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A TINY BARBET-LIKE BIRD FROM THE LOWER OLIGOCENE OF GERMANY: THE SMALLEST SPECIES AND EARLIEST SUBSTANTIAL FOSSIL RECORD OF THE PICI (WOODPECKERS AND ALLIES)

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ABSTRACT.—*Rupelramphastoides knopfi*, a new genus and species of the Pici (barbets, woodpeckers, and allies), is described from Frauenweiler, a Lower Oligocene (30–34 mya) fossil site in Germany. The disarticulated skeleton of the new species constitutes the first associated remains of a fossil member of the Pici and is the smallest known species and earliest substantial fossil record of this taxon. Despite an overall resemblance to modern Ramphastidae, *R. knopfi* appears to be distinguished from crown group Pici by several plesiomorphic characteristics. It is classified “family *incertae sedis*,” pending discovery of additional, better-preserved specimens. The fossil record and geographic occurrence of the basal lineages within the crown group are in concordance with an Old World origin of the Pici. The reasons that led to extinction of tiny Pici in Europe remain uncertain, but food competition with passeriform birds during periods of limited food availability may have played a major role. *Received 27 October 2004, accepted 24 April 2005.*

Key words: fossil birds, Oligocene, Pici, Piciformes, *Rupelramphastoides knopfi* gen. et. sp. nov.

Ein Winziger Bartvogelähnlicher Vogel aus dem Unter-Oligozän Deutschlands: Die Kleinste Art und der Älteste Substantielle Fossilnachweis der Pici (Spechte und Verwandte)

ZUSAMMENFASSUNG.—*Rupelramphastoides knopfi*, eine neue Gattung und Art der Pici (Bartvögel, Spechte und Verwandte), wird aus dem Unteroligozän (vor 30–34 Millionen Jahren) der Fossilfundstelle Frauenweiler in Deutschland beschrieben. Das disartikulierte Skelett der neuen Art stellt die ersten zusammenhängenden Reste eines fossilen Vertreters der Pici dar, und ist die kleinste bekannte Art und der älteste Fossilnachweis dieses Taxons. Trotz einer Gesamtähnlichkeit zu modernen Ramphastidae, unterscheidet sich *R. knopfi* von den Krongruppen-Pici in einigen plesiomorphen Merkmalen. Vorbehaltlich der Entdeckung weiterer, besser erhaltener Skelette, wird die neue Art daher in Familie *incertae sedis* klassifiziert. Der Fossilnachweis und die geographische Verbreitung der basalen Linien innerhalb Krongruppen-Pici stehen im Einklang mit einem altweltlichen Ursprung der Pici. Die Gründe, welchen zum Aussterben sehr kleiner Vertreter dieser Gruppe in Europa führten, sind unbekannt, aber Nahrungskonkurrenz mit Singvögeln während Zeiten beschränkten Nahrungsangebotes könnte eine wichtige Rolle gespielt haben.

THE FOSSIL RECORD of woodpeckers and allies (Pici) is very poor, but the members of this group—barbets and toucans (Ramphastidae including “Capitonidae”; see Prum 1988); honeyguides (Indicatoridae); and woodpeckers,

wrynecks, and piculets (Picidae)—today have an almost worldwide distribution and occur in most forested habitats (del Hoyo et al. 2002).

Paleogene (pre-Miocene; i.e. older than 23 Ma) remains of the Pici were described from the Lower Oligocene of Belgium (Mayr and Smith 2001) and the Upper Oligocene of Germany (Mayr 2001) but consist of fragmentary

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tarsometatarsi only, and their affinities to the modern taxa are uncertain.

The earliest Ramphastidae are known from the Lower to Middle Miocene of Germany and France (Ballmann 1969a, b, 1983); the specimens from Germany were classified in the extinct genus *Capitonides* (Ballmann 1969a). Indicatoridae have no Tertiary fossil record. The earliest skeletal remains of the Picidae are from the Middle Miocene of North America (Olson 1985) and the Upper Miocene of Italy (Ballmann 1976). Laybourne et al. (1994) further assigned a feather from Dominican amber to the Picidae; according to those authors, the minimum age of this specimen is Lower Miocene.

