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SHORT COMMUNICATION

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The oldest European fossil songbird from the early Oligocene of Germany

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Abstract We report on the oldest European songbird (Passeriformes), from the early Oligocene (30–34 million years ago) of Frauenweiler in Germany. The specimen represents the earliest associated remains of an early Tertiary passerine described so far. It ties the first appearance of Passeriformes in Europe to a minimum age of 30 million years. Passeriform birds are absent in Eocene deposits that yielded abundant remains of small land birds and apparently dispersed into Europe around the Eocene/Oligocene boundary (about 34 million years ago), not at the Oligocene/Miocene boundary (about 24 mya) as hitherto thought. This possibly relates the appearance of songbirds in Europe to a well-known major faunistic break at the Eocene/Oligocene boundary, called the "*grande coupure*". The Frauenweiler songbird most notably differs from extant Passeriformes in having a larger processus procoracoideus on the coracoid and appears to be outside Eupasseres, the taxon which includes Oscines (all modern European and most Old World songbirds) and Suboscines (most South and Central American songbirds). It shows that there were earlier dispersal events of non-oscine songbirds into Europe before the arrival of Oscines from the Australian continental plate towards the late Oligocene.

Introduction

Although songbirds (Passeriformes) today include more than half of all extant avian species, little is known about the fossil history of this group. The earliest fossil records are fragmentary bones from the early Eocene, about 50 million years ago, of Australia (Boles 1995). There are no records of early Tertiary songbirds from Africa and Asia and the oldest New World songbirds are of early Miocene age (Olson 1985; Noriega and Chiappe 1993).

In Europe, songbirds are absent among the numerous remains of small land birds from the Lower Eocene London Clay of England (e.g., Daniels in Feduccia 1999: Tab. 4.1), the Middle Eocene of Messel in Germany (e.g., Mayr 2000a), and the Middle to Upper Eocene fissure fillings of the Quercy in France (e.g., Mourer-Chauviré 1996). The hitherto earliest described European record of songbirds are a few isolated bones from the Upper Oligocene French localities Coderet and Gannat (Mourer-Chauviré et al. 1989) which have an age of about 24 million years (Mourer-Chauviré 1996; Legendre and Lévêque 1997). Most recently, Roux (2002) mentioned a songbird specimen from the early Oligocene (about 31 mya, Mourer-Chauviré 1996; Legendre and Lévêque 1997) of Céreste in France which has, however, not yet been described.

The lack of fossil songbirds in early Tertiary deposits of the northern hemisphere led to the assumption that passeriform birds originated in the southern hemisphere (e.g., Feduccia and Olson 1982; Olson 1989; Maclean 1990; Cracraft 2001) and arrived in Europe toward the end of the Oligocene (Mourer-Chauviré et al. 1989; Olson 1989; Blondel and Mourer-Chauviré 1998). Molecular studies have recently shown that Oscines, to which all European and most Old World passerines belong, indeed dispersed into Europe from the Australian continental plate (Barker et al. 2002; Ericson et al. 2002a, 2003). However, although the pattern of passerine evolution and dispersal has become much clearer in recent years, the dating of the major events of passerine evolution is still uncertain due to the lack of adequate fossils.

Here we describe the oldest fossil songbird from the northern hemisphere, which is at least 6 million years older than the above-mentioned songbird fossils from the late Oligocene of France. These are the first associated remains of an early Tertiary passerine described so far.

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Systematic paleontology

Aves Linnaeus, 1758

Passeriformes (Linnaeus, 1758)

Genus and species indeterminate.

Referred specimen

SMF Av 497 (Fig. 1); deposited in Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; dissociated skeleton including skull, sternum, and limb elements.

Locality and geological setting

Frauenweiler, south of Wiesloch (Baden-Württemberg, Germany), claypit of the Bott-Eder GmbH ("Grube Unterfeld"); Rupelian, early Oligocene (Micklich and Parin 1996; Trunkó and Munk 1998; Mayr 2000b; Mayr et al. 2002).

Measurements (maximum length in millimeters)

Rostrum, from naso-frontal hinge to tip, ~12.7; mandible, 24.5; sternum, 21.8; right humerus, 28.1; left carpometacarpus, ~13.2; right femur, ~17.0; right tibiotarsus, 29.5.

