Palaeobio Palaeoenv (2009) 89:1–6
DOI 10.1007/s12549-009-0001-9

ORIGINAL PAPER

A well-preserved second trogon skeleton (Aves, Trogonidae) from the middle Eocene of Messel, Germany

Gerald Mayr

Received: 15 March 2009 / Revised: 8 April 2009 / Accepted: 15 April 2009 / Published online: 20 May 2009

Abstract A second skeleton of a trogon is reported from the middle Eocene of Messel in Germany, which represents the best preserved Eocene record of this group of birds known to date. The new specimen shows that the Messel trogon, which was originally described as ?*Primotrogon pumilio*, differs from *Primotrogon* in a narrower spatium intermetacarpale of the carpometacarpus and a proportionally longer hallux. The middle Eocene species is thus assigned to the new taxon *Masillatrogon*. The plesiomorphically narrow spatium intermetacarpale supports a position of *Masillatrogon* outside a clade including *Primotrogon* and crown group Trogoniformes, and the presence of successive sister taxa of extant Trogonidae in the Paleogene and early Neogene of Europe indicates an Old World origin of the crown group. *Masillatrogon* and *Primotrogon* further lack derived features of the wing skeleton of extant Trogonidae, and these early trogons thus probably employed a somewhat different flight and foraging technique.

Keywords Fossil birds · Messel · Eocene · Trogonidae · *Masillatrogon* n. gen

Introduction

Trogons (Trogonidae) are brightly colored, insectivorous or frugivorous tree-dwelling birds, and the only avian group with heterodactyl feet, i.e., permanently retroverted second toes. Today, they occur in the tropical and subtropical parts of the New World, continental Africa, and Asia. Already in the nineteenth century, however, trogon fossils were reported from the early Miocene of France (Milne-Edwards 1867–1871), and early Oligocene trogons have previously been described from Switzerland (Olson 1976), France (Mayr 1999, 2001), and Germany (Mayr 2005). The skeletons from the Lubéron area in France were assigned to *Primotrogon wintersteini* Mayr, 1999, while the taxonomic identity of those from Switzerland and Germany has not yet been established.

Irrespective of this recent increase of Paleogene trogon fossils, pre-Oligocene, i.e. Eocene, records of trogoniform birds are still very rare (Mayr 2009). Kristoffersen (2002) described a cranium of a trogon from the Fur Formation in Denmark as *Septentrogon madseni*, and as yet undescribed trogon remains were also found in the early Eocene London Clay in England (Mayr 1999). A still undescribed partial skeleton of a putative trogon was reported from the early Eocene Green River Formation in North America (Weidig 2003). However, the only published record of a largely complete Eocene trogon skeleton is from the middle Eocene of Messel in Germany, and was described as ?*Primotrogon pumilio* by Mayr (2005). The holotype of this species is poorly preserved and does not allow close examination of osteological details, but here I describe a recently identified well-preserved second skeleton of *M. pumilio* from Messel, which provides information on previously unknown osteological details of this middle Eocene trogon.

Material and methods

Osteological terminology follows Baumel and Witmer (1993). Comparisons were made with skeletons of the following extant species of Trogonidae (all in the collection of Forschungsinstitut Senckenberg): *Harpactes ardens*, *H.*

G. Mayr (✉)
Sektion Ornithologie, Forschungsinstitut Senckenberg,
Senckenberganlage 25,
60325 Frankfurt/M, Germany
e-mail: Gerald.Mayr@senckenberg.de

