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The Early Pliocene avifauna of Langebaanweg (South Africa): a review and update

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Abstract — The present paper provides an overview of the famous but still insufficiently known early Pliocene avifauna of the Varswater Formation at Langebaanweg (South Africa). This site produced one of the largest pre-Pleistocene bird bone accumulations worldwide. According to latest estimates, over 35 bird families with at least 90 species have been recorded and most of them mark the earliest family records for the African continent. There is a great diversity of both seabirds such as petrels, prions, and shearwaters (Procellariidae), penguins (Spheniscidae), and terrestrial taxa such as shorebirds (Charadriiformes) and songbirds (Oscines, Passeriformes). Recent identifications of new species shed new light on the palaeoenvironment and palaeoecology of the site and reveal the co-existence of two distinct terrestrial habitats. Honeyguides (Indicatoridae) and several cavity-nesting birds such as parrots (Psittaciformes) and woodpeckers (Picinae) indicate the presence of woodlands. Two species of sandgrouse (Pteroclidae) and at least one species of large ostriches (*Struthio* cf. *asiaticus*) are characteristic of arid to semi-arid landscapes.

Key words: Upper Varswater Formation, palaeoenvironmental reconstructions, palaeoecology, birds

Introduction

The Upper Varswater Formation of Langebaanweg, 110 km NNW of Cape Town, South Africa (32°58′ S, 18°7′ E) (Fig. 1), dates from the earliest Pliocene (5.2 Ma; Roberts *et al.* 2011) and ranks among the richest fossil vertebrate sites in Africa and the world (Werdelin 2010: p. 31). It stands out against other African fossil localities by the vast number of well preserved, though generally disarticulated bird remains (Rich 1980; Hendey 1981), which can be referred to at least 90 species representing both marine and terrestrial taxa, most of which have yet to be described (Tab. 1). The Upper Varswater Formation is also exposed at Duinefontein, *c*. 30 km N of Cape Town and at Ysterplaat Air Force Base, Cape Town, but these sites produced comparatively few and less well-preserved bones of mainly marine taxa (Simpson 1973, 1979b; Olson 1985b) (Fig. 1). Langebaanweg is one of the largest pre-Pleistocene bird bone accumulations worldwide (Rich 1980),

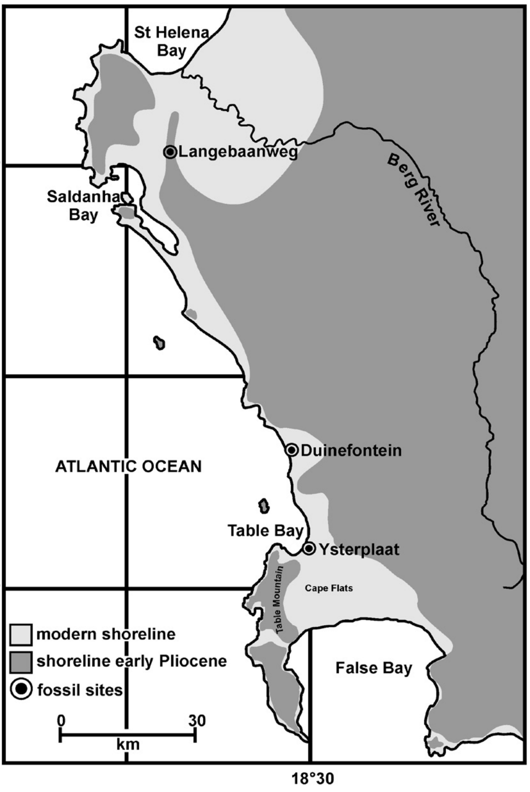

FIGURE 1. Map of Western Cape Province, South Africa showing fossil sites with outcrops of Early Pliocene Upper Varswater Formation, i.e. Langebaanweg, Duinefontein, and Ysterplaat. The modern shoreline is shown in comparison with shoreline at the climax of the Early Pliocene marine transgression with sea-levels *c.* 50 m higher than today resulting in a series of large offshore islands as suitable breeding sites for seabird colonies (after Olson 1983, 1985a).

comparable to other famous fossil localities such as Saint-Gérand-le-Puy (Early Miocene, France; Cheneval 1984; Mourer-Chauviré 1992) or Lee Creek Mine (Early Pliocene, North Carolina; Olson & Rasmussen 2001).

