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THE EARLIEST RECORD FOR HONEYGUIDES (AVES: INDICATORIDAE), FROM THE EARLY PLIOCENE OF SOUTH AFRICA

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Abstract. Two new species of honeyguides (Indicatoridae) are described from the Lower Pliocene Upper Varswater Formation at Langebaanweg, South Africa. One of these species is referred to the genus *Indicator*, as *Indicator* sp. (taxon A), and comparable in size to the Lesser Honeyguide (*I. minor*). It is represented by a partial coracoid as well as 12 humeri, eight carpometacarpi, and two tarsometatarsi. The second species is slightly smaller than the Least Honeyguide (*I. exilis)*. It is known from a fragmentary proximal humerus, a carpometacarpus and two tarsometatarsi, and cannot be referred to a particular genus of modern Indicatoridae, hence it is referred to Indicatoridae indet. (taxon B). Both species form the as yet earliest record of honeyguides in Africa and the world, and confirm the presence of woodland with mature trees suitable for cavity-nesting species at Langebaanweg during the Early Pliocene.

Introduction

The honeyguides (Indicatoridae) are a small group of piciform birds that probably originated in sub-Saharan Africa, where most of the extant 17 species occur. Only two species are distributed along the southern slopes of the Himalaya and in SE Asia, respectively, but are generally supposed to be of African origin (Fry et al. 1988; Short & Horne 2002). Brood parasitism as well as the capability to digest waxy secretions of insects, such as the coating of scale insects (Coccoidea) or beeswax, are supposed to be part of the stem species pattern of Indicatoridae, although both properties are known

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for few especially well-studied species only (Short and Horne 2002; Spottsiwoode & Koorevaar 2012). Morphology as well as DNA-sequence data indicate that honeyguides form the sister group of woodpeckers (Simpson and Cracraft 1981; Johansson & Ericson 2003), and because the earliest evidence for crown-group Picidae stems from the Early Miocene or probably late Oligocene (De Pietri et al. 2011), the split of both lineages presumably occurred towards the end of the Palaeogene. In fact, Friedmann (1955) had supposed that the taxon Indicatoridae is at least of Miocene age, and that its present distribution is the result of its diversification and spread during the Pliocene.

The splitting between the Indicatoridae and Picidae lineages now appears, from genomic data, to have occurred near 30 Ma, with the beginning of diversification of crown Indicatoridae around 26 Ma (both dates Oligocene; see One-Zoom Tree of Life Explorer; Jetz et al. 2012; Rosindell & Harmon 2012). The fossil record for honeyguides, however, only dates back to the Lower Pliocene Upper Varswater Formation at Langebaanweg, South Africa (Olson 1985: 138), which is well known for its highly diverse and well-preserved fossil avifauna (Rich 1980; Hendey 1981; Manegold et al. 2013). Furthermore, representatives of Indicatoridae are unknown from any other fossil locality. Olson (1985) and Manegold et al. (2013) first mentioned the presence of Indicatoridae in the Upper Varswater Formation at Langebaanweg, but their fossil remains were never described in detail.

The fossil remains described therein come from the Langeberg Quartz Sand Member (QSM) and Muishond Fontein Pelletal Phosphorite Member (PPM) of the Upper Varswater Formation exposed at Langebaanweg, Western Cape, South Africa (Fig. 1) during the intense mining activities for the phosphate extraction (Hendey, 1981; Roberts et al., 2011). The QSM is 0.5-2 m thick, and it is constituted mainly by quartzose sand with local silty enclosures and reflect fluvio-estuarine environments with local salty marsh and tidal flat deposition recorded by the silty facies. The fossil remains are very abundant and without any depositional structure or main orientation. The overlying PPM is the main phosphatic bearing layer of the succession and it is up to 11 metres in thickness. Its lower part shows a sharp, slightly erosional contact with the QSM and the fossil remains occur mainly as lag deposits within southwesterly orientated linear channels, with some elements possibly reworked from the underlying QSM. From a biochronological point of view, the two fossiliferous members are dated to the Early Pliocene and the age difference between QSM and PPM is minimal, even if the more derived characters of some taxa in PPM suggest a difference in age, still to be investigated (Roberts et al. 2011).

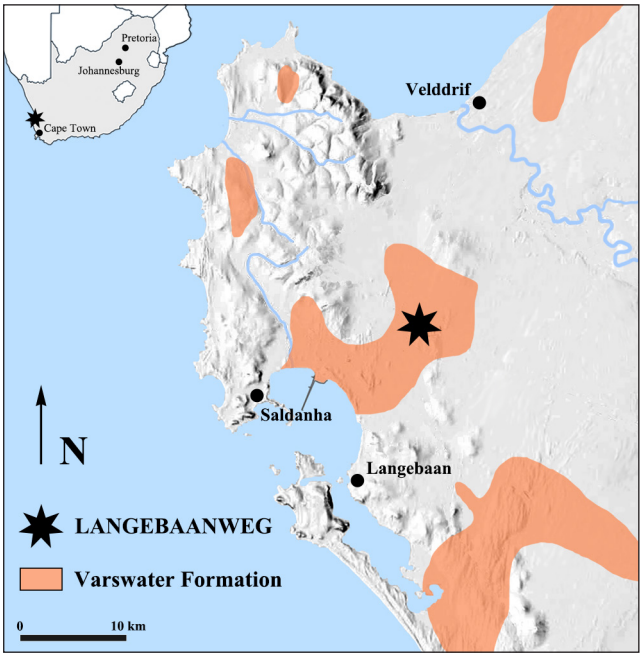

Fig. 1 - Geographical position of Langebaaweg fossil locality (Western Cape, South Africa) with the extension of the Neogene Varswater Formation highlighted in orange.

Searching previously unsorted material produced not only additional remains of honeyguides, but also evidence that not only one, but two species of very small Indicatoridae can be distinguished. They are here assigned to the genus *Indicator* sp. (taxon A), and to Indicatoridae indet. (taxon B), respectively. In this contribution, we provide the first thorough description and illustrations of the fossil sample attributed to the family Indicatoridae found at LBW, comprising the material already mentioned by Olson (1985) and Manegold et al. (2013), but also the material recently discovered.

Material and methods

All fossil specimens are part of the Cenozoic collections of the Iziko South African Museum, Cape Town, South Africa (SAM-PQ-L, Paleontology Quaternary Langebaanweg). Skeletons of Indicatoridae are generally rare in scientific collections.

Nevertheless, comparisons with modern representatives of this taxon were limited to several specimens of five African species of *Indicator*, the Asian *I. archipelagicus* Temminck, 1832, two species of *Prodotiscus*, and partial skeletons of *Melichneutes robustus* (Bates, 1909) and the two species of *Melignomon*. The taxonomy of Indicatoridae follows Winkler et al. (2020).

The anatomical terminology follows Baumel and Witmer (1993), but we prefer the terms 'os metacarpale II' and 'os metacarpale III' over the recommended 'os metacarpale majus' and 'os metacarpale minus', respectively.

Measurements were taken in accordance with the guidelines of von den Driesch (1976) by using vernier callipers accurate to 0.1 mm.

Institutional abbreviations. FMNH, Field Museum of Natural History, Chicago, USA; LACM, Los Angeles County Natural History Museum, Los Angeles, USA; MGPT-MPOC, Marco Pavia Osteological Collection, University of Torino, Torino, Italy; NHMUK, Natural History Museum, Tring, UK; NMB, National Museum Bloemfontein, Bloemfontein, South Africa; SAM, Iziko South African Museum, Cape Town, South Africa; SMF, Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt/Main, Germany; TM, Ditsong National Museum of Natural History, Pretoria, South Africa; UCBL, collections of the Faculté des Sciences de Lyon, Université Claude Bernard Lyon 1, Villeurbanne, France; UMNHK, Kansas University Biodiversity Institute and Natural History Museum, Lawrence, USA; USNM, United States National Museum, Smithsonian Institution, Washington, D.C. USA.

