Fossil hummingbirds in the Old World

Hummingbirds today only occur in the New World. Recent discoveries show, however, that a major part of the evolution of these fascinating birds took place in the early Tertiary Period of the Old World.

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Title image. Holotype specimen of *Parargornis messelensis* (specimen HLMD Be 163 in the collection of Hessisches Landesmuseum Darmstadt; the fossil is transferred into artificial resin). Photo courtesy Hessisches Landesmuseum, Darmstadt.

Hardly any avian group is as characteristic of the New World fauna as hummingbirds (Trochilidae). These 'flying jewels' are classified into more than 300 modern species, most of which occur in South and Central America from where some have colonised North America (Schuchmann 1999). Hummingbirds do not occur in the Old World today, although the completely unrelated sunbirds (Nectariniidae) or even the hummingbird hawk-moth *Macroglossum stellatarum* (an insect), are sometimes mistaken for them.

There is general consensus among systematists that hummingbirds are the closest living relatives of the swifts (Apodidae and Hemiprocnidae), and both swifts and hummingbirds are classified within an avian group called Apodiformes. Apodiform birds in turn are most closely related to the owlet-nightjars (Aegothelidae) (Figure 1), a small group of crespuscular, insectivorous birds that occurs in the Australasian region (Mayr 2002). Hummingbirds are distinguished from swifts and all other birds by their extreme adaptations to nectarivory and sustained hovering flight, enabling them to stand motionless in front of flowers while sipping nectar (Figure 2). By contrast, owlet-nightjars and swifts have a short and wide beak and catch insects on the wing. It is thus most likely that, in the early stages of their evolution, hummingbirds were also insectivorous, gleaning insects from the underside of leaves or around flowers (Cohn 1968).

Until recently, however, virtually nothing was known for sure about early hummingbird evolution, as the oldest fossils were a few bones of modern hummingbirds from Quaternary (about 10,000-30,000 years old) cave deposits in Central and South America. This situation has now dramatically changed and, surprisingly, all Tertiary fossil hummingbirds are from the Old World, where hummingbirds had never been expected.

The first discoveries

In 1988, the Russian palaeontologist Alexandr Karhu described wing remains of a tiny apodiform bird from the Lower Oligocene (about 30-35 million years ago) of the Caucasus. These belonged to a new species which he named *Jungornis tesselatus* and classified into a new family, the Jungornithidae (Karhu 1988). About a decade later, Karhu described another species from older, Upper Eocene, deposits of the Caucasus as *Argornis caucasicus* (Karhu 1999). Karhu (1988, 1999) noted that both *Jungornis* and *Argornis* share characteristic features with modern hummingbirds, including a modified 'elbow' joint and, in *Jungornis*, humerus head that allow rotation of this bone during hovering flight. He attributed these similarities to convergence and considered *Argornis* and *Jungornis* to be aberrant swifts. However, there are no morphological traits that are exclusively shared by *Argornis*, *Jungornis*, and swifts which are not also found in hummingbirds, and a phylogenetic analysis subsequently showed *Argornis* and *Jungornis* to be on the stem lineage of modern hummingbirds (Mayr 2003a).

Argornis and *Jungornis* are known from wing and pectoral girdle bones only, but an *Argornis*-like bird was also described from the Middle Eocene (about 47 million years ago) fossil site Messel in Germany. In this specimen the complete skeleton and the feathering of a basal hummingbird are preserved (Mayr 2003b). The Messel species, *Parargornis messelensis*, has a swift-like beak but trenchantly differs from modern swifts in its feathering (title image). Whereas swifts have very long wings and a short tail, *Parargornis* combines a short and broad wing with a long tail, and its feathering thus resembles that of owlet-nightjars. The presence of a swift-like beak in *Parargornis* is in perfect agreement with earlier assumptions that hummingbirds evolved from an insectivorous ancestor, and the owlet-nightjar-like feathering may well be a primitive trait of early hummingbirds.

