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SHORT COMMUNICATION

Hummingbird with modern feathering: an exceptionally well-preserved Oligocene fossil from southern France

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Abstract Hummingbirds (Trochilidae) today have an exclusively New World distribution, but their pre-Pleistocene fossil record comes from Europe only. In this study, we describe an exceptionally preserved fossil hummingbird from the early Oligocene of southeastern France. The specimen is articulated, with a completely preserved beak and feathering. Osteological characters allow to identify it as *Eurotrochilus* sp. This genus is a stem group representative of Trochilidae and was recently described from the early Oligocene of southern Germany. The new fossil reveals that these European Trochilidae were remarkably modern in size, skeletal proportions and the shape of the wing, tail and beak and hyoid bones. These features confirm the early acquisition of the abilities of hovering and nectarivory in hummingbirds, probably before the Oligocene. In several morphological characteristics, they resemble members of the 'true hummingbirds' (subfamily Trochilinae) and differ from hermits (Phaethornithinae). These features, which include a short and square tail and a moderately long, almost straight beak, appear to be primitive within the family Trochilidae.

Keywords *Eurotrochilus* · Evolution · Oligocene · Plumage · Trochilidae

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Introduction

Extant hummingbirds (Trochilidae) are a very diversified taxon with 328 species and live only in the New World (Schuchmann 1999). However, all pre-Pleistocene fossil hummingbirds come from the Paleogene of Europe (Mayr 2004, 2007). Hummingbirds (sensu Mayr 2007) include here stem and crown-group Trochilidae as well as two closely related families. They comprise the basal Cypselavidae (*Cypselavus*, *Argornis* and *Parargornis*; middle Eocene to early Oligocene of France, middle Eocene of Germany, late Eocene of Caucasus; Mourer-Chauviré 2006) and the more derived *Jungornis* (Jungornithidae, Late Eocene of France and early Oligocene of Caucasus; Mourer-Chauviré and Sigé 2006) and *Eurotrochilus* (Trochilidae, early Oligocene of Germany; Mayr 2007). Hitherto, no complete articulated specimens, let alone one with feather preservation, were known for *Jungornis* and *Eurotrochilus* (Mayr 2007). The feathering of fossil hummingbirds is known only for the basal *Parargornis*, which had short, rounded wings, with a short and wide beak corresponding to a way of living as an aerial insectivore (Mayr 2005a). In contrast, extant hummingbirds have pointed wings and a long and slender beak associated

with nectarivory, a behavioral characteristic shared with *Eurotrochilus* (Mayr 2004, 2007). In this paper, we report on an exceptionally preserved almost complete fossil specimen of a modern-type hummingbird, which is an articulated skeleton with well-preserved remains of the plumage. The specimen provides new insights into the external appearance of the earliest hummingbirds, compared with advanced hummingbird characteristics.

Systematic paleontology

The systematic paleontology of the specimen is as follows:

- Aves Linnaeus 1758
- Apodiformes Peters 1940
- Trochilidae Vigors 1825
- *Eurotrochilus* Mayr 2004
- *Eurotrochilus* sp.

Material

The fossil (Figs. 1, 2 and 3) is in the private collection of N. Tourment, Marseille, France (see author address; collection number NT-LBR-040). A cast has been deposited in the collections of the Université Claude Bernard—Lyon 1,