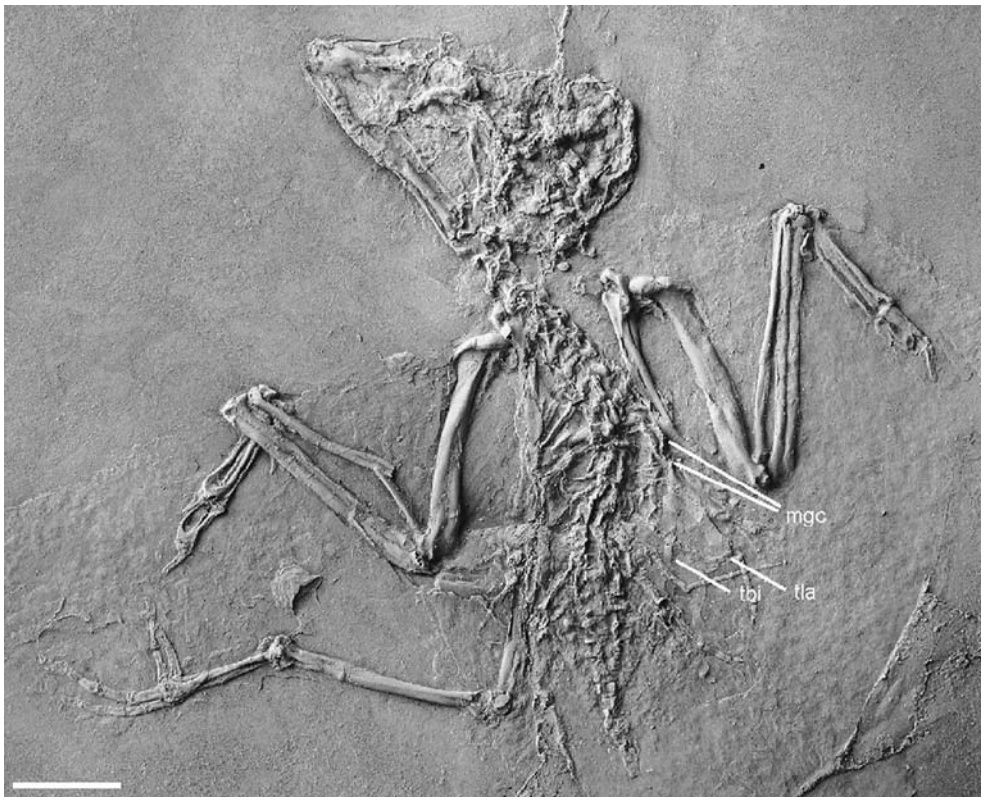

Fig. 1 *Masillatrogon pumilio* (Mayr, 2005) from the middle Eocene of Messel, referred specimen IRSNB Av81. *mgc* Margo costalis of sternum, *tbi* trabecula intermedia, *tla* trabecula lateralis. Coated with ammonium chloride; *scale bar* 10 mm

diardii, *H. erythrocephalus*, *H. oreskios*, *H. reinwardtii*, *Pharomachrus auriceps*, *P. mocinno*, *P. pavoninus* (skull), and *Trogon viridis*. In order to examine the proportions of the toes, skins of all extant species were studied.

Institutional abbreviations: IRSNB – Institut royal des Sciences naturelles de Belgique, Belgium; SMF – Forschungsinstitut Senckenberg, Frankfurt am Main, Germany.

Systematics

Trogoniformes American Ornithologists' Union, 1886
Trogonidae Lesson, 1828
Masillatrogon n. gen.

Included species

Masillatrogon pumilio (Mayr, 2005).

Differential diagnosis

Differs from *Primotrogon* Mayr, 1999 and all of the examined extant Trogonidae in the narrow spatium intermetacarpale of the carpometacarpus and the proportionally longer hallux, which is almost as long as the reversed second toe (distinctly shorter in other Trogoniformes). Comparisons with the larger *Septentrogon* Kristoffersen, 2002 are not possible owing to the poor preservation of the cranium in the two specimens of the Messel trogon (length