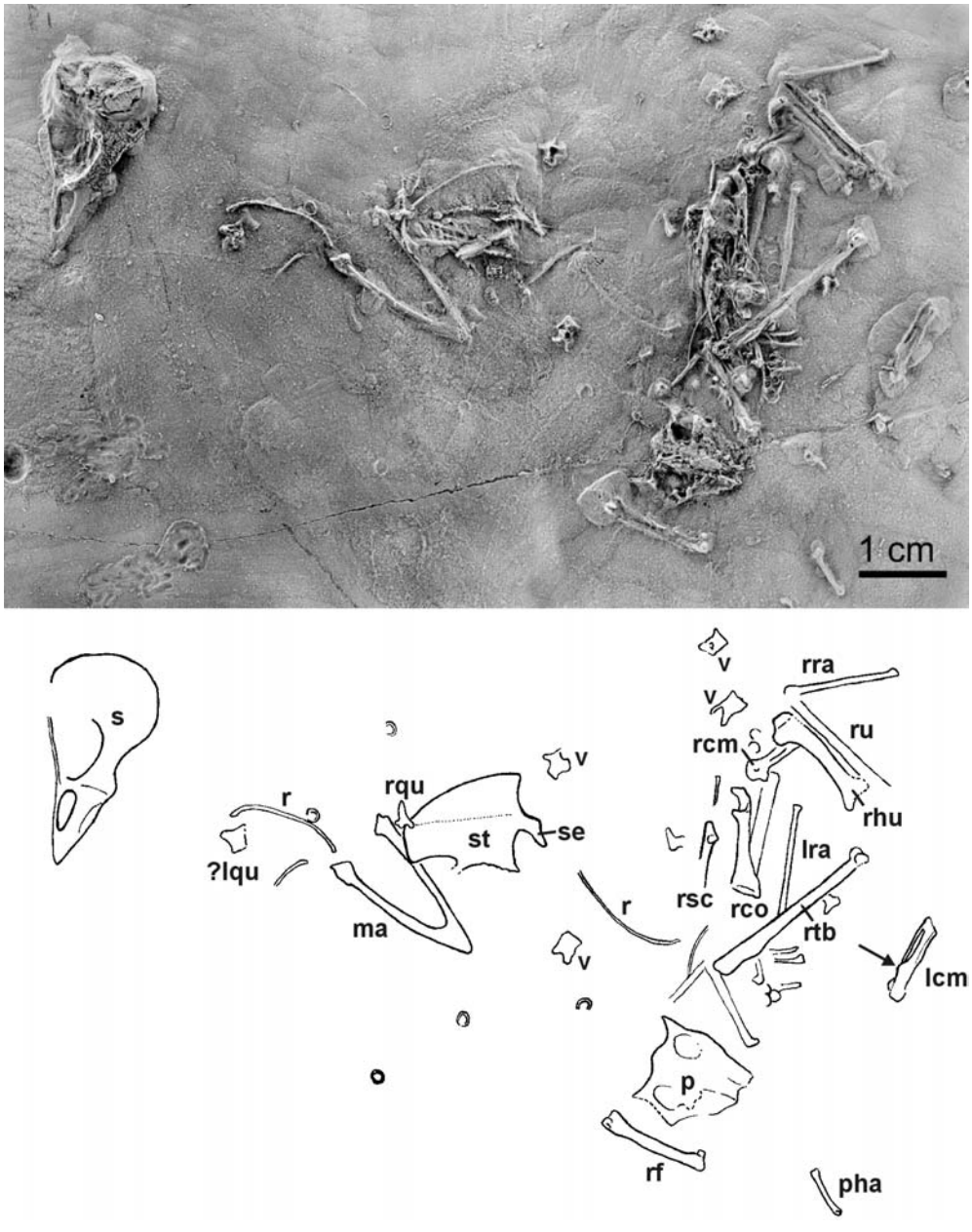

Fig. 1 Disarticulated skeleton of a passeriform bird from the early Oligocene of Frauenweiler, Germany (SMF Av 497); coated with ammonium chloride to enhance contrast. Abbreviations in the interpretative drawing of the specimen: *lcm* left carpometacarpus, *lqu* left quadrate, *lra* left radius, *ma* mandible, *p* pelvis, *pha* phalanx, *r* rib, *rcm* right carpometacarpus, *rco* right coracoid, *rf* right femur, *rhu* right humerus, *rqu* right quadrate, *rra* right radius, *rsc* right scapula, *rtb* right tibiotarsus, *ru* right ulna, *s* skull, *se* spina externa, *st* sternum, *v* vertebra. The *arrow* points to the processus intermetacarpalis of the carpometacarpus

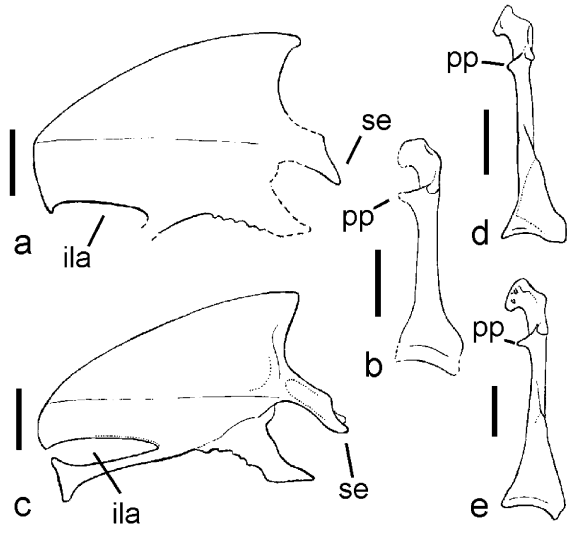

Fig. 2 **a** Sternum of the Frauenweiler songbird (SMF Av 497). **b** Right coracoid of the Frauenweiler songbird (SMF Av 497). **c** Sternum of extant *Passer griseus* (Oscines, Ploceidae). **d** Right coracoid of *Passer griseus*. **e** Right coracoid of *Pitangus sulphuratus* (Suboscines, Tyrannidae) which, for an extant passeriform bird, has an unusually large processus procoracoideus. Abbreviations: *ila* incisua lateralis, *se* spina externa, *pp* processus procoracoideus. The *scale bars* equal 5 mm

Taxonomic remarks

The specimen exhibits the uniquely derived sternum morphology of passeriform birds, with a large bifurcated spina externa and only a single pair of notches in the caudal margin (incisurae laterales, see Fig. 2). As in Passeriformes, the carpometacarpus further bears a large processus intermetacarpalis that fuses with the os metacarpale minus (Fig. 1; this character also occurs in piciform birds which otherwise, however, are clearly distinguished from