

Reappraisal of *Eocypselus*—a stem group apodiform from the early Eocene of Northern Europe

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Abstract *Eocypselus vincenti* is a small swift-like bird from the early Eocene of England and Denmark, whose phylogenetic affinities are controversial. Here, a new skeleton from the Danish Fur Formation is reported, in which for the first time the skull and pelvis are preserved. Further described are previously overlooked features of the other Fur Formation specimens, which bear on the systematic position of the species. It is detailed that *E. vincenti* falls outside crown group Apodiformes and represents the earliest diverging apodiform bird, with its osteology providing a link between that of apodiform birds and their morphologically disparate sister taxon, the Aegothelidae (owlet-nightjars). The poorly developed processus internus indicis on the proximal phalanx of the major wing digit indicates that *Eocypselus* had less elongated outer primaries than extant Apodiformes. Together with differences in the pectoral girdle, such as the lack of a coracoid/furcula articulation, this suggests that the fossil taxon was less well adapted than its extant relatives to feeding on the wing.

Keywords Fossil birds · Apodiformes · Fur Formation · Denmark · London Clay · England

Introduction

Eocypselus vincenti is one of the earliest fossil representatives of the Apodiformes (swifts and hummingbirds) and was first described by Harrison (1984), based on wing and pectoral

girdle bones of a single individual from the early Eocene London Clay in England. Harrison (1984) considered the species to be most closely related to the Hemiprocnidae (treeswifts), but assigned it to a new family, Eocypselidae. Classification of *Eocypselus* into the Hemiprocnidae was also advocated by Mourer-Chauviré (1988), whereas Karhu (1988) questioned the apodiform affinities of the taxon, and Mlíkovský (2002) transferred it to the “Caprimulgiformes” (nightjars and allies). A further hypothesis was put forward by Mayr (2003a), who included Trochilidae (hummingbirds) in a phylogenetic analysis and detailed that *Eocypselus* falls outside crown group Apodiformes and represents the earliest diverging apodiform taxon.

Until recently, determination of the affinities of *Eocypselus* was aggravated by the limited osteological information available from the type specimen. However, new data on this enigmatic bird became available through the study of Kristoffersen (2002), who reported two partial *Eocypselus* skeletons from the early Eocene Fur Formation of Denmark. These well-preserved fossils were described by Dyke et al. (2004), who also assigned *Eocypselus* to the Hemiprocnidae. Dyke et al. (2004) did not note a number of important osteological characteristics of *Eocypselus*, and the illustrations accompanying their paper do not allow the recognition of many details. The authors further largely restricted comparisons to extant swifts and did not appreciate similarities between *Eocypselus* and the “caprimulgiform” Aegothelidae (owlet-nightjars), whose sister group relationship to Apodiformes has been firmly established (Mayr 2002, 2010).

Because *Eocypselus* exhibits many plesiomorphic features, it is critical for an understanding of the early evolution of apodiform birds. The *Eocypselus* fossils are thus re-evaluated, and I further report a new specimen from the Fur Formation in which, for the first time, the skull and pelvis of this taxon are preserved.

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Fig. 1 *Eocypselus vincenti* Harrison, 1984 from the early Eocene Fur Formation of Denmark, specimens MGUH 26730 (a) and MGUH 26729 (b) with interpretative drawings. Coated with ammonium chloride to enhance contrast. *fis* Fish vertebrae, *fur* furcula, *ila* incisura lateralis, *imd* incisura medialis, *lcm* left carpometacarpus, *lco* left coracoid, *lfe* left femur, *lhu* left humerus, *lra* left radius, *ltb* left tibiotarsus, *ltm* left tarsometatarsus, *lul* left ulna, *ocu* os carpi ulnare, *ocr* os carpi radiale, *ppm* phalanx proximalis digiti majoris, *r* rib, *rcm* right carpometacarpus, *rco* right coracoid, *rhu* right humerus, *rra* right radius, *rsc* right scapula, *rul* right ulna, *ste* sternum