List of recent taxa used for comparison. Indicatoridae: *Indicator archipelagicus* Temminck, 1832 USNM 656336; *Indicator exilis* (Cassin, 1856) FMNH 429727, USNM 322550, USNM 428644; *I. indicator* (Sparrman, 1777) NMB 60-02317, MGPT-MPOC 609, NHMUK S/2005.22.13, SMF 11146, TM 71123, USNM 430329; *I. maculatus* G.R. Gray, 1847 FMNH 429417, USNM 428645, USNM 623002, USNM 630878, USNM 631581; *Indicator minor* Stephens, 1815 NHMUK S/1970.5.7, SAM ZO T36, SAM ZO T87, TM 74224, USNM 428643, USNM 558565, UMNHK 69620; *I. variegatus* Lesson, 1830 SMF 2357, SMF 10150, USNM 428639, USNM 429759; *Melichneutes robustus* (Bates, 1909) USNM 430771; *Melignomon* sp. LACM 89250, LACM 89251, LACM 89252, LACM 89253; *M. zenkeri* Reichenow, 1898 LACM 66898, LACM 84757; *Prodotiscus insignis* (Cassin, 1856) USNM 429686; *P. regulus* Sundevall, 1850 TM 33116, TM 77854, USNM 430466. **Megalaimidae**: *Psilopogon virens* (Boddaert, 1783) UCBL (no number). **Lybiidae**: *Pogoniulus bilineatus* (Sundevall, 1850) SMF 377; *Trachyphonus erythrocephalus* Cabanis, 1878 SMF 6085; *Tricholaema leucomelas* (Boddaert, 1783) SAM-ZO-58392. **Picidae**: Jynginae: *Jynx torquilla* Linnaeus, 1758 SMF 3806. Picumninae: *Picumnus albosquamatus* d'Orbigny, 1840 SMF 9600; Hemicircinae: *Hemicircus concretus* (Temminck, 1821) SMF 5088. Picinae: *Campethera abingoni* (A. Smith, 1836) SMF 473; *Celeus flavescens* (J.F. Gmelin, 1788) SMF 9608; *Dendrocopos major* (Linnaeus, 1758) SMF 5596; *Dryocopus martius* (Linnaeus, 1758) SMF 5726; *Picus viridis* Linnaeus, 1758 SMF 9707.

Systematic palaeontology

Order **Piciformes** Meyer and Wolf, 1810
Family Indicatoridae Swainson, 1837

Remarks. The coracoid, humeri, carpometacarpi and tarsometatarsi described here, are morphologically very similar to that of modern Indicatoridae and also resemble the corresponding bones of the paraphyletic barbets and allies (i.e., Lybiidae and Megalaimidae) and Picidae (all in the Piciformes). Other Piciformes (Galbulae and Ramphastidae) are morphologically very different and readily stand out. The fossil specimens are similar to Indicatoridae but differ from Lybiidae, Megalaimidae, and Picidae in the following characters (Fig. 2):

On the proximal (omal) part of the coracoid, the processus acrocoracoideus is more prominent and angular proximo-medially in Indicatoridae than in barbets with a rounded proximal end and in Picidae with a flattened proximal part. The facies articularis humeralis of the coracoid is more protruding proximally in Indicatoridae than in Picidae and barbets. The proximal end of the humerus is more constricted proximo-distally in Picidae than in barbets and Indicatoridae, with a proximally flattened and less prominent caput humeri, and a more concave crista bicipitalis, giving the impression of a more pointed ventral protrusion of the tuberculum ventrale region in the Picidae. The fossa pneumotricipitalis ventralis is deeper in Indicatoridae than in barbets and Picidae, and a deep incipient second (proximal) fossa pneumotricipitalis dorsalis exists in Indicatoridae, but neither in barbets nor Picidae (with Picumninae being an exception). A prominent tubercle on the cranial side just distal of caput humeri exists in Indicatoridae. The distal end of humerus is more extended dorso-ventrally (especially processus flexorius extending more ventrally) in barbets than in Indicatoridae and Picidae. The fossa m. brachialis is much deeper in Indicatoridae than in barbets and Picidae (but nevertheless quite deep in the Picumninae). The cotyla ventralis bears (distally) a slight concavity that is marked in Indicatoridae (especially *Indicator*), while it is rather a flattened area in barbets and Picidae. And the whole humerus is generally more curved in Picidae than in barbets and Indicatoridae. The carpometacarpus is more robust in Indicatoridae (except *Prodotiscus*)