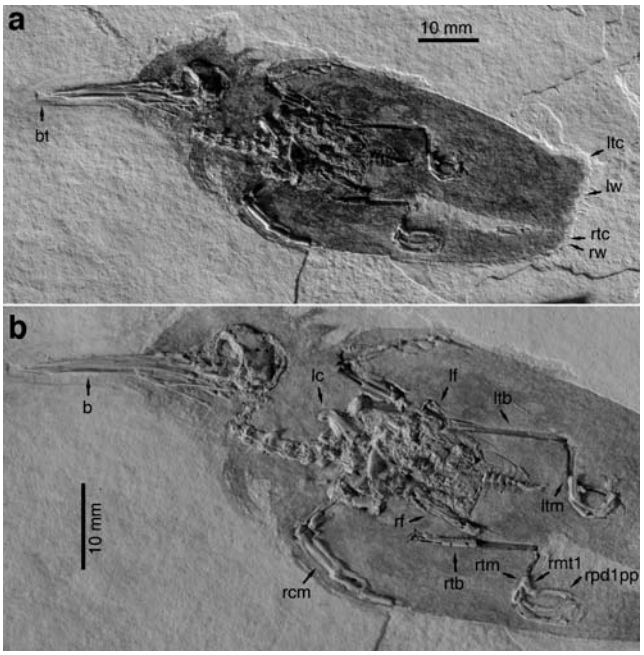

Fig. 1 *Eurotrochilus* sp. from southeastern France. **a** General view. **b** View of whole skeleton, coated with ammonium chloride. *b* Beak, *bt* beak tip, *lc* left coracoid, *lf* left femur, *ltb* left tibiotarsus, *ltc* left corner of tail, *ltm* left tarsometatarsus, *lw* left wing tip, *rcm* right carpometacarpus, *rf* right femur, *rmt1* right metatarsal I, *rpd1pp* right proximal phalanx of pedal digit I, *rtb* right tibiotarsus, *rtc* right corner of tail, *rtm* right tarsometatarsus, *rw* right wing tip

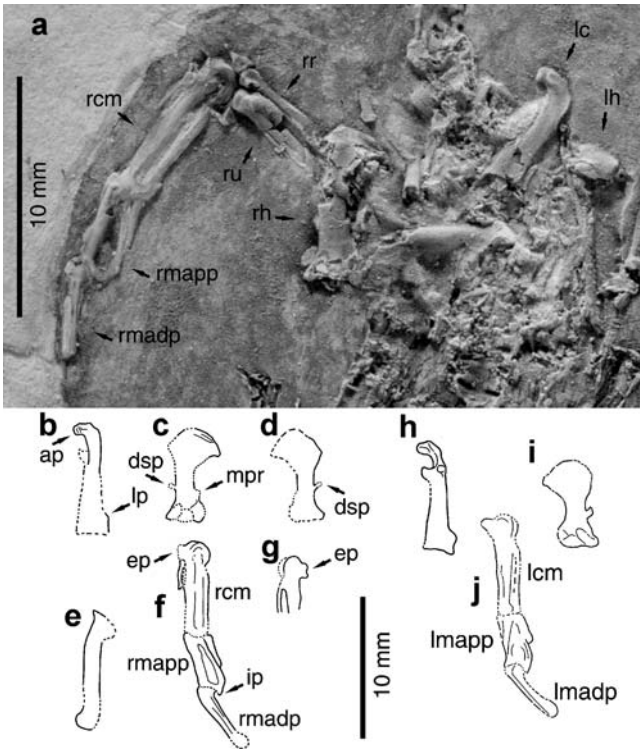

Fig. 2 *Eurotrochilus* sp. from southeastern France (**a**, **b**–**g**) and *E. inexpectatus* from Germany (**h**–**j**). **a** Detail of pectoral region, coated with ammonium chloride. **b**–**g** Interpretative drawings, all ventral views except cranial views of humeri. **b** Left coracoid (*lc*). **c** Right humerus (*rh*). **d** Left humerus (*lh*). **e** Left ulna (*lu*). **f** Bones of right hand. **g** Left carpometacarpus (*lcm*). **h**–**j** Interpretative drawings after Mayr (2004, 2007), all dorsal views except cranial view of humerus. **h** Right coracoid (*rc*). **i** Left humerus. **j** Bones of left hand. *ap* Acrocoracoid process, *dsp* dorsal supracondylar process, *ep* extensor process, *ip* internal index process, *lmadp* left wing major digit distal phalanx, *lmapp* left wing major digit proximal phalanx, *lp* lateral process, *mpr* medial process at attachment site of musculus pronator superficialis, *rcm* right carpometacarpus, *rmadp* right wing major digit distal phalanx, *rmapp* right wing major digit proximal phalanx, *rr* right radius, *ru* right ulna. Other abbreviations as in Fig. 1

