrices.

DIFFERENTIAL DIAGNOSIS

Parargornis gen. nov. differs from

- *Argornis* Karhu 1999 in: carpometacarpus relatively shorter; phalanx proximalis digiti majoris not fenestrated.
- *Cypselavus* Gaillard 1908 in: humerus slightly more abbreviated and stouter, without ventrally protruding tuberculum supracondylare ventrale; crista deltopectoralis situated somewhat further proximally.
- *Jungornis* Karhu 1988 in: humerus less abbreviated; caput humeri without distal enlargement; no ventrally protruding tuberculum musculi pronator superficialis (terminology after Karhu 1988).
- *Eocypselus* Harrison 1984 in: humerus much more abbreviated; crista deltopectoralis larger and more tapering; olecranon (ulna) narrower and more pronounced.

- *Aegialornis* Lydekker 1891 in: humerus much more abbreviated; crista deltopectoralis situated further proximally; processus supracondylaris dorsalis smaller.

- *Primapus* Harrison & Walker 1975 in: processus supracondylaris dorsalis smaller and situated further distally; crista bicipitalis less developed; crista deltopectoralis larger.

- *Scaniacypselus* Harrison 1984 in: humerus less abbreviated; processus supracondylaris dorsalis much smaller; manus relatively shorter (only known from *S. szarskii*); legs relatively longer (only known from *S. szarskii*); wings shorter and broader, and tail much longer (only known from *S. szarskii*).

ETYMOLOGY

Para (Gr.): near, the generic name refers to the great morphological similarity between the new taxon and *Argornis*. It is masculine in gender.

Parargornis messelensis, sp. nov.

HOLOTYPE

HLMD Be 163 + 193 (complete, articulated skeleton on two slabs; Figs 1–9).

DIAGNOSIS

As for genus.

TYPE LOCALITY AND HORIZON

Messel (Hessen, Germany), Lower Middle Eocene.

DIMENSIONS OF HOLOTYPE

(Dimensions of *Argornis caucasicus* in square brackets, after Karhu 1999): Coracoid, 9.6 (r) [10.0]; humerus, ~10.3 (r) [~10.4]; ulna, 16.2 (r) [~16.0]; carpometacarpus, 9.6 (l), 9.7 (r) [~11.6]; femur, 12.1 (r); tibiotarsus, ~20.1 (l), 20.3 (r); tarsometatarsus, ~9.3 (l), 9.3 (r). Pedal phalanges: dI p1, ~4.5; dI p2, 3.0; dII p1, 2.4; dII p3, ~2.0; dIII p1, 2.5; dIII p2, 2.5; dIII p3, 3.1; dIII p4, 2.8; dIV p1, 1.6; dIV p2, 1.6; dIV p3, 1.9; dIV p4, 2.2; dIV p5, 2.4.

ETYMOLOGY

The specific name refers to the type locality.

