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Source: The Auk, 131(1) : 55-60

Published By: American Ornithological Society

URL: https://doi.org/10.1642/AUK-13-134.1

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The Auk
Ornithological Advances
www.aou.org

Volume 131, 2014, pp. 55–60
DOI: 10.1642/AUK-13-134.1

RESEARCH ARTICLE

A hoatzin fossil from the middle Miocene of Kenya documents the past occurrence of modern-type Opisthocomiformes in Africa

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Received September 4, 2013; Accepted November 11, 2013; Published January 15, 2014

ABSTRACT

The fossil bird *Namibiavis senutae* from the early Miocene of Namibia was recently identified as an African stem-group representative of Opisthocomiformes (hoatzins). The species is known only from two wing and pectoral girdle bones, however, and the extent to which African Opisthocomiformes resembled their Neotropical relatives in skeletal morphology has remained elusive. I report a hoatzin tarsometatarsus from the middle Miocene of Maboko Island in Kenya, which, except for a peculiar autapomorphic fusion of the first metatarsal, closely matches the tarsometatarsus of the extant *Opisthocomus hoazin*. Although a well-founded classification on the species level is not possible, the new fossil documents the existence of essentially modern-type Opisthocomiformes in the Miocene of Africa. Being 2–2.5 Ma younger than *N. senutae*, the specimen further extends the temporal and spatial range of Miocene African Opisthocomiformes.

Keywords: biogeography, fossil birds, Maboko Island, *Namibiavis*, *Opisthocomus*

Fósil de un hoatzín del Mioceno medio de Kenia documenta la previa presencia de un Opisthocomiformes de tipo moderno en Africa

RESUMEN

El ave fósil *Namibiavis senutae* del Mioceno temprano de Namibia fue identificado recientemente como un representante del grupo raíz africano de los Opisthocomiformes (hoatzines). Sin embargo, la especie sólo se conoce de dos huesos del ala y la faja pectoral, y se ha desconocido hasta que punto los Opisthocomiformes africanos se parecen a sus parientes neotropicales en cuanto a morfología esquelética. Aqui reportamos un tarsometatarso de Opisthocomiformes del Mioceno medio de la Isla Maboko en Kenia, el cual, con la excepción de una peculiar fusión autapomórfica del primer metatarsiano, es muy similar al tarsometatarso del existente *Opisthocomus hoazin*. Aunque una clasificación bien fundamentada al nivel de especie no es possible, el nuevo fósil documenta la existencia de un Opisthocomiformes fundamentalmente de tipo moderno en el Mioceno de Africa. Siendo 2–2.5 millones de años más joven que *N. senutae*, el espécimen extiende el rango temporal y espacial de Opisthocomiformes del Mioceno africano.

Palabras clave: aves fósiles, biogeografía, Isla Maboko, *Namibiavis*, *Opisthocomus*

INTRODUCTION

The Hoatzin (*Opisthocomus hoazin*) is one of the most remarkable species of living birds, not least because of its unique foregut fermentation of ingested plant matter (Grajal et al. 1989) and its specialized nestling behavior (Thomas 1996). Its phylogenetic affinities remain unresolved, and even the most recent analyses of comprehensive molecular datasets do not result in a congruent and strongly supported placement in the avian tree of life (e.g., Sorenson et al. 2003, Ericson et al. 2006, Hackett et al. 2008, Kimball et al. 2013, McCormack et al. 2013, Yuri et al. 2013). Because their modern distribution is restricted to the riparian lowland forests of South America, hoatzins have long been regarded as endemic to that continent, and earlier authors considered it unlikely that they were more diverse and widespread in earlier times (Stresemann 1927–1934:759).

The recent identification of an opisthocomiform bird from the early Miocene (17–17.5 mya) of Namibia documents, however, that hoatzins once also occurred in Africa (Mayr et al. 2011). This African species, *Namibiavis senutae*, is represented by remains of several individuals, but only two skeletal elements are known, the coracoid and the humerus (Mourer-Chauviré 2003, Mayr et al. 2011). Given the limited fossil material, the extent of morphological congruence between African and South

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American Opisthocomiformes has remained largely unknown.