The fossil record of birds from the early Neogene of Africa is still very scarce (*e.g.*, Rich 1974; Harrison 1980; Brodkorb & Mourer-Chauviré 1982; Louchart *et al.* 2005a, b, 2008; Dyke & Walker 2008), and many findings at Langebaanweg represent the earliest evidence of certain taxa in Africa or even in the world, such as hamerkop (Scopidae), painted-snipe (Rostratulidae), honeyguides (Indicatoridae), mousebirds (Coliidae), parrots (Psittaciformes), penguins (Spheniscidae), and true woodpeckers (Picinae) (Simpson 1971; Rich 1980; Olson 1984, 1985d; Rich & Haarhoff 1985; Olson & Eller 1989; Manegold & Louchart 2012). Some bird taxa of the Upper Varswater Formation are today endemic to Africa (hamerkop, mousebirds) or evidently of African origin (honeyguides), but fossil evidence for a bird taxon of probable Eurasian origin (a malarpicine woodpecker) was reported only recently (Manegold & Louchart 2012).

Fossil assemblages close to the Miocene/Pliocene transition are particularly rare in Africa, so that Langebaanweg provides a rare insight into a period that is characterized by global cooling followed by the general spread of woodland savannahs and grasslands at the expense of forests (e.g., Cerling *et al.* 1997; Boisserie & Merceron 2011), by the first evidence for an already diverse fynbos flora in the south western Cape (Scott 1995) as well as by sea level changes and the establishment of the Benguela Upwelling System off the west coast of southern Africa (Hendey 1981; Diester-Haass *et al.* 2004; Heinrich *et al.* 2011; Rommerskirchen *et al.* 2011).

Fossil bearing units of the Upper Varswater Formation at Langebaanweg can be identified by characteristic sediments as tidal mud flats, floodplains, and salt marshes, respectively (Hendey 1981). Hypotheses on Early Pliocene palaeoenvironments at Langebaanweg and adjoining areas were largely based on the composition of the mammal fauna (Hendey 1981) and palynological studies (Scott 1995), but the composition of Langebaanweg's avifauna has also proven to be of great significance for palaeoenvironmental reconstructions (Rich 1980; Olson 1983, 1985a, c, 1994; Haarhoff 1988). The Early Pliocene seabird fauna, for example, is surprisingly diverse and can only be compared to the recent seabird diversity in the Subantarctic realm, which led Olson (1983, 1985a, b) to suppose that the Benguela Upwelling System was richer in nutrients and that its water temperatures were as cold or even colder than today. This would also be in accordance to certain morphological features of the seal *Homiphoca capensis* that were regarded as adaptations to low sea and ambient air temperatures (Hendey 1981: p. 69, but see Govender *et al.* 2012).

In comparison to the seabird fauna, the landbird fauna is less well studied, but seems dominated by two as yet unidentified species of francolins, one of them showing greatest overall similarity to the Crested Francolin, *Dendroperdix* (*Peliperdix*) *sephaena* (Rich 1980; Crowe 1992). The landbird fauna also comprises at least one species of a large ostrich (*Struthio* cf. *asiaticus*, see below), the large stork *Ciconia kahli*, the ibis *Geronticus apelex*, and the small mousebird *Colius hendeyi*, which are all supposed to be characteristic for rather open and dry habitats (Rich 1980; Hendey 1981; Olson 1985c; Rich & Haarhoff 1985; Haarhoff 1988). Evidence for a tree kingfisher *Halcyon* sp. could also indicate open savannah and bushlands, where most of its extant relatives occur (Olson 1994). Olson (1994) also tentatively referred an isolated humerus to the buttonquail *Turnix* cf. *hottentottus*, stating that the fossil could have been as characteristic for short, moist grasslands as its modern relative. Large grazers, such as the large, early hippopotamine (Hippopotaminae sp.), the rhino *Ceratotherium* sp., the gomphothere *Anacus capensis*, the elephantids *Loxodonta cookei* and *Mammuthus subplanifrons*, and the three-toed horse *Eurygnathohippus* cf. *baardi* also suggest the presence of grasslands (Hendey 1981; Franz-Odendaal *et al.* 2003; Sanders 2007; Boisserie & Merceron 2011). C_3 grasses apparently prevailed during the Late Miocene and Early Pliocene at Langebaanweg according to the study of isotopes (Franz-Odendaal *et al.* 2002) and of phytoliths (Rossouw *et al.* 2009), although in other parts of Africa C_4 grasses had already expanded considerably (Cerling *et al.* 1997).

