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Out of Africa: Fossils shed light on the origin of the hoatzin, an iconic Neotropic bird

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Abstract We describe the earliest fossils of the enigmatic avian taxon Opisthocomiformes (hoatzins) from the Oligo-Miocene (22–24 mya) of Brazil. The bones, a humerus, scapula and coracoid, closely resemble those of the extant hoatzin, *Opisthocomus hoazin*. The very similar osteology of the pectoral girdle in the new Brazilian fossil compared to the extant *O. hoazin*, in which it reflects peculiar feeding adaptations, may indicate that hoatzins had already evolved their highly specialized feeding behavior by the mid-Cenozoic. We further show that *Namibiavis senutae* from the early Miocene of Namibia is another, previously misclassified representative of Opisthocomiformes, which documents that the extant Neotropic distribution of hoatzins is relictual. Because of the weak flight capabilities of hoatzins, their occurrence on both sides of the South Atlantic is of particular biogeographic interest. We detail that this distribution pattern is best explained by dispersal from Africa to South America, and that Opisthocomiformes provide the first example of transatlantic rafting among birds.

Keywords Opisthocomiformes · Biogeography · Miocene · Brazil · Namibia

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Introduction

The hoatzin, *Opisthocomus hoazin*, is the sole extant representative of the avian taxon Opisthocomiformes and one of the most distinctive birds of tropical South America. It lives in riparian lowland vegetation of the Amazon and Orinoco basins and is an obligate folivore with an unusually large crop. The latter allows it to process plant matter with a ruminant-like foregut fermentation (Thomas 1996; Grajal *et al*. 1989). The phylogenetic affinities of the hoatzin are unresolved (Hughes and Baker 1999; Sorenson *et al*. 2003; Ericson *et al*. 2006; Livezey and Zusi 2007; Hackett *et al*. 2008) and its evolutionary history is virtually unknown.

The only previously reported fossil referable to Opisthocomiformes is a cranium fragment from the Middle Miocene (Villavieja Formation, 11.8–13.5 mya; Kay and Madden 1997) of Colombia, which documents the occurrence of hoatzins west of the Andes (Miller 1953). This species was described as *Hoazinoides magdalenae* and is slightly larger than the extant *O. hoazin*. *Onychopteryx simpsoni* from the lower Eocene of Argentina is based on a proximal tarsometatarsus fragment (Cracraft 1971). The species was classified in a monotypic family (Onychopterygidae) and was considered to be hoatzin-like in the original description. Cracraft (1971: 232) himself noted, however, that "the evidence is far too scanty to conclude this with any degree of confidence". *Foro panarium*,

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another early Eocene species from North America (Olson 1992), exhibits a hoatzin-like skull, but markedly differs from extant Opisthocomiformes in postcranial anatomy. The species was also assigned to a new family (Foratidae), and although Olson (1992: 135) noted that "something similar" could have given rise to Opisthocomiformes, a convincing case that it is indeed a stem group representative of Opisthocomiformes has not been put forward.

Here, we describe the earliest unambiguous hoatzin fossils from the Oligo-Miocene (22–24 mya) of Brazil, and further show that a previously described species from the early Miocene of Namibia is another stem group representative of Opisthocomiformes.

Material and methods

The fossils are deposited in the Museu de História Natural de Taubaté, Brazil (MHNT) and the Geological Survey, Ministry of Mines and Energy, Windhoek, Namibia (GSMME).

A phylogenetic analysis was performed with the heuristic search modus of NONA 2.0 (Goloboff 1993) through the WINCLADA 1.00.08 interface (Nixon 2002), using the commands hold 10.000, mult*1.000, hold/10, and max*. The character matrix (Supplementary Information) includes 45 taxa and 151 morphological characters and is based on an emended and slightly revised previously published matrix (Mayr and Clarke 2003). Three characters (149, 150, and 151) are newly added, scorings of 11 corrected (6, 22, 31, 32, 44, 57, 58, 65, 85, 100, 105, 106), and the description of four (15, 44, 67, and 94) modified. Three characters (55, 71, and 91) were coded as additive. Bootstrap support values were calculated with 1.000 replicates, three searches holding one tree per replicate, and TBR branch swapping without max*.

