

A NEW TROGON FROM THE MIDDLE OLIGOCENE OF CÉRESTE, FRANCE

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ABSTRACT.—A new genus and species of trogon (order Trogoniformes, family Trogonidae) is described from the Middle Oligocene (approximately 33 million years ago) of Céreste, France. The new taxon, *Primotrogon wintersteini*, is the oldest trogon that has been named so far and closely resembles living species; differences mainly concern proportions of the skull. The species most likely is the sister taxon of the extant trogons. In contrast to most of its recent relatives, *Primotrogon wintersteini* lived in an arid environment. Received 17 December 1997, accepted 21 September 1998.

THE ORDER TROGONIFORMES comprises a single family, the Trogonidae, with 37 to 39 living species (Morony et al. 1975, Sibley and Monroe 1990). Extant trogons are found in the tropics and subtropics of Asia, Africa, and America. They feed on insects and fruits, and apart from size and plumage coloration, all members of the order are quite similar morphologically.

Until recently, several species of the Archaeotrogonidae from the Upper Eocene to Upper Oligocene (40 to 20 million years ago) Phosphorites du Quercy, France, were considered to be the earliest trogons (e.g. Mourer-Chauviré 1980). Members of this family lacked the heterodactyl foot of the Trogoniformes, however, and Mourer-Chauviré (1995a) proposed a closer relationship to the Caprimulgiformes. The fossil record of trogons is very scanty, with only two known early Tertiary taxa. *Paratrogon gallicus* (Milne-Edwards, 1867–1871) is known from the Lower Miocene (22 million years ago) of France and closely resembles living species. Olson (1976) identified an incomplete skeleton of a trogon from the early Oligocene “Glarner Fischeschiefer” of Matt, Switzerland, which was originally assigned to the Alcedinidae (Peyer 1957). This bird undoubtedly is a trogon but it is poorly preserved and lacks important elements (e.g. the skull).

The new specimen presented here is the most complete fossil trogon known and also is the first bird described from the Middle Oligocene (ca. 33 million years ago) deposits of Céreste, France. This locality is well known for impressions of isolated feathers, but complete skele-

tons are extremely rare (Stemvers-van Bommel 1984, Mourer-Chauviré 1995b).

SYSTEMATICS

The measurements reported below represent the overall length along the longitudinal axis except for the length of the carpometacarpus, which represents the distance between the proximal end of the trochlea carpalis and the distal end of the os metacarpale majus. Anatomical terminology follows Baumel and Witmer (1993).

Members of the Trogonidae are characterized by their unique heterodactyl foot in which the second toe and the trochlea metatarsi II of the tarsometatarsus are turned plantad. Within this family, the monophyly of the eight living genera (*Trogon*, *Pharomachrus*, *Euptilotis*, *Priotelus*, *Temnotrogon*, *Apaloderma*, *Heterotrogon*, and *Harpactes*) is supported by the following two features of the coracoid: (1) a small process on facies articularis clavicularis overhanging the sulcus musculi supracoracoidei; and (2) a notch on the medial side of extremitas sternalis. These two characters certainly are derived within neognathous birds, because character 1 is not found in any other recent bird, and character 2 only occurs within the Momotidae (Coraciiformes) and a few other birds.

Primotrogon gen. nov.

Type species.—*Primotrogon wintersteini* Mayr.

Diagnosis.—*Primotrogon* exhibits the heterodactyl foot of all trogoniforms, but the two derived characters of the living genera mentioned

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FIG. 1. *Primotrogon wintersteini*, holotype (BSP 1997 I 38). Scale (lower left) in mm.

above are absent. This suggests that the new genus is the sister taxon of extant trogons. *Primotrogon* further differs from all recent trogons in the smaller orbitae, the narrower base of the bill, the less protruding facies articularis digitalis minor, and the shorter processus extensorius of the carpometacarpus. The status of these characters (i.e. if they are derived or primitive within trogoniforms) is unknown and can only be solved by an exhaustive phylogenetic analysis including most of the "higher" land birds; such an analysis is beyond the scope of this paper.