Here, I describe a disarticulated skeleton of a tiny new species of the Pici from the Lower Oligocene (Rupelian; i.e. 30–34 mya) near-shore marine deposits of Frauenweiler in southern Germany (Figs. 1 and 2). This site has already yielded a diverse avifauna, and the hitherto reported taxa include tubenoses (Procellariiformes; Mayr et al. 2002), loons (Gaviiformes; Mayr 2004a), mousebirds

(Coliidae; Mayr 2000), songbirds (Passeriformes; Mayr and Manegold 2004), and stem group hummingbirds (Trochilidae; Mayr 2004b).

MATERIAL AND METHODS

Osteological terminology follows Baumel and Witmer (1993). Measurements are in millimeters and represent the maximum length of the bone along its longitudinal axis. The fossil specimen is deposited in Forschungsinstitut Senckenberg, Frankfurt a. M., Germany (SMF). It was transferred into a slab of artificial resin, and skeletal details are visible through the transparent reverse.

Comparisons were made with skeletons of the following extant piciform taxa (Picumninae from the U.S. National Museum, Smithsonian Institution, Washington, D.C.; all others in the collection of Forschungsinstitut Senckenberg): Ramphastidae: *Aulacorhynchus derbianus*, *Bailloni bailloni*, *Capito squamatus*, *Eubucco bourcierii*, *Lybius minor*, *L. vieilloti*, *Megalaima*

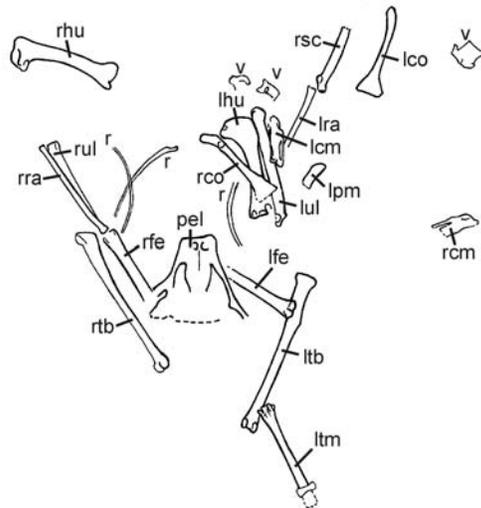


FIG. 1. *Rupelramphastoides knopfi*, gen. et sp. nov., holotype, from the Lower Oligocene of Frauenweiler, Germany. Specimen SMF Av 500a with interpretive drawing. Abbreviations: lcm = left carpometa-carpus, lco = left coracoid, lfe = left femur, lhu = left humerus, lpm = left *phalanx proximalis digiti majoris*, lra = left radius, ltb = left tibiotarsus, ltm = left tarsometatarsus, lul = left ulna, pel = pelvis, r = rib, rcm = right carpometa-carpus, rco = right coracoid, rfe = right femur, rhu = right humerus, rra = right radius, rsc = right scapula, rtb = right tibiotarsus, rul = right ulna, v = vertebra. Fossil specimen coated with ammonium chloride to enhance contrast. Scale bar equals 10 mm.