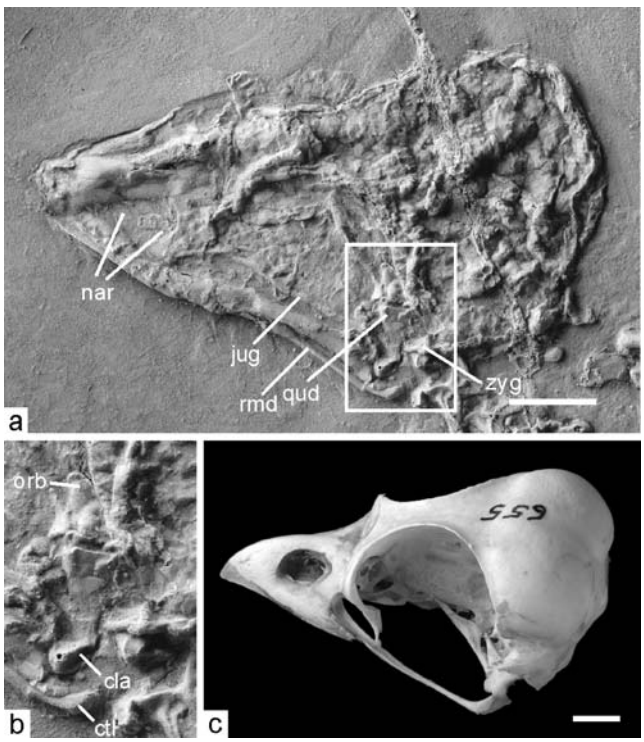

Fig. 2 Skull in comparison. **a** *Masillatrogon pumilio* (Mayr, 2005), specimen IRSNB Av81; **b** enlarged detail of the quadratum (framed area in **a**); **c** skull of the extant Philippine Trogon (*Harpactes ardens*). *cla* Condylus lateralis, *ctl* cotyla lateralis, *jug* os jugale, *nar* narial opening, *orb* processus orbitalis, *qud* quadratum, *rmd* left ramus mandibulae, *zyg* processus zygomaticus. *Scale bars* 5 mm

of cranium from nasofrontal hinge 21 mm versus 25 mm in *Septentrogon madseni*).

Etymology

The taxon name has been derived from “masilla”, the old Latin name of Messel.

Masillatrogon pumilio (Mayr, 2005)
2005 ?*Primotrogon pumilio* Mayr: 513, Figs. 1 and 2

Referred specimen

IRSNB Av81 (articulated skeleton lacking right leg; Fig. 1).

