



Research Paper

A new species of Lovebird (Aves, Psittaculidae, *Agapornis*) from the Plio-Pleistocene of the Cradle of Humankind (Gauteng, South Africa) [☆]

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ARTICLE INFO

Article history:

Received 29 November 2023

Revised 13 April 2024

Accepted 21 May 2024

Available online 9 August 2024

Keywords:

Birds

Parrot

Osteology

Paleoecology

Cooper's Cave

Kromdraai

Swartkrans

ABSTRACT

A new parrot species of the genus *Agapornis* (Aves, Psittaculidae), namely *Agapornis longipes* nov. sp., is described from the Plio-Pleistocene of Kromdraai, Cooper's Cave, and Swartkrans in the Cradle of Humankind, South Africa. The new species is represented by all major wing bones (humerus, ulna, and carpometacarpus) and by the tarsometatarsus, together with a fragmentary mandible and coracoid. The size of the bones indicates a small species of *Agapornis* with an elongated tarsometatarsus, proportionately the longest of all known species of *Agapornis*. This lengthening of the legs might be related to feeding adaptation of the extinct species, as the longer legs may have favored this ground feeder in the high and dense grassland characteristic of the Cradle of Humankind during the Plio-Pleistocene transition and the Early Pleistocene.

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1. Introduction

Lovebirds (Psittaculidae, genus *Agapornis*) are small-sized parrots endemic to sub-Saharan Africa and Madagascar; they currently include nine species living in woodlands or wooded savannahs where they breed in tree cavities and feed on grass seeds or fruits collected primarily on the ground and, to a lesser degree, on trees (del Hoyo et al., 1997).

According to genetic data, psittaciforms colonized Africa in the late Eocene/early Oligocene and *Agapornis* only colonized Africa from Australasia in the late Oligocene/Early Miocene, ca. 24 Ma; *Psittacula krameri* is the latest parrot to have dispersed into the

continent, near the Plio-Pleistocene boundary (2.5–1.5 Ma; Groombridge et al., 2004; Schweizer et al., 2010, 2011). The fossil record of parrots in Africa is very scarce and the oldest dates back to the Early Pliocene of Langebaanweg (Manegold, 2013). Remarkably, most of the African fossils were attributed to *Agapornis*, the oldest of which is represented by *Agapornis attenboroughi* described from the Early Pliocene of Langebaanweg, South Africa (Manegold, 2013). Louchart et al. (2009) reported at least two, or perhaps three, still undescribed species of *Agapornis* from the Early Pliocene of Aramis in Ethiopia, and a single bone referred to *Agapornis* was reported from the slightly younger locality of Asa Issie (White et al., 2006). From the Late Pliocene of Ahl al Oughlam, Morocco, Mourer-Chauviré and Geraads (2010) described *Agapornis atlanticus*, which is the only *Agapornis* species ever reported north of the Sahara Desert. In addition, two species of *Agapornis* were reported from the Plio-Pleistocene of Olduvai, Tanzania

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(Brodkorb, 1985; Prassack, 2010). In the Cradle of Humankind, South Africa, several remains of two *Agapornis* species were reported by Pocock (1969). The presence of a single small-sized *Agapornis* species was reported from the Plio-Pleistocene of Kromdraai (Stidham 2009; Pavia, 2020) and the Early Pleistocene of Cooper's Cave (Pavia et al., 2022). Additionally, a single quadrate of a very small species was described from the late Early Pleistocene of Plovers Lake (Stidham, 2010); this quadrate bone was not available for this study. It is worth mentioning here that the bird material from Kromdraai studied by Pocock was considered lost by Stidham (2009, 2010: 123). This has proved to be inaccurate as this material is curated at the Evolutionary Study Institute at the University of the Witwatersrand, Johannesburg, South Africa, and is included in this study.

The evidence for African fossil parrots other than *Agapornis* includes *Khwenena leopoldinae*, a fossil species of the extinct endemic genus *Khwenena* described from the Early Pliocene of Langebaanweg (Manegold, 2013); a large still undescribed parrot species from the same locality (Stidham, 2006); a single tarsometatarsus of *Poicephalus* sp. from the Early Pliocene of Aramis (Louchart et al., 2009); and different remains of *Poicephalus robustus* from the Late Pleistocene of Sibudu Cave, South Africa (Val, 2016).

In this paper, we analyze the Lovebird fossil bones found at the localities of Kromdraai, Cooper's Cave, and Swartkrans in the Cradle of Humankind (Fig. 1). The analyzed bones can be referred to a new species of *Agapornis*, which is described below.

2. Fossil localities

The fossils examined here were retrieved from three localities in the UNESCO World Heritage site of the Cradle of Humankind (Gauteng Province, South Africa), a key area for understanding early hominin evolution in southern Africa (Fig. 1). The Cradle of Humankind contains several hominin-bearing localities that span

from the Late Pliocene to the Late Pleistocene and their studies illuminate the paleoecological and paleoenvironmental contexts surrounding the appearance of the genus *Homo* in the region, as well as its relationship with contemporaneous australopithecines and *Paranthropus*. Despite extensive research through the collections of the Evolutionary Studies Institute of the University of Witwatersrand and the Ditsong National Museum of Natural History, we did not find *Agapornis* remains from other localities in the Cradle of Humankind.

The three fossil sites of Swartkrans, Cooper's Cave and Kromdraai are a few hundred meters from each other, located in the southern part of the Cradle, respectively 1 km east and ca. 1.5 km northeast of the Sterkfontein Caves (Fig. 1). Like all other hominin-bearing sites of the Bloubaan Valley, Cooper's Cave, Kromdraai, and Swartkrans open in the Archean dolomites of the Monte Christo Fm. (Malmani Subgroup, Transvaal Supergroup).

Cooper's Cave is a karstic system that extends for more than 0.6 km² and contains three distinct fossiliferous localities, namely Cooper's A, B, and D (Berger et al., 2003). The material analyzed here comes from Cooper's D, which is the most fossiliferous Early Pleistocene locality in the region (Pickering et al., 2019; Hanon et al., 2022; Pavia et al., 2022). Cooper's D is a narrow fissure along an east–west trend, which contains fossil-bearing calcified and decalcified sediments. Published studies on fossil mammals and birds from Cooper's D generally consider the remains retrieved from the different facies and across the deposits as roughly contemporaneous and usually as part of a unique assemblage (de Ruiter et al., 2009; Hanon et al., 2022; Pavia et al., 2022).