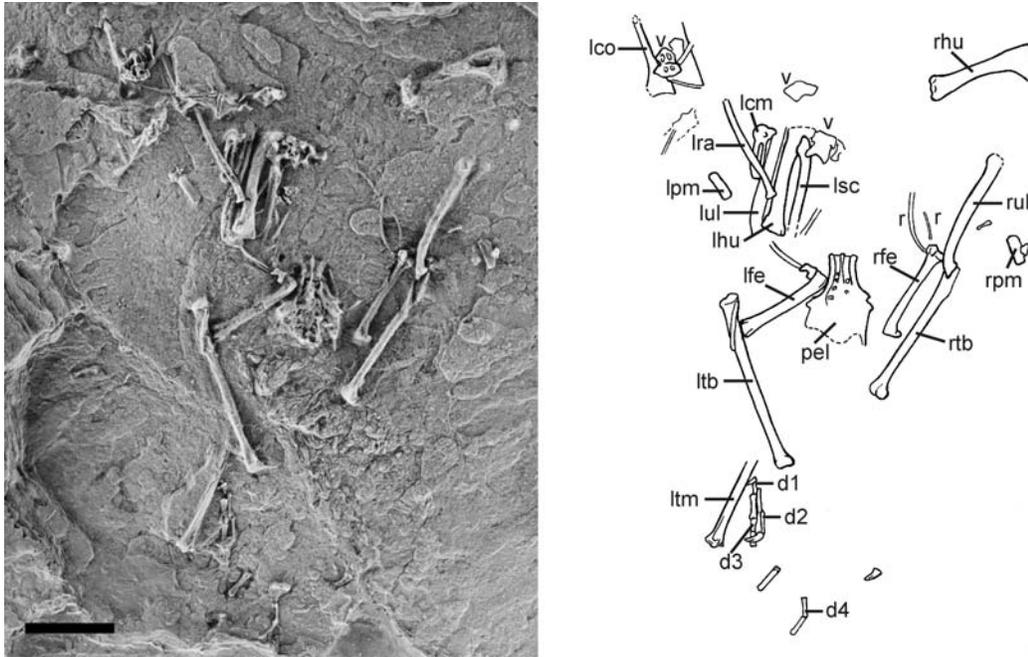


FIG. 2. *Rupelramphastoides knopfi*, gen. et sp. nov., holotype, from the Lower Oligocene of Frauenweiler, Germany. Specimen SMF Av 500b with interpretative drawing. Abbreviations: d1–d4 = left pedal digits 1–4, lsc = left scapula, rpm = right *phalanx proximalis digiti majoris*; others as in Fig. 1. Specimen coated with ammonium chloride to enhance contrast. Scale bar equals 10 mm.

armillaris, *M. asiatica*, *M. javensis*, *M. mystacophanos*, *M. virens*, *Pogoniulus bilineatus*, *P. scolopaceus*, *Psilopogon pyrolophus*, *Pteroglossus aracari*, *P. castanotis*, *P. viridis*, *Ramphastos ambiguus*, *R. toco*, *R. vitellinus*, *Selenidera culik*, *S. maculirostris*, *Trachyphonus margaritatus*; Indicatoridae: *Indicator variegatus*; Picidae: Jynginae: *Jynx ruficollis*, *J. torquilla*; Picumninae: *Picumnus exilis*, *Sasia africana*; Picinae: *Campethera abingoni*, *C. cailliautii*, *C. nivosa*, *Chrysocolaptes lucidus*, *Colaptes auratus*, *Dendrocopos major*, *D. medius*, *D. minor*, *Dendropicus fuscescens*, *Dinopium javense*, *Dryocopus martius*, *Hemicircus concretus*, *Melanerpes carolinus*, *Picoides nuttallii*, *Picus canus*, *P. viridis*, and *Sphyrapicus varius*.

The term “crown group Pici” as used here denotes a clade including the last common ancestor of modern Pici as well as all its extinct and extant descendants.

SYSTEMATIC PALEONTOLOGY

The new taxon is assigned to the Pici because of the following derived characteristics: (1) ulna

with marked *papillae remigales*; (2) carpometacarpus with large *processus intermetacarpalis* that reaches the *os metacarpale minus*, (3) *os metacarpale minus* protruding much farther distally than *os metacarpale majus*, and (4) *processus pisiformis* shifted toward the cranial margin of the bone; (5) tibiotarsus, proximally protruding *cristae cnemiales* and *crista patellaris* forming a ridge that circumscribes a groove on the cranial side of the bone; and tarsometatarsus with (6) prominent *eminentia intercotylaris*, (7) very narrow *trochlea metatarsi II*, and (8) large *trochlea accessoria* that reaches distally beyond the *trochlea metatarsi III*.

Piciformes (Meyer and Wolf, 1810)
Pici (*sensu* Simpson and Cracraft 1981)
Family *incertae sedis* (confer Ramphastidae
Vigors, 1825)

Rupelramphastoides, gen. nov.

Type species.—*Rupelramphastoides knopfi*, sp. nov.

Differential diagnosis.—Tiny birds that are

characterized by: (1) one of caudalmost cervical vertebrae and (2) cranialmost synsacral vertebra with deep lateral excavations (Fig. 3), (3) humerus without marked *impressio coracobrachialis* (Fig. 4), (4) carpometacarpus with weakly developed *fossa supratrochlearis* (Fig. 4), and (5) tarsometatarsus with mediolaterally narrow

trochlea accessoria (Figs. 5 and 6). Character (2) is probably an autapomorphy of the new taxon; characters (1), (3), (4), and (5) are probably plesiomorphic characteristics and distinguish the new taxon from crown group Pici (see below).

