

New trogons from the early Tertiary of Germany

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A new trogon (Aves, Trogoniformes), *Primotrogon? pumilio* sp. nov., is described from the Middle Eocene (49 Ma) of Messel in Germany. It is the first articulated skeleton of an Eocene trogon, of which only very few fragmentary remains were hitherto known. It is also the earliest complete skeleton of a trogon, exceeding previous finds (*Primotrogon wintersteini* Mayr 1999) by at least 15 million years. An isolated wing of a trogon is further identified from the early Oligocene (about 30–34 Ma) of the fossil site Frauenweiler in Germany. *Primotrogon? pumilio* and all other sufficiently well-preserved early Tertiary trogons appear to be stem group representatives of the Trogoniformes, corresponding with molecular clock data indicating a mid-Tertiary origin of crown group Trogoniformes.

Trogons (Trogonidae, Trogoniformes) as a group are characterized by a unique modification of the toes, the so-called heterodactyl foot, in which the second (inner) toe is permanently directed backwards. Today trogons occur in the tropical and subtropical regions of Africa, Asia and the New World. Apart from seasonal altitudinal movements, they are non-migratory forest birds with very poor long-distance dispersal abilities (Eisenmann 1985, Collar 2001).

Molecular clock data of Espinosa de los Monteros (1998) indicate that the basalmost split within modern Trogoniformes, that between the African genera and the rest, occurred between 19.7 and 35.6 Ma; New World and Old World trogons diverged between 18 and 32.6 Ma. Johansson (1998), however, assumed monophyly of Old World trogons and a sister-group relationship between Old World and New World trogons, stating that a 'possible vicariance event creating this split is the opening of the Atlantic Ocean in the Late Cretaceous'. Owing to plate tectonics and the temporary existence of land connections and geographical barriers (e.g. Smith *et al.* 1994, Cox 2000), possible dispersal routes for trogons were different in the Cretaceous and in the mid-Tertiary, and the extant distribution of trogons certainly is influenced by the time of divergence of the crown group (i.e. the clade including the stem species of extant trogons as well as its extant and extinct descendants).

Although two isolated humeri of *Paratrogon gallicus* (Milne-Edwards 1871) have long been known from

the early Miocene of France (Milne-Edwards 1867–71), early Tertiary and more complete fossil remains of these birds have only recently been described. The first of these records is an incomplete post-cranial skeleton of an unnamed trogon that was identified from the Oligocene of Switzerland (Olson 1976). From the early Oligocene of France, Mayr (2000, 2001) described articulated skeletons of the hitherto only completely preserved early Tertiary trogon, *Primotrogon wintersteini* Mayr 1999.

The earlier Eocene trogons that have repeatedly been mentioned in the literature (e.g. Eisenmann 1985, Mayr 1988) actually refer to the non-heterodactyl Archaeotrogonidae (see Mourer-Chauviré 1980), which are no longer considered to be closely related to trogons (Mourer-Chauviré 1995). The only trogoniform remains from Eocene deposits are an as yet undescribed tarsometatarsus of a heterodactyl bird from the Lower Eocene London Clay in England which is housed in a private collection (Mayr 1999), and a three-dimensionally preserved cranium from the Lower Eocene of Denmark that was described as *Septentrogon madseni* (Kristoffersen 2002).

Here I describe new specimens of fossil trogons from the Middle Eocene and early Oligocene of Germany. These are the first records of trogons from Germany, and the Messel specimen is the earliest known articulated skeleton of a fossil trogon.

MATERIALS AND METHODS

Osteological terminology follows Baumel and Witmer (1993); dimensions are given in millimeters.

