UAB
Universitat Autònoma de Barcelona

Dipòsit digital de documents de la UAB

This is the **accepted version** of the journal article:

Pavia, Marco [et al.]. «A new species of swift (Aves, Apodidae) from the Early Pliocene of Langebaanweg, South Africa». *Paläontologische Zeitschrift*, Vol. 99, Num. 1 (March 2025), p. 185-192 DOI 10.1007/s12542-024-00711-y

This version is available at https://ddd.uab.cat/record/308518

under the terms of the IN COPYRIGHT license.

Post-print version of:

Pavia M, Louchart A., Govender R. & Delfino M., 2025. A new species of Swift (Apodidae) from the early Pliocene of Langebaanweg, South Africa. PalZ (advance online publication) doi: 10.1007/s12542-024-00711-y

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

Marco Pavia[1,2,3], Antoine Louchart[4], Romala Govender[2,5], Massimo Delfino[1,6]

[1] Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso 35, 10125 Torino, Italy

[2] Research and Exhibitions, Iziko Museums of South Africa, 25 Queen Victoria Street, Cape Town 8001, South Africa

[3] Evolutionary Studies Institute, University of the Witwatersrand, PO WITS, 2050 Johannesburg, South Africa

[4] Univ Lyon, Univ Lyon 1, ENSL, CNRS, LGL-TPE, Villeurbanne, France

[5] Biological Sciences, University of Cape Town, Private Bag, Rondebosch 7701, Cape Town, South Africa

[6] Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICTA-ICP, c/ Columnes s/n, Campus de la Universitat Autònoma de Barcelona, 08193 Cerdanyola del Vallès, Barcelona, Spain

Orcid:

Marco Pavia: 0000-0002-5188-4155

Antoine Louchart: 0000-0003-3847-6007

Romala Govender: 0000-0002-3796-9830

Massimo Delfino: 0000-0001-7836-7265

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).

Zoobank urn:lsid:zoobank.org:pub:3924B65B-1478-4862-B87B-EA251FBCF2DB

**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.

**Acknowledgement** We would like to thank the people of the South African Heritage Resources Agency for their continuous support. We warmly thank Yolanda Michaels (Iziko South African Museum, Cape Town) for her invaluable help with the sorting of the Langebaanweg fossil collection during our stays at Iziko. We also thank Jofred Opperman (Iziko South African Museum, Cape Town), Mpho Malematja (Ditsong National Museum of Natural History, Pretoria), Judith White (Natural History Museum, Tring UK) who provided access to the modern samples under their care. We also warmly thank A. Manegold and G. Mayr for their comments and suggestions that greatly improved the manuscript. This is the publication number 377 of the Museo di Geologia e Paleontologia collections at the Università degli Studi di Torino.

**Funding** MP and MD were funded by Università degli Studi di Torino (grants ex-60% 2022 and 2023) and by the Palaeontological Scientific Trust (PAST), Johannesburg, South Africa.

**Data availability** All data are included in the paper.

**Statement and Declarations** The authors declare no conflict of interest.

## References

Ballmann, P. (1976). Fossile Vögel aus dem Neogen der Halbinsel Gargano (Italien). Zweiter Teil. *Scripta Geologica*, 38, 1–59.

Baumel, J. J. & Witmer, L. M. (1993). Osteologia. In J. J. Baumel, A. S. King, J. E. Breazile, H. E. Evans, & J. C. Vanden Berge (Eds.), *Handbook of Avian Anatomy: Nomina Anatomica Avium*, (2nd edition, pp. 45–132). Publications of the Nuttall Ornithological Club.

Boev, Z. (2000). The presence of *Apus baranensis* Janossy, 1977, (Aves: Apodidae) in the Late Pliocene of Bulgaria. *Acta zoologica bulgarica*, 52, 43–52.

Brodkorb, P. (1985). Preliminary report on Pliocene/Pleistocene birds of East Africa. In V. D. Ilyichev & V. M. Gavrilov (Eds.), *Proceedings of the 18th International Ornithological Congress, Moscow, August 16–24, 1982* (pp. 174–177). Nauka.