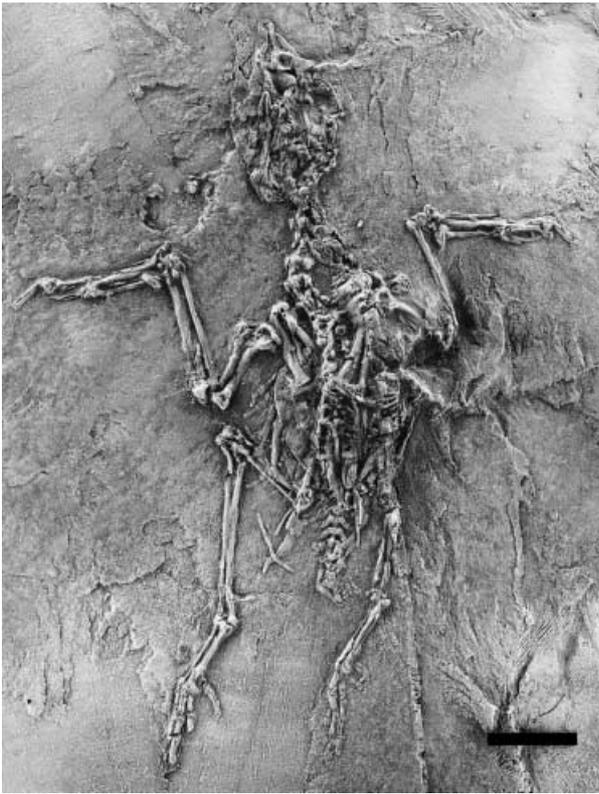


Figure 1. *Parargornis messelensis*, holotype (HLMD Be 163), skeleton in ventral view. Coated with ammonium chloride to enhance contrast; scale bar equals 10 mm.

REMARKS

Mayr and Peters (1999) described a fragmentary cranial half of an articulated skeleton of a swift-like bird from Messel which does not belong to *Scaniacypselus szarskii*. In size, this bird (HLMD Me 15405, Mayr & Peters 1999: Fig. 3) corresponds to *Parargornis messelensis*, gen. nov., sp. nov. Although its beak appears to be longer than in the type of *P. messelensis*, this could be an artefact of preservation. Unfortunately, specimen HLMD Me 15405 is too poorly preserved to make a reliable assignment to either *Parargornis* or another apodiform taxon. Other specimens of *Parargornis messelensis*, gen. nov., sp. nov. are currently unknown.

DESCRIPTION AND COMPARISON

The poorly preserved skull has similar proportions to that of recent swifts. The beak is short and wide, with a pointed tip, and measures about one-third of the entire length of the skull. The narial openings are



Figure 2. *Parargornis messelensis*, X-ray photograph of specimen HLMD Be 163.

very long. The ossa maxillaria are similar in shape to those of recent swifts, and are also widely separated. The part of the frontale between the orbitae is slightly wider than in recent *Hemiprocne comata* (in the extant Common Swift *Apus apus* it is much narrower).

The lacunae interzygapophysiales of the cervical vertebrae are deep, but otherwise the vertebrae do not allow a meaningful description. Six free tail vertebrae can be counted, which bear long processus transversi.

The coracoid resembles the corresponding bone of *Jungornis* and *Argornis*. The extremitas omalis is relatively smaller than in recent Apodidae and Hemiprocnidae. The processus procoracoideus (visible on the left side of HLMD Be 193) is well-developed and of similar shape to *Argornis* (Karhu 1999: Fig. 3). As in all other apodiform birds, but contrary to the majority of other 'higher' landbirds, a foramen nervi supracoracoidei is present (Fig. 5). The angulus medialis protrudes far medially. As in *Jungornis* and *Argornis*, the processus lateralis reaches beyond the level of the angulus lateralis (HLMD Be 193, right side; Fig. 5).

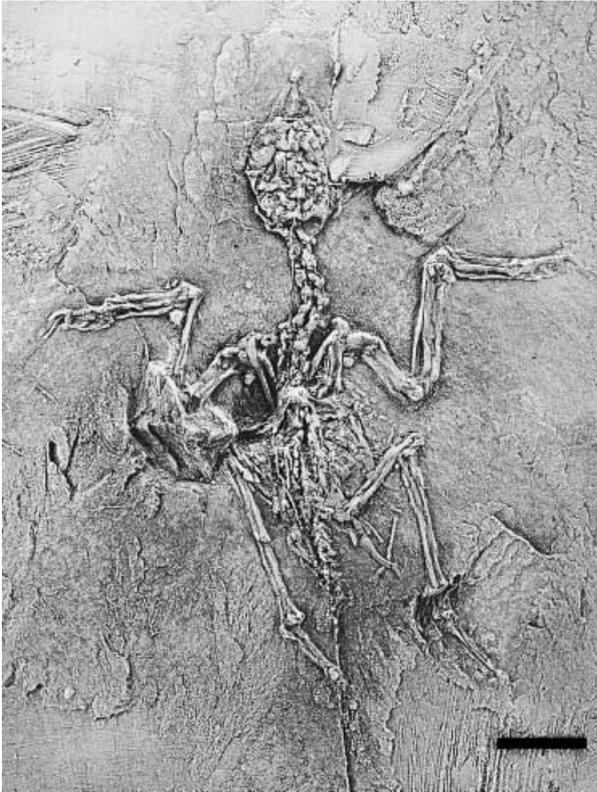


Figure 3. *Parargornis messelensis*, holotype (HLMD Be 193), contrast; scale bar equals 10 mm.