Etymology.—The genus name refers to Rupelian, the age of the Frauenweiler deposits,

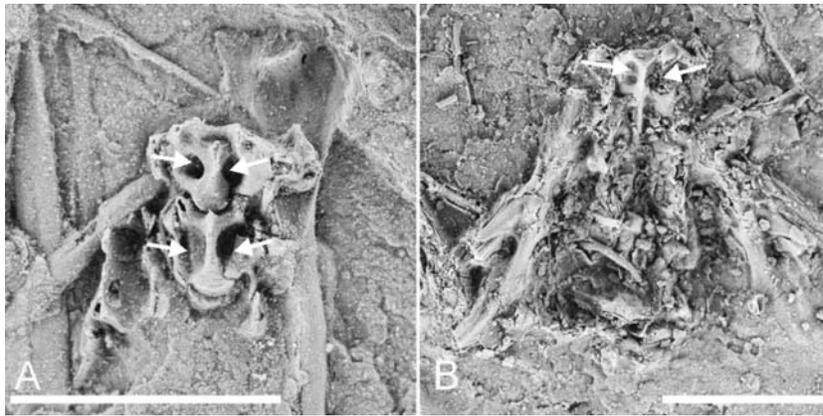


FIG. 3. *Rupelramphastoides knopfi*, gen. et sp. nov. (A) Caudalmost cervical vertebrae (SMF Av 500b); (B) pelvis in ventral view (SMF Av 500a). Arrows indicate the lateral depressions in the *corpus vertebrae* (see text). Specimen coated with ammonium chloride to enhance contrast; scale bars equal 5 mm.



FIG. 4. *Rupelramphastoides knopfi*, gen. et sp. nov. (A) Left humerus, ulna, and carpometacarpus (SMF Av 500a) in comparison with (B) humerus and carpometacarpus of modern *Baillonius bailloni* (Ramphastidae). See Figure 1 for an interpretative drawing of the bones. Abbreviations: ico = *impressio coracobrachialis*, sup = *fossa supratrochlearis*; others as in Fig. 1. Specimen coated with ammonium chloride to enhance contrast; scale bars equal 5 mm.

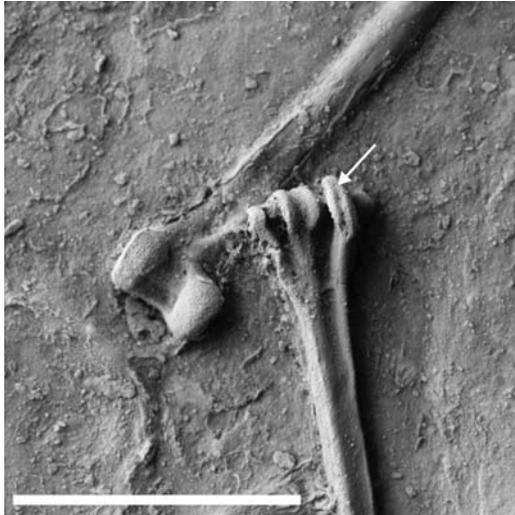


FIG. 5. *Rupelramphastoides knopfi*, gen. et sp. nov. Distal ends of left tibiotarsus and tarsometatarsus (SMF Av 500a). Arrow indicates the furrow on the *trochlea accessoria*. Specimen coated with ammonium chloride to enhance contrast; scale bar equals 5 mm.

and the overall similarity between the fossil taxon and modern Ramphastidae.

Rupelramphastoides knopfi, sp. nov.

Holotype.—SMF Av 500a+b (disarticulated skeleton on two slabs, lacking skull, furcula, sternum, right foot, and tail vertebrae; Figs. 1 and 2).

Type locality and horizon.—Frauenweiler south of Wiesloch (Baden-Württemberg, Germany), former clay pit of the Bott-Eder GmbH (“Grube Unterfeld”); Rupelian, Lower Oligocene (Micklich and Parin 1996, Trunkó and Munk 1998).

Diagnosis.—Only species of genus, thus the diagnosis is the same as for the genus. Smallest known species of the Pici, ~90% the size of the Golden-spangled Piculet (*Picumnus exilis*), which is among the smallest modern Pici.

Measurements.—See Table 1.

Etymology.—Named after the finder of the holotype, Charles Knopf, who donated the specimen to Forschungsinstitut Senckenberg.