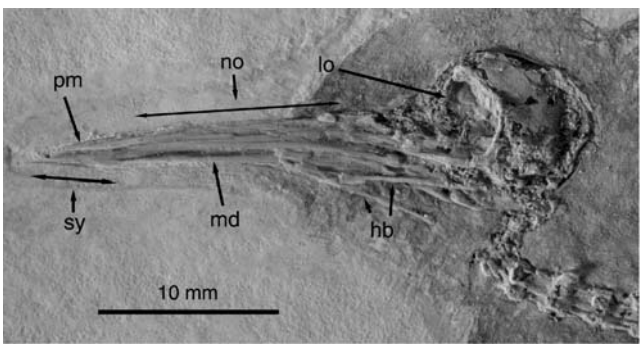

Fig. 3 *Eurotrochilus* sp. from southeastern France. Detail of skull, coated with ammonium chloride. *hb* Hyoid bones, forming the base of the two branches of the fork of the hyoid apparatus; *lo* left orbit, *md* mandible, *no* nasal opening (approximate length), *pm* premaxillary, *sy* mandibular symphysis

Villeurbanne, France (collection number FSL-367.079). The fossil consists of an almost complete articulated skeleton on a slab, in very fine limestone laminites. It shows the body and limbs in ventral view and the head in left lateral view. Only few parts of the skeleton are lacking or are not visible (sternum, parts of left humerus, ulna, radius, carpometacarpus, parts of right tibiotarsus and tarsometatarsus and minor parts of a few other bones); some missing limb bones left imprints on the slab. Small areas of the skeleton are crushed (e.g. parts of skull, femora and pelvis). The complete feathering is preserved as a thin layer of dark organic matter, showing the shape of the tail and of the folded wings.

Locality, age and geological and paleoenvironmental context

NT-LBR-040 comes from the Le Grand Banc strata (near Oppedette, Luberon, southeastern France) of Rupelian age (28–34 million years ago; Cavelier 1984). The remarkably complete preservation of the fossil indicates little or no transport and rapid burial in fine sediment in a calm depositional setting generating laminites, freshwater or possibly very slightly brackish coastal lagoons. Apart from pelagic jellyfish from the nearby sea, most organisms preserved in these levels are continental. These include fishes, plants, insects and other invertebrates, whereas amphibians, reptiles, mammals and birds are much rarer. The avian remains so far discovered include a cormorant (Phalacrocoracidae), an ibis (Threskiornithidae), a crane-like bird (Gruiformes), a buttonquail-like bird (Charadriiformes), a wader (Scolopacidae), a cuckoo-like bird (Cuculiformes), a trogon (Trogonidae) and passerines (Roux 2002; Mayr 2005b,c, 2006). Some of these birds, as well as other elements of the fauna and flora, such as freshwater fishes (*Dapalis*, *Prolebias*), peneid crustaceans, molluscs (Potaminidae), crocodiles (*Diplocynodon*), turtles (*Trionyx*) and plants like Arecaceae (*Sabal*) and Sapotaceae, indicate that the local climate was sub-tropical to tropical (see e.g. Stemvers van Bemmel 1984; Châteauneuf and Nury 1995).

Measurements

For the measurements, see Table 1.

Description (osteological terminology follows Baumel and Witmer 1993, translated from Latin into English)

The new fossil is an adult specimen and differs from all Apodiformes other than *Jungornis* and Trochilidae (*Eurotrochilus* and crown group hummingbirds; Mayr 2004, 2007; Mourer-Chauviré and Sigé 2006) by the combination of the following features: humerus, ulna and radius stocky and short, tiny size, thin and elongated beak and marked medial process at attachment site of musculus pronator superficialis of humerus.

NT-LBR-040 differs from *Jungornis* and matches *Eurotrochilus* by the following: ratio of humerus length/ulna length of 0.74 (*Eurotrochilus*: 0.74–0.77; *Jungornis tesselatus*: 0.62; Mayr 2004, 2007) and dorsal supracondylar process of humerus (Mayr 2007; Mourer-Chauviré and Sigé 2006) situated more proximal on the shaft than in *Jungornis*. As in extant hummingbirds and *E. inexpectatus* (Mayr 2004), the beak of NT-LBR-040 is long and slender, and the hind toe is long and attaches at the distal third of the tarsometatarsus. As in modern hummingbirds, the new fossil has long nasal openings and very large hyoid bones. The latter confirm nectarivory, as a large hyoid apparatus