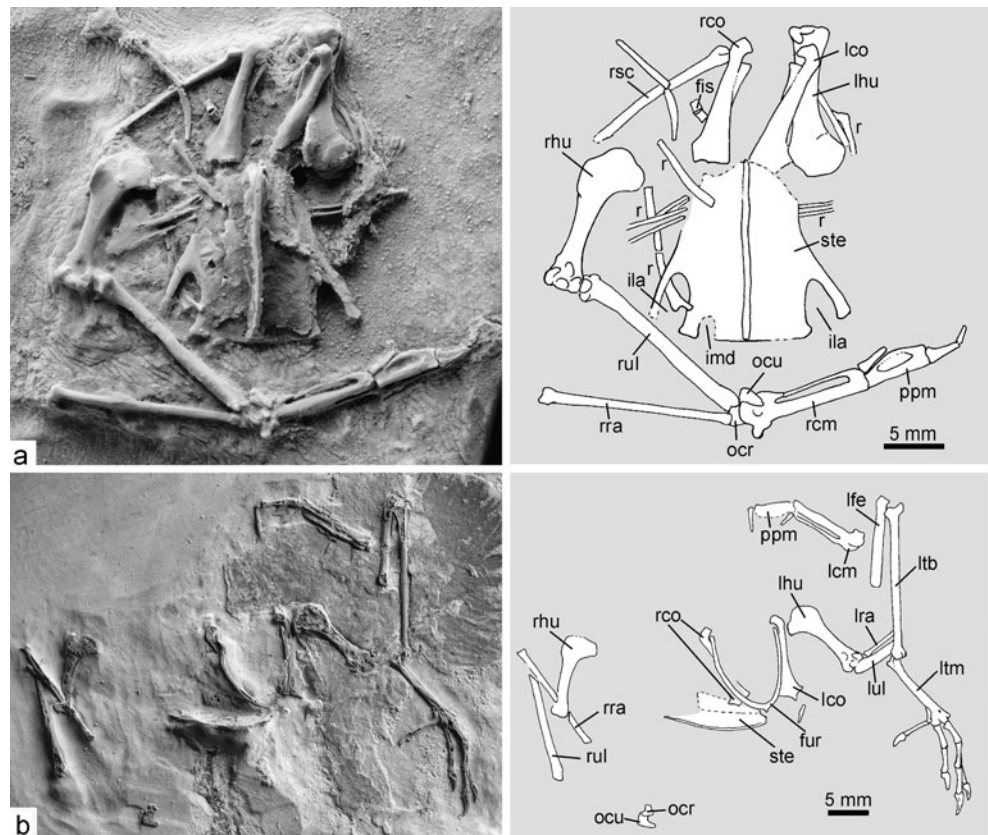


Fig. 2 *Eocypselus vincenti* Harrison, 1984 from the early Eocene Fur Formation of Denmark, specimen MGUH 29278. Silicone peel with interpretative drawing. Coated with ammonium chloride to enhance contrast. *fit* Foramina intertransversaria, *ila* incisura lateralis, *imd* incisura medialis, *lcm* left carpometacarpus, *lco* left coracoid, *lsc* left scapula, *lhu* left humerus, *ltb* left tibiotarsus, *ltm* left tarsometatarsus, *pel* pelvis, *ppm* phalanx proximalis digiti majoris, *r* rib, *rcm* right carpometacarpus, *rco* right coracoid, *rhu* right humerus, *rtb* right tibiotarsus, *rtm* right tarsometatarsus, *sku* skull, *ste* sternum, *toe* toes, *v* vertebra

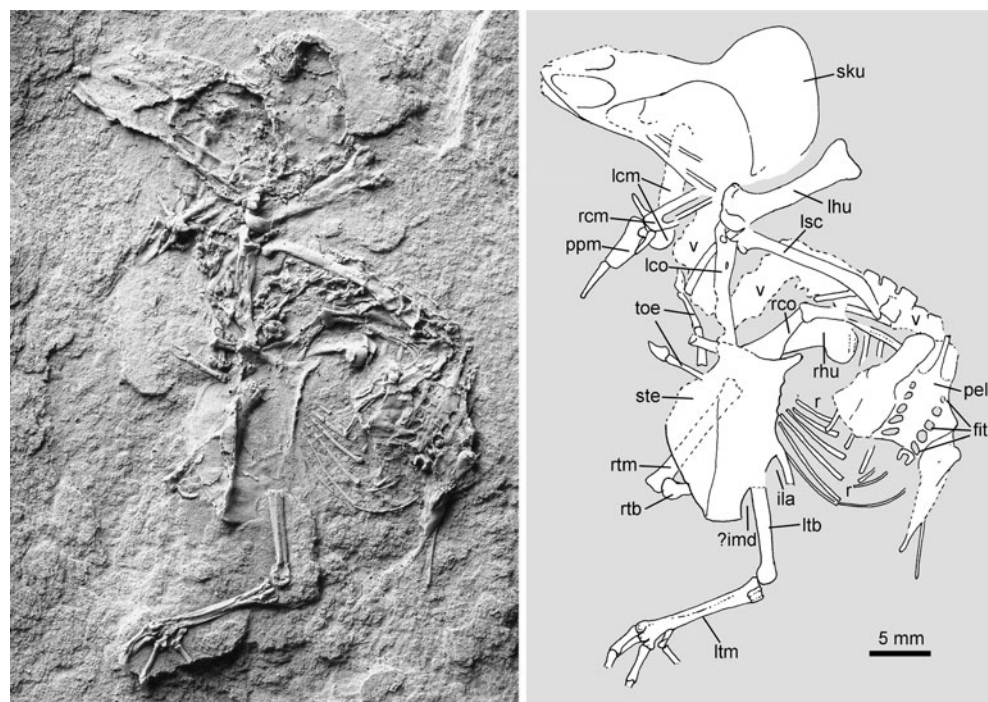


Table 1 Dimensions of major limb bones of the three Fur Formation specimens of *Eocypselus vincenti* Harrison, 1984 and the London Clay holotype in comparison (left/right, in mm)

Specimens	Coracoid	Humerus	Ulna	Carpometacarpus	Femur	Tibiotarsus	Tarsometatarsus
NHM A 5429 (holotype) ^a	10.7/-	11.9/-	~16.5 (est.)/-	–	–	–	–
MGUH 26729	11.2/-	11.5/-	—	10.2/-	11.4/-	20.2/-	10.9/-
MGUH 26730	11.4/-	12.4/12.4	~/~16.4	~/10.7	–	–	–
MGUH 29278	–	11.8/-	–	10.6/-	–	–	10.9/-

^a After Harrison (1984)

Material and methods

Osteological terminology follows Baumel and Witmer (1993). Measurements are in millimeters. Of specimen MGUH 29278, which is only preserved as an imprint in a diatomite slab, a silicone peel has been made.

Institutional abbreviations: MGUH, Geological Museum of the University of Copenhagen, Denmark; NHM, The Natural History Museum, London.

Systematic palaeontology

Apodiformes Peters, 1940

Eocypselidae Harrison, 1984

Eocypselus Harrison, 1984

Eocypselus vincenti Harrison, 1984

Referred specimens: MGUH 26729 [Fig. 1; pectoral girdle, both wings, and left foot, designated danekræ (i.e., specially protected under Danish law) DK 7]; MGUH 26730 (Fig. 1; sternum, pectoral girdle, left humerus, and right wing, designated danekræ DK 22; the specimen originally consisted of two slabs, which were glued together and acid-prepared); MGUH 29278 (Fig. 2; imprint of skeleton preserved in a slab).

Locality and horizon: Isle of Mors, Denmark, early Eocene Fur Formation. MGUH 29278 was found by Henning Bekker and purchased in 2003; for collecting details of MGUH 26729 and MGUH 26730, see Dyke et al. (2004).

Measurements: See Table 1.

Description and comparisons: Specimens MGUH 26729 and MGUH 26730 have been described by Kristoffersen (2002) and Dyke et al. (2004), and in the following only features are mentioned that went unnoticed by these authors; note that Dyke et al. (2004) did not illustrate the complete specimen MGUH 26729 and incorrectly stated that only one forelimb is preserved (Dyke et al. 2004, p. 51).