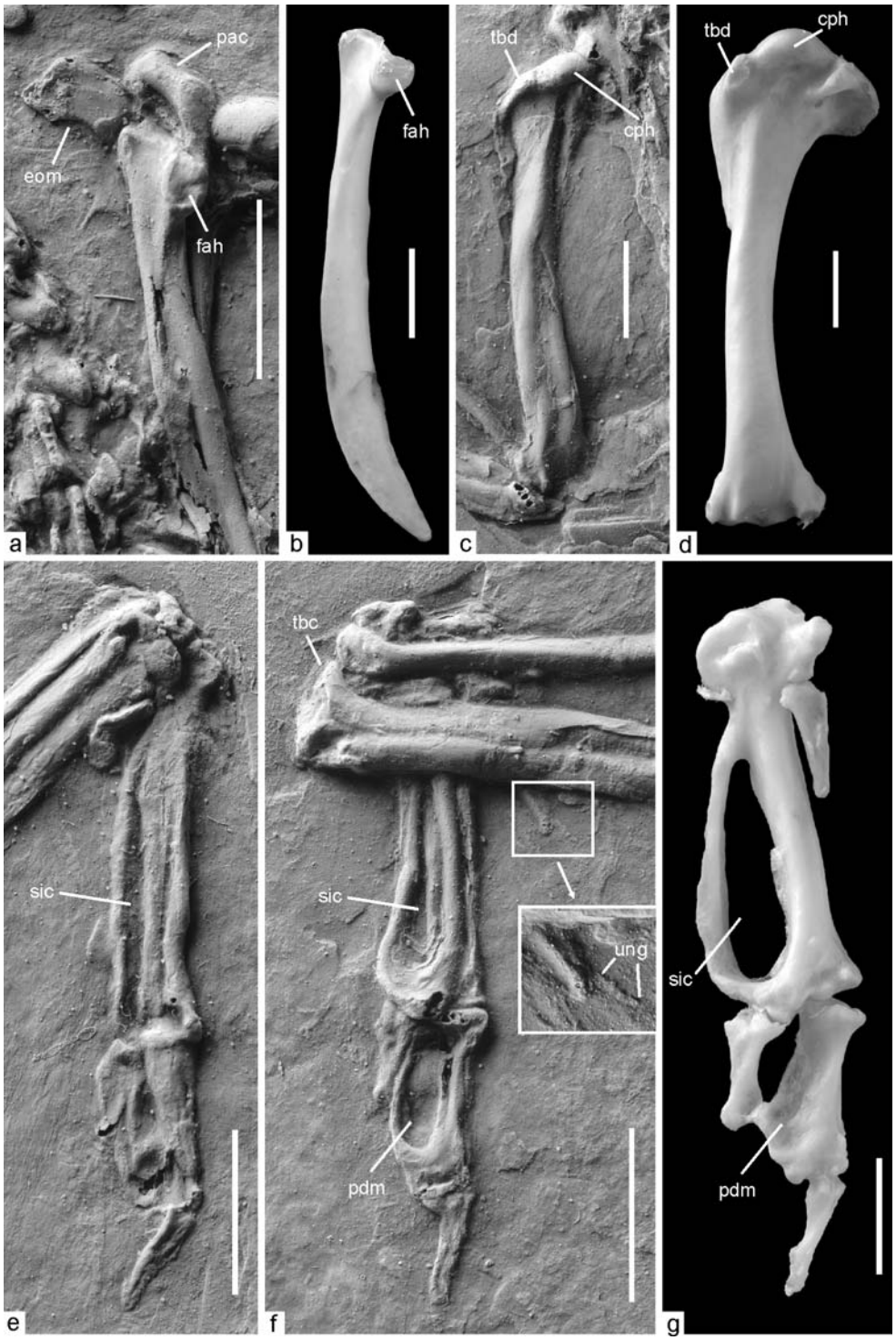

Fig. 3 Select postcranial bones of *Masillatrogon pumilio* (Mayr, 2005), specimen IRSNB Av81, in comparison. **a** *M. pumilio*, right extremitas omalis of furcula, extremitas omalis of right coracoid, and acromion of right scapula; **b** right right scapula of the extant Philippine Trogon, *Harpactes ardens*; **c** *M. pumilio*, left humerus in caudal view; **d** left humerus of *H. ardens*; **e** *M. pumilio*, right manus in dorsal view; **f** *M. pumilio*, left manus in ventral view with enlarged detail of framed area; **g** left manus (ventral view) of the extant Javan Trogon, *H. reinwardtii*. *cph* Caput humeri, *eom* extremitas omalis of furcula, *fah* facies articularis humeralis of scapula, *pac* processus acrocoracoideus of coracoid, *pdm* phalanx proximalis digiti majoris, *sic* spatium intermetacarpale, *tbc* tuberculum carpale of ulna, *tbd* tuberculum dorsale, *ung* ungual phalanx of phalanx digiti alulae. Specimen of *M. pumilio* coated with ammonium chloride. *Scale bars* 5 mm