The first fossil at “the Kromdraai farm” was discovered in 1895 by David Draper (Braga et al., 2022), and in 1938 Robert Broom started the field research activities that led to the discovery of the holotype of *Paranthropus robustus* (Broom, 1938). The locality is since well-known for its large and diverse fossil assemblage. From 2014 onwards, the Kromdraai Research Group started extensive new excavation campaigns that uncovered a plethora of vertebrate remains, including hominins (Braga et al., 2017, 2022; Braga and Grine, 2024). After reevaluating the stratigraphy at the Kromdraai site, its various localities (KA, KB, KC, and KE) are now acknowledged as a unified locality (Braga et al., 2017), characterized by a single, notably intricate stratigraphic sequence of hard and soft breccias detailed by Bruxelles et al. (2016). The parrot remains described here were collected from different parts of the Kromdraai site, which cannot be correlated easily with one another. Pocock (1969) described the presence of two species of *Agapornis* among the material collected by Brain (excavation campaign 1955–1956). Later, Stidham (2009) reported a single *Agapornis* humerus discovered in the material collected by Vrba (excavation campaign 1977–1980), and Pavia (2020) described another single humerus from Unit P, previously known as Member 2. The stratigraphic succession of Kromdraai has recently been revised by Braga et al. (2022), who pointed out that the oldest fossiliferous deposits of Kromdraai are those of Unit P and the underlying (older), recently discovered Unit O. In addition, these authors correlated the new stratigraphic nomenclature of Kromdraai with the previous studies and thus emphasize that the fossil samples recovered before the new excavation campaigns started in 2014 are not easily tied with the current stratigraphy and cannot be considered as temporally equivalent. However, for the scope of this paper, we treat the fossils from Kromdraai analyzed here as a broadly contemporaneous sample dated near the Plio-Pleistocene boundary.

The bird bones described here were collected from the Lower Bank of Member 1 at Swartkrans. Member 1 is the earliest fossil deposit at Swartkrans, dated to the Early Pleistocene (Kuman et al., 2021), and has yielded abundant fossils of early hominins attributed to both *Paranthropus robustus* and early *Homo*, associ-

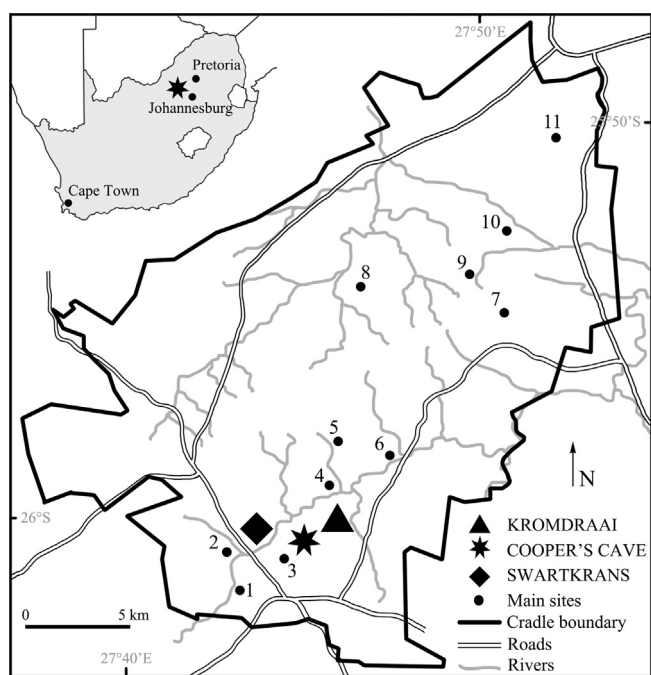


Fig. 1. Map of the Cradle of Humankind in Gauteng, South Africa. The triangle indicates the position of Kromdraai, the star indicates the position of Cooper's Cave, and the diamond indicates the position of Swartkrans. Main sites: 1, Bolt's Farm; 2, Rising Star; 3, Sterkfontein; 4, Minnaars; 5, Drimolen; 6, Plovers Lake; 7, Motsetse; 8, Gladysvale; 9, Malapa; 10, Haasgat; 11, Gondolin.

ated with lithic artefacts characteristic of the Oldowan industry. The Lower Bank was first excavated in the 1970s (Brain, 1993) and has been continuously explored by the Swartkrans Paleoanthropology Research Project (SPRP) since 2005 (Kuman et al., 2021). The material described here was collected between 1979 and 1986 by Bob Brain during the first excavation of the Lower Bank.

3. Material and methods

The bird specimens described here are curated in the Evolutionary Studies Institute at the University of the Witwatersrand, Johannesburg, South Africa (Cooper's Cave and Kromdraai) and in the Plio-Pleistocene Section, Ditsong National Museum of Natural History, Pretoria, South Africa (Swartkrans). The materials are catalogued using the acronyms CD for Cooper's Cave D (Pavia et al., 2022), KW for Kromdraai Unit P (Pavia, 2020), and SKX for Swartkrans Lower Bank of Member 1 preceding the specimen number. The fossils from Kromdraai studied by Pocock are catalogued with the acronym KWPOC preceding the specimen number. The fossil bones were compared to skeletons of extant birds in the collections of the Ditsong National Museum of Natural History, Pretoria, South Africa (TM); Iziko South African Museum Natural History, Cape Town, South Africa (SAM-ZO); Marco Pavia Ornithological Collection, University of Torino, Italy (MGPT-MPOC). Comparisons were also made with fossil material from the Pliocene of Langebaanweg, South Africa, preserved at the Iziko South African Museum Natural History, Cape Town, South Africa (SAM-PQ-L).

The anatomical nomenclature follows Baumel and Witmer (1993) unless stated otherwise. The species taxonomy follows del Hoyo et al. (1997) and Joseph et al. (2012) for suprageneric nomenclature. Measurements follow the guidelines of von den Driesch (1976) and were taken with a vernier caliper accurate to 0.1 mm.

List of specimens studied for comparative analysis:

- **Psittacidae.** *Psittacus erithacus*: MGPT-MPOC 873, MGPT-MPOC 1084; *Poicephalus robustus*: MGPT-MPOC 1071, SAM-ZO 56336, SAM-ZO 56402; *Poicephalus meyeri*: MGPT-MPOC 411, SAM-ZO 57640; *Poicephalus senegalus*: MGPT-MPOC 1880, MGPT-MPOC 1940, MGPT-MPOC 1960;
- **Psittaculidae.** *Agapornis canus*: MGPT-MPOC 412; *Agapornis pullarius*: TM 45247, SAM-ZO 56881; *Agapornis taranta*: MGPT-MPOC 2715; *Agapornis roseicollis*: MGPT-MPOC 1395, MGPT-MPOC 1860, MGPT-MPOC 1918, MGPT-MPOC 2091; *Agapornis fischeri*: MGPT-MPOC 2263; *Agapornis personatus*: MGPT-MPOC 2293, MGPT-MPOC 2712, MGPT-MPOC 2713, MGPT-MPOC 2714; *Agapornis nigrigenis*: SAM-ZO 58892.