Systematic palaeontology

Aves Linnaeus, 1758.
Opisthocomiformes Sharpe, 1891.
Opisthocomidae Swainson, 1837.
Hoazinavis Alvarenga, Mayr and Mourer-Chauviré, gen. nov.

Type species. *Hoazinavis lacustris* gen. et sp. nov.

Differential diagnosis. *Hoazinavis* is very similar to the extant hoatzin in the morphology of the preserved bones and can be confidently identified as an opisthocomiform bird by the following derived features: (1) coracoid with pneumatic opening at the base of the procoracoid process (this feature otherwise only occurs in Tinamidae, Otididae, and a few species of Cuculidae), (2) humerus with a marked brachial fossa, and (3) the deltopectoral crest situated far distally on the shaft of the bone. The new taxon differs from *Opisthocomus* in that coracoid and furcula are not fused, and in that the scapula has a proportionally shorter acromion and smaller humeral articular facet, and lacks a pneumatic foramen at the base of the acromion. It is distinguished from *Namibiavis* in the derived presence of a marked brachial fossa on the humerus and a pneumatic opening at the base of the procoracoid process of the coracoid. *H. lacustris*, gen. et sp. nov. is significantly smaller than *H. magdalenae* from the Middle Miocene of Colombia, whose skull is slightly larger than that of *O. hoazin*, but owing to the lack of overlapping skeletal elements, the two species can otherwise not be compared.

Etymology. From hoatzin, the vernacular name of *O. hoazin*, and *avis* (Lat.) bird.

Hoazinavis lacustris Alvarenga, Mayr and Mourer-Chauviré, gen. et sp. nov.

Holotype. MHNT-VT 5332; complete right humerus, omal end of right coracoid, and cranial extremity of right scapula of a single individual; found in 2008 (Fig. 1).

Locality and horizon. Tremembé Formation, Taubaté Basin, State of São Paulo, Brazil; late Oligocene to early Miocene (Upper Deseadan; 22–24 mya; Alvarenga 1999).

Etymology. From *lacustris* (Lat.), in reference to the lacustrine deposits of the Tremembé Formation.

Measurements (in mm; range of three individuals of O. hoatzin in parentheses). Humerus, length, 59.0 (68.9–73.5); proximal width, 14.7 (19.0–20.6); least shaft width, 5.2 (6.2–6.6); and distal width, 12.6 (15.9–16.2).

Diagnosis. As for genus. *H. lacustris* is the smallest known species in Opisthocomiformes (see measurements above).

Description and comparison. Judging from the morphologies of the bones, i.e., their smooth surface structure and well differentiated articular ends, the remains are those of an adult individual. Apart from being proportionally smaller, the humerus closely resembles that of *O. hoazin* (Fig. 1k–n). As in the latter and *Namibiavis*, the deltopectoral crest is situated far distally on the shaft of the bones, and there is a marked brachial fossa (absent in *Namibiavis*). In contrast to *O. hoazin*, the coracoid and the furcula are separated (late ontogenetic fusion of these bones is autapomorphic for *O. hoazin*). The coracoid is very similar to that of juvenile *O. hoazin* (Fig. 1b–e) and agrees with the extant species in the derived presence of a pneumatic opening at the base of the procoracoid process, the strap-like procoracoid