Nevertheless, large browsers such as *Sivatherium* or the okapi-like *Paleotragus* in the fossil record imply the presence of woodlands as well (Hendey 1981, but see Franz-Odendaal & Solounias 2004; Boisserie & Merceron 2011: p. 356). Dental micro- and mesowear texture analyses of bovid teeth further indicate that six out of seven bovid species studied were browsers, not grazers as previously thought, and that *Simatherium demissum* probably was the only obligate grazer among Langebaanweg's bovids (Ungar *et al.* 2007; Stynder 2011). This might indicate that the palaeoenvironment was rather heavily wooded and not dominated by grass (Stynder 2011). Among the micromammals, two species of archaic *Myosorex* shrews were also supposed to be indicative of woodlands based on habitat preferences of their modern relatives (Matthews & Stynder 2011).

The presence of a slow-streaming river with a system of drainage channels and small pools, swamps, and marshes is indicated by fossil evidence for a hippopotamine, as yet unidentified species of ducks, geese, and allies (Anatidae), a few rails (Rallidae), a crane (Gruidae), the Dabchick *Tachybaptus ruficollis* and another species of grebe *Podiceps*? sp., an ibis *Threskiornis* aff. *aethiopicus*, numerous waders (Charadriiformes), among them an extinct species of painted-snipe *Rostratula minator*, a cerylid kingfisher *Ceryle* sp., intermediate in size between the African Pied Kingfisher *Ceryle rudis* and Giant Kingfisher *Megaceryle maxima* (Olson 1994), as well as numerous remains of several frog species (Rich 1980; Hendey 1981; Olson & Eller 1989; Olson 1994; Boisserie & Merceron 2011) and evidence for pollen referable to aquatic and semi aquatic Ranunculaceae (Scott 1995: p. 67).

Hendey (1982) proposed that the decrease in temperature and rainfall during the Miocene-Pliocene transition caused woodland to be increasingly confined to the immediate vicinity of the river whereas grasslands became more and more extensive. Accordingly, the palaeoenvironment at Langebaanweg could be imagined as a large "stream in a rather open savannah" (Olson 1994).

Evidence for one species of Gerbillinae, which are characteristic for deserts and savannahs, indicates open and rather dry habitats in the area, though it is unlikely that such habitats were very extensive (Matthews *et al.* 2007). However, the discovery of a new species of golden mole (Chrysochloridae) even suggests presence of arid, sandy habitats (Asher & Avery 2010). The humerus of the new species †*Chrysochloris arenosa* Asher & Avery, 2010 is very similar to that of its distant modern relative, the Grant's Golden Mole *Emeritalpa granti*, which could indicate similar adaptations for 'sand-swimming' in both of these species: Grant's Golden Mole dwells in large dune fields along the west coast of South Africa as well as in the Namib desert, where the sandy soil immediately collapses behind it while it moves through the sand.

Recent insights into the composition of the bird fauna (Stidham 2006; Manegold 2010a, b,