The earliest and most substantial New World fossil record of a hoatzin is *Hoazinavis lacustris* from the late Oligocene–early Miocene (22–24 mya) of Brazil (Mayr et al. 2011). This species is likewise represented by wing and pectoral girdle bones only, which closely resemble those of the modern *O. hoazin*. *Hoazinavis* shares derived features with *Opisthocomus* that are absent in *Namibiavis*, and a dispersal from Africa to South America, possibly by transoceanic rafting, was considered most likely, given the interrelationships of fossil and extant Opisthocomiformes as well as the predominant paleocurrents and paleowinds (Mayr et al. 2011).

Here, I report a hoatzin from the middle Miocene of Maboko Island in Lake Victoria, Kenya. This fossil site is well-known for its mammalian fauna, and primate fossils are especially abundant (e.g., Andrews et al. 1981, Benefit 1999, Geraads et al. 2012). Maboko Island also yields a comparatively rich avifauna, which, however, remains little studied. The few described fossils are mainly fragmentary remains assigned to Ciconiidae, Ardeidae, Threskiornithidae, Phoenicopteridae, and Otididae (Harrison 1980, Rich and Walker 1983, Dyke and Walker 2008); on the basis of unpublished data, Retallack et al. (2002) listed further, predominantly aquatic, taxa for the avifauna of Maboko Island. The fossil reported here, which was first recognized during a visit to the Kenya National Museum in 2012, not only provides a temporal and spatial range extension of the opisthocomiform fossil record in Africa, but also suggests that Miocene African Opisthocomiformes already had an essentially modern-type morphology.

METHODS

Osteological terminology follows Baumel and Witmer (1993). Measurements are in millimeters. The fossils are deposited in the paleontological collections of the Kenya National Museum, Nairobi (KNM).

RESULTS

Opisthocomiformes Sclater, 1880
Opisthocomidae Swainson, 1837
?*Namibiavis* Mourer-Chauviré, 2003
?*Namibiavis* sp.

Referred specimen. KNM-MB 21692, left tarsometatarsus (Figure 1).

Locality and horizon. Maboko Island (Lake Victoria, Kenya), Maboko Main, bed 5, white clay (field no. Mb 4306/87); Maboko Formation, middle Miocene, ~15 mya (Feibel and Brown 1991, Retallack et al. 2002, Geraads et al. 2012).

Measurements. Length, 47.3; proximal width, 10.7; distal width, 10.4; minimum width of shaft, 5.1; width of trochlea metatarsi III, 3.2.

Comments on taxonomy. Assuming similar proportions to *Opisthocomus hoazin*, the tarsometatarsus KNM-MB 21692 corresponds with the coracoid and humerus of *Namibiavis senutae* in size, with the dimensions of all bones matching those of *O. hoazin*. A well-founded species-level assignment is not possible, however, because the tarsometatarsus of *N. senutae* and other fossil Opisthocomiformes is unknown. The Maboko material in KNM also includes a fragmentary extremitas sternalis of a left coracoid (KNM-MB 33477; Figure 2A–C), which exhibits a large and deeply excavated fossa on its ventral surface. This derived feature occurs in Opisthocomiformes, Anseranatidae (magpie geese), Anhimidae (screamers), and Gruidae (cranes), and the fossil resembles the extremitas sternalis of *Namibiavis* in its overall morphology and proportions (Figure 2). Unlike *Namibiavis*, however, the medial margin of KNM-MB 33477 is dorsoventrally very wide and has a flat surface, whereas it forms a ridge in *Namibiavis*. Further unlike *Namibiavis* and *Opisthocomus*, the fossa on the dorsal surface is a deep cavity rather than a marked hollow that excavates the shaft of the bone, and the medial portion of the ventral surface of the bone bears a distinct depression (Figure 2B). If KNM-MB 33477 can be confidently referred to the same species as the tarsometatarsus, it would show the Kenyan opisthocomiform to be clearly distinct from *Namibiavis senutae*. In overall morphology, however, the specimen is actually more similar to the extremitas sternalis of the coracoid of the putatively "gruiform" species *Geranopsis hastingsiae* Lydekker, 1891, from the late Eocene of England (Mayr 2009: fig. 9.4a) than to *Namibiavis*, and I refrain from a definitive referral of KNM-MB 33477 to Opisthocomiformes. The possibility that the Kenyan opisthocomiform is conspecific with *N. senutae* can thus not be excluded with the material at hand, and a sound species-level classification is not possible.