Description and comparison.—Several vertebrae and ribs are scattered over the slab. Of these, the caudalmost cervical vertebrae, probably the

13th and 14th, bear marked, pit-like excavations on each side of their corpora (Fig. 3). Such excavations occur in many avian taxa, including the Galbulae, the closest modern relatives of the Pici, but are more strongly reduced or absent in all extant Pici that I examined.

The *processus procoracoideus* of the coracoid is strongly reduced as in all Pici. The *extremittas omalis* is not as strongly elongated as in the Ramphastidae. The *extremittas sternalis* bears a distinct notch on its medial side that is a derived feature of piciform birds, but indistinct in the Picumninae and Picinae.

The scapula resembles that of modern Ramphastidae and Indicatoridae. Its caudal end does not exhibit the highly derived, hook-like shape found in the Picumninae and Picinae (fig. 3 in Höfling and Alvarenga 2001). Whether the acromion was bifurcated, with an additional medial process as in many modern Pici, cannot be discerned; there are no subacromial foramina (unlike in most modern Ramphastidae; see Höfling and Alvarenga 2001).

The humeri are poorly preserved. The bone has a large proximal end, as in all modern Pici. In contrast to the latter, however, there is no marked *impressio coracobrachialis*, and the *processus flexorius* on the distal end appears to be somewhat stouter and less protruding.

The olecranon of the ulna is long and narrow, the *processus cotylaris dorsalis* not as strongly protruding as in the Picidae (fig. 16 in Ballmann 1976). The distal end of the bone is also very similar to the distal ulna of modern Pici; the *tuberculum carpale* is elongated as in the latter, whereas it is more pointed in most other birds.

The carpometacarpus (Figs. 4 and 6) is proportionally shorter than the carpometacarpus of most Picinae (fig. 12 in Ballmann 1969a) and resembles that of the Miocene *Capitonides* and some modern Ramphastidae (e.g. *Trachyphonus*) in its proportions. The *processus extensorius* is well developed. There is a *fossa supratrochlearis (incisura externa* of fig. 12 in Ballmann 1969a) on the *trochlea carpalis* that is, however, less marked than in crown group Pici; the distocaudal margin of the ventral portion of the *trochlea carpalis* is set apart from the dorsal portion by an “edge” and does not gradually merge into it as in crown group Pici (Fig. 4).

The *phalanx proximalis digiti majoris* exhibits the derived morphology of modern Pici, in that its caudal margin is reduced. Whether there is a