Etymology.—The generic name is Latin for "first trogon."

Remarks.—The unnamed trogon from the "Glarner Fischechiefer" (see above) might also belong to the genus *Primotrogon*, but the only known specimen is too poorly preserved for detailed comparisons. It is larger than *P. wintersteini*; according to Peyer (1957), the measurements (in mm) are ulna, about 35; tibiotarsus, about 36; and tarsometatarsus, about 19.

Primotrogon wintersteini sp. nov.

Holotype.—See Figures 1 and 2. Slightly disintegrated incomplete skeleton, which is deposited in the Bayerische Staatssammlung für Paläontologie und Historische Geologie (BSP),

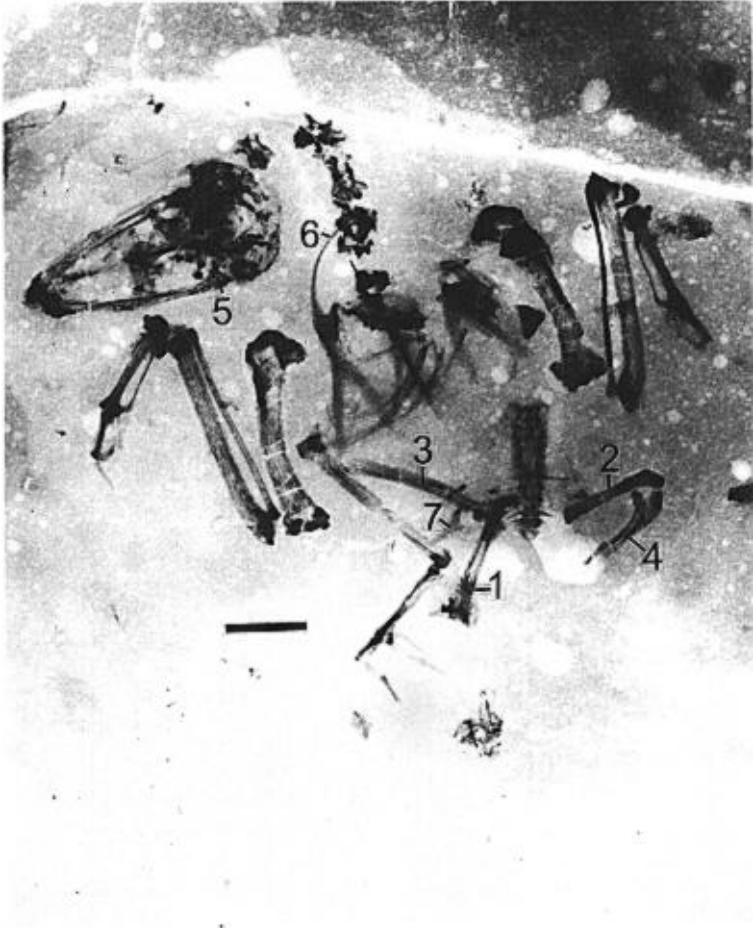


FIG. 2. X-ray photograph of *Primotrogon wintersteini* holotype. Numbers indicate left coracoid (1); right coracoid (2); left scapula (3); unidentified bone (4); proximal end of mandible (5); scapus clavicularae (6); and ala ischii (7). Scale = 10 mm.

München, Germany (collection number 1997 I 38).

Diagnosis.—Same as for genus. *Primotrogon wintersteini* is slightly smaller than the extant *Trogon violaceus*.

Measurements.—Skull (total length), about 34 mm; left coracoid, 19.8 mm; humerus, 27.2 mm (left), about 27.2 mm (right); ulna, 31.0 mm (left), 31.0 mm (right); carpometacarpus, 14.7 mm (left), 14.9 mm (right); left tibiotarsus, 24.9 mm; left tarsometatarsus, 12.7 mm; left pedal phalanges, I1, 3.5 mm; II1, 5.5 mm; II2, about 4.3 mm; III1, 4.0 mm; III2, 4.1 mm; III3, 4.7 mm; IV1, 2.6 mm; IV2, about 2.6 mm; IV3, about 2.6 mm; longest feather of wing, about 90 mm.