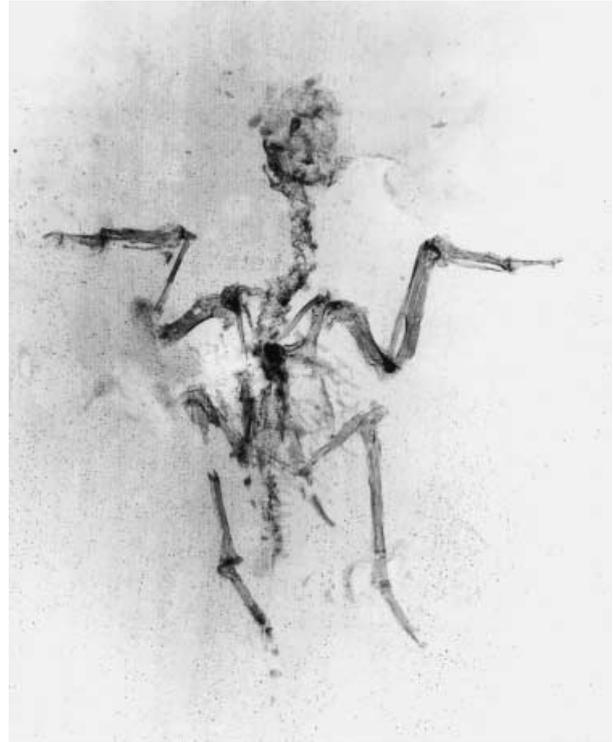


Figure 4. *Parargornis messelensis*, X-ray photograph of specimen HLMD Be 193.

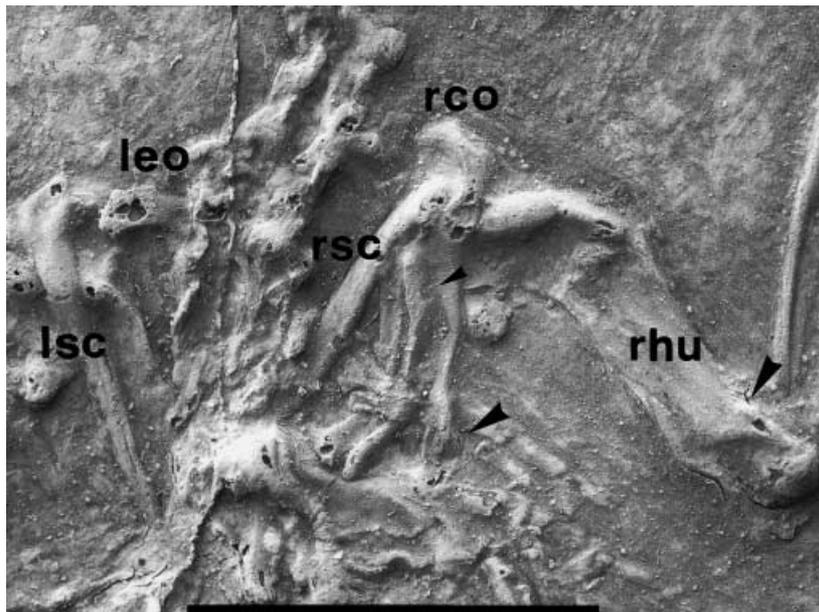


Figure 5. *Parargornis messelensis*, holotype (HLMD Be 193), detail of the pectoral region, dorsal view. Coated with ammonium chloride to enhance contrast; scale bar equals 10 mm. Abbreviations: leo – left extremitas omalis of furcula, lsc – left scapula, rco – right coracoid, rhu – right humerus, rsc – right scapula. The small arrow indicates the foramen nervi supracoracoidei (which is poorly visible in the coated specimen), the large left arrow points to the processus lateralis, the large right arrow to the processus supracoracoideus dorsalis.

