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A new species of swift (Aves, Apodidae) from the Early Pliocene of Langebaanweg, South Africa

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Abstract

We describe a new species of *Apus* (Aves, Apodidae) from the Early Pliocene of Langebaanweg (Cape Province, South Africa). A single swift humerus was reported from Langebaanweg's extraordinary rich fossil bird association, but it was never analyzed in detail. More recently, we located a second bone, a carpometacarpus, and completed the comparison of these two specimens with the corresponding bones of as many species of Apodidae as possible, leading to the description of the new species *Apus boanoi* sp. nov. The new species represents the largest species of the genus *Apus* known so far and the oldest from Africa; it represents an important calibration point for the split between *Apus* and *Tachymarptis*. The rarity of the new species in the very rich Langebaanweg fossil bird assemblage fits with the current paleoenvironmental reconstruction of a flat fluvial and coastal environment not suitable as breeding area for *Apus* swifts.

Keywords Fossil birds, Aves, Taxonomy, Paleoenvironment, Paleornithology

Introduction

The Varswater Formation at Langebaanweg, about 110 km NNW of Cape Town, South Africa, dated to the Early Pliocene, is one of the most important Neogene fossil localities in Africa with more than one million specimens of vertebrate found so far (Hendey, 1981, Roberts et al., 2011). This locality yielded a great number of well-preserved fossil bird bones, and it was considered one of the largest pre-Pleistocene fossil bird assemblages in the World already after a preliminary account made by Rich (1980), where she listed about 60 species of 28 families. Some bird groups were subsequently studied in detail, and now the bird assemblage of the "E Quarry" of Langebaanweg comprises more than 90 species representing over 37 families (Manegold et al., 2013, 2014; Pavia et al., 2015; Pavia pers. obs. 2023), with

some taxa still to be analyzed in detail. The presence of a swift at Langebaanweg was reported by Rich (1980), and Manegold et al. (2013) indicated that this taxon is represented by a single bone. In the last few years all the unsorted and unidentified bird material stored at Iziko South African Museum has been sorted and identified at family level, including an almost complete carpometacarpus of a swift, which is added to the previously known complete humerus, and both bones are described herein.

Even though the fossil record of early Apodiformes is quite rich (Mayr, 2022), the evolutionary history of apodiform birds remains poorly understood (Mayr & Kitchener, 2024). The modern Apodidae is a widespread taxon with a large number of genera and species distributed worldwide (Winkler et al., 2020), but its presence in the fossil record is remarkably scarce. The oldest representative of the genus *Apus* is *A. gaillardi* from the Middle Miocene of France (Ennouchi, 1930), followed by *A. wetmorei* and *A. baranensis* from the latest Miocene of Italy (Ballmann, 1976) and Pliocene of Bulgaria (Boev, 2000) respectively. In the Late Pleistocene, fossils of *Apus* and *Tachymarptis* are not uncommon in Western Palearctic localities (Tyrberg, 1998, 2008; Carrera et al., 2018, 2021). Apart from Langebaanweg, swifts are found as fossils in few African localities and they were never identified to species level. Two species of Apodidae are reported from the Pliocene of Kanapoi, Tanzania (Field, 2020) and in the Late Pleistocene of Sibudu Cave, South Africa (Val, 2016), an Apodidae is reported from the Pliocene of Aramis, Ethiopia (Louchart et al., 2009), the Early Pleistocene of Olduvai, Tanzania (Brodkorb, 1985), and *Apus* sp. is reported from the Early Pleistocene of Cooper's Cave, South Africa (Pavia et al., 2022).

Materials and methods

The fossil bones described here are part of the Cenozoic collections of the Iziko South African Museum, Cape Town, South Africa (SAM-PQ L, Paleontology Quaternary

Langebaanweg). The comparisons were made with eight species of Apodidae of the genus *Apus*, *Cypsiurus*, and *Tachymarptis*, which represent the most widespread African genera, and the non-African genera *Aeronautes*, *Chaetura*, *Collocalia*, *Cypseloides*, and *Hemiprocne* (Appendix 1). No comparisons were made with the other African taxa of the genera *Neafrapus*, *Rhapidura*, *Schoutedenapus*, *Telacanthura*, and *Zoonavena* and other non-African species because no skeletons of those taxa are available. The comparison with the similar-sized Asian genus *Hirundapus* was based on Serrano et al. (2020). The nomenclature of Apodidae follows del Hoyo & Collar (2014).

The anatomical terminology follows Baumel and Witmer (1993), except where stated otherwise. The measurements were taken by using Vernier caliper accurate to 0.1 mm in accordance with von den Driesch (1976).

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Systematic paleontology

Class **Aves** Linnaeus, 1758

Order **Caprimulgiformes** Ridgway, 1881

Family **Apodidae** Hartert, 1897

Genus ***Apus*** Scopoli, 1777

Type species. *Apus apus* (Linnaeus, 1758), Recent, Europe.

Apus boanoi sp. nov. Pavia & Louchart

Figures 1 and 2.