Table 1 Measurements of *Eurotrochilus* sp., NT-LBR-040, from southeastern France and corresponding measurements of *E. inexpectatus* from southern Germany

	Eurotrochilus sp., NT-LBR-040, France	*E. inexpectatus*, Germany (Mayr 2004, 2007)
Total skull length	~32.0	~26.0; ~28.0
Beak length from naso-frontal hinge to tip	~20.0	15.5; 16.8
Ratio beak length/total skull length	0.63	0.60; 0.60
Coracoid length	~8.0[a]	7.6
Humerus length	6.5[b]	6.0; 6.0
Humerus minimal shaft width	~1.2; 1.2	
Ratio humerus minimal width/total length	0.19	
Ulna length	~8.8; ~8.8	7.6–8.2 (n=5)
Carpometacarpus length	~7.5	6.9; 7.2
Length of wing major digit proximal phalanx	~4.8; ~4.9	
Length of wing major digit distal phalanx	~5.2; 5.2	
Femur length	10.1	~9.0
Tibiotarsus length	15.1; ~15.1	14.9; ~15.0
Tarsometatarsus length	6.8; ~6.8	6.4; 6.5; 6.7
Ratio humerus length/ulna length	0.74	0.74; 0.77
Ratio humerus length/coracoid length	~0.81[a]	0.79

All in millimeters
[a] Estimated
[b] Taking in account the fact that the ventral condyle is crushed and thus artificially slightly extended distally

supports the long protractile tongue used by hummingbirds to lap up nectar. The symphysis of the mandible seems to be short as in *E. inexpectatus* (Mayr 2007).

The specimen matches *Eurotrochilus* and differs from crown group Trochilidae (Mayr 2004, 2007) because in contrast to the latter, (1) a lateral process is present on the coracoid, (2) an osseous bridge connecting procoracoid and acrocoracoid processes is lacking, (3) the insertion of the dorsal supracondylar process on the humeral shaft is situated more distal, (4) the medial process of the humerus originates more ventro-distally, (5) the carpometacarpus lacks a marked dentiform process and (6) the proximal phalanx of major digit of the wing bears a distally less developed internal index process. The angle formed ventrally between the symphysis and, in lateral view, the rami of the mandible is more marked than in modern hummingbirds.

NT-LBR-040 differs from *E. inexpectatus* by the following: slightly larger size, extensor process of carpometacarpus less protruding, phalanges of major digit of wing relatively larger with regards to the carpometacarpus and tibiotarsus and tarsometatarsus relatively shorter with regards to the rest of the body (Table 1). These differences to the German specimens may be owing to either sexual or specific distinctness. Thus, we do not assign the specimen to any particular species of *Eurotrochilus*.

As in modern hummingbirds, the wings of the new fossil specimen are falcate and relatively short. The wings are folded, and their tips reach only the tip of the short tail. Hence, wing shape is consistent with hovering flight, by comparison with extant hummingbirds, a capacity previously deduced for *Eurotrochilus* from humerus features (Mayr 2004). The tail is square as in a number of extant hummingbirds (Altshuler et al. 1999; Schuchmann 1999). The beak is relatively straight and moderately long. Within crown group Trochilidae, this character combination occurs in many 'true hummingbirds' (the speciose subfamily Trochilinae) but not in hermits (Phaethornithinae; Altshuler et al. 1999; Schuchmann 1999). Most Trochilinae have a proportionally longer or equally sized beak to the fossil, but in a few species, it is shorter. With a total length (TL) of 92 mm (tip of beak to tip of tail feathers), NT-LBR-040 lies in the size range of extant Trochilinae, most of which measure 60 to 100 mm (Altshuler et al. 1999; Schuchmann 1999). The beak of the fossil is very slightly curved downwards and is relatively thicker than in most hummingbirds. Similar proportions and beak and tail shapes are found in some Trochilinae such as females of *Aglaiocercus* spp. and *Sephanoides sephaniodes*, males of *Heliothryx* spp., as well as *Colibri delphinae* (TL for these birds, 95–137 mm), *Augastes geoffroyi* (TL: 86–93 mm), *Lophornis adorabilis* and some species of *Chlorostilbon* (TL: 65–90 mm). *Florisuga mellivora* (Trochilinae) is even more similar to the fossil concerning beak and tail shape and general appearance but is slightly larger (TL=110–120 mm).