Type locality.—Céreste, Département Alpes-de-Haute-Provence, France.

Type horizon.—The fossils from Céreste are found in the "Calcaires de Montfuron" or in the "Calcaires de Vachères" (C. Mourer-Chauviré pers. comm.). These formations are of Middle Oligocene (MP 24) age (Ducreux et al. 1985).

Referred specimens.—None.

Etymology.—The species is named after Wilhelm Winterstein, whose generous financial support made it possible to purchase the specimen.

REMARKS

The taphonomy of the skeleton is very odd. Both coracoids and the left scapula are separated from the pectoral girdle and displaced far caudally (Fig. 2, nos. 1 to 3). This would be

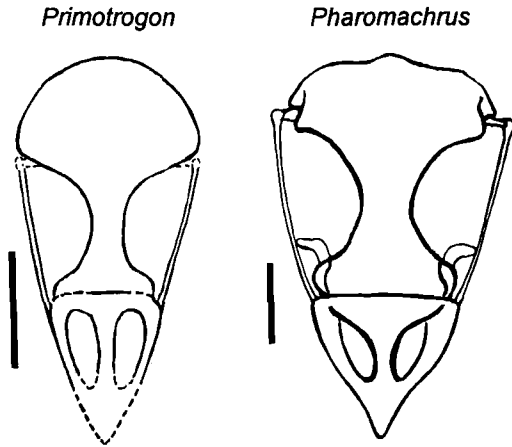


FIG. 3. Skull of *Primotrogon wintersteini* (on left; generalized reconstruction that is not to be relied on for details) and *Pharomachus pavoninus* (on right). Scale = 10 mm.

quite unusual if it was due to decomposition, because in birds the pectoral girdle, the sternum, and the wings are joined tightly to each other. It is also striking that both wings and the left leg are preserved near to their original position, although the elements connecting them to the rest of the body are either absent (left femur) or displaced (coracoids). Some of the skeletal elements (e.g. vertebral column, left scapula, right coracoid, and furcula) are incomplete, and the right leg and the tail are entirely absent. It is difficult to interpret this taphonomic situation. Possibly, the skeleton was disturbed by an animal feeding on the carcass.

A large bone lying next to the left coracoid (Fig. 2, no. 4) certainly does not belong to *P. wintersteini*, yet I have been unable to identify it. It looks somewhat like the caudal end of an avian ramus mandibulae, but besides the fact that it would be too large for *P. wintersteini*, both rami mandibulae are connected to the skull as can be seen on the x-ray photograph (Fig. 2, no. 5).

Description and comparison.—Probably *P. wintersteini* differs most strongly from living trogons in the proportions of the skull (Fig. 3), which resemble some passeriforms (e.g. *Bombycilla garrulus*). In the extant trogons, the orbitae take up most of the cranium, whereas the cranial cavity is distinctly larger and more rounded in *P. wintersteini*. The distal part of the cranium (os frontale and os lacrimale) and the proximal part of the beak are narrower in this

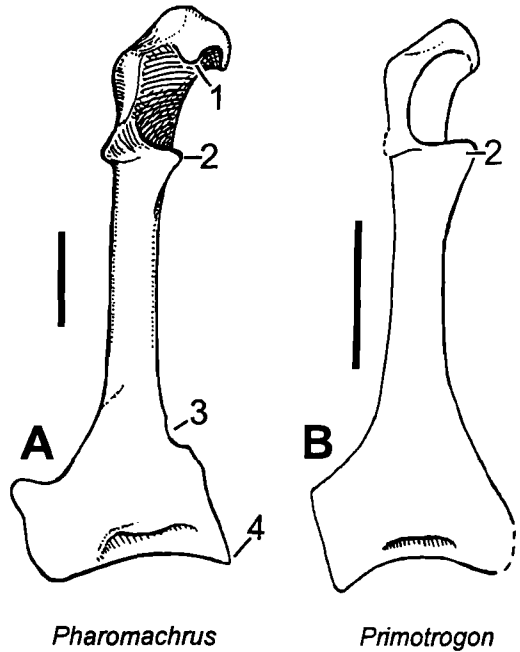


FIG. 4. Left coracoid of (A) *Pharomachus pavoninus* and (B) *Primotrogon wintersteini*. Numbers indicate process overhanging the sulcus musculi supracoracoidei (1); processus procoracoideus (2); notch on medial side of extremitas sternalis (3); and angulus medialis (4). Scale = 5 mm.