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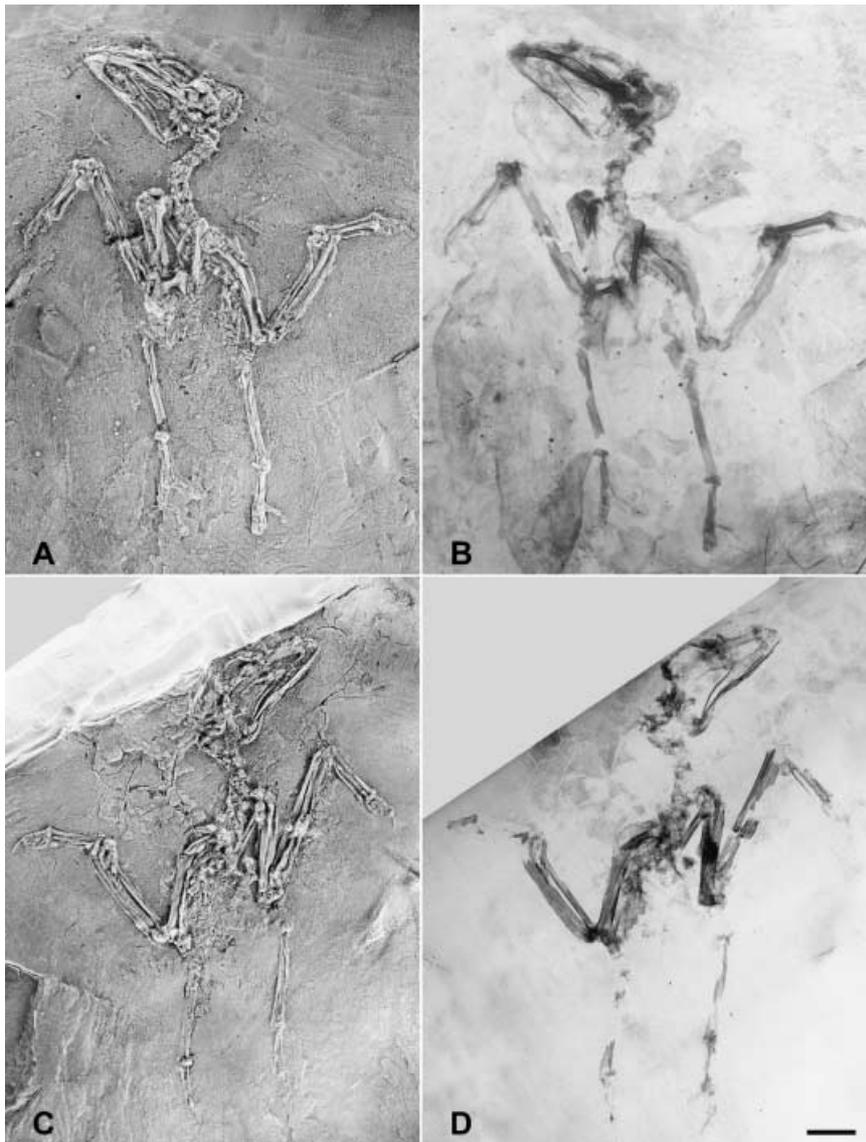


Figure 1. *Primotrogon? pumilio* n. gen. et. sp., holotype. A, specimen SMNS 55222b; B, X-ray photograph of specimen SMNS 55222b; C, specimen SMNS 55222a; D, X-ray photograph of specimen SMNS 55222a. Specimens in A and C are coated with ammonium chloride; scale bar = 10 mm.

Institutional abbreviations: SMF, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; ZMB, Museum für Naturkunde, Berlin.

SYSTEMATIC PALAEOLOGY

Trogoniformes American Ornithologists' Union 1886
 Trogonidae Lesson 1828
Primotrogon? Mayr 1999
Primotrogon? pumilio sp. nov.

HOLOTYPE

SMNS 55222 a+b (nearly complete articulated but poorly preserved skeleton on a slab, Figs 1 & 2).