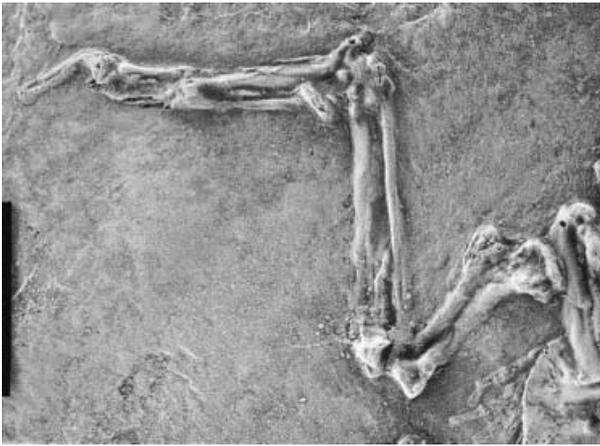


Figure 6. *Parargornis messelensis*, holotype (HLMD Be 163), right wing in ventral view. Coated with ammonium chloride to enhance contrast; scale bar equals 10 mm.

The extremitas omalis of the furcula (HLMD Be 193, left side; Fig. 5) is of similar shape to that of *Argornis*. As in the latter genus and *Jungornis*, but contrary to recent Apodiformes, the transition between the scapus claviculae and the processus acromialis is not pronounced (see Karhu 1988: Fig. 5). The extremitas sternalis (HLMD Be 193) is slightly wider than in *Argornis*.

The scapula bears a short acromion. As far as preservation allows comparison, it resembles the scapula of *Jungornis* and *Argornis*.

The sternum appears to have been of similar relative length to that of *Jungornis* and recent Hemiprocnidae, and is not as elongated as in Apodidae and Trochilidae. As preserved, the sternal ends of the coracoids are widely separated, which indicates that the facies articulares coracoidei of the sternum are also widely separated, as in *Jungornis* (in recent Apodiformes they are situated close together). As in *Jungornis*, the carina sterni is somewhat lower than in recent Apodiformes (the sternum of *Argornis* is too fragmentarily preserved to allow meaningful comparisons). The caudal margin of the sternum appears to bear a small incisura lateralis (HLMD Be 193, right side; HLMD Be 163, right side), whereas in recent Hemiprocnidae and Apodidae, as well as in recent hummingbirds, there are no incisions at all (although recent swifts often exhibit foramina in various parts of the corpus sterni). In *Jungornis* there is a fenestra lateralis.

The humerus of *Parargornis messelensis* (Figs 5 and 6) has similar proportions to that of *Argornis caucasicus*, *Cypselavus gallicus* and recent *Hemiproctne longipennis*. It is less abbreviated than the corresponding bone of *Jungornis*, the Trochilidae, and recent and fossil Apodidae. The proximal end is large and strongly