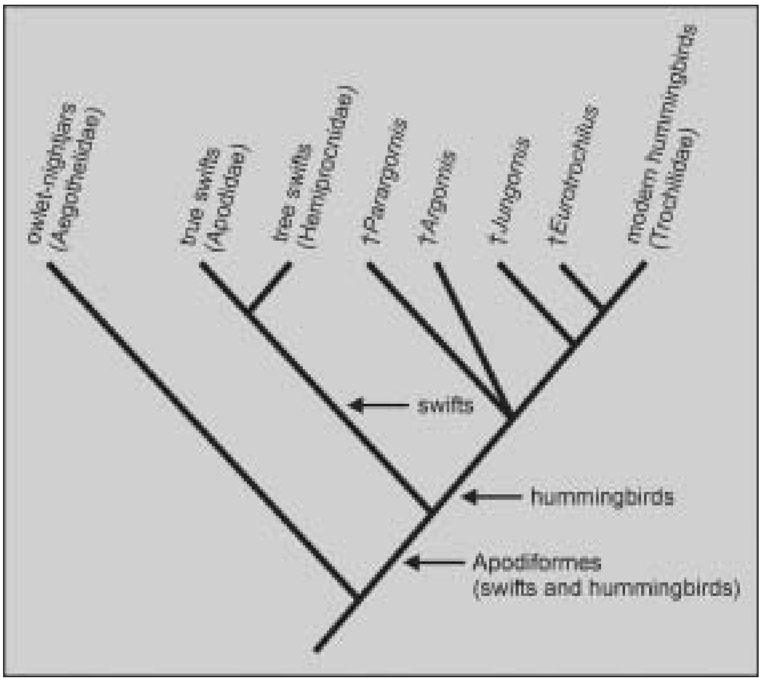

Figure 1. Phylogenetic relationships between hummingbirds and their closest modern relatives, owlet-nightjars and swifts. Extinct groups are indicated by a dagger symbol.

Finds in Germany

As *Jungornis* and *Argornis* are known only from a few skeletal remains and as these and *Parargornis* are quite different from modern hummingbirds, the finds would probably not have convinced sceptics of the presence of early hummingbirds in the Old World Tertiary. In December 2003, however, I was looking through the collection drawers of the Stuttgart natural history museum and found two unidentified tiny bird skeletons from the Lower Oligocene fossil locality Wiesloch-Frauenweiler in Southern Germany (Figures 3 and 4). After further

Figure 2. Cinnamon Hummingbird (*Amazilia rutila*) feeding at a flower of *Ipomoea neei* (Convolvulaceae). Photo: J Ferdinand.

preparation and careful examination they turned out to be conclusive evidence for the presence of hummingbirds of an essentially modern type in the European Tertiary Period.

The two specimens belong to a new species that was described as *Eurotrochilus inexpectatus*, the 'unexpected European hummingbird' (Mayr 2004). Most skeletal elements are preserved, and *Eurotrochilus* is well-characterised as an apodiform bird by its extremely abbreviated humerus and ulna which hummingbirds share with their closest relatives, the swifts. There are no other, extinct or extant birds, in which these bones are equally shortened. As in *Jungornis*, the proximal articulation surface of the humerus shows morphological specialisations that enable rotation of this bone during hovering flight (Mayr 2004). The beak is greatly elongated which, together with the hovering adaptations in the wing bones, indicates that *Eurotrochilus* was nectarivorous like modern hummingbirds. No other birds exhibit the combination of these features, i.e. tiny size, extremely abbreviated humerus which exhibits adaptations to hovering flight, and greatly elongated beak.