Camelliti, G., & Boano, G. (2002). Nidificazione di Rondone *Apus apus* in cavità di alberi a Torino. *Picus*, 28, 105–107.

Carrera, L., Pavia, M., Romandini, M., & Peresani, M. (2018). Avian fossil assemblages at the onset of the LGM in the eastern Alps: a palaecological contribution from the Rio Secco Cave (Italy). *Compte Rendu Palevol*, 17, 166–177. https://doi.org/10.1016/j.crpv.2017.10.006

Carrera, L., Scarponi, D., Martini, F., Sarti, L. & Pavia, M. (2021). Mid-Late Pleistocene Neanderthal landscapes in southern Italy: paleoecological contributions of the avian

assemblage from Grotta del Cavallo, Apulia, southern Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 567, 110256. https://doi.org/10.1016/j.palaeo.2021.110256

Chantler, P., Boesman, P. F. D., & Kirwan, G. M. (2020). Common Swift (*Apus apus*), version 1.0. In J. del Hoyo, A. Elliott, J. Sargatal, D.A. Christie, & E. de Juana (Eds.), *Birds of the World*. Cornell Lab of Ornithology, Ithaca, NY, USA. Retrieved September 30, 2024, from https://doi.org/10.2173/bow.comswi.01

Cramp, S. (1994). *Handbook of the Birds of Europe, the Middle East, and North Africa. Vol. IV. Terns to Woodpeckers*. Oxford University Press.

del Hoyo J. & Collar N. J. (2014). *HBW and BirdLife International illustrated checklist of the birds of the World. Volume I: Non-passerines*. Lynx Edicion.

Ennouchi, E. (1930). *Contribution à l'étude de la faune du Tortonien de la Grive-Saint-Alban (Isère)*. Les Presses Modernes.

Field D. J. (2020). Preliminary paleoecological insights from the Pliocene avifauna of Kanapoi, Kenya: Implications for the ecology of *Australopithecus anamensis*. *Journal of Human Evolution*, 140, 102384. https://doi.org/10.1016/j.jhevol.2017.08.007

Hartert, E (1897). *Das Tierreich: Podargidae, Caprimulgidae und Macropterygidae*. Friedländer und Sohn.

Hendey, Q. (1981). Palaeoecology of the late Tertiary fossil occurrences in 'E' Quarry, Langebaanweg, South Africa, and a reinterpretation of their geological context. *Annals of the South African Museum*, 84, 1–104.

Linnaeus, C. (1758). *Systema naturae per regna tria naturae* (10th edition, 2 vols). Holmiae: L. Salmii.

Louchart, A., Wesselman, H., Blumenschine, R. J., Hlusko, L. J., Njau, J. K., Black, M. T., Asnake, M., & White, T. D. (2009). Taphonomic, Avian, and Small-Vertebrate indicators

of *Ardipithecus ramidus* habitat. *Science*, 326, 66e1–66e4. https://doi.org/10.1126/science.1175823

Manegold, A., Louchart, A., Carrier, J., & Elzanowski, A. (2013). The early Pliocene avifauna of Langebaanweg (South Africa): a review and update. In U. B. Gohlich, & A. Kroh (Eds.), *Paleontological Research 2013 - Proceedings of the 8th International meeting of the Society of Avian Palaeontology and Evolution* (pp. 135–152). Naturhistorisches Museum Wien.

Manegold, A., Pavia, M., & Haarhoff, P. (2014). A new species of *Aegypius* vulture (Aegypiinae, Accipitridae) from the early Pliocene of South Africa. *Journal of Vertebrate Paleontology*, 34, 1394–1407. https://doi.org/10.1080/02724634.2014.863204

Mayr, G. (2022). *Paleogene fossil birds* 2nd edition). Springer

Mayr, G. & Kitchener, A. C. (2024). New fossils of *Eocypselus* and *Primapus* from the British London Clay reveal a high taxonomic and ecological diversity of early Eocene swift-like apodiform birds. *Ibis*, 1–19 https://doi.org/10.1111/ibi.13323.