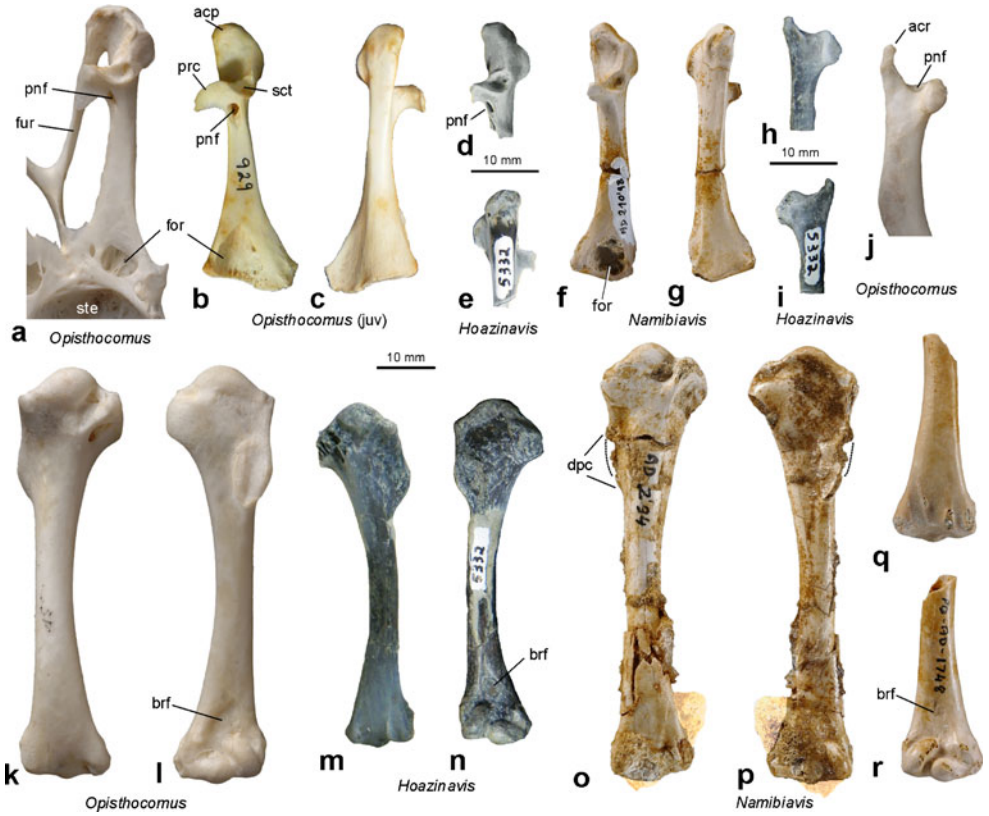

Fig. 1 Bones of *Hoazinavis lacustris* gen. et sp. nov. and *Namibiavis senutae* in comparison to extant *Opisthocomus hoazin*. **a**–**c** Right coracoids of adult (**a**) and juvenile (**b**, **c**) *O. hoazin*. **d**, **e** Right omal extremity of coracoid of *Hoazinavis lacustris* (holotype, MHNT-VT 5332) in dorsal (**d**) and ventral (**e**) views. **f**, **g** Right coracoid of *N. senutae* (holotype, GSMME AD 210′98) in dorsal (**f**) and ventral (**g**) views. **h**, **i** Right cranial extremity of scapula of *Hoazinavis lacustris* (holotype, MHNT-VT 5332) in lateral (**h**) and medial (**i**) views. **j** Right cranial extremity of scapula of *O. hoazin*. **k**, **l** Left humerus of *O. hoazin* in caudal (**k**) and cranial (**l**) views. **m**, **n** Right humerus of *Hoazinavis lacustris* (holotype, MHNT-VT 5332) in caudal (**m**) and cranial (**n**) views. **o**, **p** Left humerus of *N. senutae* (GSMME AD 2′94) in caudal (**o**) and cranial (**p**) views; the *dotted lines* indicate the reconstructed course of the deltopectoral crest, matrix adherent to the distal end was digitally colored and lightened. **q**, **r** Distal right humerus of *N. senutae* (GSMME PQ AD 1748) in caudal (**q**) and cranial (**r**) views. Same scale for all bones except **d**, **e**, **h**, and **i**. Scapula and coracoid of *Hoazinavis* were coated with ammonium chloride. Abbreviations: *acp* acrocoracoid process, *acr* acromion, *brf* brachial fossa, *dpc* deltopectoral crest, *for* foramen in sternal end of coracoid, *fur* furcula, *pnf* pneumatic foramen, *prc* procoracoid process, *sct* scapular cotyla, *ste* sternum

process, which is directed perpendicular to the long axis of the bone, and the deeply excavated scapular facet, which extends medially onto the procoracoid process and bears a small fossa in its center. The acromion of the scapula is proportionally shorter than in *O. hoazin*, the humeral articulation facet is smaller, and the shaft narrower; in contrast to *O. Hoazin*, there is no pneumatic foramen at the base of the acromion (Fig. 1h, j).