MGUH 29278 preserves an impression of the dorsal surface of the skull. In its proportions and most osteological details that can be discerned, it resembles the skull of extant swifts. The beak measures about one third of the entire length of the skull. The narial openings are large and ovate as in Aegothelidae, Hemiprocnidae and Apodidae. The postnarial bar, however, which borders the caudal end of the nostril and is formed by the processus maxillaris of the os nasale and the processus nasalis of the os maxillare, meets the arcus jugalis at an acute angle as in Aegothelidae, Trochilidae and most other birds; in extant Apodidae, by contrast, it is more dorsoventrally oriented and almost perpendicular to the os quadratojugale. If the putative impression of this bone is correctly interpreted (Fig. 3), the os ectethmoidale has a similar size to that of extant swifts; in

Fig. 3 Comparison of skulls. **a** *Eocypselus vincenti* Harrison, 1984 (MGUH 29278). **b** *Aegothales cristatus* (Aegothelidae). **c** *Cypseloides senex* (Apodidae). Fossil coated with ammonium chloride to enhance contrast. *ect* os ectethmoidale, *iof* interorbital section of os frontale, *lhu* left humerus, *pnb* postnarial bar, *ppo* processus postorbitalis. Scale bars: 5 mm

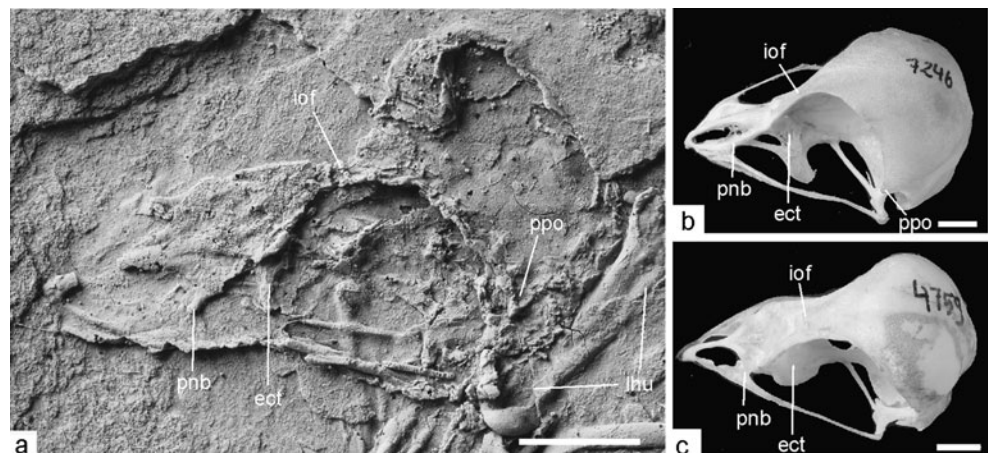
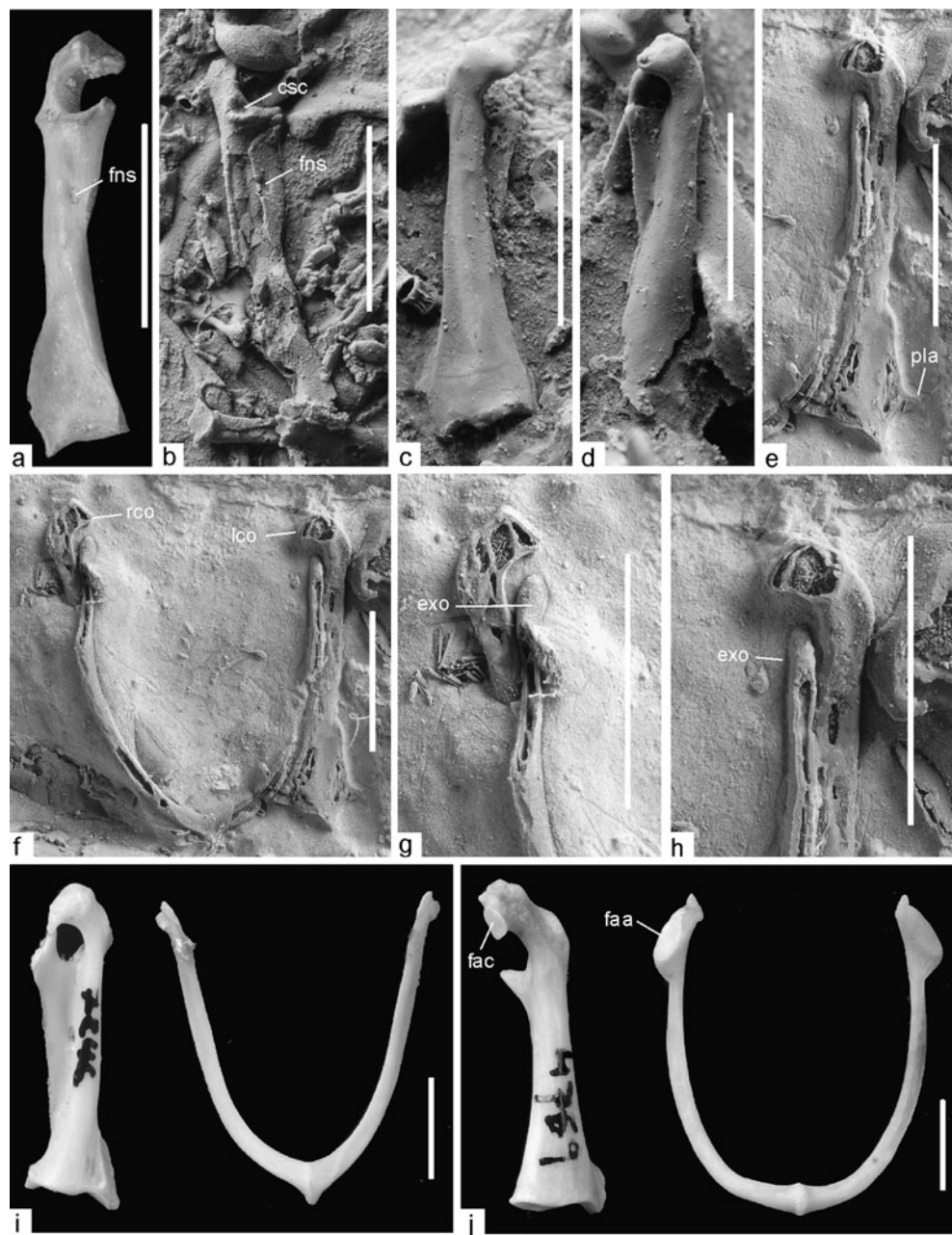