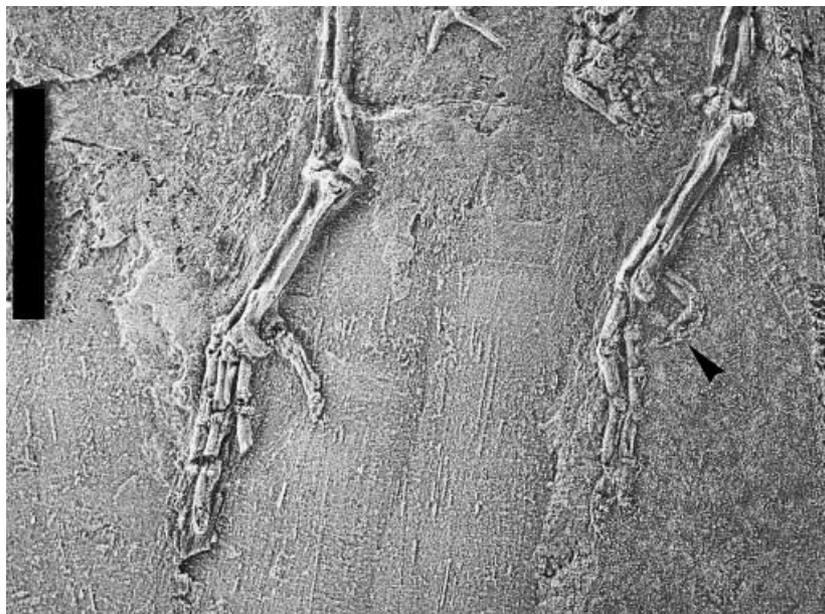


Figure 7. *Parargornis messelensis*, holotype (HLMD Be 163), detail of the feet. The arrow indicates the large claw on the hind toe. Coated with ammonium chloride to enhance contrast; scale bar equals 10 mm.

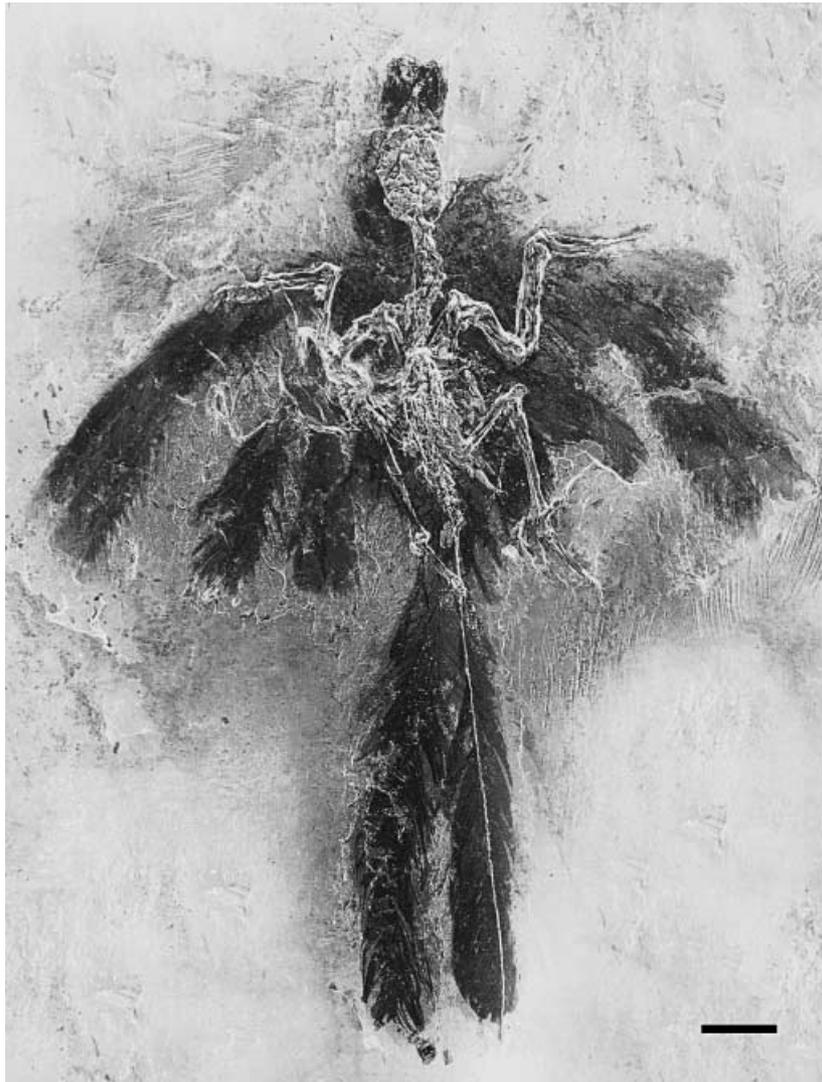


Figure 8. *Parargornis messelensis*, holotype (HLMD Be 193), uncoated specimen to show the excellently preserved feathering; scale bar equals 10 mm.