Despite its similarities to modern hummingbirds, however, *Eurotrochilus* still exhibits a number of primitive features which show *Eurotrochilus* to be outside the crown group of Trochilidae, i.e. the group including the stem species of the modern taxa and all its descendants (Mayr 2004). Although *Eurotrochilus* is a 'modern-type' hummingbird and probably would have looked very similar to modern hummingbirds when seen alive, it is not closely related to any particular modern hummingbird species. Discovery of hummingbirds in the Old World thus does not conflict with the assumption that the last common ancestor of the modern species evolved in South or Central America (Bleiweiss 1998). However, it indicates that hummingbirds had a different, probably wider distribution in the past and this has interesting implications for the evolution of ornithophilous (bird-pollinated) flowers in the Old World.

Bird-flower co-evolution in the Old World

Plants that are adapted to pollination by hummingbirds exhibit a characteristic flower morphology, in that they produce a great amount of nectar, are often coloured brightly red, have a long corolla, and do not provide perches near the flower. This last feature distinguishes most New World ornithophilous flowers from those in the Old World, as nectarivorous Old World birds are not capable of sustained hovering flight and usually have to sit on branches near the flower, or parts of the flower itself, while feeding at the nectar (note that the flower in Figure 2 is not a typical hummingbird-flower, and appears to be primarily adapted to bats rather than hummingbirds).

However, it has been recognised by botanists that some Old World plants exhibit a very similar flower morphology to those pollinated by hummingbirds in the New World, although they occur in areas without hovering avian pollinators,

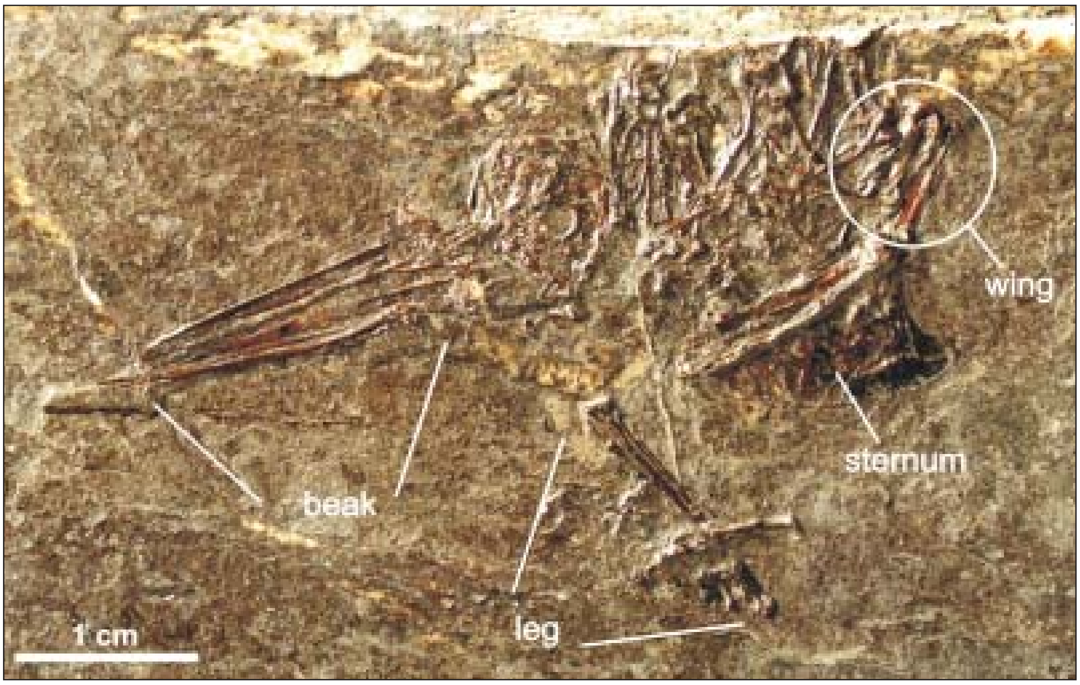

Figure 3. Holotype specimen of *Eurotrochilus inexpectatus* (specimen SMNS 80739/4 in the collection of *Hessisches Landesmuseum Darmstadt*; the fossil is transferred into artificial resin). Photo by A Hebs.