Etymology. The species is dedicated to Giovanni Boano, Italy's foremost swift specialist and world-renowned for his studies on the Pallid Swift, for his role in Italian ornithology, for his passion for natural science that served as an example for generations of naturalists, and for

his interest in natural history collections as a research tool for past, present and future biodiversity.

Holotype. Right humerus, SAM-PQL-43334, complete (Fig. 1).

Paratype. Left carpometacarpus, SAM-PQL-60037S, complete (Fig. 2).

Material. Holotype and paratype only.

Type horizon. Upper Varswater Formation; Early Pliocene, about 5.1 Ma (Roberts et al., 2011).

Type locality. "E" Quarry, Langebaanweg (18°9' E, 32°58' S), approximately 110 km NNW of Cape Town, South Africa.

Diagnosis. A swift of the genus *Apus* of very large size, only slightly smaller than the two *Tachymarptis* species, and larger than any other living species of *Apus* (Table 1). The humerus of *Apus boanoi* sp. nov. is characterized by the distal edge of the intumescentia humeri which is prolongated by a crest that reaches the caudal side of the bone proximally to the tuberculum dorsale, and it is distinguished from *Tachymarptis melba* and *T. aequatorialis* by a well-marked continuous crest joining the processus supracondylaris dorsalis and the epicondylus dorsalis, and from other *Apus* species by the very weak tuberculum for musculus extensor metacarpalis radialis (Ballmann, 1976). The carpometacarpus of *Apus boanoi* sp. nov. shows the processus pisiformis and the processus alularis more developed than in the recent species of *Apus* used for comparison.

Description and comparisons. *Apus boanoi* sp. nov. is described on the basis of two almost complete bones. It can be referred to Apodidae because of its very peculiar humerus which is stout and with a very strong and narrow crista deltopectoralis and for the very short and deep sulcus humerotricipitalis (see also Ballmann, 1976). The carpometacarpus is characteristic of Apodidae in having a very strong and straight os metacarpale major contrasting with the relatively small proximal end in which the processus extensorius is small

and thin and protrudes medially perpendicular to the os metacarpale major. The two bones can be referred to the same species because, besides clearly showing all the diagnostic characters of a large swift, their proportions match those observed in single extant species of Apodidae (Table 1).*Hirundapus*, although similar in size, can be ruled out because the humerus is generally more elongated with a less pointed crista deltopectoralis and a more developed processus supracondylaris dorsalis, and because the carpometacarpus shows a less pointed processus extensorius and a more rounded ventral projection of the os metacarpale major. The other non-African taxa are smaller in size and show morphological differences in the two analyzed bones.

Among the African Apodidae, *Cypsiurus parvus* can be easily ruled out because of the very small size of the various bones (Table 1).

The humerus of *Apus boanoi* differs from those of *Tachymarptis melba* and T. *aequatorialis* by various characters in the proximal and distal ends of the bone: in particular, the caput humeri is less developed in the new species, particularly in cranio-caudal direction; the tuberculum dorsale is more pointed and the crest between the caput humeri and the tuberculum dorsale is sharper in caudal view. The intumescentia humeri is partially broken in *A. boanoi*, but its impression goes as distal as the crista deltopectoralis, whereas it ends more proximally in the recent *Tachymarptis* and *Apus* species (including *A. barbatus*). The fossa pneumotricipitalis ventralis is smaller and less developed in the fossil species than in *Apus barbatus* and other *Apus* species. In the holotype humerus SAM-PQL-43334 there is a continuous well-marked crest between the processus supracondylaris dorsalis and the epicondylus dorsalis, whereas it is interrupted by a flat area just proximally to the epicondylus dorsalis in *Tachymarptis*. In the latter genus, the processus flexorius is more protruding caudally for the major development of an accessory tuberculum on the caudal surface of the processus flexorius, and the condylus dorsalis is more developed ventrally. The

humerus of *Apus boanoi* can be distinguished from the other species of the genus *Apus* used for comparison, in particular the closer-in-size *A. barbatus*, by the longer, deeper, and wider sulcus ligamenti transversus with its distal ridge less developed. In the holotype humerus SAM-PQL-43334, the distal limit of the intumescentia humeri is represented by a crest that reaches the caudal side of the bone just proximally to the tuberculum dorsale. This character is not present in any species used for comparison. The tuberculum for the musculus extensor metacarpi radialis (Ballmann 1976) is very weak in *Apus boanoi*, compared with all the other species. The tuberculum supracondylare ventrale is proportionately more developed in *Apus boanoi* than in all the other recent species, such as the secondary tuberculum just proximal to it.