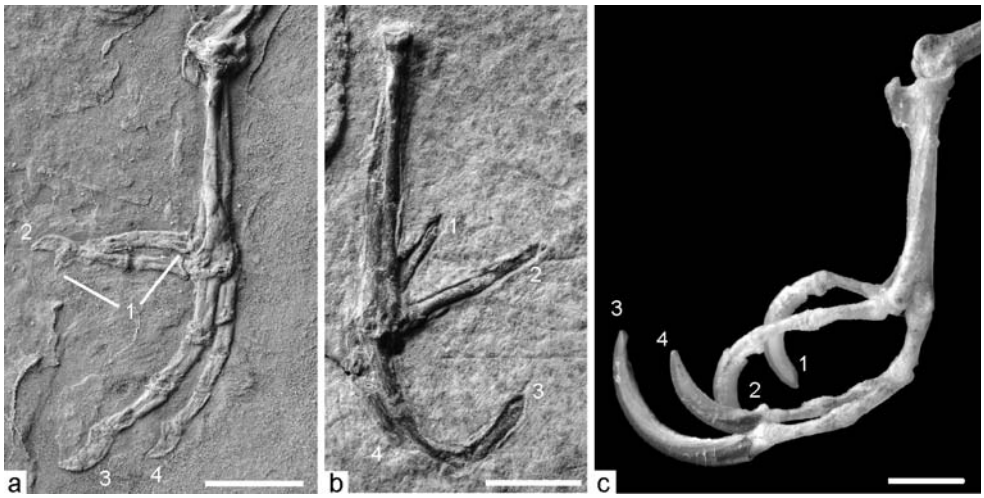

Fig. 4 Foot of *Masillatrogon pumilio* (Mayr, 2005), specimen IRSNB Av81, in comparison. **a** *M. pumilio*, left foot; **b** right foot of *Primotrogon wintersteini* Mayr, 1999 from the early Oligocene of France (SMF Av 423); **c** left foot of the extant Red-headed Trogon, *Harpactes erythrocephalus* (captive individual with very long claws). The toes are numbered; note that the foot of *P. wintersteini* lacks ungual phalanges. Specimen of *M. pumilio* coated with ammonium chloride. *Scale bars* 5 mm

Locality and horizon

Messel near Darmstadt, Hessen, Germany; middle Eocene, about 47 million years ago.

Measurements

Left/right in mm; dimensions of holotype in brackets: skull, 32.0 [31]; humerus, 21.9/22.3 [~24.5]; ulna, 25.0/~25.5 (est.) [~26.0]; carpometacarpus, ~11.2/~11.8 [~12.2/~12.6]; femur, ~15.4/–; tibiotarsus, 21.8/– [~20.8]; tarsometatarsus, 10.8/– [~9.0]. Pedal phalanges: I1, 4.8; I2, 2.1; II1, 2.6; II2, 2.8; II3, 2.0; III1, 3.3; III2, 3.2; III3, 3.6; III4, 2.9; IV1, 2.8; IV2, 2.1; IV3, 2.0; IV4, 2.3; IV5, 2.3.

Description

The skull is visible in dorsolateral view. The beak appears to have been somewhat wider than that of *Primotrogon*, but because it is crushed and flattened, its original proportions are difficult to reconstruct. As already noted by Mayr (2005), however, its tip is less pointed than that of extant Trogonidae. The narial opening is circular and caudally bordered by a broad processus maxillaris of the os nasale (Fig. 2a). Details of the os praefrontale/os ectethmoidale complex cannot be unambiguously identified. The interorbital portion of the os frontale is of similar width to *S. madseni* and the extant taxa *Trogon* and *Pharomachrus*, whereas it is narrower in the species of *Harpactes*. Also as in *S. madseni* and extant Trogonidae, the processus postorbitalis appears to have been very short and the processus zygomaticus is flattened and has a rounded tip (Kristoffersen 2002; Fig. 2). The left quadratum is visible in lateral view and has a similar shape to that of extant trogons, with a long processus orbitalis and a prominent condylus lateralis (Fig. 2b). A part of the dorsal surface of the proximal end of the left ramus mandibulae is exposed and allows recognition of the convex cotyla lateralis (Fig. 2b).

As far as comparisons are possible, the vertebrae resemble those of extant Trogonidae; the first cervical vertebrae are hidden under the skull. A small fish tooth is preserved next to one of the cervical vertebrae. The pygostyle has a large and elongate lamina pygostyli.

Only the right extremitas omalis of the furcula is visible, which has a similar shape to that of extant trogons, with a subtriangular tip and a concavity on its ventral margin (Fig. 3a). The facies articularis clavicularis on the extremitas omalis of the coracoid overhangs the sulcus supracoracoideus. The facies articularis humeralis of the scapula is narrower and more elongate than in crown group Trogoniformes (Figs. 3a, b), a fact that is presumably correlated with the less protruding caput humeri of *M. pumilio*. The acromion is short and slightly bipartite; the distal end of the scapular corpus is only weakly angled.