Discussion

The new hummingbird from southeastern France reveals that stem group representatives of the Trochilidae had essentially modern-type wing and tail shapes as early as about 30 million years ago, in addition to modern-type large hyoid bones, an adaptation to nectarivory. Despite some plesiomorphic osteological features, *Eurotrochilus* was very like modern 'true hummingbirds' (Trochilinae) in external shape and limb proportions, beak shape and relative lengths of tail and wing feathers. Most likely, these similarities, which distinguish the fossil from the Phaethornithinae, are primitive within Trochilidae.

In addition, NT-LBR-040 extends the known geographical distribution of *Eurotrochilus* and adds evidence to the unexpected discovery of European stem group hummingbirds. Sedimentary contexts needed to preserve such tiny and fragile bones are very rare. European hummingbirds like *Eurotrochilus* may thus have been more widespread in space and time than the rarity of preserved remains, all of which have an early Oligocene age, suggests.

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References

Altshuler DN, Bündgen R, Calder WA, Chai P, Fjeldså J, Heindl M, Heynen I, Hinkelmann C, Peterson AT, Powers DR, Rappole JH, Roy MS, Sánchez Osés C, Schuchmann KL, Scott PE, Stiles FG, Weller AA, Züchner T (1999) Species accounts of Trochilidae. In: Del Hoyo J, Elliott A, Sargatal J (eds) Handbook of the birds of the world, 5: barn-owls to hummingbirds. Lynx Edicions, Barcelona, pp 536–680

Baumel JJ, Witmer LM (1993) Osteologia. In: Baumel JJ, King AS, Breazile JE, Evans HE, Vanden Berge JC (eds) Handbook of avian anatomy: nomina anatomica avium. Publ Nuttall Ornithol Club 23:45–132

Cavelier C (1984) Paléogène. In: Debrand-Passard S (ed) Synthèse Géologique du Sud-Est de la France. Mémoires BRGM France 125:389–468

Châteauneuf JJ, Nury D (1995) La flore de l'Oligocène de Provence méridionale: implications stratigraphiques, environnementales et climatiques. Géol Fr 2:43–55

Mayr G (2004) Old World fossil record of modern-type hummingbirds. Science 304:861–864

Mayr G (2005a) Fossil hummingbirds in the Old World. Biologist 52:12–16

Mayr G (2005b) A chicken-sized crane precursor from the early Oligocene of France. Naturwissenschaften 92:389–393

Mayr G (2005c) The Paleogene fossil record of birds in Europe. Biol Rev 80:515–542

Mayr G (2006) A specimen of *Eocuculus* Chandler, 1999 (Aves, ? Cuculidae) from the early Oligocene of France. Geobios 39: 865–872

Mayr G (2007) New specimens of the early Oligocene Old World hummingbird *Eurotrochilus inexpectatus*. J Ornithol 148:105–111

Mourer-Chauviré C (2006) The avifauna of the Eocene and Oligocene Phosphorites du Quercy (France): an updated list. Strata Ser 1 13:135–149

Mourer-Chauviré C, Sigé B (2006) Une nouvelle espèce de *Jungornis* (Aves, Apodiformes) et de nouvelles formes de Coraciiformes s.s. dans l'Eocène supérieur du Quercy. Strata Ser 1 13:151–159

Roux T (2002) Deux fossiles d'oiseaux de l'Oligocène inférieur du Luberon. Courr Sci Parc Nat Rég Luberon 6:38–57

Schuchmann KL (1999) Trochilidae. In: Del Hoyo J, Elliott A, Sargatal J (eds) Handbook of the birds of the world, 5: barn-owls to hummingbirds. Lynx Edicions, Barcelona, pp 468–535

Stemvers van Bemmel J (1984) Een Oligocene fauna in het Bekken van Apt-Manosque-Forcalquier: Zuidfranse vogels en vissen begraven in kalkslib. Gea 17:134–138