DIAGNOSIS

Smallest species of the Trogoniformes, distinctly smaller than *Septentrogon madseni* Kristoffersen 2002 (length of cranium ~18 vs. ~25 mm in *S. madseni*), the unnamed trogon from Switzerland (Olson 1976), and all extant

Table 1. Dimensions of the skull and major limb bones (left/right, maximum length in mm) of *Primotrogon? pumilio* sp. nov. (holotype) in comparison with other fossil trogons and specimens of the extant Cuban Trogon (*Priotelus temnurus*), Blue-billed Trogon (*Harpactes reinwardtii*) and Resplendent Quetzal (*Pharomachrus mocinno*). The Cuban Trogon is the smallest, the Quetzal the largest of the extant taxa.

| | Skull | Humerus | Ulna | Carpometacarpus | Tibiotarsus | Tarsometatarsus |
|--|-------|------------|-----------|-----------------|-------------|-----------------|
| <i>Primotrogon? pumilio</i> sp. nov. | 31 | ~24.5/– | –/~26.0 | ~12.2/~12.6 | ~20.8/– | –/~9.0 |
| <i>Primotrogon wintersteini</i> Mayr 1999 ^a | ~34 | 27.2/~27.2 | 31.0/31.0 | 14.7/14.9 | 24.9/– | 12.7/ |
| Unnamed trogon from Switzerland ^b | | | ~35/ | | ~36/~34 | /~19 |
| <i>Priotelus temnurus</i> | 39 | 29.1/29.1 | 33.8/33.8 | 17.1/17.3 | 31.2/31.2 | 17.4/17.6 |
| <i>Harpactes reinwardtii</i> | 44 | 32.4/32.2 | 36.7/36.9 | 18.7/18.7 | 32.0/31.7 | 15.3/15.7 |
| <i>Pharomachrus mocinno</i> | 53 | 45.3/45.0 | 51.0/51.1 | 25.6/25.0 | 39.2/38.8 | 19.0/18.8 |

^aAfter Mayr (1999).

^bAfter Peyer (1957).



Figure 2. Foot of *Primotrogon? pumilio* n. gen. et. sp. in medio-dorsal view, holotype, specimen SMNS 55222b. The toes are numbered; note the reversed second toe. Coated with ammonium chloride; scale bar = 10 mm.

species (Table 1). Further differs from *Primotrogon wintersteini* Mayr 1999 in the proportionally shorter tarsometatarsus (ratio of ulna : tarsometatarsus ~2.4 in *P. wintersteini* vs. ~2.9 in *P.? pumilio* sp. nov.).

TYPE LOCALITY AND HORIZON

Messel near Darmstadt, Hessen, Germany (see Schaal & Ziegler 1988 for a description of the locality, and Mayr 2000 concerning the avifauna of the site); early Middle Eocene, about 49 Ma (Legendre & Lévêque 1997).

DIMENSIONS OF HOLOTYPE (THOSE OF *P. WINTERSTEINI* IN BRACKETS, AFTER MAYR 1999)

Skull: 31 [~34]. Humerus: ~24.5 (left) [27.2 (left), ~27.2 (right)]. Ulna: ~26.0 (right) [31.0 (left), 31.0

(right)]. Carpometacarpus: ~12.2 (left), ~12.6 (right) [14.7 (left), 14.9 (right)]. Tibiotarsus: ~20.8 (left) [24.9 (left)]. Tarsometatarsus: ~9.0 (right) [12.7 (left)].

ETYMOLOGY

From *pumilio* (Lat.): dwarf; the specific name refers to the small size of the new species.

TAXONOMIC REMARKS

Primotrogon? pumilio sp. nov. closely resembles modern trogons in overall morphology of its skeleton and shares with other Trogoniformes the presence of a heterodactyl foot, an unquestionably derived character which is only known for trogons (see Fig. 2 and description below). The new species is tentatively referred to *Primotrogon* Mayr 1999, which it closely resembles in overall morphology of the preserved skeletal elements, as far as the specimens are comparable owing to the rather poor preservation of the fossil from Messel. This assignment is tentative because it is based on overall similarity and not on shared derived characters. The cranium of the much larger Lower Eocene *Septentrogon madseni* Kristoffersen 2002, the only other named early Tertiary trogon, unfortunately does not allow for meaningful comparisons with the poorly preserved of new species from Messel.