The sternum also corresponds to that of extant Trogonidae in its shape. The margo costalis is short and four processus costales can be counted (Fig. 1). The caudal margin bears four incisions of similar depth to those of extant trogons. Also as in the latter, the trabeculae laterales have broad caudal ends, whereas the trabeculae intermediae and the trabecula mediana are narrow.

The humerus is more slender than that of extant Trogonidae, with the caput humeri being more caudally inflected and the tuberculum dorsale smaller (Figs. 3c, d). The crista deltopectoralis is less cranially deflected and has a concave caudal surface. As in extant Trogonidae, the ulna has a long and protruding tuberculum carpale and a well-developed olecranon, and the crus longum of the os carpi ulnare is very long. The distal end of the wing, however, exhibits a more plesiomorphic morphology than that of crown group Trogonidae in that the spatium intermetacarpale of the carpometacarpus is narrower, and the caudal margin of the phalanx proximalis digiti majoris not reduced

Fig. 5 *Masillatrogon pumilio* (Mayr, 2005), specimen IRSNB Av81 uncoated to show the preservation of the feathers. Note that the slab has been painted black around the skeleton and feather impressions. *Scale bar* 10 mm

to a thin blade (Figs. 3e-g). Overlain by the distal end of the left ulna is a small elongated ossicle, which I consider to be the tip of the phalanx digiti alulae (Fig. 3f). If this interpretation is correct, the bone bears a rudimentary ungual phalanx, which is absent in *Primotrogon wintersteini*, the early Oligocene trogon from Switzerland (Peyer 1957), and extant Trogonidae.

The pelvis has similar overall proportions to that of extant Trogonidae but is too poorly preserved for detailed comparisons. The tuberositas musculi tibialis cranialis of the tarsometatarsus is prominent and situated at the medial margin of the bone. The tarsometatarsal trochleae are poorly preserved, but the presence of a heterodactyl foot is indicated by the fact that, as in other fossil trogon skeletons (Olson 1976; Mayr 1999, 2001, 2005), the second toe is preserved in a reversed position (Fig. 4a). Being almost as long as the reversed second toe, the hallux is proportionally longer than that of *P. wintersteini*, the unnamed trogon from the early Oligocene of Switzerland, and extant Trogonidae, where it is distinctly shorter than the second toe (Fig. 4 and Olson 1976: Fig. 3). Whereas *M. pumilio* has a slightly smaller overall size than *P. wintersteini* (length of humerus about 22 vs 24.5 mm), the proximal phalanx of its hallux is distinctly longer (4.8 vs 3.5 mm); in an exemplar and representative individual of the extant Javan Trogon (*Harpactes reinwardtii*) it measures 4.1 mm, com-

pared to a humerus length of 29 mm. The ungual phalanges are short, with that of the third toe being the longest.

In the specimen, remains of the feathering of the wings and the tail are preserved (Fig. 5). The longest primary of the left wing measures about 57 mm. Disregarding the unusual long tail of the males of the Resplendent Quetzal (*Pharomachrus mocinno*), the tail of *M. pumilio* has a similar length and shape to that of extant Trogonidae, with the longest tail feather having a length of 60 mm. Unfortunately, neither the number of the wing feathers nor of the tail feathers is discernible.

Discussion

Masillatrogon pumilio differs most notably from extant Trogonidae in the morphology of the wing and foot skeleton. The plesiomorphic (by outgroup comparison with other "higher land birds") morphologies of the less protruding caput humeri and smaller tuberculum dorsale of the humerus, as well as the well-developed caudal margin of the phalanx proximalis digiti majoris, support a position of this middle Eocene species outside crown group Trogoniformes. The plesiomorphic presence of a narrow spatium intermetacarpale and, possibly (see description), an ungual phalanx on the phalanx digiti alulae indicates that *M. pumilio* is further outside a clade including the early Oligocene *Primotrogon* and crown group Trogoniformes. In addition, the hallux of *M. pumilio* is proportionally longer than that of all other fossil or extant trogons, which may also be a plesiomorphic trait of trogoniform birds.