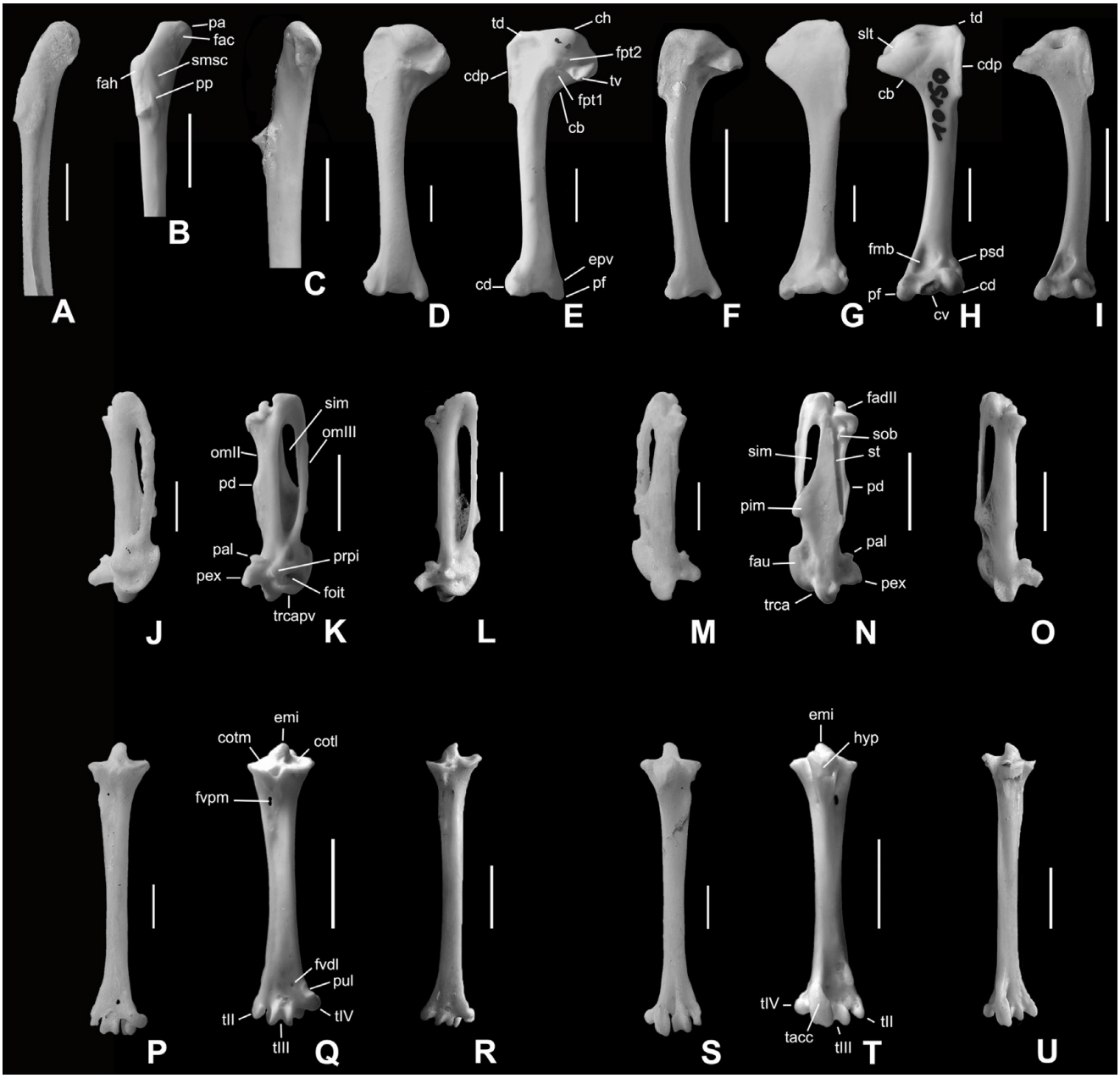

Fig. 2 - Coracoids, humeri, carpometacarpi and tarsometatarsi of extant Megalaimidae (barbets), Indicatoridae (honeyguides) and Picidae (woodpeckers) for comparisons. (A–C) proximal coracoids, dorsal views. (D–I) humeri in caudal (D–F) and cranial (G–I) views. (J–O) carpometacarpi in ventral (J–L) and dorsal (M–O) views. (P–U) tarsometatarsi in dorsal (P–R) and plantar (S–U) views. All bones are left side except (C, L, O, R, U), which are reversed to facilitate the comparison. On the left of each series of three elements-views is (A, D, G, J, M, P, S) a bone of a barbet (*Psilopogon virens*, Megalaimidae); in the middle is (B, E, H, K, N, Q, T) a bone of a honeyguide (*Indicator variegatus*, Indicatoridae); on the right is (C, F, I, L, O, R, U) a bone of a woodpecker (Picidae) as follows: (C) *Picus viridis*; (F, I) *Picumnus albosquamatus*; (L, O, R, U) *Dendrocopos major*. Abbreviations: cb, crista bicipitalis; cd, condylus dorsalis; cdp, crista deltopectoralis; ch, caput humeri; cotl, cotyla lateralis; cotm, cotyla medialis; cv, condylus ventralis; emi, eminentia intercotylaris; epv, epicondylus ventralis; fac, facies art. clavicularis; fadII, facies art. digitalis II; fah, facies art. humeralis; fau, facies art. ulnocarpalis; fmb, fossa m. brachialis; foit, fossa infratrochlearis; fpt1, first fossa pneumotricipitalis = fossa pneumotricipitalis ventralis (even if it is rather a distal fossa in Piciformes); fpt2, second fossa pneumotricipitalis = fossa pneumotricipitalis dorsalis (even if it is rather a proximal fossa in Piciformes); fvdl, foramen vasculare distale lateralis; fvpm, foramen vasculare proximale medialis; hyp, hypotarsus; omII, os metacarpale II; omIII, os metacarpale III; pa, processus acrocoracoideus; pal, processus alularis; pd, processus dentiformis; pex, processus extensorius; pf, processus flexorius; pim, processus intermetacarpalis; pp, processus procoracoideus; prpi, processus pisiformis; psd, processus supracondylaris dorsalis; pul, pulley for tendon of m. extensor digitorum longus pars dig. IV; sim, spatium intermetacarpalis; slt, sulcus lig. transversus; smsc, sulcus m. supracoracoidei; sob, semi-osseous supratendineous bridge; st, sulcus tendineus; tII, trochlea metatarsi II; tIII, trochlea metatarsi III; tIV, trochlea metatarsi IV; tacc, 'trochlea accessoria'; td, tuberculum dorsale; trca, trochlea carpalis; trcapv, trochlea carpalis pars ventralis; tv, tuberculum ventrale. The scale bars represent 5 mm.

than in barbets and Picidae. Its processus intermetacarpalis is huge in Indicatoridae (and some barbets), obscuring the spatium intermetacarpalis almost completely, whereas it is more reduced in the Picidae. The processus dentiformis is most prominent in Indicatoridae, less prominent in barbets, and least developed in Picidae. The processus extensorius is relatively larger in Indicatoridae than in barbets and Picidae. The facies articularis digiti II extends farther cranially in Indicatoridae (especially *Indicator*) than in barbets and Picidae. On the distal carpometacarpus, dorsal side, the sulcus tendineus bears a small oblique crest at its craniodistal margin in Indicatoridae, not in barbets and Picidae (and this crest extends not only as a semi-osseous tendinal bridge over the sulcus, but as a fully osseous bridge in some taxa/individuals of Indicatoridae). On the distal tarsometatarsus, the depth of the tendinal groove separating the trochlea IV and the trochlea accessoria is shallower, in distal view, in barbets. The distal-lateral extension of the trochlea IV in dorsal view is more rounded and with a pulley for the tendon of m. extensor digitorum longus pars dig. IV less indented in barbets and Indicatoridae than in Picidae. The trochlea accessoria in distal view is thicker and its curve is less angular, in Picidae than in barbets and Indicatoridae. The trochlea II is very reduced proportionally (and with a small medial indentation in dorsal or plantar view) in barbets, compared with the Picidae and Indicatoridae. The latter two taxa lack a medial indentation on trochlea II.

Genus Indicator Stephens, 1815

Type species: *Indicator indicator* Stephens, 1815; by tautonymy, *Indicator sparrmanii* Stephens = *Cuculus indicator* Sparrman, 1777.

Diagnosis: Very small to medium-sized zygodactyl birds with short tarsometatarsi, single hypotarsal canal for the tendon of M. flexor digitorum longus, osseous arcus extensorius, deep tendinal groove separating trochlea accessoria and trochlea metatarsi IV and trochlea accessoria further plantad than trochlea metatarsi III like other honeyguides and Picidae (Ballmann 1969; Simpson & Cracraft 1981; Mayr 2004, 2005).

Indicator honeyguides share with remaining taxa of Indicatoridae several derived characters such as humerus with distinct fossa pneumotricipitalis dorsalis (also present in Picumninae), prominent tubercle on cranial side just distal of caput humeri, and enlarged, deep fossa m. brachialis (also present in Picumninae); carpometacarpus with huge cranially widened proc. intermetacarpalis obscuring spatium intermetacarpalis almost completely, and sulcus tendineus with small oblique crest at its craniodistal margin.

The coracoid of *Indicator* is distinguished from honeyguides of the genus *Prodotiscus* by small, rounded, dorsoventrally flat proc. acrocoracoideus, which is continuous with shallow sulcus m. supracoracoidei (Fig. 3A–E) (proc. acrocoracoideus of *Prodotiscus* hooked and offset from concave sulcus m. supracoracoidei); the humerus shows robust, curved shaft (shaft slender and straight in *Prodotiscus*), proximodistally short crista deltopectoralis (proximodistally elongated in *Prodotiscus*), proximodistally broadened crista bicipitalis (proximodistally narrow in *Prodotiscus*), fossa pneumotricipitalis dorsalis deep (shallow in *Prodotiscus*), deep fossa m. brachialis (shallower in *Prodotiscus*), and short proc. supracondylaris dorsalis (well-developed proc. supracondylaris dorsalis in *Prodotiscus*); the carpometacarpus is robust with prominent, proximodistally elongated proc. dentiformis (carpometacarpus of *Prodotiscus* slender with indistinct proc. dentiformis); tarsometatarsus with trochlea accessoria proximodistally short, reaching not further distal than trochlea metatarsi III (trochlea accessoria projects further distal than trochlea metatarsi III in *Prodotiscus*).

The analysed bones are distinguished from honeyguides of the genera *Melichneutes* and *Melignomon* by oblique distal margin of crista bicipitalis (distal margin almost perpendicular to longitudinal axis in the humerus of *Melichneutes* and *Melignomon*), and from *Melichneutes* by less prominent crista deltopectoralis (crista deltopectoralis of *Melichneutes* projects further dorsal than in any other honeyguide studied).

Chronological and geographical distribution: Early Pliocene–Recent; fossil evidence for taxa referable to *Indicator* (and Indicatoridae) is limited to the Lower Pliocene Upper Varswater Formation of Langebaanweg, South Africa (this study); nine extant species endemic to Africa South of the Sahara, two additional extant species of apparently African origin in S and SE Asia, respectively (Fry et al. 1988; Short & Horne 2002).