DESCRIPTION AND COMPARISON

Judging from the shape of the mandible, the skull appears to have been narrower than that of extant trogons, as is the skull of *Primotrogon wintersteini*. Unlike in extant trogons but like in *Primotrogon wintersteini* (Mayr 1999, p. 430), the premaxilla does not taper

into a narrow tip (Fig. 1). The narial openings are proportionally longer than those of extant trogons. The right pterygoid is visible and exhibits an articulation facet for basipterygoid process, the presence of which is characteristic of trogons, distinguishing them from most other 'higher land birds'. The symphysis mandibulae is of similar size to that of the extant Asian genus *Harpactes*; a fenestra mandibulae is absent (in extant trogons this character is variable, being well developed in, for example, *Harpactes reinwardtii* and reduced in, for example, *Pharomachrus mocinno*).

Details of the vertebral column and the pectoral girdle cannot be discerned except that the coracoids are slender and the sternum is small relative to that of modern trogons.

The humerus resembles the corresponding bone of *Primotrogon wintersteini* in its proportions and, as in this species, appears to be somewhat more slender than that of extant trogons. As in many 'higher land birds', the ulna distinctly exceeds the humerus in length. As far as is comparable owing to the poor preservation of the specimen, the carpometacarpus appears similar to the corresponding bone of *P. wintersteini*.

Details of the pelvis and the femur cannot be discerned. As in extant trogons, the condyli of the tibiotarsus appear to have been proximo-distally

low. The tarsometatarsus is short, as is the corresponding bone of extant trogons. The trochlea metatarsi II is poorly preserved in the specimen and whether a trochlea accessoria was present cannot be discerned. However, the heterodactyl condition of the toes is clearly visible for the right foot (Fig. 2). The second toe with only three phalanges (vs. four in the third and five in the fourth toe) directs backwards. Its poorly preserved claw appears to have the same orientation as that of the hindtoe, which would not be the case if it was an accidentally reversed forward-pointing toe. Moreover, in articulated bird skeletons the toes are firmly connected to the trochleae of the tarsometatarsus and fixed in their position by strong ligaments, and I have not observed an accidentally heterodactyl position of the toes in any other of the numerous articulated bird skeletons from Messel. The three anterior toes of the left foot cluster close together and the orientation of the second toe cannot be discerned.

cf. *Primotrogon* sp.

REFERRED SPECIMEN

SMF Avenue 498 a+b (incomplete right wing on two slabs, Fig. 3).

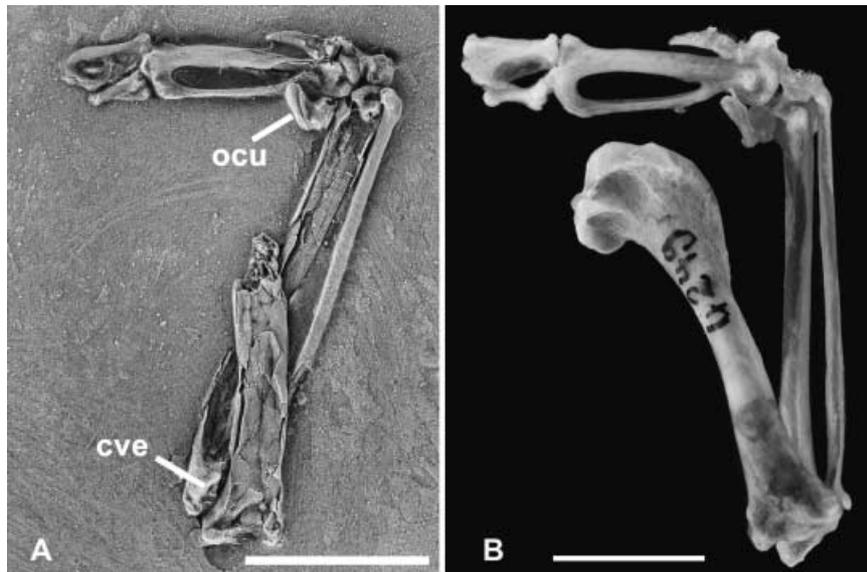


Figure 3. Incomplete right wing of a trogon from the early Oligocene (Rupelian) of Frauenweiler, Baden-Württemberg, Germany (specimen SMF Av498 a+b) (A) in comparison with the right wing of the extant Blue-billed Trogon *Harpactes reinwardtii* (SMF 4249) (B). Abbreviations: cve, cotyla ventralis of ulna; ocu, os carpi ulnare. Specimen in A coated with ammonium chloride to enhance contrast; scale bars = 10 mm.