Description and comparison. KNM-MB 21692 is nearly complete, but the specimen is broken in its midsection and has a partially eroded bone surface. It closely resembles the tarsometatarsus of *Opisthocomus* in its proportions and most morphological details (Figure 1A–L). The hypotarsus exhibits the characteristic, derived morphology of *O. hoazin* in that the crista medialis is strongly plantarly protruding and its distal end forms a marked hook (Figure 1E); as in *Opisthocomus*, it encloses a single canal. It is, however, distinguished from the hypotarsus of *Opisthocomus* in that there are no marked sulci for the tendons of musculus flexor hallucis longus and the superficial flexor muscles (Figure 1L). In plantar

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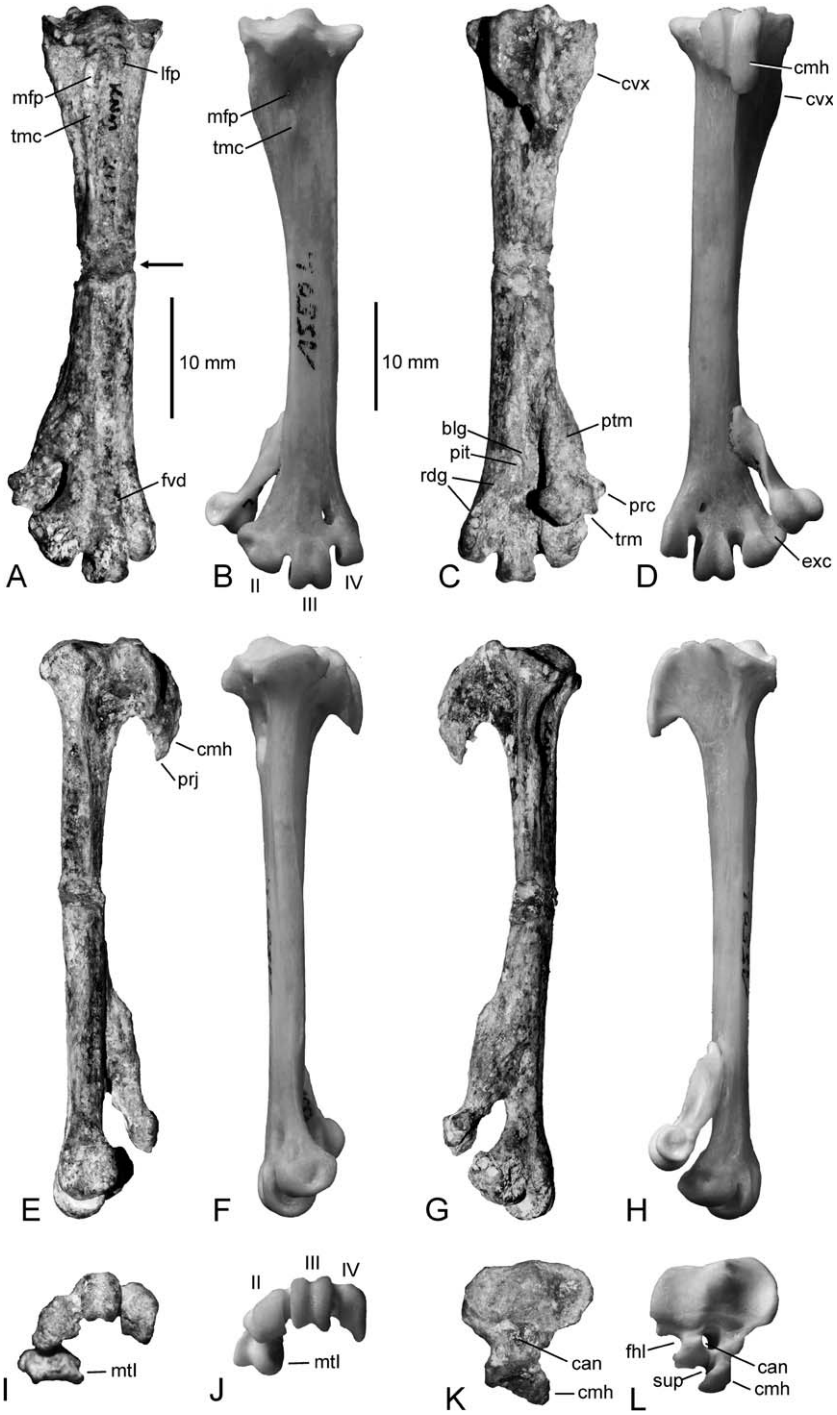