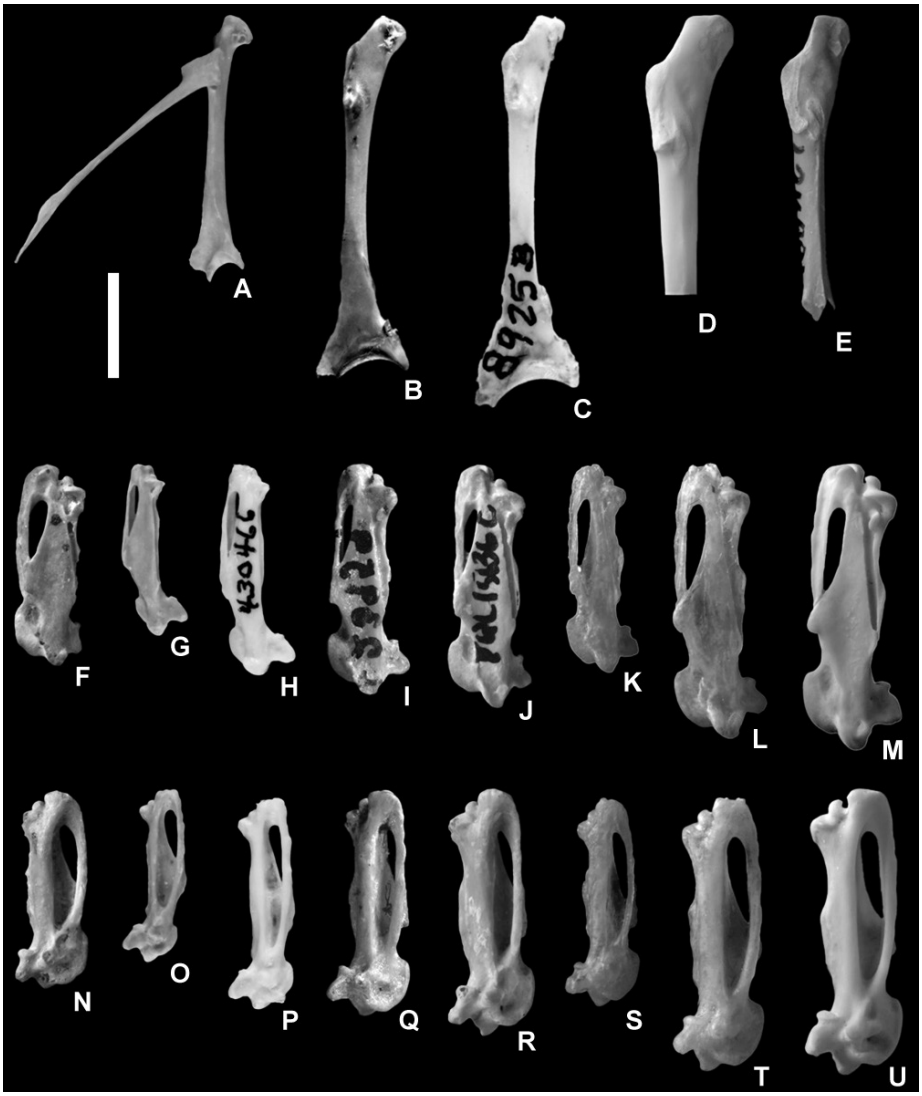

Fig. 3 - Coracoids and carpometacarpi of fossil honeyguides from the Lower Pliocene Upper Varswater Formation in comparison to those of extant Indicatoridae. A–E, left coracoids, dorsal views, of (A) *Prodotiscus insignis*, (B) *Melignomon zenkeri*, (C) *Melignomon eisentrauti*, (D) *Indicator variegatus*, and (E) *Indicator* sp. (taxon A) SAM-PQ-L24001MP. F–U, left carpometacarpi of (F, N) Indicatoridae indet. (taxon B) SAM-PQ-L28425 (F dorsal and N ventral views); (G, O) *Prodotiscus insignis* (G dorsal and O ventral views); (H, P) *Prodotiscus regulus* (H dorsal and P ventral views); (I, Q) *Indicator* sp. (taxon A) SAM-PQ-L23959 (mirrored right carpometacarpus, I dorsal and Q ventral views); (J, R) *Indicator* sp. (taxon A) SAM-PQ-L15136C (J dorsal and R ventral views); (K, S) *Indicator exilis* (K dorsal and S ventral views); (L, T) *Indicator maculatus* (L dorsal and T ventral views); (M, U) *Indicator variegatus* (M dorsal and U ventral views). The scale bar represents 5 mm.

Indicator sp. (taxon A)

Figs. 3–5

Referred specimens: SAM-PQ-L24001MP, incomplete left coracoid (Fig. 3D). SAM-PQ-L70282, complete left humerus (Fig. 4A); SAM-PQ-L20733, proximal left humerus; SAM-PQ-L24001IJ, proximal left humerus (Fig. 4B); SAM-PQ-L24001MC, proximal left humerus; SAM-PQ-L24213L, proximal left humerus; SAM-PQ-L17161B, distal left humerus; SAM-PQ-L28469I, distal left humerus; SAM-PQ-L28469T, distal left humerus; SAM-PQ-L24001RV, almost complete right humerus ; SAM-PQ-L28433J, proximal right humerus (Fig. 4D); SAM-PQ-L28842, proximal right humerus; SAM-PQ-L43364I, distal right humerus. SAM-PQ-L15136C, complete left carpometacarpus (Fig.3J, 3R); SAM-PQ-L25255, almost complete left carpometacarpus; SAM-PQ-L42849BK, complete left carpometacarpus; SAM-PQ-L28422, distal left carpometacarpus; SAM-PQ-L17165D, complete right carpometacarpus lacking os metacarpale III; SAM-PQ-L23959, complete right carpometacarpus (Fig. 3I, 3Q); SAM-PQ-L25544, complete right carpometacarpus; SAM-PQ-L28843, complete right carpometacarpus. SAM-PQ-L28423GS, left distal tarsometatarsus (Fig. 5A–B); SAM-PQ-L20423, tarsometatarsus lacking proximal end.

Geographic and stratigraphic range. 'E' Quarry, Langeberg Quartz Sand Member and Muishond Fontein Pelletal Phosphorite Member (Appendix 1), Upper Varswater Formation, Lower Pliocene at Langebaanweg (18°9' E, 32°58' S), South Africa, c. 110 km NNW of Cape Town (Hendey 1981; Roberts et al. 2011) (Fig. 1).

Measurements: See Tables 1–3.

Description and comparison. The bones of *Indicator* sp. (taxon A) from Langebaanweg are generally well preserved, and even the fragmented specimens show various anatomical details, which facilitates comparisons with recent Indicatoridae.

Coracoid. The omal part of the single fragmentary coracoid from Langebaanweg can be distinguished from the corresponding bone of *Prodotiscus* and non-indicatorid piciform birds by its small, rounded, dorsoventrally flat proc. acrocoracoideus, which is also continuous with the shallow sulcus m. supracoracoidei (Fig. 3D). These are derived features shared with modern species of *Indicator*, *Melignomon* and *Melichneutes*. In the latter, the proc. acrocoracoideus is even more strongly flattened

Tab. 1 - Measurements (mm) of humeri of fossil Indicator sp. (taxon A) and Indicatoridae indet. (taxon B) from the early Pliocene at Langebaanweg (South Africa) in comparison to those of modern honeyguides (taxa sorted by size). The fossil taxa are highlighted in bold.

Specimens	Greatest length	Proximal width	Distal width	Minimal width
***Indicator* sp. (taxon A)**	**21.0 (n = 1)**	**7.4 (7.1-7.7) (n = 7)**	**5.1 (5.0-5.2) (n = 4)**	**2.0 (1.9-2.5) (n = 10)**
Indicatoridae indet. (taxon B) (n = 1)	**–**	**6.2**	**–**	**–**
Indicator variegatus (n = 2)	26.3 (26.1-26.5)	8.9 (8.8-8.9)	6.3 (6.0-6.4)	2.2 (2.1-2.3)
Indicator indicator (n = 4)	26.2 (26.4-26.9)	8.7 (7.4-8.8)	6.5 (6.3-6.9)	2.5 (2.4-2.6)
Indicator maculatus (n = 5)	26.0 (25.6-26.7)	7.8 (7.4-8.7)	6.1 (6.0-6.3)	2.4 (2.3-2.4)
Melichneustes robustus (n = 1)	24.1	7.0	6.1	2.3
Indicator archipelagicus (n = 1)	23.0	6.5	5.3	2.2
Indicator minor (n = 6)	21.2 (20.1-22.2)	6.9 (5.6-7.3)	5.1 (5.0-5.2)	1.9 (1.8-2.0)
Protodiscus regulus (n = 2)	20.3 (19.9-20.7)	5.2 (5.0-5.3)	4.1 (4.0-4.1)	1.7 (1.6-1.7)
Indicator exilis (n = 3)	17.7 (15.8-19.4)	5.4 (4.9-6.3)	4.2 (3.8-4.5)	1.6 (1.5-1.6)
Protodiscus insignis (n = 1)	16.5	4.4	3.6	1.4

and the facies articularis humeralis is less extended laterally. The proc. acrocoracoideus of *Prodotiscus* is offset from the concave sulcus m. supracoracoidei and bears a small hook as well as a pneumatic foramen (Fig. 3A). A pneumatised extremitas omalis coracoidei was otherwise only noted for *I. indicator*. As in all Piciformes, the processus procoracoideus is greatly reduced.