DIMENSIONS

Ulna, ~25.4. Carpometacarpus, 12.3.

LOCALITY AND HORIZON

Frauenweiler near Wiesloch (Baden-Württemberg, Germany), clay pit of the Bott-Eder GmbH ('Grube Unterfeld'); Rupelian, early Oligocene, about 30–34 Ma (see Micklich & Parin 1996, Legendre & Lévêque 1997).

DESCRIPTION AND COMPARISON

The specimen is of similar size to *Primotrogon? pumilio*. It consists of an incomplete right wing lacking the proximal half of the humerus and the distal phalanx of the major digit; the processus extensorius of the carpometacarpus is broken. Although it is fragmentary, it can be assigned reliably to the Trogonidae because it exhibits the following combination of derived characters (Fig. 3) that are characteristic for trogons, absent in basal neornithine birds such as waterfowl (Anseriformes) and present in few other avian taxa: (1) ulna with very large cotyla ventralis; (2) carpometacarpus with wide spatium intermetacarpale; and (3) os carpi ulnare with greatly elongated crus longum (see Mayr 2003, fig. 3). In overall morphology the fossil remains also closely resemble the wing bones of extant trogons (Fig. 3), which are clearly distinguished from those of other birds by the combination of the above characters.

DISCUSSION

Apart from differences in size and proportions, extant trogons have a very uniform osteology. Of the fossil taxa, *Primotrogon wintersteini* differs from modern trogons in the narrower skull (Fig. 4), proportionally smaller orbitae and the absence of derived characters of the coracoid (see Mayr 1999), differences that suggest this species does not belong to crown group Trogoniformes.

Owing to the poor preservation of the only known specimen, most of these features cannot be discerned in *Primotrogon? pumilio* sp. nov., which is, however, also distinguished from crown group Trogoniformes based on the shape of its beak (Fig. 1 and description above). Furthermore, both *Primotrogon wintersteini* and *P.? pumilio* are much smaller in size than their extant relatives.

According to Kristoffersen (2002), the cranium of the Eocene *Septentrogon madseni* differs from that of extant Trogonidae in that the naso-frontal hinge is proportionally narrower, the processus zygomaticus somewhat smaller, and the articulation facet for the quadrate less caudally situated than in extant trogons. Again, the corresponding condition in extant trogons is probably derived, suggesting that *Septentrogon* is outside the crown group of Trogoniformes.

The incomplete trogoniform (Olson 1976) skeleton from the Oligocene of Switzerland (Peyer 1957, plates 9–11) is considerably distorted and its exact systematic position within Trogoniformes is uncertain. Similarly,