4. Systematic paleontology

Aves Linnaeus, 1758
 Psittaciformes Wagler, 1830
 Psittaculidae Vigors, 1825
 Agapornithinae Salvin, 1882
 Genus *Agapornis* Selby, 1836

Remarks: The specimens examined here belong to a small species of parrot, which shows the following apomorphies of Agapornithinae: humerus with tuberculum craniodistalis (Manegold, 2013) well separated from the dorsal margin of the shaft and located ventrally to the condylus dorsalis (Fig. 2(F)); carpometacarpus with a ridge-shaped craniocaudally elongated processus pisi-formis, which is apomorphic for *Agapornis* (Manegold, 2013); tibiotarsus with a complete pons supratendineus, which is characteristic of *Agapornis* among the African parrots (Manegold, 2013). Together with the presence of the medial foramen vasculare prox-

imale (Mayr and Göhlich, 2004) on the proximal tarsometatarsus, the single canal for the musculus flexor hallucis longus and musculus flexor digitorum longus well separated from the large bony canal for the superficial flexor tendons (Mayr, 2008) is exclusive of *Agapornis* and *Loriculus*, the latter being only distributed in Asia. These characteristics allow us to refer the fossil to *Agapornis* and not to other Agapornithinae and other African parrots, also according to Manegold (2013).

Agapornis longipes nov. sp.

Fig. 2

1969. *Agapornis* (Smaller species) - Pocock, p. 3.

1969. *Agapornis* (Larger species) - Pocock, p. 3.

2009. *Agapornis* sp. - Stidham, fig. 1A-B.

2020. *Agapornis* sp. - Pavia, fig. 4C.

2022. *Agapornis* sp. - Pavia et al., fig. 4G.

Derivation of the name: The new species shows the longest tarsometatarsus of all extant and extinct species of *Agapornis* in proportion to the humerus, as shown by the ratio of humerus to tarsometatarsus lengths.

Holotype: KWPOC 70e, complete right tarsometatarsus (Fig. 2 (A–C)).

Paratypes: From Kromdraai: KW 7951, complete left humerus (Fig. 2(J)); KWPOC 244d, complete left ulna (Fig. 2(G)); KWPOC 167c, complete left carpometacarpus (Fig. 2(H)). From Cooper's Cave: CD 16332, incomplete left coracoid (Fig. 2(I)); CD 16165b, complete right humerus (Fig. 2(E, F)); CD 16312c, complete left ulna. From Swartkrans: SKX 18159, complete left humerus; SKX 18593b, distal left tibiotarsus; SKX 18624, damaged complete tarsometatarsus (Fig. 2(D));

Referred material: From Kromdraai: KWPOC 70 g, complete left humerus; KWPOC 70 h, complete right humerus; KWPOC 70i, complete left humerus; KWPOC 70j, complete right humerus; KWPOC 70 k, complete right humerus; KWPOC 70 l, complete right humerus; KWPOC 167a, complete right humerus; KWPOC 244a, proximal left humerus; KWPOC 244b, complete right humerus; KWPOC 245, proximal right humerus; KWPOC 70a, complete left ulna; KWPOC 70b, complete left ulna; KWPOC 70c, complete left ulna; KWPOC 167b, complete left ulna; KWPOC 244e, complete right ulna; KWPOC 244f, complete left ulna; KWPOC 244c, complete left carpometacarpus; KWPOC 70f, complete right tarsometatarsus; KWPOC 167d, complete left tarsometatarsus.

From Cooper's Cave: CD 16381e, partial mandible (Fig. 2(J)); CD 16308, proximal right coracoid; CD 01692, complete left humerus; CD 15497, complete left humerus; CD 16324c, complete left humerus; CD 18435b, complete left humerus; CD 05539b, complete right humerus; CD 06658, complete right humerus; CD 18929c, complete right humerus; CD 21641a, complete right humerus; CD 16190c, proximal left humerus; CD 16316b, proximal left humerus; CD 15501, proximal right humerus; CD 16280b, proximal right humerus; CD 16389c, complete left ulna; CD 16297b, complete right ulna; CD 16386d, complete right ulna; CD 16381c, proximal left carpometacarpus; CD 16381, complete right tarsometatarsus; CD 16376c, distal left tarsometatarsus; CD 16386b, distal left tarsometatarsus.

From Swartkrans: SKX 6558, damaged complete left humerus; SKX 13502, complete left humerus; SKX 18328, complete left humerus; SKX 18479, complete left humerus; SKX 18514, complete left humerus; SKX 18527, complete left humerus; SKX 6559, complete right humerus; SKX 13083, complete right humerus; SKX 15323, complete right humerus; SKX 18482, complete right humerus; SKX 18502, complete right humerus; SKX 18663, damaged complete right humerus; SKX 18926, complete right humerus; SKX 18951, complete right humerus; SKX 18969,



Fig. 2. *Agapornis longipes* nov. sp. from the Plio-Pleistocene of the Cradle of Humankind. **A–C.** Holotype, right tarsometatarsus KWPOc 70e from Kromdraai in dorsal (A), plantar (B), and proximal (C) views. **D.** Paratype, left tarsometatarsus SKX 18624 from Swartkrans in proximal view. **E, F.** Paratype, right humerus CD 16165b from Cooper's Cave in caudal (E) and cranial (F) views. **G.** Paratype, left ulna KWPOc 244d from Kromdraai in ventral view. **H.** Paratype, left carpometacarpus KWPOc 167c from Kromdraai in ventral view. **I.** Paratype, left coracoid CD 16332 from Cooper's Cave in dorsal view. **J.** Paratype, left humerus KW 7951 from Kromdraai in caudal view. **K.** Rostrum mandibulae CD 16381e from Cooper's Cave in dorsal view. Abbreviation: tcd, tuberculum craniodistalis. Scale bar: 10 mm.

complete right humerus; SKX 14484, proximal left humerus; SKX 15856, damaged proximal left humerus; SKX 18520, proximal left humerus; SKX 18856, proximal left humerus; SKX 18329, proximal right humerus; SKX 18373, proximal right humerus; SKX 18453, proximal right humerus; SKX 18508, proximal right humerus; SKX 18799, damaged proximal right humerus; SKX 18862, proximal right humerus; SKX 18545, distal left humerus; SKX 18593a, distal left humerus; SKX 18753, distal left humerus; SKX 18958, distal left humerus; SKX 18973, distal left humerus; SKX 17873, distal right humerus; SKX 18512, distal right humerus; SKX 18588, distal right humerus; SKX 18641a, distal right humerus; SKX 18652a, distal right humerus; SKX 18652b, distal right humerus; SKX 18686, distal right humerus; SKX 18759, distal right humerus; SKX 18762, distal right humerus; SKX 18927, distal right humerus; SKX 18954, distal right humerus; SKX 17959a, complete

right carpometacarpus; SKX 17959b, complete right carpometacarpus; SKX 18372, complete right carpometacarpus; SKX 18584, distal left carpometacarpus; SKX 18543, distal right carpometacarpus; SKX 18527b, distal right carpometacarpus; SKX 18593b, distal left tibiotarsus; SKX 18641b, complete right tarsometatarsus.