Namibiavis Mourer-Chauviré, 2003.
N. senutae Mourer-Chauviré, 2003.

Holotype: GSMME AD 210′98 (right coracoid; Fig. 1f, g).

Locality and horizon. Fluviatile deposits of a palaeochannel of the Proto-Orange River at Arrisdrift in Namibia; late early Miocene (17–17.5 mya; Mourer-Chauviré 2003).

Comments on revised phylogenetic position. *N. senutae* is known from three coracoids and six humeri; a referred femur (Mourer-Chauviré 2003) is here assigned to Galliformes, which constitute the majority of avian bones from Arrisdrift. *Namibiavis* was classified in the extinct taxon Idiornithidae in the original description, which are stem group representatives of the South American seriemas (Cariamidae) and were very widespread and diversified in the Cenozoic. As noted by previous authors, the humerus and other wing bones of Idiornithidae show a great resemblance to those of Opisthocomiformes (Milne-Edwards 1892; Mourer-Chauviré 1983; Olson 1985). Distinctive differences between *Namibiavis* and idiornithids were, however, noted (Mourer-Chauviré 2003), and our restudy of the fossils shows that the identification cannot be upheld.

In fact, the coracoid of *Namibiavis* closely resembles that of *Hoazinavis* (Fig. 1d–g) and exhibits diagnostic features of Opisthocomiformes, whose distinctive coracoid

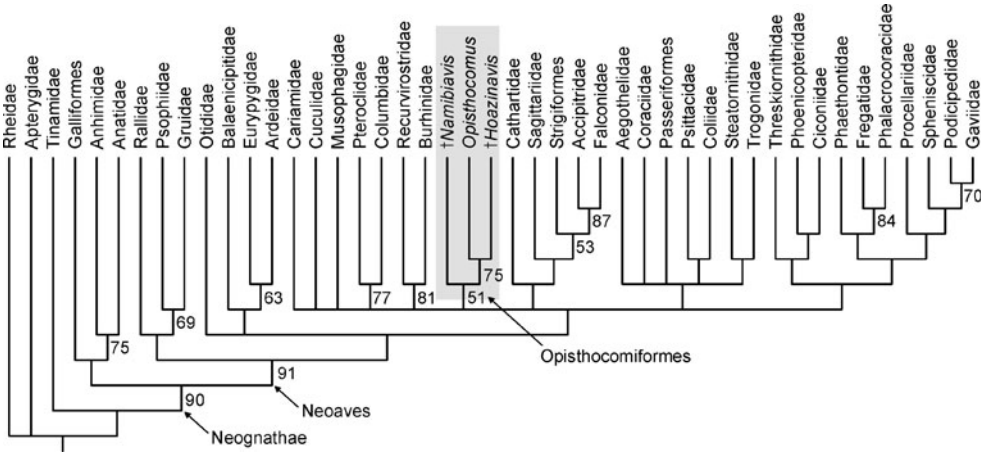

Fig. 2 Phylogenetic placement of *Hoazinavis* gen. nov. and *Namibiavis* in a strict consensus cladogram of seven most parsimonious trees (length, 762, consistency index, 0.21) resulting from analysis of 151 morphological characters. Bootstrap support values are indicated next to the nodes

morphology is not matched by other taxa including idiornithids. In particular, the bone is characterized by the presence of a marked opening on the dorsal surface of the sternal end (Fig. 1f), which elsewhere only occurs in the clearly distinguished coracoids of some anseriform (Anhimidae and Anseranatidae) and gruiform (Gruidae) birds. The derived morphologies of the procoracoid process and scapular facet correspond with *Opisthocomus* and *Hoazinavis*, and as in juvenile *Opisthocomus* and *Hoazinavis*, the medial border of the short acrocoracoid process forms a straight line with the shaft of the bone. The *Namibiavis* coracoid is, however, distinguished from that of *Opisthocomus* and *Hoazinavis* in the plesiomorphic absence of a pneumatic foramen below the procoracoid process (Fig. 1f). The humerus of *Namibiavis* is more elongated than that of *Opisthocomus* and *Hoazinavis* and has a straighter shaft (Fig. 1k–p), but otherwise its shape corresponds with that of other Opisthocomiformes. Unlike idiornithids, the deltopectoral crest is situated distal to the bicipital crest and the proximodorsal portion of the bone has a sigmoidally curved margin and a markedly concave caudal surface. The brachial fossa of *Namibiavis* is less marked than in *Opisthocomus* and *Hoazinavis* (Fig. 1r).