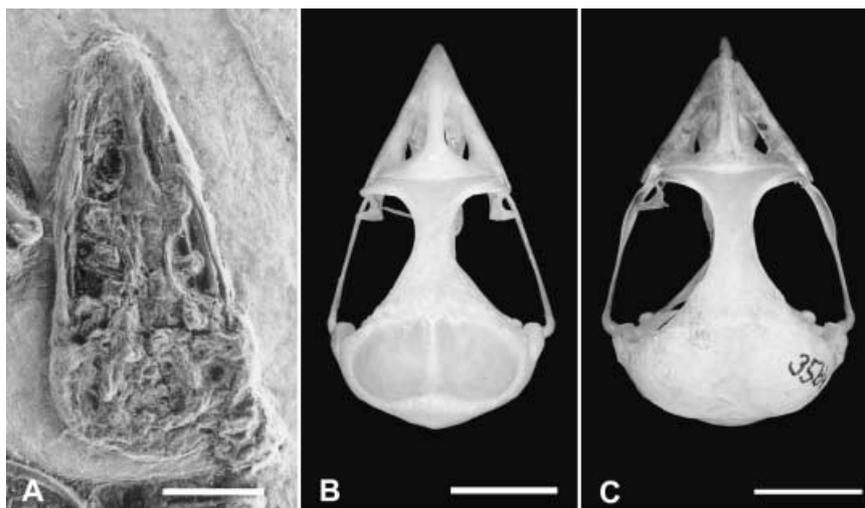


Figure 4. *Primotrogon wintersteini* Mayr 1999, skull of the holotype (A) in comparison with the skull of the extant Cuban Trogon (*Priotelus temnurus*, ZMB 36648) (B) and Orange-breasted Trogon (*Harpactes oreskios*, SMF 3564) (C). The Cuban Trogon has the narrowest skull of the extant taxa examined. Specimen in A coated with ammonium chloride; scale bars = 10 mm.

the new specimen from Frauenweiler is too fragmentary for its phylogenetic affinities within Trogoniformes to be assessed with confidence.

The early Miocene *Paratrogon gallicus* was referred to the extant African genus *Apaloderma* by Mlíkovský (2002, p. 224f) but no convincing evidence for this assignment has been presented, and the listed similarity of the humeri of *Paratrogon* and *Apaloderma* ('entepicondylar prominence large and distinct') may well be plesiomorphic within Trogoniformes.

The fact that all sufficiently well-preserved early Tertiary trogons appear to be outside the crown group of Trogoniformes thus supports molecular studies indicating a mid-Tertiary (Espinosa de los Monteros 1998), rather than a late Cretaceous (Johansson 1998), divergence of the crown group.

Crown group Trogoniformes may have 'dispersed into the New World either early across the North Atlantic land connection or later via the Bering land bridge' (Feduccia 1999, p. 336). Whether they reached South America before or after the late Miocene/Pliocene (e.g. Cox & Moore 1993, Marshall & Liebherr 2000) closure of the Panamanian Isthmus is unknown, as the earliest trogon fossils in the New World are from the Pleistocene of the Dominican Republic and Brazil (Brodkorb 1971).

Assuming that mousebirds (Coliiformes) are the sister taxon of trogons, Espinosa de los Monteros (1998, p. 948) noted that the divergence between Coliiformes and Trogoniformes was 'between 25.5 and 46.1 Ma. However, as trogons closely resembling the modern taxa were already present in the early Eocene (49 Ma) the divergence between trogons and their sister taxon (possibly the Steatornithidae, see Mayr & Clarke 2003, Mayr 2003) may be considerably older.