the specimen described in this study). Other features that identify the bird as a passerine are a strongly protruding processus flexorius on the distal humerus and a long tibiotarsus. The combination of these characters clearly distinguishes the fossil from any other avian taxon, including the superficially similar mousebirds (Coliiformes) that have also been reported from the Frauenweiler deposits (Mayr 2000b).

Description (terminology after Baumel and Witmer 1993)

The specimen consists of an associated partial skeleton, the bones of which are scattered over the slab. It was prepared with the resin transfer method (Kühne 1961) and most bones are preserved as casts.

The beak is short and finch-like, suggesting a granivorous/frugivorous rather than an insectivorous diet, the narial openings are large and of oval shape. As in extant Passeriformes, the ossa praefrontalia are greatly reduced, the interorbital section of the os frontale is narrow. The part of the cranium caudal to the orbitae was fabricated by the preparator. The caudal ends of the mandible bear short processus retroarticulares. Ossified tracheal rings are scattered over the slab.

The fossil species most notably differs from extant Passeriformes in that the coracoid bears a decidedly larger processus procoracoideus (Fig. 2, although the tip of this process is not visible in the fossil specimen, the remaining part clearly indicates that it was much larger than in extant songbirds) and has a dorsoventrally less flattened extremitas omalis. The processus lateralis of the coracoid is greatly reduced, as in all extant songbirds. The acromion of the scapula is large and lacks a well-developed ventromedial process for articulation with the processus procoracoideus.