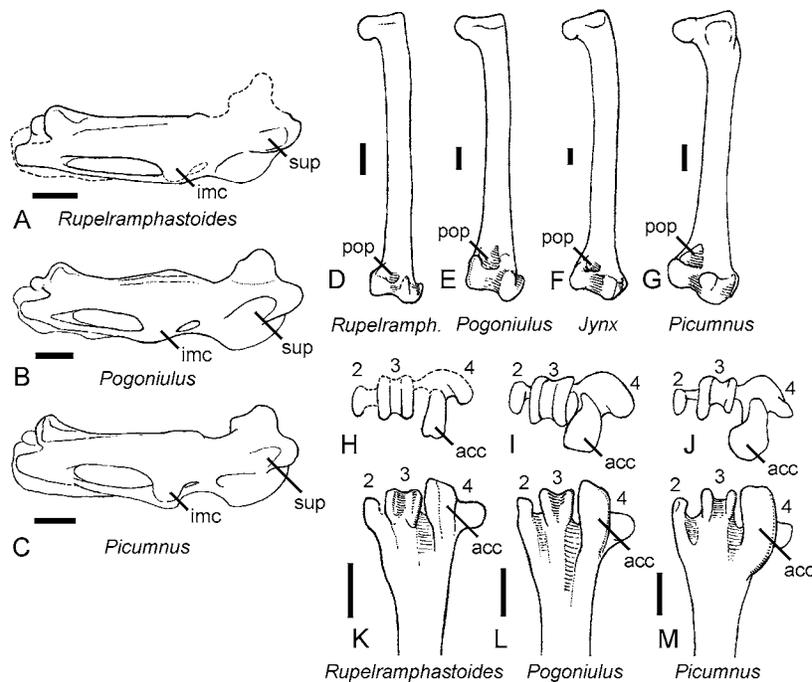


FIG. 6. *Rupelramphastoides knopfi*, gen. et sp. nov. Selected skeletal elements in comparison: (A–C) left carpometacarpus, (D–G) right femur, (H–J) left tarsometatarsus in distal, and (K–M) plantar view. (A, D, H, K) *Rupelramphastoides knopfi*, gen. et sp. nov. (family *incertae sedis*); (B, E, I, L) *Pogoniulus bilineatus* (Ramphastidae); (F) *Jynx torquilla* (Jynginae, Picidae); (C, G, J, M) *Picumnus exilis* (Picumninae, Picidae). Abbreviations: acc = *trochlea accessoria*, imc = *processus intermetacarpalis*, pop = *fossa poplitea*, sup = *fossa supratrochlearis*. Tarsometatarsal trochleae are numbered. Scale bars equal 1 mm.

proximally protruding process on its proximal end, a synapomorphy of Piciformes (fig. 2 in Mayr et al. 2003), cannot be discerned.

The pelvis is poorly preserved but appears to have been of similar proportions to that of modern Pici, with prominent antitrochanters and narrow *alae praeacetabulares*. Most of the caudal portion of the ilium, as well as the *alae ischii*, are not preserved. Most notably, the cranialmost synsacral vertebra bears deep lateral excavations (Fig. 3). Within Pici, I found such excavations only in *Picoides nuttallii* (Picidae) and, although much shallower, in *Pogoniulus*; they are absent in the Galbulae but occur in several passerines (Passeriformes; e.g. *Megarhynchus pitangua* [Tyrannidae], *Menura novaehollandiae* [Menuridae], and *Delichon urbica* [Hirundinidae]).

The femur is slender and in its proportions resembles the corresponding bone of modern nonclimbing Pici (Fig. 6). The distal end is wide,

the *fossa poplitea* marked. As in modern Pici, the *condylus lateralis* is very prominent and bears a marked *trochlea fibularis*.

The tibiotarsus is the longest limb element. The condyli of the distal end are about equal in size to those of *Sasia africana*, whereas in many other modern Pici the *condylus lateralis* is smaller than the *condylus medialis*. The *trochlea cartilaginiis tibialis* is shallow.

The tarsometatarsus is fairly long and slender, about as long as the ulna, as in most Ramphastidae (except *Megalaima*); this bone is much shorter than the ulna in Indicatoridae and Picidae (Table 1). As in the Ramphastidae, but in contrast to the Picoidea (Indicatoridae + Picidae) and the unnamed Upper Oligocene species described by Mayr (2001), the *arcus extensorius* on the proximal end is only incompletely ossified (most modern birds completely lack this derived characteristic; see Baumel and Witmer 1993). The *trochlea metatarsi* III (Figs.

TABLE 1. Dimensions of major limb bones (in millimeters) and ratio ulna (ulu)/tarsometatarsus (tmt) of *Rupelramphastoides knopfi*, gen. et sp. nov. (left/right) in comparison with selected small to medium-sized species of extant Pici.

	Humerus	Ulna	Carpometacarpus	Femur	Tibiotarsus	Tarsometatarsus	Ratio uln/tmt
<i>R. knopfi</i>	11.5/-	13.9/-	6.0/-	-/10.8	19.0/18.5	~12.8/-	1.09
	Family incertae sedis						
	Ramphastidae						
<i>Pogoniulus bilineatus</i>	13.8	16.7	7.4	11.8	21.1	14.3	1.17
<i>Trachyphonus margaritatus</i>	25.0	27.6	12.0	23.8	40.1	26.9	1.03
<i>Megalaima virens</i>	39.1	50.8	21.6	33.8	58.8	34.5	1.47
	Indicatoridae						
<i>Indicator variegatus</i>	26.2	31.8	14.2	19.2	29.0	17.2	1.85
	Picidae						
<i>Jynx torquilla</i>	22.7	24.7	11.7	19.5	29.9	18.8	1.31
<i>Sasia africana</i>	14.1	15.3	6.6	11.6	-	12.0	1.28
<i>Picumnus exilis</i>	14.1	15.3	6.6	11.6	18.6	11.7	1.31
<i>Dendrocopos minor</i>	21.2	25.1	11.8	16.1	24.5	15.3	1.64

5 and 6) bears a more shallow furrow than in the climbing Picidae. The *trochlea accessoria* is more slender than in crown group Pici. It bears a distinct, narrow furrow along its plantar surface (Fig. 5) that also occurs in some modern Ramphastidae (e.g. *Psilopogon*, *Pteroglossus*). Meaningful comparisons between the tarsometatarsus of *R. knopfi* and that of the unnamed Lower Oligocene species described by Mayr and Smith (2001) are not possible, owing to the very fragmentary preservation of the latter.