Fig. 4 Coracoid and furcula in comparison. **a–h** *Eocypselus vincenti* Harrison, 1984: **a** holotype, NHM A 5429, **b** MGUH 29278, **c, d** MGUH 26730, **e–h** MGUH 26729. **i** *Aegothales cristatus* (Aegothelidae). **j** *Cypseloides senex* (Apodidae). *csc* Cotyla scapularis, *exo* extremitas omalis of furcula, *faa* facies articularis acroracoroidea, *fac* facies articularis clavicularis, *fns* foramen nervi supracoracoidei, *lco* left coracoid, *pla* processus lateralis, *rco* right coracoid. Fossil specimens are coated with ammonium chloride to enhance contrast. Scale bars: 5 mm

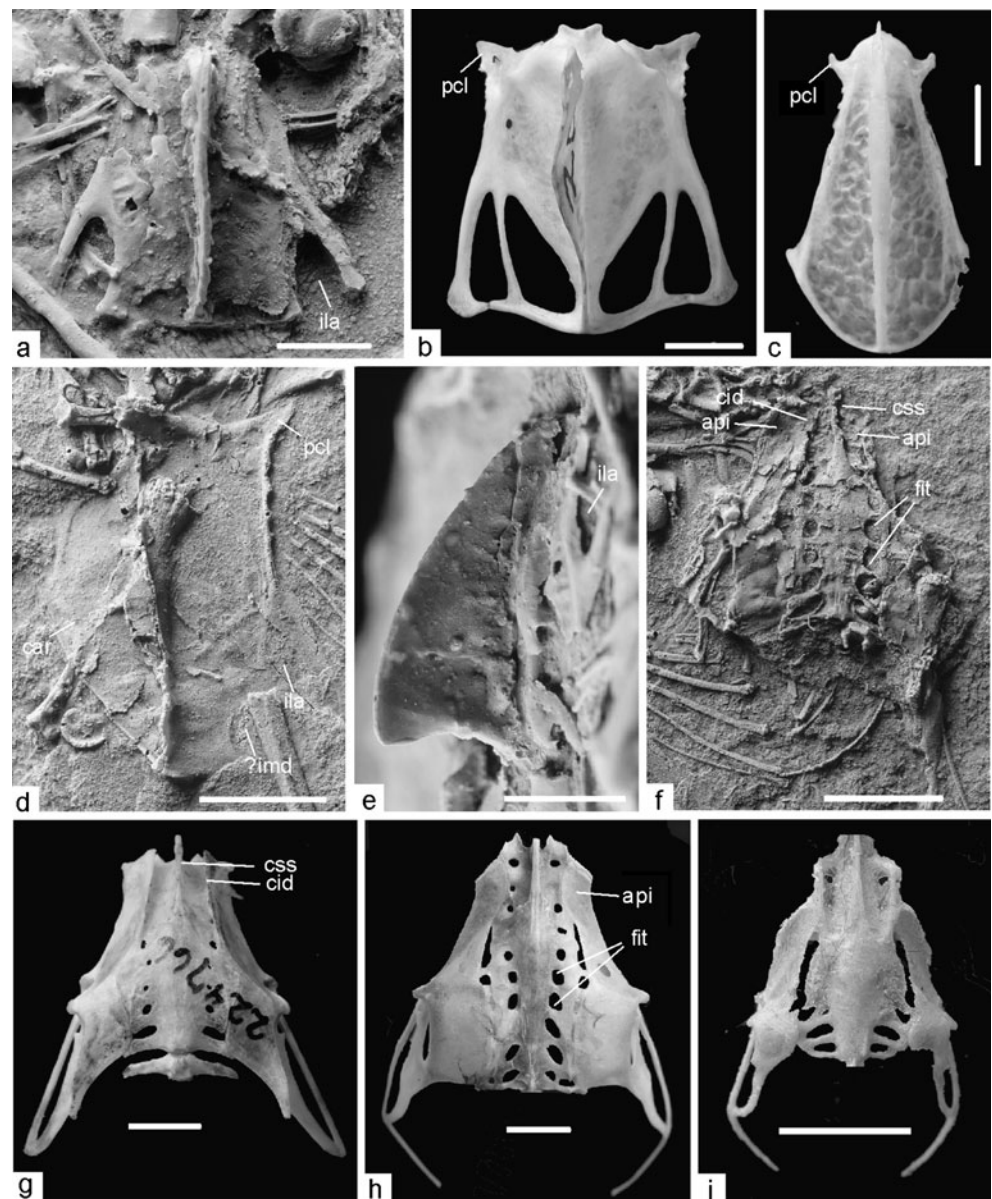


Trochilidae it is much larger, and in Aegothelidae distinctly smaller (Fig. 3). The nasofrontal section, formed by the base of the beak and the rostral part of the os frontale, is as wide as in crown group Apodiformes, whereas it is narrow in Aegothelidae. The midsection of the interorbital part of the os frontale, however, appears much narrower than that in crown group Apodiformes, and more closely approaches the condition in Aegothelidae. The processus postorbitalis is short and resembles that of Apodidae and Hemiprocnidae (in Aegothelidae it is larger and wider). Further details of the cranium and the palate are not visible.