species, too. The bill is more elongated, and although its tip is not clearly visible, it seems to be less pointed than that of the recent trogons. The narial openings are large and oval-shaped. The mandible does not articulate as far caudally as it does in living trogons (its proximal end is visible on the x-ray photograph; Fig. 2, no. 5).

Most of the cervical and some thoracic vertebrae are preserved, but no details are visible. The caudal vertebrae including the pygostyle have been lost entirely. Six left (?) vertebral ribs can be counted.

The coracoid is similar to that of extant trogons in its proportions, yet it differs in some details (Figs. 4A, B). The facies articularis clavicularis of the processus acrocoracoideus does not exhibit the small projection overhanging the sulcus musculi supracoracoidei (Fig. 4A, no. 1), and the processus procoracoideus (Fig. 4A, no. 2) is broader. The extremitas sternalis differs from that of the living genera in the absence of a notch on the medial margin (Fig. 4A, no. 3) and in the form of the angulus medialis (Fig. 4A, no. 4), which does not taper off to a

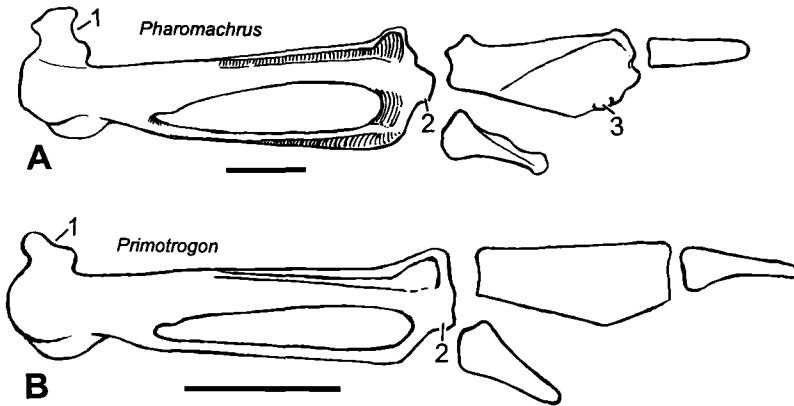


FIG. 5. Right manus of (A) *Pharomachus pavoninus* and (B) *Primotrogon wintersteini*. The digitus alulae is not shown. Numbers indicate processus extensorius (1); facies articularis digitalis minor (2); and tubercle on phalanx proximalis digiti majoris (3). Scale = 5 mm.

point; the angulus lateralis of the processus lateralis is less pronounced.

Much of the corpus of the left scapula (Fig. 2, no. 3) is preserved but does not show any peculiarities. A single scapus clavicularae is visible near the cranial end of the sternum (Fig. 2, no. 6). It becomes broader toward its extremitas omalis.

The sternum is short and very wide (its caudal width even exceeds the length of the humerus). The processus craniolaterales and the margo cranialis are not visible. Three processus costales can be counted on the x-ray photograph. The margo caudalis shows four incisurae, of which the incisurae laterales are deeper than the incisurae mediales. The trabeculae lack transverse processes at their caudal end. Like in the recent genera, the trabecula mediana is triangular.

The humerus differs in some details from that of recent trogons. An enlarged crista bicipitalis, which is characteristic of the humerus of living genera, apparently is absent. The fossa pneumotricipitalis is single, whereas in recent trogons a shallow second fossa ends beneath the caput humeri. The tuberculum dorsale is weak. There is a slight notch between the tuberculum ventrale and the crus ventrale fossae. Like in living trogons, the crista deltopectoralis seems to be bent toward the cranial side of the humerus. It is not visible in the specimen or in the x-ray photograph (both humeri are slightly turned in dorsocranial direction). The processus flexorius is short; the sulcus scapulopectoralis is shallow. The processus supracondylar-

is dorsalis is small, and the condylus dorsalis and the condylus ventralis resemble those of extant genera (see Fig. 2).