Type locality and horizon: Kromdraai site (26°00'41"S, 27°44'60"E) in the Cradle of Humankind, Gauteng, South Africa (Fig. 1); Plio-Pleistocene transition.

Other localities: Cooper's Cave (26°00'47"S, 27°44'44"E); Swartkrans (26°55'45"S, 27°47'20"E), in the Cradle of Humankind, Gauteng, South Africa (Fig. 1); Early Pleistocene.

Measurements: See Tables 1 and 2.

Diagnosis: Small-sized species of *Agapornis* with the size of the known wing bones (humerus, ulna, and carpometacarpus) comparable to those of *A. fischeri*, *A. lilianae*, *A. nigrigenis*, and the extinct

Table 1

Measurements (in mm) of the complete humeri of *Agapornis longipes* nov. sp. from Cooper's Cave, Kromdraai, and Swartkrans. Abbreviations: GL, greatest length; Wd, distal width; Wp, proximal width; Ws, smallest width of shaft.

Humerus	GL	Wp	Wd	Ws
<i>Agapornis longipes</i> nov. sp. CD 16165b PARATYPE	18.8	5.8	3.8	2.2
<i>Agapornis longipes</i> nov. sp. KW 7951 PARATYPE	20.0	6.7	4.3	2.2
<i>Agapornis longipes</i> nov. sp. SKX 18159 PARATYPE	19.1	5.9	3.8	2.2
<i>Agapornis longipes</i> nov. sp. CD 01692	19.4	6.2	3.9	2.1
<i>Agapornis longipes</i> nov. sp. CD 05539b	18.7	5.8	3.9	2.1
<i>Agapornis longipes</i> nov. sp. CD 06658	18.9	5.7	3.9	2.1
<i>Agapornis longipes</i> nov. sp. CD 15497	19.4	6.2	3.9	2.2
<i>Agapornis longipes</i> nov. sp. CD 16324c	19.4	6.2	3.9	2.3
<i>Agapornis longipes</i> nov. sp. CD 18435b	18.9	5.5	4.0	2.1
<i>Agapornis longipes</i> nov. sp. CD 18929c	19.3	—	4.1	2.1
<i>Agapornis longipes</i> nov. sp. CD 21641a	18.2	5.4	—	2.0
<i>Agapornis longipes</i> nov. sp. KWPoc 70 g	19.2	6.0	4.3	2.2
<i>Agapornis longipes</i> nov. sp. KWPoc 70 h	18.3	6.4	3.8	2.2
<i>Agapornis longipes</i> nov. sp. KWPoc 70i	18.3	6.4	4.0	2.2
<i>Agapornis longipes</i> nov. sp. KWPoc 70j	19.2	6.2	4.1	2.3
<i>Agapornis longipes</i> nov. sp. KWPoc 70 k	19.2	—	4.1	2.3
<i>Agapornis longipes</i> nov. sp. KWPoc 70 l	18.8	6.0	4.0	2.2
<i>Agapornis longipes</i> nov. sp. KWPoc 167a	19.5	5.8	—	2.3
<i>Agapornis longipes</i> nov. sp. KWPoc 244b	18.7	5.8	4.2	2.3
<i>Agapornis longipes</i> nov. sp. SKX 6558	19.3	—	4.0	2.2
<i>Agapornis longipes</i> nov. sp. SKX 6559	19.4	6.3	4.1	2.3
<i>Agapornis longipes</i> nov. sp. SKX 13083	18.1	6.1	3.7	2.1
<i>Agapornis longipes</i> nov. sp. SKX 13502	18.9	6.2	3.9	2.1
<i>Agapornis longipes</i> nov. sp. SKX 15323	19.6	6.3	—	2.2
<i>Agapornis longipes</i> nov. sp. SKX 18328	19.5	6.2	4.2	1.9
<i>Agapornis longipes</i> nov. sp. SKX 18479	18.7	—	4.0	2.1
<i>Agapornis longipes</i> nov. sp. SKX 18482	18.5	6.1	4.1	2.2
<i>Agapornis longipes</i> nov. sp. SKX 18502	18.0	6.1	3.8	2.1
<i>Agapornis longipes</i> nov. sp. SKX 18514	17.7	5.9	3.7	2.1
<i>Agapornis longipes</i> nov. sp. SKX 18527	19.4	6.2	4.1	2.2
<i>Agapornis longipes</i> nov. sp. SKX 18926	18.7	6.0	3.7	2.0
<i>Agapornis longipes</i> nov. sp. SKX 18951	18.0	5.7	3.9	2.0
<i>Agapornis longipes</i> nov. sp. SKX 18969	19.1	6.2	3.9	2.1

Table 2

Measurements (in mm) of various bones of *Agapornis longipes* nov. sp. from Cooper's Cave and Kromdraai. Abbreviations: see [Table 1](#).