Humerus. The humerus of *Indicator* sp. (taxon A) is morphologically similar to the corresponding bone of *I. indicator*, *I. minor*, and *I. variegatus*, though it differs in size. In particular, the proximal widths of humeri of *Indicator* sp. (taxon A) slightly exceed those of the *I. minor* specimens available for comparisons, while their total lengths agree with the latter species (Tab. 1). *Indicator* sp. (taxon A) can be distinguished from the humerus of *Prodotiscus* (Fig. 4E–F) by larger size, robust and curved shaft, proximodistally short crista deltopectoralis and proximodistally broadened crista bicipitalis, and short proc. supracondylaris dorsalis. The humeri of *Melichneutes* (Fig. 4J) and *Melignomon* (Fig. 4K) are of smaller size (*Melichneutes* distinctly, but *Melignomon* only slightly smaller) and show an oblique distal margin of crista bicipitalis and a less pronounced crista deltopectoralis. The other species of the genus are of different size (*I. maculatus* larger, *I. exilis* smaller) and show a dorsal margin of fossa m. brachialis clearly delimited in *I. exilis* and *I. maculatus*, while it is diffuse in *Indicator* sp. (taxon A) from Langebaanweg. One fragmentary humerus (SAM-PQ-L43364I) is noticeable in showing a significantly higher minimal

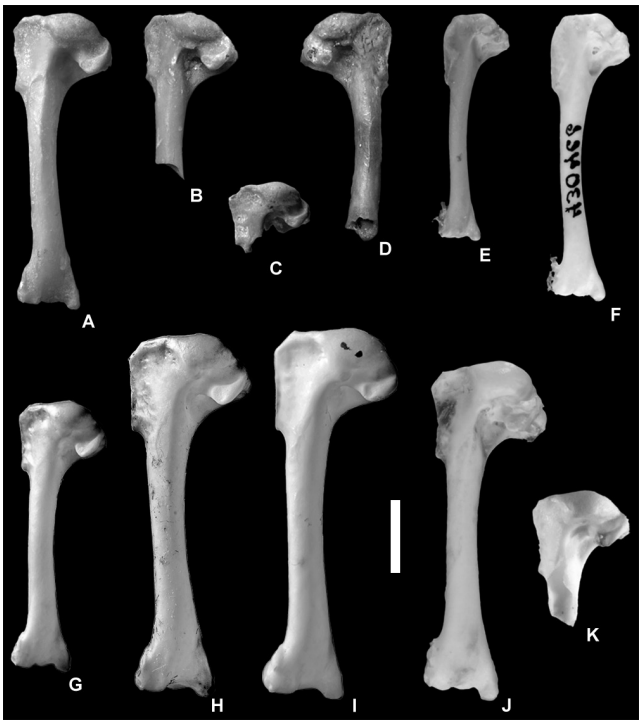

Fig. 4 - Humeri of fossil honeyguides from the Lower Pliocene Upper Varswater Formation in comparison to those of extant Indicatoridae. A) *Indicator* sp. (taxon A) SAM-PQ-L70282, left humerus cranial view; B) *Indicator* sp. (taxon A) SAM-PQ-L24001IJ, left humerus cranial view; C) Indicatoridae indet (taxon B) SAM-PQ-L28849, left humerus cranial view; D) *Indicator* sp. (taxon A) SAM-PQ-L28433J, right humerus cranial view; E) *Prodotiscus regulus*, left humerus cranial view; F) *Prodotiscus insignis*, mirrored right humerus cranial view; G) *Indicator exilis*, left humerus cranial view; H) *Indicator maculatus*, left humerus cranial view; I) *Indicator variegatus*, left humerus cranial view; J) *Melichneutes robustus*, left humerus cranial view; K) *Melignomon zenkeri*, left humerus cranial view. The scale bar represents 5 mm.

Specimens	Greatest length	Proximal width	Distal width
***Indicator* sp. (taxon A)**	**11.6 (10.9-12.1) (n = 7)**	**4.2 (4.0-4.4) (n = 6)**	**3.4 (3.2-3.6) (n = 5)**
Indicatoridae indet. (taxon B) (n = 1)	**9.5**	**3.9**	**3.1**
Indicator indicator (n = 4)	14.8 (14.5-15.1)	5.1 (5.0-5.3)	4.2 (4.0-4.3)
Indicator variegatus (n = 3)	14.4 (13.9-14.9)	5.2 (4.9-5.4)	4.1 (4.0-4.2)
Indicator maculatus (n = 5)	14.0 (13.9-14.4)	4.8 (4.7-4.9)	3.8 (3.6-4.1)
Indicator archipelagicus (n = 1)	11.7	4.3	3.2
Indicator minor (n = 7)	11.3 (10.5-12.0)	4.0 (3.7-4.1)	3.1 (2.7-3.4)
Protodiscus regulus (n = 2)	10.6 (10.5-10.7)	3.4 (3.3-3.4)	2.6
Indicator exilis (n = 3)	9.6 (8.5-10.5)	3.4 (2.9-3.8)	2.6 (2.3-2.8)
Protodiscus insignis (n = 1)	8.8	2.9	2.1

Tab. 2 - Measurements (mm) of carpometacarpi of fossil Indicator sp. (taxon A) and Indicatoridae indet. (taxon B) from the early Pliocene at Langebaanweg (South Africa) in comparison with to those of modern honeyguides (taxa sorted by size). The fossil taxa are highlighted in bold.

Specimens	Greatest length	Proximal width	Distal width	Minimal width
***Indicator* sp. (taxon A)**	**14.2***		**3.0 (2.9-3.1) (n = 2)**	**1.5 (n = 2)**
Indicatoridae indet. (taxon B)		**2.9 (n = 1)**	**2.9 (n = 1)**	**1.1 (n = 2)**
Indicator maculatus (n = 5)	17.0 (16.3-17.3)	3.8 (3.6-4.4)	4.2 (4.0-4.4)	1.6 (1.5-1.8)
Indicator indicator (n = 5)	16.9 (16.6-17.4)	3.8 (3.6-3.9)	4.0 (3.9-4.1)	1.7 (1.5-1.8)
Indicator variegatus (n = 3)	16.6 (16.4-17.0)	3.9 (3.7-4.0)	3.9 (3.9-4.0)	1.5 (1.4-1.6)
Indicator minor (n = 5)	14.9 (14.3-15.9)	3.0 (2.8-3.3)	3.2 (3.0-3.5)	1.2 (1.0-1.3)
Indicator exilis (n = 3)	13.5 (13.0-13.8)	2.6 (2.5-2.8)	2.8 (2.6-2.9)	1.0 (1.0-1.1)
Indicator archipelagus (n = 1)	13.1	3.4	3.3	1.7
Protodiscus regulus (n = 1)	12.5	2.4	2.6	1.0
Protodiscus insignis (n = 1)	12.0	2.0	2.3	0.7

Tab. 3 - Measurements (mm) of tarsometatarsi of fossil Indicator sp. (taxon A) and Indicatoridae indet. (taxon B) from the early Pliocene at Langebaanweg (South Africa) in comparison to those of modern honeyguides (taxa sorted by size). The fossil taxa are highlighted in bold. The asterisk (*) indicates estimated value.

shaft width than in *I. minor*: it might represent a third species, but could also presumably be a large outlier, and we prefer to conservatively keep it within *Indicator* sp. (A) here.

Carpometacarpus. The fossil carpometacarpi of *Indicator* sp. (taxon A) are robust and slightly larger than those of *I. minor* (Tab. 2). They bear a prominent proximodistally elongated proc. dentiformis as well as a caudally protruding and proximally truncated trochlea carpalis pars ventralis, as it is the case with extant species of *Indicator*. The carpometacarpus of *Prodotiscus* shows a proximo-distally very widened processus intermetacarpalis which occludes most of the spatium intermetacarpalis, more than in the other studied genera (Fig 3F), it also shows a more cranially protruding processus extensorius and a less defined and pointed processus alularis than in *Indicator* and in the fossil remains. The carpometacarpi of *Melichneutes* and *Melignomon* were not available for comparison.