protrudes ventrally. The caput humeri directs caudally; like in *Argornis* it lacks the distal enlargement which is characteristic for *Jungornis*. The crista deltopectoralis is large and tapering (visible on the left side of HLMD Be 163). As in *Jungornis* and *Argornis*, the processus supracondylaris dorsalis is weakly developed (Fig. 5). It is situated in a similar relative position to that of *Argornis*, about one-quarter of the length of the humerus from the distal end. Whether there was a second, distal process as in *Argornis* and *Cypselavus* cannot be said with certainty, since the area directly below the (?proximal) processus supracondylaris dorsalis is broken (the corresponding

part of the humerus is only visible on the right side of HLMD Be 193). However, if a second process was present, it must have been situated directly next to the one that is preserved (in *Argornis* the two processus are also situated close together, whereas they are more distant in *Cypselavus*). The condylus ventralis is elongated, the tuberculum supracondylare ventrale is in a similar relative position to *Argornis*. The sulcus humerotricipitalis is not as deeply excavated as in recent Apodidae.

As in recent swifts, the ulna greatly exceeds the humerus in length (Fig. 6), whereas in hummingbirds it is as short as the humerus. As far as is

comparable, its proximal end resembles the proximal ulna of *Argornis caucasicus*. As in the latter, the olecranon is more strongly developed than in *Aegialornis* and recent Hemiprocnidae (HLMD Be 163, right side). In recent Apodidae, the olecranon is pronounced in Apodinae and Chaeturinae but short in the Cypseloidinae (Collins 1976). As in *Jungornis*, *Argornis* and recent Trochilidae, the ventro-proximal edge of the cotyla ventralis is weakly pronounced (HLMD Be 163, right side), and the tuberculum ligamenti collateralis ventralis very large (in recent swifts it is distinctly smaller).

The carpometacarpus (Fig. 6) resembles that of *Argornis caucasicus* too, but is somewhat shorter than the humerus (in *Argornis* it is slightly longer). The processus extensorius strongly protrudes cranial. The os metacarpale minus runs parallel to the os metacarpale majus.

The phalanx digiti alulae lacks a claw, which is present in recent Apodidae but absent in the Hemiprocnidae. As in most recent swifts but contrary to *Argornis*, the phalanx proximalis digiti majoris is not fenestrated, and like in all other swift-like birds it bears a well-developed processus internus indicis (terminology after Stegmann 1963). On both sides of the skeleton, the distal part of the phalanx distalis digiti majoris is strongly deflected. I consider this peculiar morphology to be of taphonomic origin, otherwise it would distinguish *Parargornis* from all other avian taxa (in *Argornis*, this phalanx is straight).

The pelvis is poorly preserved but appears to have had similar proportions to that of recent swifts. As in the latter, the alae ischii are very narrow.

Details of the femur cannot be discerned.

The tibiotarsus is long and slender, much longer than in *Scaniacypselus szarskii*. The condyli are small and of similar size, the incisura intercondylaris is wide. The trochlea cartilaginis tibialis is not as deeply grooved as in recent Hemiprocnidae and Apodinae; in the Cypseloidinae as well as in the Aegialornithidae it is also shallow.

The tarsometatarsus has similar proportions to that of the Aegialornithidae, in most recent Apodiformes it is more abbreviated. The hypotarsus exhibits three cristae of similar height, whereas in most recent Apodidae only a crista medialis is present. The foramen vasculare distale appears to have been rather small. Concerning the morphology of its distal end, the bone most closely resembles the tarsometatarsus of recent Hemiprocnidae. As in the latter, the trochlea metatarsi II is very large and strongly

protrudes medially. The trochlea metatarsi III is small and medio-laterally narrow.