Päckert, M., Martens, J., Wink, M., Feigl, A., & Tietze, D. T. (2012). Molecular phylogeny of Old World swifts (Aves: Apodiformes, Apodidae, *Apus* and *Tachymarptis*) based on mitochondrial and nuclear markers. *Molecular Phylogenetics and Evolution*, 63, 606–616. https://doi.org/10.1016/j.ympev.2012.02.002

Pavia, M., Manegold, A., & Haarhoff, P. (2015). New early Pliocene owls from Langebaanweg, South Africa, with first evidence of *Athene* south of the Sahara and a new species of *Tyto*. *Acta Paleontologica Polonica*, 60, 815–828. https://doi.org/10.4202/app.00077.2014

Pavia M., Val A., Carrera L., & Steininger C. M. (2022). Fossil birds from Cooper's D aid in reconstructing the Early Pleistocene paleoenvironment in the Cradle of Humankind

(Gauteng, South Africa). *Journal of Human Evolution*, 167, 103185. https://doi.org/10.1016/j.jhevol.2022.103185

Pellegrino, I., Cucco, M., Harvey, J. A., Liberatore, F., Pavia, M., Voelker, G., & Boano, G. (2017). So similar and yet so different: taxonomic status of Pallid Swift *Apus pallidus* and Common Swift *Apus apus*. *Bird Study*, 64, 344–352. http://dx.doi.org/10.1080/00063657.2017.1359235

Rich, P. V. (1980). Preliminary report on the fossil avian remains from late Tertiary sediments at Langebaanweg (Cape Province), South Africa. *South African Journal of Science*, 76, 166–170.

Ridgway, R. (1881). A Catalogue of the birds of Illinois. *Bulletin of the Illinois State Laboratory of Natural History*, 4, 163–208.

Roberts, D. L., Matthews, T., Herries, A. I. R., Boulter, C., Scott, L., Dondo, C., Mtembi, P., Browning, C., Smith, R. M. H., Haarhoff, P., & Bateman, M. D. (2011). Regional and global context of the Late Cenozoic Langebaanweg (LBW) palaeontological site: West Coast of South Africa. *Earth-Science Reviews*, 106, 191–214. https://doi.org/10.1016/j.earscirev.2011.02.002

Rosindell, J., & Harmon, L. J. (2012). OneZoom: A Fractal Explorer for the Tree of Life. *PLoS Biol*, 10, e1001406. https://doi.org/10.1371/journal.pbio.1001406

Scopoli, G. A. (1777). *Introductio ad historiam naturalem*. Gerle.

Serrano F. J., Costa-Pérez M., Navalón G., & Martín-Serra A. (2020). Morphological Disparity of the Humerus in Modern Birds. *Diversity*, 12:, 173. https://doi.org/10.3390/d12050173

Tyrberg, T. (1998). *Pleistocene Birds of the Palearctic: A Catalogue*. Publications of the Nuttall Ornithological Club No. 27.

Tyrberg, T. (2008). Pleistocene Birds of the Palaearctic. Retrieved September 30, 2024, from https://epe.lac-bac.gc.ca/100/201/300/palaeontologia/2015/v18n02/web.telia.com/_u11502098/pleistocene.pdf

Val, A. (2016). New data on the avifauna from the Middle Stone Age layers of Sibudu Cave, South Africa: Taphonomic and palaeoenvironmental implications. *Quaternary International*, 421, 173–189. https://doi.org/10.1016/j.quaint.2014.11.068

von den Driesch, A. (1976). A guide to the measurement of animal bones from archaeological sites. *Peabody Museum Bulletin*, 1, 1–137.

Winkler, D. W., Billerman, S. M., & Lovette, I. J. (2020). Swifts (Apodidae), version 1.0. In S. M. Billerman, B. K. Keeney, P. G. Rodewald, & T. S. Schulenberg (Eds.). *Birds of the World*. Cornell Lab of Ornithology. Retrieved September 30, 2024, from https://doi.org/10.2173/bow.apodid1.01

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.