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REFERENCES

- Baumel, J.J. & Witmer, L.M.** 1993. Osteologia. In Baumel, J.J., King, A.S., Breazile, J.E., Evans, H.E. & Vanden Berge, J.C. (eds) *Handbook of Avian Anatomy: Nomina Anatomica Avium*: 45–132. Publications of the Nuttall Ornithological Club **23**.
- Brodkorb, P.** 1971. Catalogue of fossil birds: Part 4 (Columbiformes through Piciformes). *Bull. Florida State Museum Biol. Sci.* **15**: 163–266.
- Collar, N.J.** 2001. Family Trogonidae (Trogons). In del Hoyo, J., Elliott, A. & Sargatal, J. (eds) *Handbook of the Birds of the World*, Vol. 6: 80–127. Barcelona: Lynx Edicions.
- Cox, C.B.** 2000. Plate tectonics, seaways and climate in the historical biogeography of mammals. *Mem. Inst. Oswaldo Cruz* **95**: 509–516.
- Cox, C.B. & Moore, P.D.** 1993. *Biogeography; an Ecological and Evolutionary Approach*, 5th edn. Oxford: Blackwell Science.
- Eisenmann, E.S.B.** 1985. Trogon. In Campbell, B. & Lack, E. (eds) *A Dictionary of Birds*: 609–610. Calton: Poyser.
- Espinosa de los Monteros, A.** 1998. Phylogenetic relationships among the trogons. *Auk* **115**: 937–954.
- Feduccia, A.** 1999. *The Origin and Evolution of Birds*, 2nd edn. New Haven: Yale University Press.
- Johansson, U.** 1998. The early evolution of the Trogonidae. *Ostrich* **69**: 402.
- Kristoffersen, A.V.** 2002. An early Paleogene trogon (Aves: Trogoniformes) from the Fur Formation, Denmark. *J. Vertebrate Paleontol.* **22**: 661–666.
- Legendre, S. & Lévêque, F.** 1997. Etalonnage de l'échelle biochronologique mammalienne du Paléogène d'Europe occidentale: vers une intégration à l'échelle globale. In Aguilar, J.-P., Legendre, S. & Michaux, J. (eds) *Actes du Congrès Biochrom '97*: 461–473. Mémoires et Travaux de l'Ecole Pratique des Hautes Etudes, Institut de Montpellier 21.
- Marshall, C.J. & Liebherr, J.K.** 2000. Cladistic biogeography of the Mexican transition zone. *J. Biogeogr.* **27**: 203–216.
- Mayr, E.** 1988. Plattentektonik und die Geschichte der Vogelfaunen. In *Proceedings of the International 100. DO-G Meeting, Current Topics in Avian Biology, Bonn*: 1–17. editors: van den Elzen, R., Schuchmann, K.-L. & Schmidt-Koenig, K. publisher: Deutsche Ornithologen-Gesellschaft, Bonn.
- Mayr, G.** 1999. A new trogon from the Middle Oligocene of Céreste, France. *Auk* **116**: 427–434.
- Mayr, G.** 2000. Die Vögel der Grube Messel – ein Einblick in die Vogelwelt Mitteleuropas vor 49 Millionen Jahren. *Natur Museum* **130**: 365–378.
- Mayr, G.** 2001. A second skeleton of the early Oligocene trogon *Primotrogon wintersteini* Mayr 1999 (Aves: Trogoniformes: Trogonidae) in an unusual state of preservation. *Senckenbergiana Lethaea* **81**: 335–338.
- Mayr, G.** 2003. On the phylogenetic relationships of trogons (Aves, Trogonidae). *J. Avian Biol.* **34**: 81–88.
- Mayr, G. & Clarke, J.** 2003. The deep divergences of neornithine birds: a phylogenetic analysis of morphological characters. *Cladistics* **19**: 527–553.
- Micklich, N. & Parin, N.** 1996. The fishfauna of Frauenweiler (Middle Oligocene, Rupelian; Germany): first results of a review. *Publ. Especiales Inst. Español Oceanografía* **21**: 129–148.
- Milne-Edwards, A.** 1867–71. *Recherches anatomiques et paléontologiques pour servir à l'histoire des oiseaux fossiles de la France*. Paris: Victor Masson et fils.
- Mlíkovský, J.** 2002. *Cenozoic Birds of the World. Part 1: Europe*. Praha: Ninox Press.
- Mourer-Chauviré, C.** 1980. The Archaeotrogonidae from the Eocene and Oligocene deposits of Phosphorites du Quercy (France). *Natural History Museum Los Angeles County, Contrib. Sci.* **330**: 17–31.
- Mourer-Chauviré, C.** 1995. Les Garouillas et les sites contemporains (Oligocène, MP 25) des Phosphorites du Quercy

- (Lot, Tarn-et-Garonne, France) et leurs faunes de Vertébrés. 3. Oiseaux. *Palaeontographica (a)* **236**: 33–38.
- Olson, S.L.** 1976. Oligocene fossils bearing on the origins of the Todidae and the Momotidae (Aves: Coraciiformes). *Smithsonian Contrib. Paleobiol.* **27**: 111–119.
- Peyer, B.** 1957. *Protornis glaronensis* H. v. Meyer Neubeschreibung des Typusexemplars und eines weiteren Fundes. *Schweiz. Paläontol. Abh.* **73**: 1–47.

- Schaal, S. & Ziegler, W.** 1988. *Messel – Ein Schaufenster in die Geschichte der Erde und des Lebens*. Frankfurt: Kramer.
- Smith, A.G., Smith, D.G. & Funnell, B.M.** 1994. *Atlas of Mesozoic and Cenozoic Coastlines*. Cambridge: Cambridge University Press.

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