Tarsometatarsus. The tarsometatarsus of *Indicator* sp. (taxon A) is broad and in respect of its robustness more similar to the corresponding bone of the much larger *I. maculatus*, but it is shorter than in the

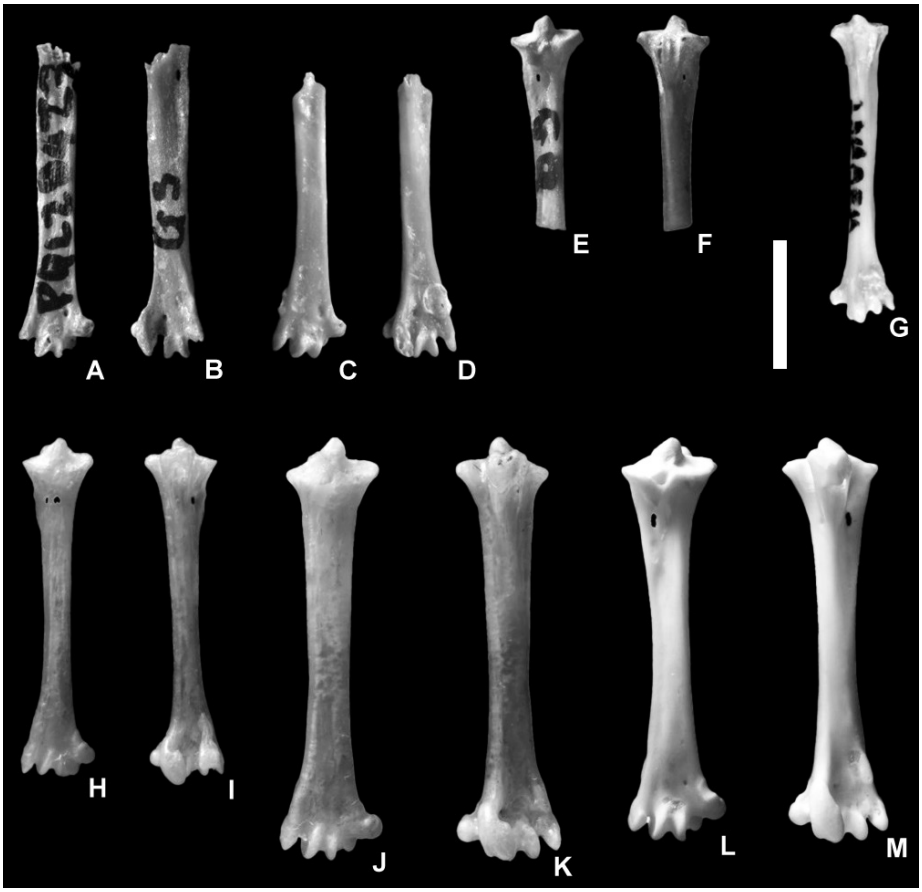

Fig. 5 - Tarsometatarsi of fossil honeyguides from the Lower Pliocene Upper Varswater Formation in comparison to those of extant Indicatoridae. A–B) *Indicator* sp. (taxon A) SAM-PQ-L28423GS, right tarsometatarsus in dorsal (A) and plantar (B) views; C–D) Indicatoridae indet. (taxon B) SAM-PQ-L28208, mirrored left tarsometatarsus in dorsal (C) and plantar (D) views; E–F) Indicatoridae indet. (taxon B) SAM-PQ-L28423GQ, right tarsometatarsus in dorsal (E) and plantar (F) views; G) *Prodotiscus regulus*, mirrored left tarsometatarsus in plantar view; H–I) *Indicator exilis*, right tarsometatarsus in dorsal (H) and plantar (I) views; J–K) *Indicator maculatus*, right tarsometatarsus in dorsal (J) and plantar (K) views; L–M) *Indicator variegatus*, right tarsometatarsus in dorsal (L) and plantar (M) views. The scale bar represents 5 mm.

latter species, as shown by the estimated length of SAM-PQ-L20423. Similarly, the tarsometatarsus of *Indicator* sp. (taxon A) is slightly shorter and simultaneously more robust, than in *I. minor* (Tab. 3). The distal end of the trochlea accessoria is on level with the distal end of trochlea metatarsi III as it is the case with extant species of *Indicator*, but in contrast to the situation in *Prodotiscus*, in which the trochlea accessoria projects further distally (Fig. 5G). The tarsometatarsi of *Melichneutes* and *Melignomon* were not available for comparison.

Indicatoridae indet. (taxon B)

Figs. 2-4

Referred specimens: SAM-PQ-L28849, proximal left humerus (Fig. 3C). SAM-PQ-L28425F, complete left carpometacarpus (Fig. 4F, 4N). SAM-PQ-L28423GQ, proximal right tarsometatarsus (Fig. 4E–F); SAM-PQ-L28208, distal left tarsometatarsus (Fig. 4C–D).

Geographic and stratigraphic range: 'E' Quarry, Langeberg Quartz Sand Member and Muishond Fontein Pelletal Phosphorite Member (Appendix 1), Upper Varswater Formation, Lower Pliocene at Langebaanweg (18°9' E, 32°58' S), South Africa, c. 110 km NNW of Cape Town (Hendey 1981; Roberts et al. 2011) (Fig. 1).

Measurements: See Tables 1–3.

Description and comparison. The bones of Indicatoridae indet. (taxon B) from Langebaanweg, though only fragmentarily preserved as in the case of a single proximal humerus, show critical anatomical details that allow their analysis.

Humerus. SAM-PQ-L28849 is a very fragmentary proximal humerus, but two features characteristic of Indicatoridae, i.e. the clearly delimited fossa pneumotricipitalis and the distinct tubercle just distal to caput humeri, are preserved. Given its very fragmentary status, no other characters are discernible, including the shape of the crista bicipitalis and of crista deltopectoralis, thus SAM-PQ-L28849 cannot be distinguished from the humeri assigned to *Indicator* sp. (taxon A) except for its smaller size.

Carpometacarpus. The almost complete left carpometacarpus SAM-PQ-L28425F is even smaller than the corresponding bone of *I. exilis*, one of the smallest extant species of *Indicator*, but much more robust with craniocaudally deeper ossa metacarpalia II and III. The os metacarpale III is curved and wider than any other recent Indicatoridae used for comparison. The processus extensorius is slightly tilted proximally and less extended cranially than in any other recent Indicatoridae and the fossil *Indicator*

sp. (taxon A) described in this paper. In contrast to extant species of *Indicator*, the tip of proc. intermetacarpalis does not protrude caudally over os metacarpale III. The cranial margin of the proc. dentiformis is broken off, but its vast proximodistal extension is still evident. In contrast to *Indicator* sp. (taxon A) and modern species of *Indicator*, the trochlea carpalis pars ventralis of Indicatoridae indet. (taxon B) is not truncated distally, but merges gradually into os metacarpale III. The small crest at the craniodistal margin of the sulcus tendineus is fused to the caudodistal margin of the sulcus, thus forming an osseous supratendinal bridge, which was otherwise noted for *Prodotiscus*, *I. indicator*, and *I. minor* only. In *I. exilis*, the crest is proximodistally broadened and craniocaudally elongated but remains separate from the caudal margin of the sulcus tendineus.

Tarsometatarsus. The tarsometatarsus of Indicatoridae indet. (taxon B) is slender and comparable in size with that of *I. exilis* (Tab. 1–3), but the fossil's eminentia intercotylaris appears to be slenderer and more pointed, and its sulcus extensorius broader compared to the last mentioned species.

Discussion

Systematic Palaeontology

As detailed above, the fossil honeyguides from Langebaanweg belong to two different taxa. The more common one can be referred to the genus *Indicator* on the basis of several derived characters, which are primarily absent in *Prodotiscus*, as well as few additional characters that distinguish them from *Melichneutes* and *Melignomon*. Comparative material was, however, limited to six of the ten species of the genus *Indicator*, represented by less than six specimens each, or even on partial skeletons only. Thus, even though it displays characteristics that differ from all the species examined, we prefer to leave it as *Indicator* sp. (taxon A) rather than to describe it as a new species. As the size of the latter species is relatively small, additional comparisons, especially with the smaller representatives of *Indicator* such as *I. meliphilus, I. pumilio*, and *I. willcocksi*, might be crucial for a sound hypothesis on the systematic position of the fossil taxon. The differences in the skeleton between *I. exilis* and *I. pumilio* pointed out by Friedmann (1963) concern the length of coracoids and furcula in relation to the length of the carina sterni of the sternum, so they are not applicable in this study. A species of the genus *Indicator* in the Early Pliocene (ca. 5 Ma) of Langebaanweg is congruent with current genomic data that point to an age of 16.6 Ma for the origin of the genus *Indicator* (Jetz et al. 2012; Rosindell & Harmon 2012).