Ulna	GL	Wp	Wd	Ws
<i>Agapornis longipes</i> nov. sp. KWPoc 244d PARATYPE	22.5	3.4	2.7	1.7
<i>Agapornis longipes</i> nov. sp. CD 16312c PARATYPE	22.0	3.2	2.1	1.5
<i>Agapornis longipes</i> nov. sp. CD 16297b	—	3.2	2.3	1.6
<i>Agapornis longipes</i> nov. sp. CD 16386d	—	3.5	2.6	1.7
<i>Agapornis longipes</i> nov. sp. CD 16389c	—	3.4	2.4	1.7
<i>Agapornis longipes</i> nov. sp. KWPoc 70a	22.0	3.5	2.5	1.6
<i>Agapornis longipes</i> nov. sp. KWPoc 70b	23.7	3.6	2.6	1.7
<i>Agapornis longipes</i> nov. sp. KWPoc 70c	21.4	3.3	2.4	1.6
<i>Agapornis longipes</i> nov. sp. KWPoc 167b	22.5	3.5	2.7	1.6
<i>Agapornis longipes</i> nov. sp. KWPoc 244e	22.2	3.5	2.4	1.7
<i>Agapornis longipes</i> nov. sp. KWPoc 244f	21.5	3.2	2.5	1.7
Carpometacarpus	GL	Dp	Wd	Ws
<i>Agapornis longipes</i> nov. sp. KWPoc 167c PARATYPE	15.1	4.4	2.7	1.3
<i>Agapornis longipes</i> nov. sp. CD 16381c	—	4.3	—	1.4
<i>Agapornis longipes</i> nov. sp. KWPoc 244c	15.7	4.3	2.5	1.3
<i>Agapornis longipes</i> nov. sp. SKX 17959a	15.0	4.4	2.4	1.3
<i>Agapornis longipes</i> nov. sp. SKX 17959b	15.0	4.1	2.4	1.3
<i>Agapornis longipes</i> nov. sp. SKX 18372	15.5	4.2	2.7	1.4
Tibiotarsus	GL	Dp	Wd	Ws
<i>Agapornis longipes</i> nov. sp. SKX 18372 PARATYPE	—	—	2.9	1.3
Tarsometatarsus	GL	Dp	Wd	Ws
<i>Agapornis longipes</i> nov. sp. KWPoc 70e HOLOTYPE	13.2	2.9	3.8	1.5
<i>Agapornis longipes</i> nov. sp. SKX 18624 PARATYPE	—	2.8	—	1.5
<i>Agapornis longipes</i> nov. sp. CD 16376c	—	—	3.8	1.4
<i>Agapornis longipes</i> nov. sp. CD 16381 g	13.0	—	—	1.5
<i>Agapornis longipes</i> nov. sp. KWPoc 70f	13.5	3.1	3.6	1.6
<i>Agapornis longipes</i> nov. sp. KWPoc 167d	13.3	3.0	4.0	1.5
<i>Agapornis longipes</i> nov. sp. SKX 18641b	13.1	—	3.6	1.5

A. attenboroughi. Tarsometatarsus similar to those of the largest species in the genus: *A. fischeri*, *A. personatus*, *A. roseicollis*, and *A. taranta*. The humerus shows a distinct fossa pneumaticipitalis dorsalis, shallower than in *A. attenboroughi*, but larger than in *A. roseicollis* and the other extant species; it lacks the distal extension on the caudal surface of the caput humeri as in *A. atlanticus*. The

tarsometatarsus shows a more distally protruding trochlea metatarsi III, which is also wider than in other species.

Description: *Agapornis longipes* nov. sp. is described on the basis of 96 complete and sub-complete bones from Kromdraai, Cooper's Cave and Swartkrans. The ratio of humerus to tarsometatarsus length (h/t; Manegold, 2013) in *Agapornis longipes* nov. sp. is the smallest of all *Agapornis* taxa known (Table 3).

Table 3

Measurements (in mm) and the humerus/tarsometatarsus ratio of *Agapornis longipes* nov. sp. compared with fossil and recent *Agapornis* species. The measurements of the living and fossil specimens for comparison are from Manegold (2013) and Mourer-Chauviré and Geraads (2010). The h/t is the ration between the mean values of the humerus lengths and the tarsometatarsus lengths, following Manegold (2013).