Discussion

The phylogenetic analysis supports assignment of *Hoazinavis* and *Namibiavis* to Opisthocomiformes and resulted in sister group relationship between *Namibiavis* and a clade including *Hoazinavis* and *Opisthocomus* (Fig. 2). A clade including the three opisthocomiform taxa is supported by the presence of a large foramen at the sternal extremity of the coracoid (Fig. 1a, b, f; unknown for *Hoazinavis*) and the distally situated deltopectoral crest. Our analysis recovers two synapomorphies for *Hoazinavis* and *Opisthocomus*, a pneumatic opening next to the procoracoid process and a sharply delimited brachial fossa (Fig. 1l, n).

H. lacustris, gen. et sp. nov. is the earliest unambiguous representative of Opisthocomiformes. Like those of *H. magdalenae*, the remains of the new species were found outside the extant distribution of Opisthocomiformes (Fig. 3).

The extant hoatzin has one of the proportionally largest crops of all birds (Böker 1929), whose space requirements resulted in the reduction of the cranial portion of the sternal carina and in a caudal shift of the pectoral muscles (Stegmann 1964). Because of these anatomical peculiarities, the species is a notably poor long distance flier (Thomas 1996). Humeral morphology of *Hoazinavis* and *Namibiavis*, especially the shape of the low deltopectoral crest, closely corresponds to that of *O. hoazin*, and indicates that stem-Opisthocomiformes also had limited flight capabilities. If and to what extent the two fossil taxa were already folivorous cannot be said for sure. However, a large crop strongly affects the morphology of the pectoral girdle

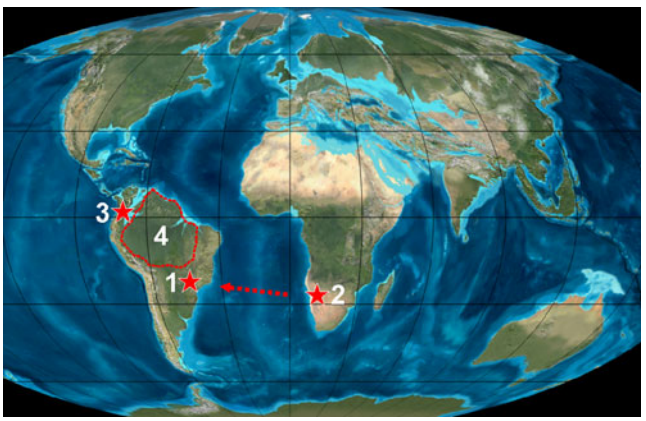

Fig. 3 Palaeomap of the continents in the early Oligocene (35 mya; copyright Ron Blakey, Colorado Plateau Geosystems, Inc.). *Asterisks* indicate localities of *Hoazinavis lacustris* gen. et sp. nov. (1), *Namibiavis senutae* (2), and *Hoazinoides magdalenae* (3). The distribution area of the extant *Opisthocomus hoazin* (4) is indicated by the *dotted lines*. The *arrow* denotes the presumed direction of hoatzin dispersal

bones (Stegmann 1964). Because humerus, coracoid, and scapula are very similar in *Hoazinavis* and *Opisthocomus*, we consider it likely that at least the Brazilian taxon had already evolved a large crop and some degree of folivory, whose pronounced development in the hoatzin suggests a long evolutionary history of this feeding specialization in the Opisthocomiformes.

Identification of stem-Opisthocomiformes in the Miocene of Africa adds hoatzins to the list of South American avian higher level taxa with a relictual extant distribution (Mourer-Chauviré 1999; Mayr 2009). *Namibiavis* is of particular biogeographic significance because it is the only stem group representative of these birds that is known from Africa. Other relictual South American taxa have a fossil record in Europe or North America (Alvarenga 1995; Mourer-Chauviré 1999, 2000; Mayr 2009). Although there are some corresponding relationships among extinct bird groups from South America and Europe (Alvarenga 1990; Mayr 2009), unambiguous stem group representatives of Opisthocomiformes are unknown from Northern Hemispheric fossil sites (Mayr 2009), and the fossil evidence indicates that at least modern type Opisthocomiformes, such as *Hoazinavis* and *Namibiavis*, evolved in the Southern Hemisphere.