The disarticulated toes of the left foot are preserved and, as in modern Pici, the second toe is very thin. A short hindtoe is present (reduced or absent in modern *Sasia*).

DISCUSSION

Rupelramphastoides knopfi is unequivocally identified as a member of the Pici by, among other features, the highly derived morphology of its distal tarsometatarsus (see above and Fig. 6). Assessment of its position within Pici is, however, more difficult, owing to the poor preservation of the single known specimen.

Rupelramphastoides knopfi is shown to be outside crown group Picoidea (Indicatoridae + Picidae) by the plesiomorphic absence of a completely ossified *arcus extensorius* on the tarsometatarsus. It further differs from crown group Picoidea, but agrees with modern Ramphastidae, in its elongated tarsometatarsus—though it is uncertain whether this characteristic is derived or primitive within the Pici.

Despite an overall resemblance to some modern Ramphastidae (e.g. *Pogoniulus*), *R. knopfi* appears to be distinguished from all modern Pici by a less marked *impressio coracobrachialis* on the proximal end of the humerus and a less marked *fossa supratrochlearis* on the *trochlea carpalis* of the carpometacarpus. A deep *impressio coracobrachialis* and *fossa supratrochlearis* are unquestionably derived within neornithine birds, and their weaker formation in *Rupelramphastoides* may indicate a position outside crown group Pici (i.e. sister group relationship to the modern taxa). The new species is further distinguished from crown group Pici by the presence of deep lateral excavations on the caudalmost cervical vertebrae. These excavations occur in the Galbulae, the closest modern relatives of the Pici, and many other birds, and their absence or great reduction in crown group

Pici may well be derived, thus also supporting a position of *R. knopfi* outside crown group Pici.

Unfortunately, the preservation of the fossil does not permit detailed comparisons of many bones, and the new species is classified “family *incertae sedis*,” pending discovery of additional, better-preserved specimens. If a position of *Rupelramphastoides* outside crown group Pici can be confirmed, the similarities with modern Ramphastidae are probably plesiomorphic within Pici (note that the early Miocene barbet-like *Capitonides* also was considered outside crown group Pici by Prum [1988], though the reasons for that judgment were questioned by Olson [1991]).

The new species represents the first associated remains of a fossil member of the Pici and is the smallest known species of this taxon. Together with the fragmentary tarsometatarsus reported by Mayr and Smith (2001), it is the earliest fossil record of the Pici.

Curiously, all known Paleogene species of the Pici are very small (Mayr 2001, Mayr and Smith 2001, present study), though the chances of discovering such tiny taxa are certainly lower than those for discovering larger species. In the Old World, tiny species of Pici today occur in the tropical regions of southeast Asia and Africa (*Sasia*, *Picumnus*, *Pogoniulus*) but are absent from the European avifauna, in which medium-sized to large Picidae occur throughout the year.

The causes of extinction of tiny Pici in Europe remain uncertain—more so because we do not know when these birds finally disappeared. Most modern Pici are sedentary (del Hoyo et al. 2002), and it is conceivable that food competition with small passeriform birds during periods with limited food availability, especially the cold Northern Hemisphere winters, may have played a major role. The earliest European remains of passeriform birds are from the Frauenweiler deposits and the early Oligocene of Céreste in France but, at least in Europe, songbirds had not yet become the dominant group of small insectivorous birds by that time (Mayr and Manegold 2004).

The distribution of the modern taxa supports an Old World origin of the Pici. Molecular phylogenies show the basal divergences within Ramphastidae to be in Asia (Moyle 2004); Indicatoridae and Jynginae, the most basal taxa of the Picidae (e.g. Stresemann 1927–1934, Sudhaus 1988), occur in Asia and Africa. The

fossil record is in concordance with this assumption, given that all known Paleogene Pici were found in Europe and the Miopiconidae, the presumed sister taxon of the Pici (Mayr 1998), are known only from the Miocene of Morocco.

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