The ulna is longer than the humerus. Papillae remigales are absent, and the olecranon is large. Other details of this bone are not visible. The carpometacarpus is comparable to that of living trogons (Figs. 5A, B). The spatium intermetacarpale is wide, and the symphysis metacarpalis distalis is short. The distal part of the os metacarpale minus is slightly tilted. The processus extensorius (Fig. 5B, no. 1) is shorter than in extant genera. The facies articularis digitalis minor is in line with the os metacarpale majus, whereas it protrudes farther distally in extant trogons (Fig. 5A, no. 2). The sulcus tendinosus opens in a shallow funnel-shaped depression.

The digitus minor is large. In recent trogons, the phalanx proximalis digiti majoris exhibits a tubercle on its caudal side opposite to the digitus minor (Fig. 5A, no. 3) that apparently is absent in *P. wintersteini* (Fig. 5B). The os carpi ulnare resembles that of the extant trogons and many other birds; its crus breve is short.

The alae ischii of the pelvis seem to be very slender like in the extant genera (Fig. 2, no. 7); the synsacrum shows no peculiarities.

The tibiotarsus is stout and similar to the corresponding bone of *Pharomachus* sp., whereas it is much more slender in other trogons, e.g. *Trogon viridis* and *Priotelus temnurus*. The condylus lateralis protrudes only slightly toward the cranial surface of the bone.

The tarsometatarsus is short and robust. It

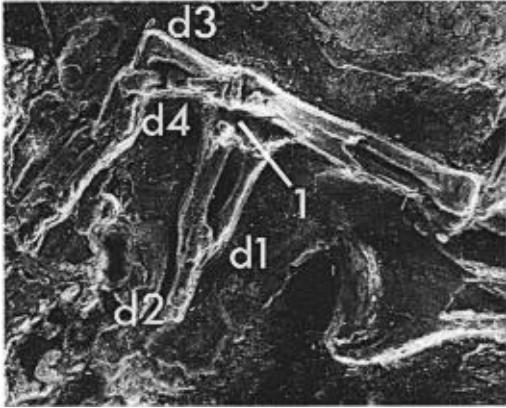


FIG. 6. Left foot of *Primotrogon wintersteini*. The digits are numbered from d1 to d4; 1 is trochlea metatarsi II.

closely resembles that of most extant species, although in *Priotelus temnurus* it is distinctly longer and more narrow. In lateral view the central section of the shaft is broad. The hypotarsus is very prominent and seems to exhibit two sulci on its lateral side. The trochlea metatarsi II (Fig. 6) is turned as far plantad as in recent trogons. The trochlea metatarsi IV is small and round when seen from its lateral side.

The arrangement of the toes clearly is heterodactyl. The phalange formula and the proportions of the phalanges are normal. The hallux is weak, and no claws have been preserved on any of the toes. The processus articularis tarsometatarsalis of the os metatarsale I is short.

The impressions of the remiges correspond in relative length with those of recent trogons. However, it is not clear whether the distal primaries are shortened like in recent species (a short feather on the outer side of the left wing is not the most distal primary because it does not insert on the phalanx distalis digiti major). Trogons possess very long tail feathers; unfortunately those of *P. wintersteini* have been lost together with the pygostyle.

DISCUSSION

Contrary to their extant relatives, early Tertiary trogons are known only from Europe. The oldest New World fossils are from Pleistocene deposits in the Dominican Republic and Brazil (Brodkorb 1971). Although the fossil record

does not prove an Old World origin for the Trogoniformes, this notion is supported by a recent cladistic analysis of living species (Espinoso de los Monteros 1998). *Primotrogon wintersteini* is the earliest known trogonid, but a tarsometatarsus of an unquestionably heterodactyl bird closely resembling that of a trogoniform has been collected in the Lower Eocene (53 million years ago) London Clay of Essex, England (private collection M. Daniels). Surprisingly, trogons have not been found in the extensive and well-studied material of the Phosphorites du Quercy. This is odd because the locality is geographically and stratigraphically close to Céreste.