FIGURE 1. Left tarsometatarsus of ?*Namibiavis* sp. from the middle Miocene of Maboko Island, Kenya (KNM-MB 21692, left), in comparison to the extant Hoatzin (*Opisthocomus hoazin*, right): dorsal (**A**, **B**), plantar (**C**, **D**), left lateral (**E**, **F**), right lateral (**G**, **H**), distal (**I**, **J**), and proximal (**K**, **L**) views. Abbreviations: blg = bulge, can = hypotarsal canal for tendon of musculus flexor digitorum longus, cmh = crista medialis hypotarsi, cvx = convexity of proximal tarsometatarsus, exc = excavation of trochlea metatarsi II, fhl = sulcus for tendon of musculus flexor hallucis longus, fvd = foramen vasculare distale, lfp = lateral foramen vasculare proximale, mfp = medial foramen vasculare proximale, mtI = os metatarsale I, pit = subovate pit, prc = lateral process of trochlea metatarsi I, prj = distal projection of crista medialis hypotarsi, ptm = processus articularis tarsometatarsalis of os metatarsale I, rdg = ridge, sup = sulcus for tendons of superficial flexor muscles, tmc = tuberositas musculi tibialis cranialis, trm = trochlea metatarsi I. In (**B**) and (**J**), the trochleae are numbered. The arrow in (**A**) indicates the breakage of the shaft. All recent and fossil bones are shown to the same scale, respectively.

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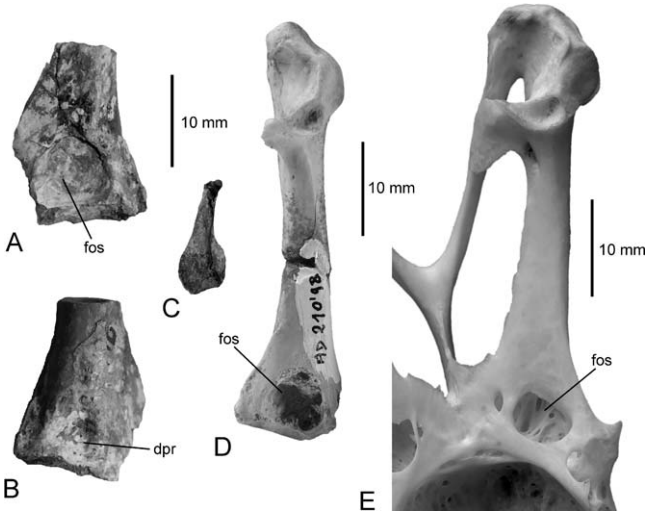