Extant trogons are "sallying substrate gleaners" (Collar 2001: 90), that are able to hover over a short period to feed on fruits or to pick up insects from leaves and trunks (Collar 2001). The derived morphology of their wing skeleton most likely constitutes an adaptation to this feeding behavior, in which case the absence of the above features in *M. pumilio* indicates that the Eocene species employed a somewhat different flight technique and foraging behavior than its extant relatives.

Trogons today have a nearly pantropical distribution, and the area of origin of the crown group is debated. Whereas Espinosa de los Monteros (1998) assumed that the stem species of extant trogons lived in the Old World, possibly in Africa, Moyle (2005) considered a New World origin of crown group Trogoniformes more likely. Both authors based their hypotheses on phylogenies derived from molecular analyses. The fossil record is more consistent with an Old World origin of crown group Trogoniformes. Although there is an as yet unpublished record of a putative stem group representative from the early Eocene North America (Weidig 2003), all unambiguously identified Eocene trogon fossils and all Oligocene and Miocene records are from the Old World, i.e., Europe. *Masillatrogon* and *Primotrogon* are successive sister taxa of crown group Trogonidae, and *Paratrogon gallicus* (Milne-Edwards, 1867–1871) from the early Miocene of France already exhibits the derived humerus morphology of crown group Trogoniformes (Mlíkovský 2002 even assigned the species to the extant taxon *Apaloderma*, but this classification is poorly established and based on a presumably plesiomorphic overall similarity). The fact that successive sister taxa of crown group Trogonidae occur in European fossil sites is most parsimoniously explained by the assumption that the lineage leading to crown group Trogoniformes evolved in the Old World, and trogons may have dispersed into the New World in the late Paleogene or early Neogene (when the first modern-type trogons are known).

Acknowledgements I thank Thierry Smith and Annelise Folie (both IRSNB) for the loan of the fossil specimen, Sven Tränkner for taking the photographs, and two anonymous referees for comments on the manuscript.

References

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

Collar NJ (2001) Family Trogonidae (Trogons). In: del Hoyo J, Elliott A, Sargatal J (eds) Handbook of the birds of the world, vol 6. Lynx Edicions, Barcelona, pp 80–127

Espinosa de los Monteros A (1998) Phylogenetic relationships among the trogons. Auk 115:937–954

Kristoffersen AV (2002) An early Paleogene trogon (Aves: Trogoniformes) from the Fur Formation, Denmark. J Vertebr Paleontol 22:661–666

Mayr G (1999) A new trogon from the Middle Oligocene of Céreste, France. Auk 116:427–434

Mayr G (2001) A second skeleton of the early Oligocene trogon *Primotrogon wintersteini* Mayr 1999 (Aves: Trogoniformes: Trogonidae) in an unusual state of preservation. Senck leth 81:335–338

Mayr G (2005) New trogons from the early Tertiary of Germany. Ibis 147:512–518

Mayr G (2009) Paleogene fossil birds. Springer, Heidelberg

Milne-Edwards A (1867-71) Recherches anatomiques et paléontologiques pour servir à l'histoire des oiseaux fossiles de la France. Victor Masson, Paris

Mlíkovský J (2002) Cenozoic birds of the world. Part 1: Europe. Ninox Press, Praha

Moyle RG (2005) Phylogeny and biogeographical history of Trogoniformes, a pantropical bird order. Biol J Linn Soc 84:725–738

Olson SL (1976) Oligocene fossils bearing on the origins of the Todidae and the Momotidae (Aves: Coraciiformes). Smithson 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

Weidig I (2003) Fossil birds from the Lower Eocene Green River Formation (USA). PhD thesis, Johann-Wolfgang-Goethe-Universität, Frankfurt/M