The toes (Fig. 7) are fairly long, the third toe is the longest and exceeds the tarsometatarsus in length. The pedal phalanges have the usual number, as in recent Hemiprocnidae, the three proximal phalanges of the fourth toe are somewhat shorter than the fourth phalanx. In some recent Apodidae (e.g. *Apus*, *Panyptila* and *Cypsiurus*), the proximal pedal phalanges of the three anterior toes are greatly abbreviated, and the most proximal phalanges of the third and fourth toe are completely reduced. The hallux is of similar length to that of recent Hemiprocnidae. The claws of the three anterior toes are robust, only slightly curved and resemble those of recent Hemiprocnidae, too. As in the latter, but contrary to recent Apodidae, the tubercula flexoria are weakly developed. The claw of the hallux is longer and more straight than those of the anterior toes.

The specimen exhibits well-preserved feather remains (Fig. 8), and even the barbulae can be discerned. Whereas all recent swifts have very long, narrow and pointed wings, those of *Parargornis* are short, broad and rounded. In hummingbirds also the wing is very short, but much narrower than in *Parargornis* and pointed, too. The approximate length of the four outermost primaries is as follows (the length of the primaries of the equally sized 'Messel-swift' *Scaniacypselus szarskii* is given in parentheses): ?P10: ~25 (~74); ?P9: ~37 (~72); ?P8: ~43 (~72); ?P7: ~45 (~62); the innermost (?) primary (?P1) measures ~46 (~31). Hence contrary to what is seen in recent swifts and hummingbirds, in *Parargornis* the outermost primaries are shorter than the proximally adjacent ones. Furthermore, the primaries of *Parargornis* are only slightly asymmetric, and the secondaries are distinctly longer than in recent swifts and hummingbirds. Wing coverts are preserved on the left wing of HLMD Be 193 and measure about 15 mm.

Two long, broad and fairly symmetric tail feathers are preserved which measure about 65 mm. A third one is situated between these feathers and is about 35 mm long. Apart from these three feathers, only a fourth, growing tail feather can be discerned, which might indicate that the specimen is a moulting individual. In all recent swifts with elongated tail feathers (*Panyptila*, *Hemiproctne*), these are narrow and tapering, not broad and symmetric as in *Parargornis*. A similar tail (at least in shape) is, however, found among some recent hummingbirds (*Lesbia nuna*, *Sappho sparganura*).

DISCUSSION

Parargornis messelensis, gen. nov., sp. nov. exhibits a completely unexpected wing morphology, which sharply contrasts with that of recent swifts. The short and rounded wings clearly show that the new taxon was not adapted to gliding, and was certainly less aerial than recent true swifts. According to the shape of its bill, *Parargornis* was catching insects on the wing, although it must have had a different feeding strategy from recent swifts, and most other aerial insectivores which tend to have long and narrow wings.

The fact that fossils of *Parargornis* are rarer than those of the 'Messel-swift' *Scaniacypselus* (of which at least six specimens are known to me) might indicate that the former mainly caught its prey in the dense vegetation surrounding the ancient Messel lake, whereas *Scaniacypselus* certainly also hunted insects above the lake surface, and accordingly had a greater chance to become fossilized. This assumption accords with the feathering of the new taxon, because short, broad wings and a long tail are often found in birds which are adapted to agile manoeuvrability in dense vegetation, like hawks, owls or turacos (e.g. Rayner 1988, p. 30).

Small birds with similar feathering also occur among some recent passeriform families, e.g. ovenbirds (Furnariidae), antbirds (Formicariidae) and wrens (Troglodytidae). Most unusual, and not found in any recent avian taxon, however, is the combination of short and broad wings with greatly abbreviated humeri, as in *Parargornis*.

Short wings generally have a high wing loading (weight supported by unit wing area) and allow high wing beat frequencies and fast flight (Pennycuik 1985; Rayner 1988). Through the concentration of wing mass near the humeral joint, abbreviation of the humerus further leads to a decreasing inertia moment of the wing, and also favours intensive flapping flight (Karhu 1992). However, the high wing loading also results in high energy costs for flight (Rayner 1988) which, together with the long legs of *Parargornis* and the well-developed hind toe, might indicate that the Eocene genus caught its prey by sallying flights from a perch. The aspect ratio (wing span squared, divided by area) is very low in *Parargornis* (about 5.3, with an estimated wing area of 25 cm² and a wing span of 115 mm), and its combination with a presumably high wing loading is rare among recent birds but cannot be related to a specific flight technique (Rayner 1988, p. 40).