Humerus	GL	Wp	Wd	Ws	h/t ratio
<i>Agapornis longipes</i> nov. sp.	18.9 (17.7–20.0) N = 33	6.0 (5.4–6.7) N = 29	4.0 (3.7–4.3) N = 30	2.15 (1.9–2.3) N = 33	1.43
<i>Agapornis atlanticus</i>	22.5 (22.0–23.4) N = 8	7.4 (7.1–7.6) N = 7	4.8 (4.7–5.0) N = 11	2.7 (2.4–2.9) N = 13	–
<i>Agapornis attenboroughi</i>	19.3 (19.1–19.5) N = 3	6.9 (6.8–7.1) N = 6	4.1 (3.9–4.2) N = 10	2.1 (2.1–2.2) N = 7	1.74
<i>Agapornis taranta</i> (N = 1)	22.6	7.0	4.7	2.2	1.73
<i>Agapornis roseicollis</i> (N = 7)	21.8 (20.4–22.8)	7.5 (7.3–8.0)	4.6 (4.4–4.7)	2.2 (2.1–2.2)	1.64
<i>Agapornis fischeri</i> (N = 6)	19.9 (19.1–20.6)	6.9 (6.6–7.1)	4.2 (4.1–4.3)	2.0 (1.9–2.1)	1.53
<i>Agapornis personatus</i> (N = 3)	20.5 (20.0–20.9)	7.1 (6.8–7.5)	4.4 (4.4–4.6)	2.1 (2.1)	1.55
<i>Agapornis pullarius</i> (N = 2)	20.3 (19.7–20.8)	7.1 (7.0–7.1)	4.3 (4.3)	2.1 (2.1)	1.80
<i>Agapornis nigrigenis</i> (N = 5)	19.7 (19.5–20.1)	6.6 (6.2–7.0)	4.0 (3.8–4.2)	1.9 (1.7–2.1)	1.58
<i>Agapornis lilianae</i> (N = 1)	18.9	7.0	4.0	2.0	1.56
<i>Agapornis swinderianus</i> (N = 1)	20.3	6.9	4.4	2.1	1.93
<i>Agapornis canus</i> (N = 2)	17.7 (17.4–18.0)	6.1 (6.1)	3.9 (3.8–3.9)	1.9 (1.8–1.9)	1.53
Ulna	GL	Wp	Wd	Ws	
<i>Agapornis longipes</i> nov. sp.	22.3 (21.4–23.7) N = 7	3.4 (3.2–3.6) N = 11	2.5 (2.1–2.7) N = 11	1.6 (1.5–1.7) N = 11	
<i>Agapornis atlanticus</i>	27.0	4.0 (3.9–4.1) N = 4	–	2.0 (1.9–2.1) N = 4	
<i>Agapornis attenboroughi</i>	22.8	–	–	1.3	
<i>Agapornis taranta</i> (N = 1)	27.4	3.8	3.1	1.7	
<i>Agapornis roseicollis</i> (N = 7)	25.3 (23.7–26.1)	3.9 (3.6–4.2)	3.0 (2.9–3.2)	1.6 (1.6–1.7)	
<i>Agapornis fischeri</i> (N = 6)	24.2 (23.4–25.0)	3.5 (3.4–3.7)	2.7 (2.6–2.9)	1.4 (1.3–1.5)	
<i>Agapornis personatus</i> (N = 3)	25.2 (24.8–25.7)	3.7 (3.6–3.8)	2.8 (2.6–3.0)	1.4 (1.4–1.5)	
<i>Agapornis pullarius</i> (N = 2)	24.3 (24.1–24.4)	3.55 (3.5–3.6)	2.75 (2.7–2.8)	1.5 (1.5)	
<i>Agapornis nigrigenis</i> (N = 5)	23.6 (23.0–24.8)	3.5 (3.4–3.7)	2.6 (2.4–2.8)	1.4 (1.2–1.5)	
<i>Agapornis lilianae</i> (N = 1)	22.3	3.3	2.8	1.3	
<i>Agapornis swinderianus</i> (N = 1)	24.7	–	–	1.6	
<i>Agapornis canus</i> (N = 2)	21.2 (20.7–21.6)	3.1 (2.9–3.3)	2.45 (2.4–2.5)	1.3 (1.2–1.3)	
Carpometacarpus	GL	Dp	Wd	Ws	
<i>Agapornis longipes</i> nov. sp.	15.3 (15.0–15.7) N = 5	4.3 (4.1–4.4) N = 6	2.5 (2.4–2.7) N = 5	1.3 (1.3–1.4) N = 6	
<i>Agapornis atlanticus</i>	21.2 (21.0–21.4) N = 2	5.6 (5.5–5.7) N = 4	–	–	
<i>Agapornis attenboroughi</i>	15.5 (15.1–15.8) N = 2	4.1 (4.0–4.2) N = 3	2.3 (2.3–2.4) N = 4	–	
<i>Agapornis taranta</i> (N = 1)	17.5	4.9	2.8	1.6	
<i>Agapornis roseicollis</i> (N = 7)	17.2 (16.4–17.8)	4.4 (4.2–4.6)	2.6 (2.4–3.0)	1.5 (1.4–1.6)	
<i>Agapornis fischeri</i> (N = 6)	16.2 (15.5–17.0)	4.1 (4.0–4.3)	2.3 (2.1–2.5)	1.4 (1.3–1.5)	
<i>Agapornis personatus</i> (N = 3)	16.9 (16.7–16.9)	4.4 (4.3–4.6)	2.4 (2.3–2.5)	1.5 (1.4–1.6)	
<i>Agapornis pullarius</i> (N = 2)	15.9 (15.5–15.8)	4.4 (4.3–4.4)	2.4 (2.3–2.5)	1.35 (1.3–1.4)	
<i>Agapornis nigrigenis</i> (N = 5)	16.2 (16.0–16.7)	4.1 (4.0–4.3)	2.4 (2.3–2.5)	1.4 (1.3–1.5)	
<i>Agapornis lilianae</i> (N = 1)	15.2	4.0	2.5	1.4	
<i>Agapornis swinderianus</i> (N = 1)	16.0	4.3	2.4	–	
<i>Agapornis canus</i> (N = 2)	14.6 (14.3–14.9)	3.8 (3.8)	2.3 (2.2–2.3)	1.35 (1.3–1.4)	
Tarsometatarsus	GL	Dp	Wd	Ws	
<i>Agapornis longipes</i> nov. sp.	13.2 (13.0–13.5) N = 5	2.95 (2.8–3.1) N = 4	3.8 (3.6–4.0) N = 5	1.5 (1.4–1.6) N = 6	
<i>Agapornis attenboroughi</i>	11.1	3.0	4.0 (3.9–4.2) N = 6	1.4 (1.4) N = 2	
<i>Agapornis taranta</i> (N = 1)	13.1	3.4	4.6	1.6	
<i>Agapornis roseicollis</i> (N = 7)	13.3 (12.5–14.0)	3.4 (3.3–3.6)	4.6 (4.4–4.8)	1.6 (1.5–1.7)	
<i>Agapornis fischeri</i> (N = 6)	13.0 (12.2–14.0)	3.2 (3.0–3.3)	4.1 (3.9–4.2)	1.4 (1.4–1.5)	
<i>Agapornis personatus</i> (N = 3)	13.2 (12.7–13.6)	3.3 (3.3–3.4)	4.3 (4.3–4.4)	1.6 (1.5–1.6)	
<i>Agapornis pullarius</i> (N = 2)	11.3 (11.1–11.4)	3.3 (3.3)	4.6 (4.5–4.6)	1.5 (1.5)	
<i>Agapornis nigrigenis</i> (N = 5)	12.5 (12.3–12.9)	3.1 (2.9–3.1)	3.9 (3.5–4.3)	1.3 (1.2–1.4)	
<i>Agapornis lilianae</i> (N = 1)	12.1	3.1	4.2	1.6	
<i>Agapornis swinderianus</i> (N = 1)	10.5	3.1	4.4	1.6	
<i>Agapornis canus</i> (N = 2)	11.6 (11.1–12.0)	2.7 (2.6–2.7)	3.3 (3.1–3.5)	1.1 (1.0–1.2)	

Abbreviations: GL, greatest length; Lm, medial length; Wd, distal width; Wp, proximal width; Ws, smallest width of shaft.

Although this cannot be confirmed by the tibiotarsus, this ratio reflects the lengthening of the distal part of the hindlimb.

Coracoid. The single coracoid lacks the sternal part and shows a large facies articularis clavicularis with a ventrally located projection, a deep pneumatic fossa underneath the overhanging facies articularis clavicularis, and a rounded tuberculum on the dorsal side of the sulcus musculi supracoracoidei between the sulcus and the proximal end of the facies articularis humeralis. All the observed characters are typical of parrots in general, and *Agapornis* in particular (Manegold, 2013), and support the attribution of the coracoid to the new species.

Humerus. The caput humeri of the fossil species is offset ventrally from crista deltopectoralis as in other *Agapornis* species and the tuberculum craniodistalis (Manegold, 2013) is located proximoventrally in respect to the condylus dorsalis (Fig. 2(E)). The tuberculum dorsale is less prominent than in *A. fischeri* and *A. nigrigenis* but is similar to that in the extinct *A. attenboroughi*. The longitudinal fossa pneumotricipitalis dorsalis is well defined and dorsally limited by a ridge. This fossa is absent or faintly evident in the extant *Agapornis* species, but deeper and more defined in the fossil *A. attenboroughi*, while in *A. atlanticus* the ridge dorsally to the fossa pneumotricipitalis dorsalis is more defined and sharper. The proximal part of the margo caudalis in *A. longipes* nov. sp. is flat and not as sharp as in *A. attenboroughi*, and the fossa musculi brachialis is deeper and more defined in the new species

than in the extant ones. The presence of the fossa pneumotricipitalis dorsalis was not recognized by Manegold (2013: 132) as he examined the picture of Stidham (2009: fig. 1) where the bone was still covered by sediment that hid its detailed morphology, especially along the shaft, as already supposed by the author himself (Manegold, 2013: 132).