Here, the second species of honeyguide from Langebaanweg is conservatively referred to Indicatoridae indet. (taxon B), because of the few and mostly fragmentary remains referable to it. Nevertheless, the morphology of the carpometacarpus SAM-PQ-L- L28425F is distinctive and differs markedly from that of all the taxa used for comparisons. The analyses of the recent species unavailable for the present study, as well as additional fossil remains from Langebaanweg, seem to be necessary for clarifying the taxonomy of this rare species.

One significantly larger distal humerus (SAM-PQ-L43364I), assigned here to *Indicator* sp. (taxon A) might represent yet a further, larger honeyguide species, but more material will be needed to confirm it or not.

Palaeoenvironmental and palaeoecological implications

Evidence for two honeyguide species of small size at the same fossil site (see Appendix 1) is unexpected, but not without modern analogies. In different parts of its distribution area, *I. exilis* occurs in sympatry with *I. meliphilus*, *I. pumilio*, and *I. willcocksi*, respectively (Chapin 1962; Friedmann 1968a, 1976; Winkler et al. 2020). Even co-occurrence of three small honeyguide species is reported, e.g., *I. exilis* and *I. willcocksi* are sympatric with either *I. minor* or *I. pumilio* in certain areas of west Uganda (Friedmann 1968a), but their potential ecological separation in sympatry is unknown.

Honeyguides can be found in various types of forest and woodlands, but their ancestral habitat probably was tropical forest, where taxa like *I. exilis, I. minor, I. maculatus*, *Melignomon zenkeri* and *M. eisentrauti*, *Melichneutes robustus*, and *Prodotiscus insignis* still occur (Friedmann 1955). Other species became adapted to rather open woodlands and savannahs, such as *I. indicator, I. minor, I. variegatus*, and *Prodotiscus regulus* (Friedmann 1955), but the honeyguides apparently avoid very open, treeless savannahs and grasslands (Harrison et al. 1997). Extant species of Indicatoridae strongly rely on bees and scale insects for food (Moreau 1966) but being obligate brood

parasites they also depend on the presence of suitable host species, such as cavity-nesting barbets, bee-eaters, kingfishers, hoopoes, woodhoopoes, rollers, woodpeckers, swallows, and starlings, while *Prodotiscus* honeyguides can also lay eggs in nests of non-cavity nesters such as Monarchidae, Zosteropidae, and Nectariniidae (Friedmann 1955, 1968b; Frey et al. 1988; Short & Honre 2002; Lowther 2020; Winkler et al. 2020). Interestingly, the Western Cape region was probably only recently colonized by *I. indicator*, *I. minor*, and *Prodotiscus regulus* after forestation with allochthonous trees (e.g., pine and eucalyptus plantations), and further triggered by the expansion of potential foster species, such as Pied Barbet (*Tricholaema leucomelas*) in the case of *I. minor* (Harrison et al. 1997).

Thus, fossil evidence for honeyguides does not only strongly indicate the presence of woodlands, but also of sufficient populations of potential tree cavity-nesting foster species. This indication is also supported by the presence of other secondary tree cavity-nesters in the same levels: two parrots, one of them relatively common (Manegold 2013) and the owl *Athene inexpectata* (Pavia et al. 2015), which indicate at least the presence of suitable nest sites in tree cavities. Surprisingly, barbets and bee-eaters, which rank among the most common foster species at least for *I. indicator* and *I. minor* (Friedmann 1955, 1958, 1968b; Short & Horne 2002), are unknown from the Upper Varswater Formation, as are also hoopoes, rollers, and woodhoopoes. On the other hand, those taxa are very scarce in the fossil record worldwide (Brodkorb 1971; Olson 1985) and Langebaanweg, despite its great bird diversity, follows this pattern (Manegold et al. 2013). One could speculate that the woodpecker *Australopicus nelsonmandelai*, which is comparable in size to extant *Dendrocopos major* and *Melanerpes carolinus* (Manegold & Louchart 2012), and a kingfisher (*Halcyon* sp.) comparable in size to *Halcyon albiventris* (Olson 1994) served as foster species for the fossil honeyguide species. Both species probably reached more than 2.5 times the weight of the fossil honeyguides from Langebaanweg, but such size differences between foster species and brood parasite are also evident for *Indicator minor* and some of its modern hosts, i.e. *Campethera bennettii* and *C. abingoni* are on average more than 2.5 times as heavy as female *I. minor* (Tab. 4). In fact, most of the species fostered by *I. minor* are at least twice its body weight (Tab. 4). The other kingfisher *Ceryle* sp. reported by Olson (1994) is supposed to be five times the body weight of the fossil *Indicator* sp., hence too large to be considered as a putative foster species for the small honeyguides reported here. *Indicator* species and other honeyguides are also recorded to parasite other cavity-nesters such as Hirundinidae and Sturnidae (Lowther 2020), which are recorded for the Early Pliocene of Langebaanweg (Manegold 2010; Manegold et al. 2013; Manegold & Pavia, pers. obs. 2023). No precise palaeoenvironment indications can be obtained from the other fossil honeyguide (taxon B) described in this paper, as it is not possible to assign it to any extant genus of Indicatoridae.

This study continues the long-term project on the tremendous fossil bird association found at Langebaanweg. The data presented here indicate that at least one modern genus of honeyguide was already established in the Early Pliocene of southern Africa and that there is at least another hon-

Species	body weight	body weight host/ body weight *I. minor*
Indicator minor	25.6	1.0
Merops pusillus	14.5	0.6
Hirundo albigularis	21.8	0.9
Merops oreobates	22.0	0.9
Petronia superciliaris	24.0	0.9
Tricholaema diademata	29.7	1.2
Tricholaema leucomelas	32.2	1.3
Halcyon chelicuti	39.6	1.5
Cinnyricinclus leucogaster	44.0	1.7
Stactolaema anchietae	48.0	1.9
Stactolaema olivacea	50.1	2.0
Jynx ruficollis	50.3	2.0
Lybius torquatus	52.4	2.0
Lybius leucocephalus	57.6	2.3
**Halcyon albiventris*	65.0	2.5
**Melanerpes carolinus*	66.0	2.6
Campethera bennettii	67.0	2.6
Campethera abingoni	70.0	2.7
**Dendrocopos major*	72.7	2.8
**Chloroceryle amazona*	132.5	5.2
**Megaceryle alcyon*	147.6	5.7

Tab. 4 - Average body weight of female *I. minor* in comparison to the average body weight of their foster species and selected non-foster species indicated by an asterisk (*). Data for non-foster species serve as approximation for the weights of the woodpecker *Australopicus nelsonmandelai* and kingfishers in the fossil record of Langebaanweg. Weights in grams according to Fry et al. (1988).

eyguide taxon with uncertain affinities, confirming once again the importance of these studies in the knowledge of the evolution of the present-day African avifauna.

Data Availability Statement. The data supporting the results of this research are available upon request. Interested researchers may contact the corresponding author to obtain access

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References

Ballmann P. (1969) - Die Vögel aus der altburdigalen Spaltenfüllung von Wintershof (West) bei Eichstätt in Bayern. *Zitteliana*, 1: 5-60.

Baumel J.J. & Witmer L.M. (1993) - Osteologia. In: Baumel J.J., King A.S., Breazile J.E., Evans H.E. & Vanden Berge J.C. (Eds) - Handbook of Avian Anatomy: Nomina Anatomica Avium. second edition: 45-132. Nuttall Ornithological Club, Cambridge, Massachusetts.

Chapin J.P. (1962) - Sibling species of small African honeyguides. *Ibis*, 104: 40-44.

De Pietri V.L., Manegold A., Costeur L. & Mayr G. (2011) - A new species of woodpecker (Aves; Picidae) from the early Miocene of Saulcet (Allier, France). *Swiss Journal of Palaeontology*, 130: 307-314.

Friedmann H. (1955) - The honey-guides. *United States National Museum Bulletin*, 208: 1-292.

Friedmann H. (1963) - Morphological data on two sibling species of small honey-guides. *Los Angeles County Museum Contributions to Science*, 79: 1-5.

Friedmann H. (1968a) - Additional data on brood parasitism in the honey-guides. *Proceedings of the United States National Museum*, 124: 1-8.

Friedmann H. (1968b). Parallel evolution in the small species of *Indicator* (Aves). *Proceedings of the United States National Museum*, 125: 1-10.

Fry C.H., Keith S. & Urban E.K. (1988) - The Birds of Africa. Volume 3. Parrots to Woodpeckers, Academic Press, London, 611 pp.