With respect to the recent species of the genus *Apus*, the carpometacarpus of *A. boanoi* shows cranio-caudally wider processus extensorius and processus pisiformis, and processus alularis more developed in length and wider with a rounded crest joining the processus pisiformis with the proximal end of the os metacarpale minus separating the shaft from the proximal end of the bone. In dorsal view the paratype carpometacarpus SAM-PQL-60037S shows a well-marked fovea between the os metacarpale alulare and the proximal end with a tuberculum just distally to the dorsal side of the trochlea carpalis. The fovea and the tuberculum are less developed in the recent *Tachymarptis* species, where the tuberculum is also situated more medially. *Apus boanoi* shows a more rounded and relatively less developed processus for the articulation with phalanx digit minoris in comparison with *Tachymarptis*, even less developed than in *Apus apus*, *A. barbatus*, *A. caffer*, and *A. pallidus*. With respect to *Apus barbatus*, *A. boanoi* shows the ventral projection of the os metacarpale major more pointed with the dorsal outline angled in distal view and not straight as in *A. barbatus*. The trochlea carpalis dorsalis is less developed proximally in *Apus barbatus* than in *Apus boanoi*.

The new species described here shows several morphological characters that allow its strong affiliation with the genus *Apus* and exclude the other genera used for comparison. This well-supported attribution can also safely exclude the other African Apodidae not directly examined, all of which show a smaller size (Winkler et al., 2020).

Measurements. See Table 1.

Stratigraphic and geographical range. Langeberg Quartz Sand Member or Muishond Fontein Pelletal Phosphorite Member, Upper Varswater Formation at Langebaanweg,
Early Pliocene of South Africa (Roberts et al., 2011).

Discussion

Apus boanoi sp. nov. is the oldest representative of the Apodidae known from Africa, and the first large representative of the crown Apodidae, as the other fossil species are all diminutive, smaller than the recent *Apus apus*: *Apus gaillardi* from the Middle Miocene of France (Ennouchi, 1930), *A. wetmorei* from the latest Miocene of Italy (Ballmann, 1976), and *A. baranensis* from the Pliocene of Hungary and Bulgaria (Boev, 2000).

Fossil swifts are rare in the African fossil record and *Apus boanoi* represents the first identified at specific level. All the other African records of swifts are referred to small taxa of the size of *Apus horus* or smaller (Field, 2020; Pavia et al., 2022; Louchart pers. obs. 2024).

The morphological analysis of the two remains of *Apus boanoi* indicates its affinities with the genus *Apus* instead of *Tachymarptis*, even if the size of the bones may have suggested an assignment at first glance. *Apus* and *Tachymarptis* are monophyletic groups genetically well separated (Päckert et al., 2012), even if the time of their divergence has not been estimated yet (but see the indication of 16.6 Ma from OneZoom; Rosindell and Harmon, 2012). The presence of a modern-type *Apus* in the Early Pliocene of Africa could represent an

important calibration point in the reconstruction of the *Apus* evolutionary history (Pellegrino et al., 2017) and in the separation between *Apus* and *Tachymarptis*.

The fact that Swift remains are so rare at Langebaanweeg fits perfectly with the paleoenvironmental reconstructions of a flat humid area with woods, bushlands, and open patches. In fact, all the *Apus* swifts are cavity nesters that use rocky outcrops or cliffs, except for some remote populations of *Apus apus* that breed in tree holes or other occasional records (Cramp, 1994; Camelliti & Boano, 2002; Chantler et al., 2020) and use the flat areas only during foraging activities. This study is part of the detailed ongoing studies on the various marine and terrestrial bird groups found at Langebaanweg and confirms the diversity of the African avifauna since the Early Pliocene. The new data are shedding new light on the evolution of the present-day African avifauna, which started in the Early Pliocene with the establishment of the modern genera, and on its significance in terms of paleobiogeography and paleoenvironment.

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Data availability All data are included in the paper.

Statement and Declarations The authors declare no conflict of interest.

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FIGURE CAPTIONS



Fig. 1. Holotype right humerus (SAM-PQL-43334) of *Apus boanoi* sp. nov. from the Early Pliocene of Langebaanweg (a, d, g, j, m, p) compared with recent *Apus barbatus* (ZO 56847) (b, e, h, k, n, q), and *Tachymarptis melba* (MGPT-MPOC 2196) (c, f, i, l, o, r), in caudal (a-c), dorsal (d-e), cranial (g-i), ventral (j-l), proximal (m-o), and distal (p-r) views. Scale bar represents 10 mm. Abbreviations: **cih**, crista of the intumescentia humeri; **ed**, epicondulus dorsalis; **psd**, processus supracondylaris dorsalis; **slt**, sulcus ligament transversus; **td**, tuberculum dorsale; **tmr**, tuberculum for musculus extensor metacarpalis radialis; **tsv**, tuberculum supracondylare ventral.



Fig. 2. Paratype left carpometacarpus (SAM-PQL-60037S), of *Apus boanoi* sp. nov. from the Early Pliocene of Langebaanweg (a, d, g, j, m, p) compared with recent *Apus barbatus* (ZO 56847) (b, e, h, k, n, q), and *Tachymarptis melba* (MGPT-MPOC 2196) (c, f, i, l, o, r), in ventral (a-c), cranial (d-f), dorsal (g-i), caudal (j-i), proximal (m-o), and distal (p-r) views. Scale bar represents 10 mm. Abbreviations: **pa**, processus alularis; **pe**, processus extensorius; **pp**, processus pisiformis; **tcd**, trochela carpalis dorsalis.