let alone hummingbirds. Examples include the Himalayan *Agapetes* spp. (Ericaceae) (Figure 5), the East African *Canarina eminii* (Campanulaceae), and West African *Impatiens sakeriana* (Balsaminaceae) (Westerkamp 1991), as well as the West African *Sabicea speiosa* (Rubiaceae) and the South African *Tecomaria capensis* (Bignoniaceae) (S Vogel, personal communication). Discovery of fossil hummingbirds in Europe now suggests that the flower traits of these plants may indeed be primarily an adaptation to pollination by hummingbirds. After the disappearance of hummingbirds from the Old World, their pollination may have been taken over by long-tongued bees and other insects, as many Neotropical plants today are still visited by both hummingbirds and insects (e.g. Stiles 1978).

There are probably further unrecognised examples of Old World plants whose flower morphology goes back to co-evolution with hummingbirds in the early Tertiary. Many hummingbird-pollinated flowers in North America are derived from bee-pollinated ones (Grant 1994), and it has been shown that hummingbird flowers can switch into bee-pollinated ones by a single mutation that changes flower colouration from red (for hummingbirds) into violet (for bees) (Bradshaw and Schemske 2003).

Extinction in the Old World

It is quite possible that early hummingbirds had a wider distribution in the Tertiary and also occurred in South and Central America, although this cannot be proven owing to the non-existence of Tertiary hummingbird fossils in the New World. Whereas early hummingbirds became extinct in the Old World, the New World representatives evolved further into modern hummingbirds.

Unfortunately the reasons that led to extinction of hummingbirds in the Old World are still unknown. Modern hummingbirds include migratory species that occur in mountainous areas and temperate zones. It is thus unlikely that the extinction of hummingbirds in the Old World was due to climatic cooling in the Tertiary, so much the more as hummingbirds today are also absent from the tropic or subtropic regions of Asia and Africa.

To explain the extinction of hummingbirds in the Old World, it may be helpful to focus on the ecological characteristics that distinguish New World biotas, especially in South and Central America, from those in the Old World. Could it be that the much higher biomass density of large herbivores in the paleotropics led to hummingbird extinction in the Old World, as the nectar-rich and highly nutrient flowers that are pollinated by hummingbirds in the Neotropics would be eaten by these large herbivores (Cristoffer and Peres 2003)? Did food competition with other birds or insects lead to hummingbird extinction in the Old World?

As shown by the still very swift-like *Parargornis* and *Argornis*, 'modern' hummingbirds were probably absent in the Eocene period, and seem to have appeared towards the Lower Oligocene. Any hypothesis about hummingbird extinction in the Old World is, however, made difficult by the fact that we do not know when they ultimately disappeared from the Old World. Hummingbird bones are very small and so preserved only under especially fortunate circumstances. Have the tiny bones of these birds been overlooked in Upper Oligocene or early Miocene localities, or did they indeed only occur in the Lower Oligocene? Did the birds survive over a longer period of time in Southern Asia or Africa, where the fossil record for small birds is almost non-existent? Future finds will have to shed light on these questions.

Figure 4. Paratype specimen of *Eurotrochilus inexpectatus* (specimen SMNS 80739/3a+b in the collection of *Hessisches Landesmuseum Darmstadt*; the fossil is transferred into artificial resin and consists of two slabs). Photo by A Hebs.

Figure 5. Flower of the Himalayan *Agapetes serpens* (Ericaceae) – an Old-World 'hummingbird-flower'? Photo by K Stüber.

Concluding remarks

Although the discovery of hummingbirds in the Old World was very unexpected, there were other avian groups in the early Tertiary of Europe whose closest relatives today are also restricted to the New World, such as potoos (Nyctibiidae), idiornithids (close relatives of modern seriemas, Cariamidae), and New World Vultures (Cathartidae) (*e.g.* Mourer-Chauviré 1999). Hummingbirds are thus just another group of modern birds that had a different distribution in the past.