FIGURE 2. (**A**–**C**) Hoatzin-like extremitas sternalis of a left coracoid from the middle Miocene of Maboko Island (KNM-MB 33477) in (**A**) dorsal, (**B**) ventral, and (**C**) sternal view. (**D**) Right coracoid of *Namibiavis senutae* from the early Miocene of Namibia (holotype in dorsal view; from Mayr et al. 2011: fig. 1f). (**E**) Right coracoid of the extant *Opisthocomus hoazin* (dorsal view). Abbreviations: dpr = depression on extremitas sternalis, fos = fossa on extremitas sternalis. Same scale for (**A**–**C**).

view the distal margin of the hypotarsus is laterally slanting (Figure 1C). As in *O. hoatzin*, the proximal end of the bone exhibits a derived morphology in that the fossa infracotylaris dorsalis is very shallow, the medial foramen vasculare proximale much larger and more distally positioned than the lateral one, and the tuberositas musculi tibialis cranialis medially situated (Figure 1A). As in *Opisthocomus*, the ridge-like medial margin of the proximal shaft forms a medial convexity (Figure 1C). The foramen vasculare distale is small. Proximal of its plantar opening, there is a distinct subovate pit, which is proximomedially bordered by a low bulge and laterally adjoins a ridge that runs to the base of trochlea metatarsi IV (Figure 1C). As in *Opisthocomus*, the trochlea metatarsi II is large and medially rather than plantarly directed, but its medial surface does not bear a marked excavation (Figure 1E). The trochlea metatarsi IV is mediolaterally wider than in *Opisthocomus*, and the plantar flange on its lateral portion is longer and better developed.

A highly peculiar feature of the fossil specimen is the extensive fusion of the processus articularis tarsometatarsalis of the os metatarsale I with the tarsometatarsus. Such a fusion otherwise only occurs in tropicbirds (Phaethontidae), in which the tarsometatarsus has a very different shape and the metatarsal is fixed in a forward-directing, rather than reversed, position. The processus articularis tarsometatarsalis of KNM-MB 21692 is markedly thickened and bloated, and its fusion may, at first sight, be considered of pathological origin. The process does not, however, show the rugose bone surface to be expected for a callus formation and, as detailed below, the unusual fusion is instead regarded as indicative of strictly arboreal habits. A derived, rather than pathological, foot morphology is also indicated by the fact that the trochlea metatarsi I is much more dorsoventrally compressed than in *Opisthocomus*, with a less marked sulcus, so that the joint between the trochlea metatarsi I and the hallux acted in a hinge-like manner; unlike in *Opisthocomus*, the trochlea metatarsi I further exhibits a small lateral projection (Figure 1C). This derived shape of the trochlea also renders unlikely a fusion due to a very high individual age of the bird.

DISCUSSION

Specimen KNM-MB 21692 closely resembles the distinctive tarsometatarsus of the extant Hoatzin and can be unambiguously assigned to Opisthocomiformes because of (1) the characteristic derived shape of the hook-like crista medialis of the hypotarsus, (2) the presence of a medial convexity on the proximal shaft, and (3) the large and medially directed trochlea metatarsi II. Because the specimen had not been recognized when an African occurrence of Opisthocomiformes was first proposed (Mayr et al. 2011), it provides independent evidence for the existence of hoatzins in the Miocene of this continent. In fact, the fossil is so similar to the tarsometatarsus of the extant Hoatzin that even the existence of essentially modern-type Opisthocomiformes can now be inferred for the middle Miocene of Africa. That hoatzins indeed evolved their characteristic postcranial osteology by that time is also suggested by the Brazilian *Hoazinavis lacustris*, which lived 7–9 Ma before the Kenyan opisthocomiform, and the known bones of which closely agree with those of *O. hoazin* (Mayr et al. 2011).