Like its recent relatives, *Parargornis* exhibits a well-developed processus internus indicis on the proximal phalanx of the major wing digit. This process leads the tendon of musculus interosseus ventralis, which flexes the distal phalanx of the major wing digit. Stegmann (1963) considered a well-developed process to be functionally related to increasing aerodynamic forces on the distal primaries. This process is usually therefore well developed in rapidly flying species with long and pointed wings (Stegmann 1963). Its presence in *Parargornis* is unexpected and might indicate either that the short wings of the Eocene genus evolved from typical swift-like wings with long primaries, or that it might be due to a high wing beat frequency.

The phylogenetic relationships between the Jungornithidae (*sensu* Karhu 1999) and other apodiform birds have not been convincingly resolved so far. Contrary to most other authors, who proceed from monophyly of the taxon (Hemiprocnidae + Apodidae), Karhu (1988, p. 87; 1992, p. 383) considered Jungornithidae, Apodidae and Trochilidae to be monophyletic. He did not comment explicitly on the exact phylogenetic relationships between the three families, but – because of their absence in *Argornis* – ascribed the unique derived features shared by *Jungornis* and recent Trochilidae (most notably a distal protrusion of the caput humeri, a strongly protruding tuberculum musculi pronator superficialis, and a crest distal to the processus supracondylaris dorsalis) to parallel evolution (Karhu 1999).

However, if swifts and hummingbirds are monophyletic and if owl-nightjars are their sister taxon (Mayr 2002), one might expect that the ancestor of hummingbirds had a 'swift-like' or 'aegothelid' beak also. Given the unique derived characters shared by *Jungornis* and recent hummingbirds, as well as the peculiar wing morphology of *Parargornis*, it is thus tempting to assume that the Trochilidae (which also have unusually short wings) evolved from a jungornithid-like ancestor.

A presumably derived character shared by *Argornis*, *Parargornis*, *Jungornis* and recent Trochilidae is the weakly pronounced ventro-proximal edge of the cotyla ventralis on the proximal end of the ulna. According to Karhu (1999), this feature facilitates rotation of the elbow joint in the spread wing. Although hummingbirds have a much narrower, semi-elliptical wing with a high aspect ratio in which the outermost primary is the longest, the wing shape of *Parargornis* does not rule out the possibility that it was capable of hovering, which, for shorter periods,

is also performed by many small passeriform birds with short, broad wings (e.g. Oehme 1959).

If monophyly of Trochilidae and Jungornithidae can be confirmed by future fossil specimens, the Jungornithidae *sensu* Karhu (1999) would probably be paraphyletic, with *Jungornis* being more closely related to the Trochilidae than *Argornis* and *Parargornis*, which lack the above mentioned derived features of the humerus. This would also coincide with the temporal occurrence of the taxa, as the derived trochilid characters are present in the geologically youngest taxon, *Jungornis*.

Finally, it should be noted that, although the humerus of the putative hemiprocnid *Cypselavus* is similar to that of recent Hemiprocnidae, it also resembles the corresponding bone of the contemporaneous genus *Argornis* with which it has not been compared so far. As in *Argornis*, and contrary to *Hemiprocnis*, *Cypselavus* exhibits a large, tapering crista deltopectoralis. Furthermore, the morphology of the coracoid that was assigned to *C. gallicus* by Mourer-Chauviré (1978) concords with *Jungornis*, *Argornis* and *Parargornis*. As mentioned in the introduction, this bone was described as a new taxon of the Jungornithidae by Karhu (1988). Direct examination of the specimens will have to show whether *Cypselavus gallicus* is more closely related to *Argornis* than to recent Hemiprocnidae, and whether *Palaeocypselavus escampensis* is a junior synonym of this species.

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