Apart from being the earliest remains of modern-type hummingbirds in general and the first from the Old World, the specimens of *Eurotrochilus* provide indirect evidence that bird-flower co-evolution also dates back to at least the Lower Oligocene. Although there are no longer hummingbirds in the Old World, there are other nectarivorous birds, most of which belong to passerines (Passeriformes). Among these, the sunbirds so strikingly resemble hummingbirds in external appearance that both groups are often treated as the textbook example of convergence among birds. It now seems possible that hummingbird-flower co-evolution predated sunbird-flower co-evolution in the Old World, and that some sunbirds are adapted to ornithophilous flowers that originally evolved for pollination by hummingbirds.

The discovery of *Eurotrochilus* exemplifies how little we still know about the birds – especially the very small ones – that lived in the early Tertiary of Europe. It is not unlikely that future discoveries will lead to further examples of unexpected taxa, thus keeping palaeornitholgy among the most exciting fields of vertebrate palaeontology.

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References

Bleiweiss R (1998) Origin of hummingbird faunas. *Biological Journal of the Linnean Society* **65,** 77-97.

Bradshaw H D and Schemske D W (2003) Allele substitution at a flower colour locus produces a pollinator shift in monkeyflowers. *Nature* **426,** 176-178.

Cohn J M W (1968) *The convergent flight mechanism of swifts (Apodi) and hummingbirds (Trochili) (Aves).* PhD dissertation, University of Michigan, Ann Arbor.

Cristoffer C and Peres C A (2003) Elephants versus butterflies: the ecological role of large herbivores in the evolutionary history of two tropical worlds. *Journal of Biogeography* **30,** 1357-1380.

Grant V (1994) Historical development of ornithophily in the western North American flora. *Proceedings of the National Academy of Sciences USA* **91,** 10407-10411.

Karhu A (1988) [A new family of swift-like birds from the Paleogene of Europe] *Paleontological Journal* **3,** 78-88. (Russian with English abstract).

Karhu A (1999) A New Genus and Species of the Family Jungornithidae (Apodiformes) from the Late Eocene of the Northern Caucasus, with Comments on the Ancestry of Hummingbirds. In *Avian Paleontology at the Close of the 20th Century: Proceedings of the 4th International Meeting of the Society of Avian Paleontology and Evolution, Washington, DC, 4-7 June 1996* (ed. S L Olson). Smithsonian Contributions to Paleobiology **89,** 207-216.

Mayr G (2002) Osteological evidence for paraphyly of the avian order Caprimulgiformes (nightjars and allies). *Journal für Ornithologie* **143,** 82-97.

Mayr G (2003a) Phylogeny of early Tertiary swifts and hummingbirds (Aves: Apodiformes). *Auk* **120**, 145-151.

Mayr G (2003b) A new Eocene swift-like bird with a peculiar feathering. *Ibis* **145**, 382-391.

Mayr G (2004) Old World Fossil Record of Modern-Type Hummingbirds. Science **304** (5672), 861-864.

Mourer-Chauviré C (1999) Les relations entre les avifaunes du Tertiaire inférieur d'Europe et d'Amérique du Sud. *Bulletin de la Société Géologique de France* **170,** 85-90.

Schuchmann KL (1999) Family Trochilidae (Hummingbirds). In: *Handbook of the Birds of the World, vol. 5., Barn-owls to hummingbirds*. del Hoyo J, Elliot A and Sargatal J (Eds). Barcelona: Lynx Edicions, pp. 468-680.

Stiles F (1978) Ecological and Evolutionary Implications of Bird Pollination. *American Zoologist* **18,** 715-727.

Westerkamp C (1990) Bird-Flowers: Hovering Versus Perching Exploitation. *Botanica Acta* **103,** 366-371.

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