Harrison J.A., Allan D.G., Underhill L.G., Herremans M., Tree A.J., Parker V. & Brown C.J. (Eds) (1997) - The Atlas of Southern African Birds. Volume 1: Non-passerines. BirdLife South Africa, Johannesburg.

Hendey Q.B. (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.

Jetz W., Thomas G.H., Joy J.B., Hartmann K. & Mooers A.O. (2012) - The global diversity of birds in space and time. *Nature*, 491: 444-448.

Johansson U.S. & Ericson P.G.P. (2003) - Molecular support for a sister group relationship between Pici and Galbulae (Piciformes sensu Wetmore 1960). *Journal of Avian Biology*, 34: 185-197.

Lowther P.E. (2020) - Host list of avian brood parasites. - 4 - Piciformes; Indicatoridae. (accessed in November 2024). https://www.datocms-assets.com/44232/1632764065-host-list-honeyguide-16sep2020-revised.pdf.

Manegold A. (2010) - Two Swallow Species from the Early Pliocene of Langebaanweg (South Africa). *Acta Palaeontologica Polonica*, 55: 765-768.

Manegold A. (2013) - Two new parrot species (Psittaciformes) from the early Pliocene of Langebaanweg, South Africa, and their palaeoecological implications. *Ibis*, 155: 127-139.

Manegold A. & Louchart A. (2012) - Biogeographic and paleoenvironmental implications of a new woodpecker species (Aves, Picidae) from the early Pliocene of South Africa. *Journal of Vertebrate Paleontology*, 32: 926-938.

Manegold A., Louchart A., Carrier J. & Elzanowski A. (2013) - The Early Pliocene avifauna of Langebaanweg (South Africa): a review and update. In: Göhlich U.B. & Kroh A. (Eds) - Paleornithological Research 2013 Proceedings of the 8th International Meeting of the Society of Avian Paleontology and Evolution, Vienna, Austria, 11th -16th June 2012: 135-152. Naturhistorisches Museum Wien, Vienna.

Mayr G. (2004) - The phylogenetic relationships of the early Tertiary Primoscenidae and Sylphornithidae and the sister taxon of crown group piciform birds. *Journal of Ornithology*, 145: 188-198.

Mayr G. (2005) - A tiny barbet-like bird from the Lower Oligocene of Germany: the smallest species and earliest substantial fossil record of the Pici (woodpeckers and allies). *Auk*, 122: 1055-1063.

Meyer B. & Wolf J. (1810) - Taschenbuch der deutschen Vögelkunde oder kurze Beschreibung aller Vögel Deutschlands, Erster Theil. Friedrich Wilmans, Frankfurt, 310 pp.

Moreau R.E. (1966) - The bird faunas of Africa and its islands. Academic Press, London and New York.

Olson S.L. (1985) - The fossil record of birds. In: Farner D.S., King J.R. & Parkes K.C. (Eds) - Avian Biology, Volume 8: 79-238. Academic Press, New York and London.

Olson S.L. (1994) - Early Pliocene Grebes, button-quail, and kingfishers from south-western Cape Province, South Africa (Aves: Podicipedidae, Turnicidae, Halcyonidae). *Annals of the South African Museum*, 104: 49-61.

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 Palaeontologica Polonica*, 60: 815-828.

Pavia M., Louchart A., Govender R. & Delfino M. (2025) - A

new species of swift (Aves, Apodidae) from the Early Pliocene of Langebaanweg, South Africa. *PalZ*, 99:185-192.

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.

Roberts D.L., Matthews T., Herries A.I.R., Boulter C., Scott L., Musekiwa C., Mthembi 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.

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. Website: http://www.onezoom.org/OZtree/static/OZLegacy/EDGE_birds.htm (accessed 21 February 2025).

Short L.L. & Horne J.F.M. (2002) - Family Indicatoridae (Honeyguides). In: del Hoyo J., Elliot A. & Sargatal J. (Eds) - Handbook of the Birds of the World. Volume 7: 274-295. Jacamars to Woodpeckers. Lynx Edicions, Barcelona.

Simpson S.F. & Cracraft J. (1981) - The phylogenetic relationships of the Piciformes (class Aves). *Auk*, 98: 481-494.

Sparrman A. (1777) - An account of a journey into Africa from the Cape of Good-Hope, and a description of a new species of cuckow. Philosophical Transactions 67: 38-42.

Spottiswoode C.N. & Koorevaar J. (2012) - A stab in the dark: chick killing by brood parasitic honeyguides. *Biology Letters*, 8: 241-244.

Stephens J.F. (1815) - Birds. In: Shaw's General Zoolology or Systematic Natural History. Vol. 9(1). G. Wilkie, J. Walker, J. Stockdale, J. & A. Arch, London.

Swainson W. (1837) - On the natural history and classification of birds. Vol. 2. J. Taylor, London.

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) - Honeyguides (Indicatoridae), version 1.0. In: Billerman S.M., Keeney B.K., Rodewald P.G. & Schulenberg T. S. (Eds) - Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA. (Accessed in November 2024). https://doi.org/10.2173/bow.indica1.01.

Appendix 1 - Measurements (mm) of the fossil bones of Indicator sp. (taxon A) and Indicatoridae indet. (taxon B) from the early Pliocene at Langebaanweg (South Africa). The asterisk (*) indicates estimated value. For each specimen the horizon from the Upper Varswater Formation at 'E' Quarry, Langebaanweg, Early Pliocene, South Africa is provided. Abbreviations: LQSM, Langeberg Quartz Sand Member; MPPM, Muishond Fontein Pelletal Phosphorite Member (Roberts et al. 2011).

Specimens	Horizon	Greatest length	Proximal width	Distal width	Minimal width
Coracoid					
L24001MP *Indicator* sp. (taxon A)	LQSM/MPPM	-	-	-	-
Humerus					
L17161B *Indicator* sp. (taxon A)	LQSM	-	-	5.2	2.1
L20733 *Indicator* sp. (taxon A)	LQSM	-	7.7	-	-
L24001IJ *Indicator* sp. (taxon A)	LQSM	-	7.5	-	2.1
L24001MC *Indicator* sp. (taxon A)	LQSM	-	7.1	-	2.0
L24001RV *Indicator* sp. (taxon A)	LQSM	-	-	5.1	2.0
L24213L *Indicator* sp. (taxon A)	LQSM	-	7.4	-	1.9
L28433J *Indicator* sp. (taxon A)	LQSM/MPPM	-	7.2	-	1.9
L28469I *Indicator* sp. (taxon A)	LQSM/MPPM	-	-	5.1	2.0
L28469T *Indicator* sp. (taxon A)	LQSM/MPPM	-	-	5.2	2.1
L28842 *Indicator* sp. (taxon A)	LQSM/MPPM	-	7.4	-	-
L43364I *Indicator* sp. (taxon A)	LQSM/MPPM	-	-	-	2.5
L70282 *Indicator* sp. (taxon A)	LQSM	21.0	7.2	5.0	1.9
L28849 Indicatoridae indet. (taxon B)	LQSM/MPPM	-	6.2	-	-
Carpometacarpus					
L15136C *Indicator* sp. (taxon A)	MPPM	12.1	4.4	3.6	
L17165D *Indicator* sp. (taxon A)	LQSM	11.2	4.3	-	
L23959 *Indicator* sp. (taxon A)	LQSM	10.9	4.2	3.2	
L25255 *Indicator* sp. (taxon A)	LQSM	11.8	-	-	
L25544 *Indicator* sp. (taxon A)	LQSM	11.4	4.0	3.4	
L28422 *Indicator* sp. (taxon A)	LQSM/MPPM	-	-	3.5	
L28843 *Indicator* sp. (taxon A)	LQSM/MPPM	12.1	4.4	3.4	
L42849BK *Indicator* sp. (taxon A)	LQSM/MPPM	11.4	4.2	3.6	
L28425F Indicatoridae indet. (taxon B)	LQSM/MPPM	9.5	3.9	3.1	
Tarsometatarsus					
L20423 *Indicator* sp. (taxon A)	LQSM/MPPM	14.2*	-	3.1	1.5
L28423GS *Indicator* sp. (taxon A)	LQSM/MPPM	-	-	2.9	1.5
L28208 Indicatoridae indet. (taxon B)	LQSM	-	-	2.9	1.1
L28423GQ Indicatoridae indet. (taxon B)	LQSM/MPPM	-	2.9	-	1.1