Palaeobiology.—Most recent authors postulate an arid climate for Céreste during the Oligocene. Lutz (1984) assumed that the vegetation was open with only few bushes and trees, and Schmidt-Kittler and Storch (1985) considered it to be a "semi-arid open habitat on a large scale." According to Mai (1995:423), there were semi-evergreen open forests interspersed with sclerophyllous bushes and sparse pines. Because trogon feet are especially adapted to perching, and recent trogons nest in tree holes, the presence of at least isolated woodlands in and near Céreste is a reasonable conjecture. The presence of a trogon in an arid environment might be surprising, because most living trogons occur in humid subtropical or tropical forests. However, some recent species (e.g. *Trogon elegans*, *T. violaceus*, and *T. citreolus*) also occur in open woodlands and arid scrub (Sibley and Monroe 1990).

Phylogeny.—As pointed out in the diagnosis, *Primotrogon wintersteini* most likely is the sister taxon of the recent trogons. The species is remarkably similar to living trogons, and only a few other avian taxa are known to have undergone so little morphological alteration during the past 33 million years. Differences concerning the relative size of the orbitae and the more narrow beak might indicate that the Oligocene species was less specialized at catching flying insects. In its proportions, *P. wintersteini* falls within the range of recent trogons and is closest to the Asian species *Harpactes ardens* (Table 1). All New World trogons seem to have a slightly longer ulna than *P. wintersteini* and the African and Asian trogons, but this must be confirmed with a larger number of skeletons than was available to me.

TABLE 1. Wing and leg ratios* of trogons (SD in parentheses).

Species	HU:UL	HU:CM	HU:TM	UL:TM	TT:TM	HU:TT	UL:TT
Oligocene trogon from Céreste							
<i>Primitrogon wintersteini</i> (n = 1)	0.88	1.84	2.14	2.44	1.96	1.09	1.24
Recent New World trogons							
<i>Pharomachus mocinno</i> (n = 3)	0.85 (0.00)	1.77 (0.06)	2.24 (0.06)	2.63 (0.06)	2.02 (0.09)	1.11 (0.01)	1.31 (0.02)
<i>Pharomachus paoninus</i> (n = 1)	0.85	1.76	2.49	2.91	2.03	1.25	1.43
<i>Trogon violaceus</i> (n = 2)	0.82 ^b	1.75 (0.05)	2.26 (0.09)	2.64 ^b	2.03 (0.05)	1.12 (0.02)	1.33 ^b
<i>Trogon viridus</i> (n = 1)	0.85	1.82	2.35	2.78	2.08	1.13	1.33
<i>Priotelus temnurus</i> (n = 3)	0.83 (0.01)	1.77 (0.01)	1.69 (0.01)	2.02 (0.04)	1.76 (0.02)	0.96 (0.01)	1.15 (0.01)
Recent African trogons							
<i>Heterotrogon vittatus</i> (n = 1)	0.91	1.83					1.12
<i>Apaloderma narina</i> (n = 3)	0.90 (0.01)	1.79 (0.01)	1.92 (0.02)	2.12 (0.01)	1.92 (0.01)	1.00 (0.01)	1.11 (0.01)
Recent Asian trogon							
<i>Harpactes ardens</i> (n = 1)	0.89	1.86	2.23	2.49	2.13	1.04	1.17

*HU, humerus; UL, ulna; CM, carpopectacarpus; TM, tarsometatarsus; TT, tibiotarsus.
^b Ratio based on one specimen only.

Because *Primitrogon wintersteini* is very close to extant trogons, it does not give us additional information on the higher systematic position of the order Trogoniformes. Feduccia (1975) discovered that trogoniforms and some coraciiforms (Meropidae, Alcedinidae, Momotidae) share a derived morphology of the columella. A very similar type of columella, however, also occurs in the suboscine passerines (Feduccia 1975), and no other characters are known to support a relationship between trogons and coraciiforms.

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