The coracoid (Fig. 4) differs from the corresponding bone of all other—extant and fossil—Apodiformes in that the

processus lateralis of the extremitas sternalis forms a pointed projection, as it does in many non-apodiform birds. This projection is clearly visible on the extremitates sternalis of both coracoids of MGUH 26729; in the holotype coracoid of *E. vincenti*, it is broken (Fig. 4). Further, in contrast to crown group Apodiformes and the Paleogene Aegialornithidae (Mourer-Chauviré 1988), the processus acroracoroideus does not exhibit a facies articularis clavicularis (Fig. 4). Connected with the latter feature, the furcula is distinguished from that of extant apodiform birds in that the extremitas omalis lacks a facies articularis acroracoroidea, which is very prominent in crown group Apodiformes (MGUH 26729, Fig. 4). Contrary to the statement of Dyke et al. (2004, p. 51), the furcula is not

Fig. 5 Sternum (a–e) in ventral (a–c), dorsolateral (d) and lateral (e) and view, and pelvis (f–i, dorsal view) for comparison. **a, d–f** *Eocypselus vincenti* Harrison, 1984: **a, e** MGUH 26730, **d, f** MGUH 29278. **b, g** *Aegothales cristatus* (Aegothelidae). **c** *Glaucis hirsuta* (Trochilidae). **h** *Apus apus* (Apodidae). **i** *Phaethornis yaruqui* (Trochilidae). *api* Alae praeacetabularis ilii, *car* carina sterni, *cid* crista dorsolateralis ilii, *css* crista spinosa synsacri, *fit* foramina intertransversaria, *ila* incisura lateralis, *imd* incisura medialis, *pcl* processus craniolateralis. Fossil specimens are coated with ammonium chloride to enhance contrast. Scale bars: 5 mm

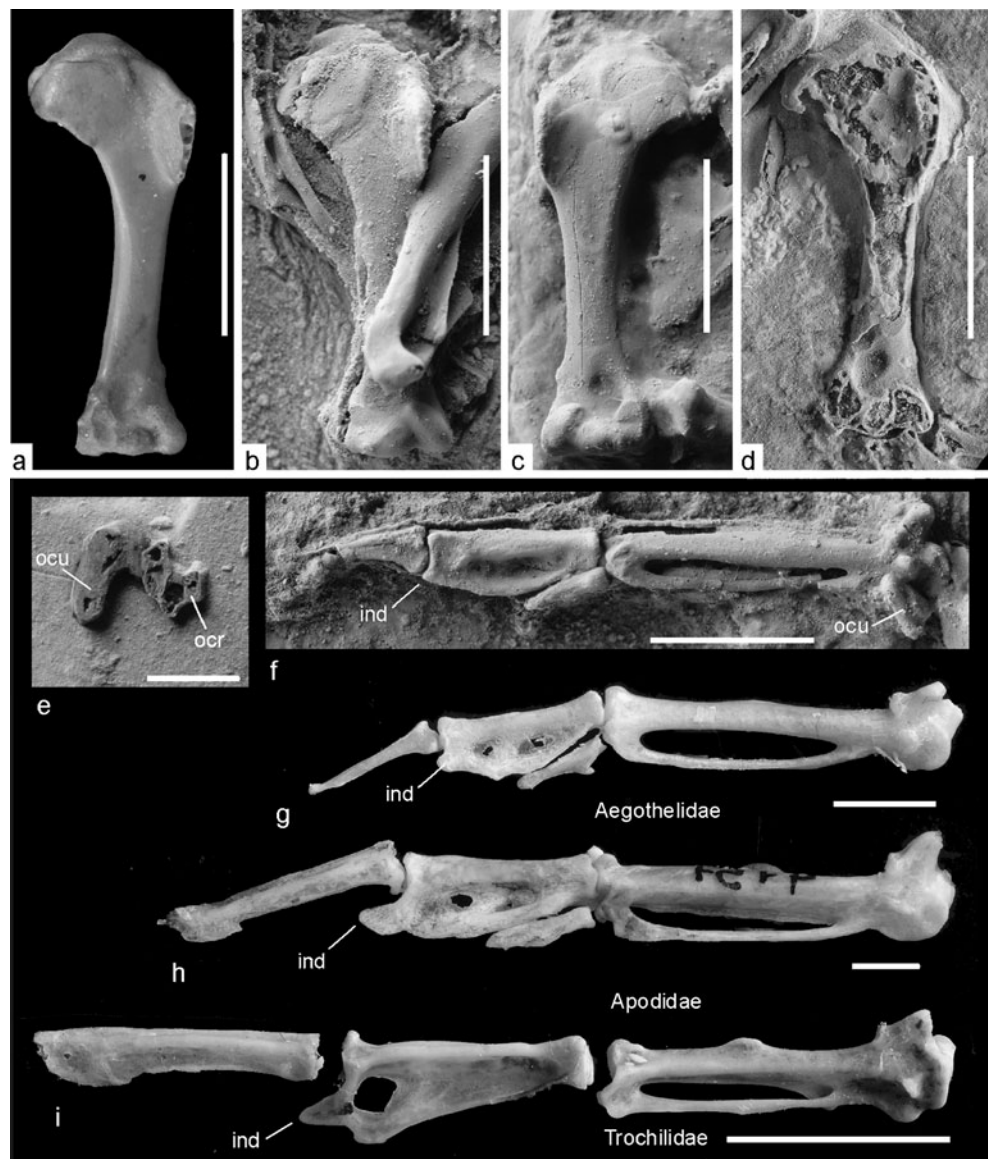


preserved as an impression in MGUH 26730, but altogether absent in this specimen (Fig. 1).