Extant Opisthocomiformes are arboreal birds with robust feet and a long hallux, and the adults are almost never seen on the ground (Strahl 1988, Thomas 1996). Studies on the functional morphology of hoatzin feet have not yet been performed, to the best of my knowledge, but the derived tarsometatarsal features of *O. hoazin* are likely related to the demands of a powerful grasping foot in these comparatively large and heavy birds. Hoatzins have a large musculus flexor hallucis brevis with an extensive area of origin (George and Berger 1966:453), and the strong development of this flexor muscle of the hindtoe may account for the marked medial convexity of the proximal tarsometatarsus shaft and the prominent crista medialis hypotarsi.

In that the processus articularis tarsometatarsalis of the os metatarsale I is extensively fused with the tarsometatarsus, the Kenyan opisthocomiform is clearly distinguished from the extant Hoatzin, although the position and orientation of the metatarsal broadly corresponds with

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that of *Opisthocomus*. As a result of this fusion and the dorsoventrally narrow, hinge-like joint between the first phalange of the hallux and the trochlea metatarsi I, the movements of the hindtoe were restricted to a parasagittal plane, and its extension toward the tarsometatarsal shaft was possible only to a limited degree. This morphology meets the demands of a grasping foot used to clutch branches but would not be functional in a ground-living species, in which a flexible articulation between the os metatarsale I and the tarsometatarsus allows for higher maneuverability of the hindtoe and presumably also has a springing function. I thus conclude that, like its extant relative, the Kenyan opisthocomiform was bound to an arboreal life and did not forage on the ground.

Because of the limited fossil record, it has remained arguable whether *Namibiavis* was specialized for a folivorous diet as modern Hoatzins are, although the great resemblance of the two known bones to those of *Opisthocomus* suggest similar modifications of the wing and pectoral girdle, which in *O. hoazin* are related to the formation of a large crop (Mayr et al. 2011). The tarsometatarsus morphology of the Kenyan opisthocomiform indicates arboreal habits, which is also consistent with a folivorous diet of Miocene African hoatzins.

The distribution of modern Hoatzins is confined to riverine and lacustrine lowland habitats. The fossiliferous sites of Maboko Island were interpreted as floodplain deposits (Andrews et al. 1981), but more recent evidence from paleosols suggests a diversity of microhabitats, from relatively dry bushland to riparian woodland (Retallack et al. 2002). The white clay of bed 5 of Maboko Main, from which the tarsometatarsus stems, is a paleosol type indicative of seasonally waterlogged wooded grassland (Retallack et al. 2002). According to my examination of the avian fossils in KNM, most birds from these sediments represent aquatic taxa, such as Pelecanidae, Phalacrocoracidae, Phoenicopteridae, and Jacanidae, and the paleoenvironment may thus have been well-suited for a middle Miocene opisthocomiform with life habits similar to those of the extant species.

With an age of ~15 Ma (Feibel and Brown 1991, Geraads et al. 2012), the Kenyan opisthocomiform is 2–2.5 Ma younger than *Namibiavis senutae* and represents the latest known occurrence of hoatzins in Africa. Hoatzin fossils have not been reported from any of the better-studied late Miocene African avifaunas (Rich 1974, Stidham 2007, Louchart et al. 2008), and current data thus suggest their extinction on this continent in the middle Miocene. Various avian taxa with closest extant relatives in South America, such as Trochilidae, Nyctibiidae, and Cariamiformes, were also reported from the Paleogene of the Northern Hemisphere, and it has been hypothesized that the extinction of at least some of these were triggered by newly immigrated faunal elements (Mayr 2009, 2011). Hoatzin extinction in Africa may also be attributable to ecological competition with species that did not reach South America, but the patchy fossil record of African vertebrates does not allow for well-founded considerations on the causes of their final disappearance from the continent.

ACKNOWLEDGMENTS

I am indebted to F. K. Manthi and M. Muungu, both of the Kenya National Museum (KNM), for providing access to the fossil material. I further thank T. Lehmann for logistic help during my visit to KNM, S. Tränkner for taking the photographs of extant hoatzin bones, and D. Steadman and an anonymous reviewer for comments on the manuscript.

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