Ulna. The shaft of *Agapornis longipes* nov. sp. is curved as in other *Agapornis* species but differs from the extant species by its stouter and less protruding olecranon and by the tuberculum carpal protruding ventrally and not distally. The only known ulna of *A. attenboroughi* shows a wider olecranon and a smaller tuberculum ligament collateralis ventralis.

Carpometacarpus. *Agapornis longipes* nov. sp. shows a processus pisiformis ridge-like, which is apomorphic for *Agapornis* (Manegold, 2013). This process is also connected to processus alularis in *A. longipes* nov. sp. by a continuous ridge, not present in any other species. The fossa supratrochlearis is shallower in the new species and the processus extensorius is more pointed and protruding medially.

Tibiotarsus. The only known tibiotarsus of *Agapornis longipes* nov. sp. shows the typical features of Psittaciformes and a complete pons supratendineus, which is incomplete or strongly reduced in the other African parrots, and it is in accordance with the general morphology of *Agapornis* (Manegold, 2013). The size

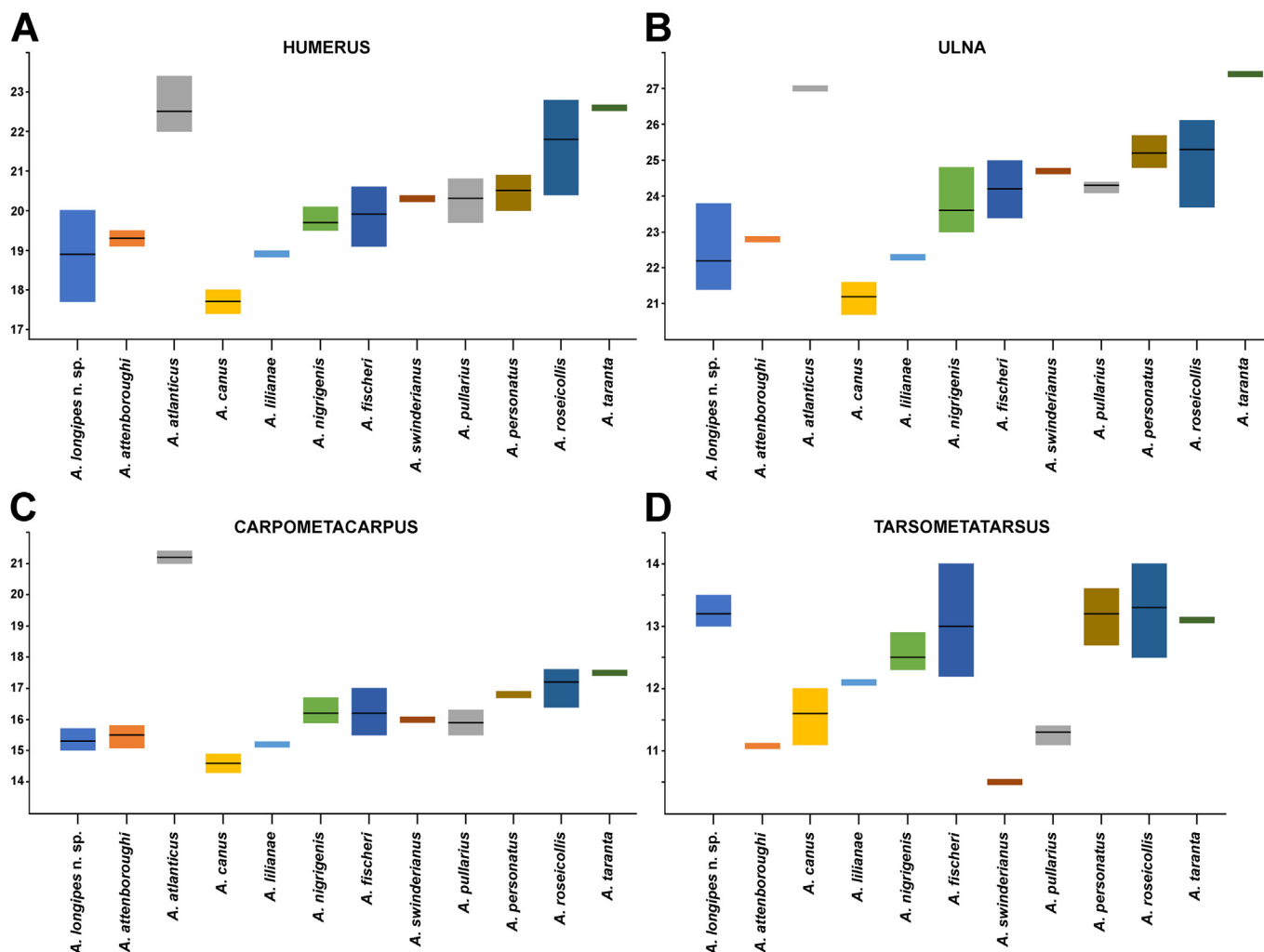


Fig. 3. Comparison of the total lengths (in mm) of the humerus (A), ulna (B), carpometacarpus (C), and tarsometatarsus (D) of *Agapornis longipes* nov. sp. with those for the fossil species *A. attenboroughi* and *A. atlanticus*, and all nine extant *Agapornis* species. The black lines represent the mean values.

of the tibiotarsus from Swartkrans (Table 2) agrees with the general small size of *Agapornis longipes* nov. sp. compared with the other lovebirds.

Tarsometatarsus. The proximal part of the tarsometatarsus of *Agapornis longipes* nov. sp. is only partially preserved in the holotype, but in the paratype SKX 8624 the common canal for the musculus flexor hallucis longus and musculus flexor digitorum longus, apomorphic for Agapornithinae, is well separated from the large bony canal that encompasses most of the superficial flexor tendons (Fig. 2(D)). This morphology is only present in *Agapornis* and *Loriculus*, the latter endemic of southern Asia (Mayr, 2008). The bone of the new species shows the shaft with straight medial margin parallel with the lateral margin and not curved and only slightly proximally widening and not as much as in the extant species. *Agapornis longipes* nov. sp. has the trochlea metatarsi III more protruding than in all the compared taxa with a wider proximal part of the trochlea.