The sternum (Fig. 5) is present in all three specimens, but only MGUH 26730 and MGUH 29278 allow the recognition of salient details. In overall proportions of the corpus sterni, the bone corresponds with the sternum of Aegothelidae and Hemiprocnidae; the sternum of Trochilidae and Apodidae, by contrast, is more elongated and narrower (Fig. 5). The processus craniolaterales are pointed and very long, as in the Aegothelidae, whereas these processes are proportionally shorter and less pointed in crown group Apodiformes. Kristoffersen (2002) and Dyke et al. (2004) noted that the caudal margin of the bone bears two pairs of incisions, namely deep lateral incisions and shallow medial ones. The deep lateral incisions are well-preserved in MGUH 26730 and MGUH 29278, reaching about one third

of the length of the corpus sterni. The medial area of the caudal portion of the corpus sterni is, however, damaged in MGUH 26730, and although there appears to be a small, subcircular incisura medialis on the right side of the bone, the left side seems to have had only a lateral incision (Fig. 5). Only a small medial incision in the right half of the sternum was also indicated by Kristoffersen (1997, fig. 2), who studied MGUH 26730 before the two slabs of which the fossil originally consisted were glued together and acid-prepared. Dyke et al.'s (2004) statement that there are medial "fenestrae" in this specimen is unfounded. In MGUH 29278, the wide trabecula mediana is well-preserved, but the area between the latter and the trabecula lateralis is damaged, although the curvature of the lateral margin of the trabecula mediana suggests the presence of an incisura medialis. Six sternal ribs can be counted in MGUH 29278, five of which

Fig. 6 Humerus (a–d), ossa carpalia (e) and hand skeleton (f–i). a–f *Eocypselus vincenti* Harrison, 1984: a holotype, NHM A 5429, b, c, f MGUH 26730, d, e MGUH 26729. g *Aegothales cristatus* (Aegothelidae). h *Streptoprocne zonaris* (Apodidae), i *Phaethornis malaris* (Trochilidae). The extant bones are from the left side and were reversed to facilitate comparisons. *ind* Processus internus indicis, *ocr* os carpi radiale, *ocu* os carpi ulnare. Fossil specimens coated with ammonium chloride to enhance contrast. Scale bars: (a–d, f–i) 5 mm, (e) 2 mm



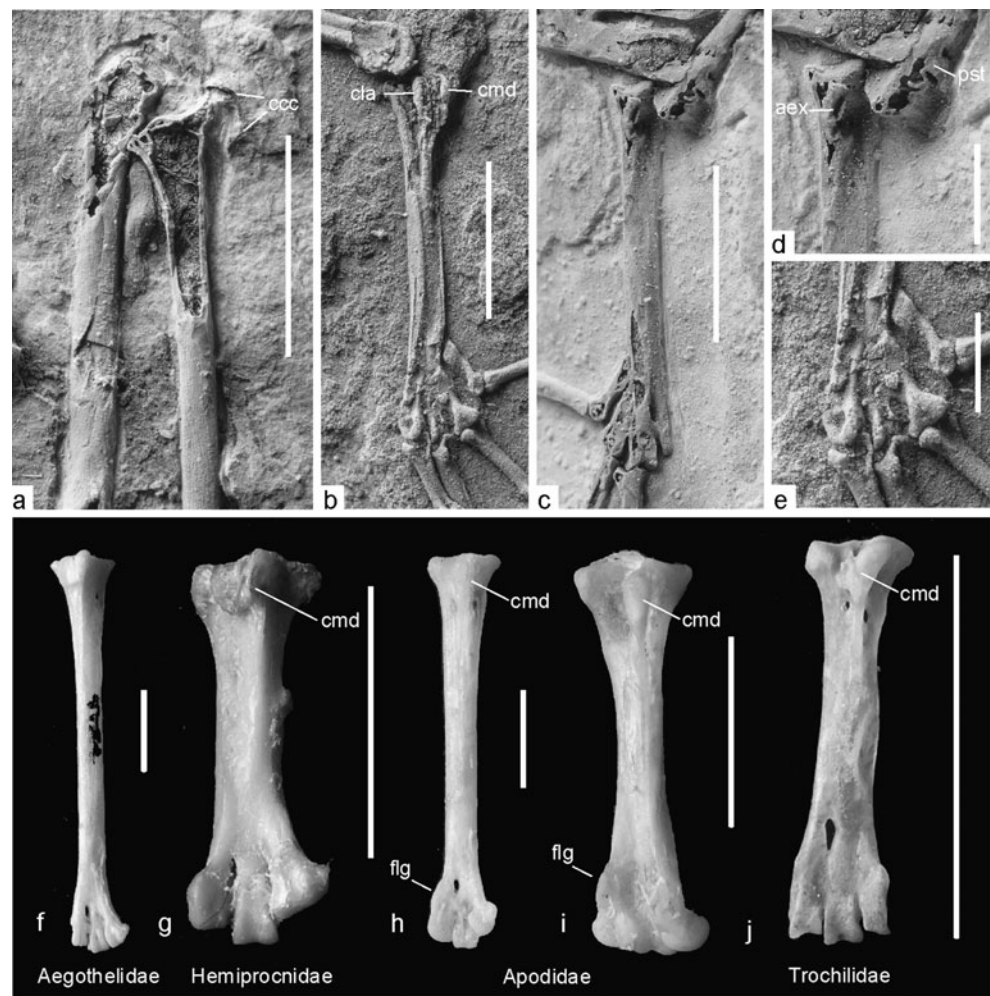
reached the sternum, as in Apodidae and Trochilidae (in Aegothelidae only four are in contact with the sternum).

The humerus of *Eocypselus* was described by Harrison (1984), but the crista deltopectoralis, which is damaged in the holotype of *E. vincenti*, is only completely preserved in MGUH 26730 (Fig. 6). It is evenly curved and better developed than the crista deltopectoralis of Trochilidae and Hemiprocnidae, but not strongly pointed as the crista deltopectoralis of the Apodidae. Only the proximal portion of the ulna is preserved in the holotype of *E. vincenti*, and the completely preserved ulna of MGUH 26730 confirms previous conclusions that the bone is less stout than that in crown group Apodiformes (with a width of 1.2 mm, the ratio length of ulna:diameter of bone is 13.6, whereas it is less than 12.0 in crown group Apodiformes; Mayr 2005). The distal end of the radius lacks the marked tubercle on the ventral surface of shaft, which is a derived characteristic

of Hemiprocnidae and Apodidae (Mayr 2003a, 2010). Except for the more centrally positioned processus pisiformis, the carpometacarpus resembles that of the Aegothelidae. The processus extensorius is not as straight as in extant swifts (Hemiprocnidae and Apodidae). Further in contrast to the latter, the processus pisiformis does not form a through-like duct for the tendon of musculus flexor digitorum profundus, which is a previously unrecognized synapomorphy of Hemiprocnidae and Apodidae. The os carpi ulnare (MGUH 26729; Fig. 6) resembles that of extant Hemiprocnidae in its shape, with the crus longum being much longer than the crus breve.