Separation of South America and Africa, former parts of the supercontinent Gondwana, was completed in the mid-Cretaceous, about 100 mya (Gheerbrant and Rage 2006). Because this event clearly predates the fossil record of crown Neornithes, let alone neognathous or neoavian birds (Mayr 2009), the distribution of stem-Opisthocomiformes must be considered the result of dispersal rather than vicariance. However, the minimum distance between South America and Africa in the earliest Cenozoic was 1,000 km in a straight line (de Oliveira *et al.* 2009). Even if Miocene hoatzins had better flight capabilities than the modern species and the early Cenozoic existence of islands in the South Atlantic is acknowledged (de Oliveira *et al.* 2009), an oceanic dispersal on the wing is highly unlikely. The distribution pattern of hoatzins thus raises the same biogeographic problems as that of some nonvolant vertebrates with a distribution in Africa and South or Central America, i.e., caviomorph rodents and platyrrhine primates as well as some amphisbaenian and gekkotan lizards, for which a Cenozoic transatlantic dispersal on floating vegetation islands is assumed (Houle 1999; Carranza *et al.* 2000; de Queiroz 2005; Vidal *et al.* 2008; de Oliveira *et al.* 2009).

Oceanic rafting is also the most plausible explanation for transatlantic dispersal of hoatzins. Because suitable flotsam, which can reach considerable dimensions (Houle 1999; Hedges 2006), is usually washed into oceans from the mouth of large rivers (Hedges 2006), the riparian, poorly flighted hoatzins are among those avian taxa, for which dispersal by rafting would be most expected, and their folivorous diet may have favored transport on floating vegetation. Although birds have better dispersal capabilities than nonvolant animals, there are few well established examples of transatlantic dispersal by flight (Vuilleumier and Andors 1993; Voelker *et al.* 2009), and our study provides the first evidence for an oceanic rafting of birds with weak flight capabilities.

Phylogenetic reconstructions suggest a dispersal from Africa to the Neotropic region for primates, rodents, and lizards (Poux *et al.* 2006; Vidal *et al.* 2008). Dispersal from South America to Africa was suggested for sirenians (Domning 2005) and some thrushes (Voelker *et al.* 2009), but the dispersal capabilities of these animals are not comparable to those of the Opisthocomiformes. Because a westward journey on a floating raft was favored by palaeocurrents and palaeowinds (de Oliveira *et al.* 2009), we consider a dispersal of stem-Opisthocomiformes from Africa to South America to be more likely than one in the opposite direction. Certainly, however, further fossils or identification of the sister taxon of Opisthocomiformes is needed for a firmly established hypothesis on the direction of dispersal of Palaeogene Opisthocomiformes. Some morphological (Hughes 2000) and molecular (Hughes and Baker 1999; Mayr *et al.* 2003) studies identified the African Musophagidae (turacos) as the closest extant relatives of Opisthocomiformes. As noted in the Introduction, however, there exists no congruent and well supported phylogenetic placement of Opisthocomiformes and more data are needed for a strongly based phylogeny.

The early and mid-Cenozoic avifaunas of Africa are very poorly known (see the reviews of Mourer-Chauviré (2003), Mourer-Chauviré *et al.* (2011a), and Mayr (2009)), and the identification of stem-Opisthocomiformes strengthens observations concerning early and mid-Cenozoic biogeographic affinities between Africa and South America, notably the proposed (Agnolin and Chimento 2011), albeit controversial (Billet and Martin 2011), afrotherian relationships of the South America notoungulates and the recent discovery of a phorusrhacid bird in the Eocene of Algeria (Mourer-Chauviré *et al.* 2011b). The reasons for the large scale extinction of "South American" taxa outside the Neotropic region are poorly understood, but recognition of hoatzins in Africa south of the Sahara substantiates previous hypotheses that climatic cooling played only a subordinate role (Mayr 2009).

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