The sternum is preserved in lateral view and has a high carina sterni. The spina externa is very long and of similar shape to that of extant Passeriformes; as in the latter it appears to have had a bifurcated tip. Five processus costales can be counted; the processus craniolaterales are long as in extant Passeriformes. Also as in most extant Passeriformes, the caudal margin of the corpus sterni bears only a single pair of notches (a four-notched sternum occurs in very few Suboscines, see Heimerdinger and Ames 1967).

The proximal end of the humerus lacks a well-developed second fossa pneumotricipitalis, which is characteristic for many extant oscine Passeriformes (Bock 1962). The distal end bears a strongly protruding processus flexorius. The shape of the processus supracondylaris dorsalis cannot be clearly discerned.

The ventral surface of the proximal right carpometacarpus is visible between the right coracoid and the proximal right humerus. The left carpometacarpus is exposed in dorsal view and bears a large processus intermetacarpalis that, as in extant Passeriformes, fuses with the os metacarpale minus. The latter protrudes distally beyond the os metacarpale majus.

The pelvis is exposed from its ventral surface and is small as in extant Passeriformes. As in extant Passeriformes but in contrast to most other “higher land birds”, the tibiotarsus is by far the longest limb element.

Discussion

The stratigraphic level of the Rupelian formation is the Mammalian Paleogene (MP) 21–25, which corresponds to an absolute age of about 30–34 million years (Legendre and Lévêque 1997). Although the exact age within this formation is unknown for the specimen described here, it allows us to assume a minimum age of 30 million years for first appearance of Passeriformes in Europe.

It is more difficult to pinpoint the maximum age for the first appearance of songbirds in Europe, as their absence in the Eocene fossil record does not prove their non-existence in Europe by that time. However, whereas there are few Lower Oligocene European avifaunas in which great numbers of small land birds have been found, the fossil record of small land birds from the Lower and

Middle Eocene London Clay and Messel deposits is extensive, covering many hundred individuals, none of which is a passeriform bird (G. Mayr, personal observation). Songbirds are also absent in the Upper Eocene Montmartre gypsum and the well-studied Upper Eocene fissure fillings of Quercy (Mourer-Chauviré 1996).

Accordingly, present evidence indicates that songbirds reached Europe around or shortly after the Eocene/Oligocene boundary (about 34 mya), which possibly relates the appearance of songbirds in Europe to the "*grande coupure*". This major faunistic break at the Eocene/Oligocene boundary, due to climatic and geographic changes (e.g., regression of the Turgai Strait between Europe and Asia), has been known for a long time in mammalian paleontology (e.g., Hartenberger 1983, 1998; Russell and Tobien 1986), but very few studies have hitherto shown its effects on the Tertiary avifauna (e.g., Mourer-Chauviré 1980).

The exact systematic position of the Frauenweiler fossil within Passeriformes is uncertain, owing to its rather poor preservation and the great osteological similarity of extant songbirds. Despite its superficially finch-like beak, it is almost certainly neither a member of Oscines, the passeriform taxon to which all extant European songbirds belong, nor Suboscines, the other major passeriform group which today has its center of distribution in the New World but was also reported from the Miocene of Europe (e.g., Ballmann 1969; Cheneval 2000). Suboscines and Oscines most notably differ from the fossil specimen in the much more reduced processus procoracoideus of the coracoid (Fig. 2). There is little variation in the morphology of the coracoid of extant Passeriformes (e.g., Höfling and Alvarenga 2001) and a well-developed processus procoracoideus is found in taxa considered to be closely related to Passeriformes, as the piciform Galbulae and most coraciiform birds. Thus its reduction in extant Oscines and Suboscines is probably derived relative to the condition seen in the Frauenweiler fossil and indicates a position of the fossil outside Eupasseres, the monophyletic taxon including Oscines and Suboscines (Ericson 2002b).

Barker et al. (2002) assumed that Oscines dispersed into Europe at the end of the isolation of the Australian continent towards the late Oligocene (Stevens 1991). As shown in this study, there were earlier dispersals of non-oscine songbirds into Europe, although it is unknown whether these came from the Asian or African continental plate.

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