The phalanges of the major wing digit are not as strongly elongated as in the crown group Apodiformes (Fig. 6). The narrow phalanx proximalis digiti majoris is not fenestrated and is distinct from that of all other apodiform birds in that it lacks a well-developed processus internus indicis. The

Fig. 7 Tibiotarsus (a) and tarsometatarsus (b–j). a–e *Eocypselus vincenti* Harrison, 1984: a, c, d MGUH 26729, b, e MGUH 29278. f *Aegothelidae*. g *Hemiprocyne comata* (Hemiprocyidae). h *Cypseloides senex* (Apodidae). i *Apus apus* (Apodidae). j *Phaethornis malaris* (Trochilidae). Fossil specimens are coated with ammonium chloride to enhance contrast. aex arcus extensorius (incompletely ossified), ccc crista cnemialis cranialis, cla crista lateralis, cmd crista medialis, flg flange along lateroplantar surface of trochlea metatarsi IV, pst pons supratendineus. Scale bars: (a, b, e–i) 5 mm, (c, d) 2 mm



processus internus indicis is also poorly developed in Aegothelidae.

The pelvis of *Eocypselus* has not been described earlier, and its imprint exposes the dorsal surface in MGUH 29278 (Fig. 5). In its proportions, it resembles the pelvis of extant apodiform birds. As in the latter—but unlike the condition in Aegothelidae—there are well-developed foramina intertransversaria. Further as in crown group Apodiformes but in contrast to the pelvis of Aegothelidae, the alae praeacetabulares ilii are horizontally oriented and the cristae iliacae dorsales are low and widely separated from the crista spinosa synsacri (Fig. 5).

The hindlimbs of *Eocypselus* are fairly long and proportionally longer than those in the Aegialornithidae and the early Eocene *Scaniacypselus* (stem group Apodidae). In MGUH 29278, only impressions of the distal tibiotarsi are preserved, with the right one being situated next to the caudal portion of the carina sterni. In MGUH 26729, it can be discerned that the proximal end of the left tibiotarsus bears a large crista cnemialis cranialis, although the corresponding area is damaged (Fig. 7; this feature was also recognized by Kristoffersen 2002). A similarly well-

developed crista cnemialis occurs in the Apodidae, whereas it is small in Aegothelidae, Hemiprocyidae and Trochilidae.

In MGUH 29278, the left tarsometatarsus is exposed in plantar view, while the right one is hidden under the sternum. The bone is slender and as long as the carpometacarpus, whereas it is much shorter than the latter bone in all other Apodiformes except for the apodid *Cypseloidini* (*Cypseloides* and *Streptoprocne*), in which the tarsometatarsus is only slightly shorter than the carpometacarpus. The tarsometatarsus of *Eocypselus* is more slender than that of Trochilidae, Hemiprocyidae and most Apodidae (Fig. 7). On the left tarsometatarsus of MGUH 26729 an incompletely ossified arcus extensorius can be discerned (Fig. 7), a feature mentioned by neither Kristoffersen (2002) nor Dyke et al. (2004). In contrast to crown group Apodiformes, and as in Aegothelidae and most other birds, the tuberositas musculi tibialis cranialis is not strongly developed. The hypotarsus is visible in plantar view in MGUH 29278 and resembles that of the Aegothelidae in that the plantar surface forms a wide platform, which is bordered by two low cristae. In extant Apodiformes, by contrast, the crista medialis hypotarsi is much more prominent and more

strongly developed than the small crista lateralis. Whether the hypotarsus of *Eocypselus* enclosed a bony canal as in Aegothelidae, Hemiprocnidae, Trochilidae and Aegialornithidae cannot be discerned. The distal end of the bone resembles the distal tarsometatarsus of *Procuruculus minutus* Harrison and Walker, 1977 from the London Clay (Mayr 2009, fig. 12.8), whose apodiform affinities were first recognized by Olson (1985). Compared to extant birds, it is more similar to the distal tarsometatarsus of Aegothelidae than to that of crown group Apodiformes, in which the trochleae and incisurae intertrochleares are proportionally shorter. The trochlea metatarsi IV lacks the elongate flange along its lateroplantar surface, which is characteristic of extant Apodidae and, in a less pronounced form, also occurs in Hemiprocnidae and Trochilidae (Fig. 7).

The toes are very long and, contrary to extant Apodidae, the proximal phalanges of the fourth toe are not abbreviated (MGUH 29278). The trochlea of the os metatarsale I is not as wide as in extant apodiform birds.

Discussion

In addition to the morphology of the short and stocky humerus (Harrison 1984; Dyke et al. 2004), assignment of *Eocypselus* to the Apodiformes is supported by the derived presence of foramina intertransversaria on the pelvis and an, albeit incompletely ossified, arcus extensorius on the proximal tarsometatarsus (this study). In many plesiomorphic aspects of its osteology, *Eocypselus* is, however, clearly distinguished from crown group Apodiformes and more closely resembles Aegothelidae. This is especially true for (1) the presence of deep incisions in the caudal margin of the sternum, (2) the absence of an articulation between coracoid and furcula, (3) the less abbreviated ulna, (4) the absence of a well-developed processus internus indicis on the phalanx proximalis digiti majoris and (5) the weakly developed crista medialis of the hypotarsus.

The Paleogene fossil record of apodiform birds was reviewed by Mayr (2009). The only other apodiform taxon outside the crown group are the Aegialornithidae, which were reported from the early Eocene to early Oligocene of Europe, and whose earliest representative, *Primapus lacki* Harrison and Walker, 1975 from the London Clay, coexisted with *E. vincenti* (Mayr 2009). Characters (2)–(5) listed above also distinguish *Eocypselus* from aegialornithids, thereby corroborating the hypothesis that eocypselids are the earliest diverging of the known apodiform birds (Fig. 8; see also Mayr 2003a, 2009).