Remarks: In his preliminary analysis of the fossil birds from Kromdraai and Sterkfontein, Pocock (1969) reported the presence of two species of *Agapornis* on the basis of a single proximal humerus larger than all the others (KWPoc 245). The size of this bone fits perfectly with the paratype KW 7951. The presence of these two humeri and the ulna KWPoc 70b in the Kromdraai assemblage collected from different stratigraphic units testify to the variability of *Agapornis longipes* nov. sp., represented at least by a few individuals slightly larger than others, even if this variability seems to have no impact to the forelimb/hindlimb ratio. In addition, the variability shown by *Agapornis longipes* nov. sp. is comparable with other *Agapornis* species (Fig. 3; Table 3). It is worth noting that the presence of sympatric species of *Agapornis* is not documented in the distribution range of the modern species (del Hoyo and Collar, 2014). We argue that sympatry of two or more species of *Agapornis* is not supported by the fossil evidence

from the Cradle of Humankind analyzed here, and we therefore exclude this possibility.

5. Discussion

The fossil remains studied here clearly belong to an extinct species of *Agapornis* distinguished from the extant nine species of the genus and from the extinct *A. atlanticus* and *A. attenboroughi* by several morphological characters and by the smallest humerus/tarsometatarsus ratio of all *Agapornis* species (Table 3). This indicates the lengthening of the leg bones of *Agapornis longipes* nov. sp. This new species shows the straight medial margin of the shaft of the tarsometatarsus and the fossa pneumaticipitalis dorsalis delimited dorsally by a ridge in the proximal humerus, which are apparently plesiomorphic characters shared with the extinct *A. attenboroughi*. However, the different relationship between wings and legs in respect to any other *Agapornis* species, prevents further phylogenetic hypotheses.

All but one *Agapornis* species are grass seed eaters and secondarily fruit eaters, and are generally related to the presence of grassland, permanent water resources and tall trees that provide either natural cavities or holes excavated by other birds such as woodpeckers or barbets (Fry et al., 1988). The elongated feet of *Agapornis longipes* nov. sp. could relate to the feeding adaptation of this extinct species. In fact, the modern species with the lower humerus/tarsometatarsus ratios (*A. canus*, *A. fischeri*, and *A. personatus*; Table 3) typically collect food on the ground, while the others also collect seeds or fruits from the trees (Fry et al., 1988). We thus hypothesize that *A. longipes* nov. sp. took advantage of its longer legs to feed on grass seeds on the ground in the tall and dense grassland of the paleo-Bloubaank valley (Fig. 4) as suggested by the paleoenvironmental reconstructions (Pavia, 2020; Pavia et al., 2022).



Fig. 4. Life reconstruction of an air of *Agapornis longipes* nov. sp. feeding on the ground in the Early Pleistocene of the Cradle of Humankind (Gauteng, South Africa) during the dry season (Artwork by Martina Cadin).

Paleoenvironmental reconstructions for Kromdraai and Cooper's Cave based on mammals and birds indicate that grassland, combined with patches of woodlands or gallery forests with tall trees along watercourses, were the dominant habitats in this area of the Cradle of Humankind at the Plio-Pleistocene boundary and the Early Pleistocene (de Ruiter et al., 2009; Fourvel et al., 2018; Badenhorst and Steininger, 2019; Cohen et al., 2019; Hanon et al., 2022; Pavia, 2020; Pavia et al., 2022; Linchamps et al., 2023). At Swartkrans, the rich faunal assemblage from Member 1 indicates a similar mosaic of habitats dominated by highveld grassland associated with riverine woodland adjacent to the Bloubaai River, while several species are typical of the rocky hillsides above the cave system (Avery, 1991; Watson, 1993; de Ruiter, 2003). These habitats provide adequate conditions for all modern species of Lovebirds and would have been perfectly suitable for *Agapornis longipes* nov. sp. This is also supported by the relative abundance of this taxon in the bird assemblages of Kromdraai and Cooper's Cave. In fact, the new species is described on the basis of 23 remains from Kromdraai and 24 remains from Cooper's Cave. At Cooper's, *Agapornis longipes* nov. sp. represents the fifth most abundant avian taxon in terms of percentage of identified specimens and the third in terms of number of individuals (Pavia et al., 2022). At Kromdraai, the species is also relatively common but, as stated above, the remains were found in different stratigraphic contexts, so it is difficult to understand their real abundance.

The present-day environment of the Cradle of Humankind and of this part of South Africa is not markedly different from that of the Early Pleistocene, and the extinction of the Lovebirds from this region during the Pleistocene was most probably related to a change in microclimatic conditions or to the extinction of specific food resources rather than to the change of general environmental conditions.

CRediT authorship contribution statement

Marco Pavia: Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **José Braga:** Writing – review & editing, Investigation, Funding acquisition. **Massimo Delfino:** Writing – review & editing, Funding acquisition. **Lazarus Kgasi:** Writing – review & editing, Investigation. **Albrecht Manegold:** Investigation, Writing – review & editing. **Christine Steininger:** Writing – review & editing, Investigation, Funding acquisition. **Bernhard Zipfel:** Writing – review & editing, Investigation, Funding acquisition. **Aurore Val:** Writing – review & editing, Investigation, Conceptualization.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank the Cradle of Humankind Management Authority and the South African Heritage Resources Agency for their continuous support and the excavation permits to JB and BZ (ID 3035, 3176, and 3888). We also thank M. Malematja (Ditsong National Museum of Natural History, Pretoria), R. Govender and J. Opperman (Iziko South African Museum, Cape Town), and S. Jirah and

Fossil Access Advisory Panel of the Evolutionary Studies Institute, University of the Witwatersrand who provided access to the modern and fossil specimens under their care. We are deeply grateful to Adriaan Kruger Lotz, trustee of the Lotz Family Trust, and his family for granting permission to conduct fieldwork at Kromdraai. We thank D. Gommerly (CNRS-MNHN-SU, Sorbonne University) for the access to the fossils from Bolt's Farm, excavation of which was funded by the IRL Homen CNRS-NRF, the MPFSA (Mission Paléoanthropologique Franco-Sud-Africaine) of Pôle Sciences humaines et sociales, Archéologie et Patrimoine (sub-directorate for Higher Education and Research) of the French Ministry of Europe and Foreign Affairs. We thank T. Molefyane for his help in pulling out the bird remains from the Cooper's D faunal sample. The excavations at Cooper's D were financially supported by the Paleoanthropological Scientific Trust (PAST), the National Research Foundation, Genus: DST-NRF Centre of Excellence in Paleosciences. 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. We also warmly thank the Editor-in-Chief G. Escarguel, the Associate Editor F.J. Serrano, T. Worthy and one anonymous reviewer for their comments and suggestions that greatly improved the manuscript. This is the publication number 373 of the Museo di Geologia e Paleontologia collections at the Università degli Studi di Torino.

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