Strisores, the clade including “Caprimulgiformes” and Apodiformes (Mayr 2010), mainly contains insectivorous birds, but the foraging methods of these taxa are very

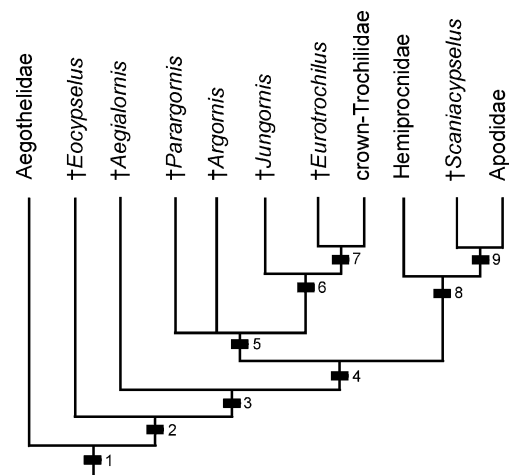


Fig. 8 Phylogenetic interrelationships of Paleogene and extant representatives of the Apodiformes; after Mayr (2003b, 2009). Selected apomorphies of the nodes: 1 *Musculus splenius capitis* with cruciform origin; coracoid with foramen nervi supracoracoidei. 2 Humerus abbreviated and stocky; pelvis with foramina intertransversaria; tarsometatarsus with arcus extensorius (incompletely ossified in some taxa). 3 Processus internus indicis of phalanx proximalis digiti majoris greatly elongated; furcula with well-developed facies articularis acroracoidea. 4 Sternal articulation facets for coracoid saddle-shaped or slightly convex, ratio length of humerus:width of shaft in midsection less than 7.0. 5 Cotyla ventralis of ulna with weakly pronounced ventro-proximal edge, olecranon elongated and narrow, deep fossa on caudal surface of proximal end of ulna (unknown for *Parargornis*). 6 Caput humeri with marked distal protrusion. 7 Beak greatly elongated and narrow (unknown for *Argornis* and *Jungornis*). 8 Tuberculum supracondylare ventrale of humerus elongated and narrow, distal end of radius with marked tubercle on ventral side of shaft, opposite to carpal tubercle of ulna, tarsometatarsus with deep sulcus on dorsal surface proximal to distal vascular foramen, outermost primaries greatly elongated, measuring at least 2.5-fold the length of the longest secondaries; salivary glands greatly enlarged. 9 Processus supracondylaris dorsalis of humerus greatly enlarged (also in Trochilidae and Aegialornithidae)

different, with Aegothelidae feeding by sallying flights from perches or picking insects from the ground and tree trunks, Trochilidae being adapted to hovering flight and Hemiprocnidae and Apodidae catching insects on the wing (e.g., del Hoyo et al. 1999). Just by consideration of the extant taxa, the foraging mode of a stem group apodiform thus cannot be deduced.

Based on the size of a *Collocalia* swiftlet, *Eocypselus vincenti* was a very small bird, and its swift-like beak indicates an insectivorous diet. The abbreviated humerus suggests that the species was already adapted to catching insects on the wing. However, the aerial locomotion of *Eocypselus* seems to have been less sophisticated than in extant Apodiformes because furcula and coracoid lack an articulation and the facies articularis sternalis of the coracoid is much narrower. *Eocypselus* is further distinguished from extant Apodiformes in that the phalanx proximalis digiti majoris does not bear a well-developed processus internus indicis. Stegmann (1963) detailed that by increasing the

lever arm of musculus interosseus ventralis, which adduces the phalanx distalis digiti majoris, a well-developed internal index process is characteristic for birds with long distal primaries that are exposed to high aerodynamic forces. The poorly developed processus internus indicis thus indicates that *Eocypselus* had less elongated outer primaries than extant apodiform birds. That the early Eocene taxon was less well adapted to feeding on the wing is also suggested by the long hallux, which testifies to perching capabilities.

The fact that the diurnal Apodiformes are nested within the nocturnal “Caprimulgiformes” raises the question of whether the stem species of Apodiformes was nocturnal or crepuscular, or whether dark-activity evolved four times independently in “caprimulgiform” birds (Mayr 2010). The skull of Aegothelidae does not have significantly larger orbits than that of crown group Apodiformes. It differs, however, in the much narrower interorbital part of the os frontale (Fig. 3), a feature that may be related to properties of the eyeball and reflect the dark-activity of owl-nightjars. The narrow interorbital section of the frontal bone of *Eocypselus* is therefore notable, even though it is certainly not possible to deduce the activity pattern of the fossil taxon from this feature alone.

Definitive records of eocypselids have so far only been found in the early Eocene of Northern Europe, but an undescribed small apodiform bird from the early Eocene Green River Formation (Wyoming, USA), which was illustrated by Feduccia (1999, p. 324), corresponds well with *E. vincenti* in the long legs and small processus internus indicis. *Eocypselus* has not yet been reported in the diversified middle Eocene avifauna of Messel in Germany, from where stem group Apodidae (*Scaniacypselus szarskii*) and stem group Trochilidae (*Parargornis messelensis*) were described (Mayr 2009). A better knowledge of Paleogene avifaunas will have to show whether the absence of eocypselids in Messel and other Middle Eocene localities reflects an incomplete fossil record, different palaeoenvironments (to date, all *Eocypselus* fossils stem from marine, near-shore deposits) or indeed indicates their disappearance after the early Eocene.

Based on the calibration of molecular data, it has been assumed that crown group Apodiformes originated in the late Cretaceous, some 70 million years ago (mya) and that Apodidae and Hemiprocnidae diverged 34 mya (Brown and Mindell 2009). The latter date is clearly refuted by the occurrence of stem group Apodidae (*Scaniacypselus*) in the Middle Eocene (47 mya), and the fossil record does not indicate a diversification of crown group Apodiformes before the early Eocene.

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