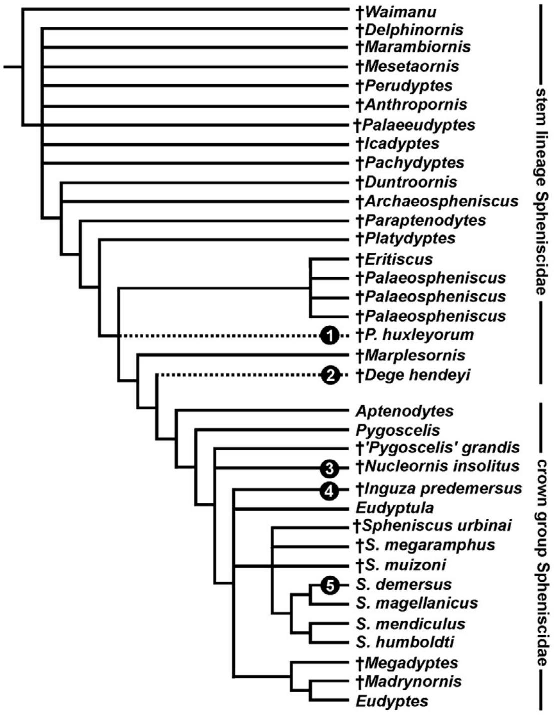

FIGURE 2. Simplified cladogram of stem-lineage and crown group penguins after Ksepka & Clarke (2010) and Ksepka & Thomas (2012). Note that †*Palaeospheniscus*? *huxleyorum* was not included in these phylogenetic analyses, but tentatively assigned by Ksepka & Clarke (2010) to a clade that also comprises other species of †*Palaeospheniscus* as well as †*Eritiscus*, †*Dege hendeyi*, †*Marplesornis*, and crown group Spheniscidae. The systematic position of †*Dege hendeyi* outside crown group Spheniscidae is based on one plesiomorphic character and regarded as being only tentative (Ksepka & Clarke 2010). Extinct species are indicated by a dagger (†), numbers (1–5) refer to the number of independent colonization events that occured by the late Miocene (1–4) and during the Plio-Pleistocene (5), respectively.

2013; Ksepka & Thomas 2012; Manegold & Louchart 2012; Louchart unpubl. data) also indicate that the palaeoenvironments were diverse and mosaic-like, and that the biogeographical history of certain taxa is more complex than previously thought. These findings are summarized and discussed in the following sections.

The Marine Avifauna

Penguins were the first fossil birds described from Langebaanweg by George Gaylord Simpson, who distinguished and named the four species *Dege hendeyi*, *Inguza predemersus*, *Nucleornis insolitus*, and *Palaeospheniscus*? *huxleyorum* (Simpson 1971, 1973, 1979a, b). All these species differ markedly in size, with *N. insolitus* being comparable in size to the largest modern penguins (*Aptenodytes*) and with *I. predemersus* being slightly smaller than the extant African Penguin (*Spheniscus demersus*) (Simpson 1971, 1973, 1979a, b; Olson 1985b). Although Simpson considered these species to be closely related, he nevertheless described them as four extinct genera. *N. insolitus*, and *P. huxleyorum* have been originally described from the Upper Varswater Formation exposed at Duinefontein and Ysterplaat, respectively, but all four species were subsequently recorded for Langebaanweg (Olson 1985b) with breeding evidence for *I. predemersus* at least (Ksepka & Thomas 2012).

Two recent cladistic analyses found no support for monophyletic Varswater penguins or for their close relationship to *S. demersus*, but indicate that probably neither *D. hendeyi* nor *P. huxleyorum* were part of crown group Spheniscidae (Ksepka & Clarke 2010: pp. 26–29), and that *Aptenodytes, Pygoscelis,* and *N. insolitus* are successive sister taxa to all the remaining crown group penguins, though the phylogenetic relationships of the aforementioned taxa to *'Pygoscelis' grandis* Walsh & Suarez, 2006 are still uncertain (Ksepka & Thomas 2012) (Fig. 2). *Inguza predemersus* turned out to be part of a clade that also comprises the extant genera *Eudyptes, Eudyptula,* and *Spheniscus* (Ksepka & Thomas 2012) (Fig. 2). Based on these hypotheses it seems evident that four penguin lineages colonized Southern Africa independently by the Late Miocene, whereas the ancestor of *S. demersus* arrived later sometime during the Plio-Pleistocene (Ksepka & Clarke 2010; Ksepka & Thomas 2012; Thomas & Ksepka 2013).

Aside from the four species of penguins, the marine avifauna of the Upper Varswater Formation comprises three species of cormorants (Phalacrocoracidae), a small booby (Sulidae; also known from Duinefontein; Olson 1985b), two species each of gulls and terns, and eight species of tubenoses (Procellariiformes) (Olson 1983; 1985a). However, some of the cormorants, gulls, and terns might also have been associated with fresh water habitats (Olson 1983).

Only tubenoses have been adequately described. Remains of juveniles indicate that an albatross, a storm-petrel, and at least one, but possibly three prion species bred close to the fossil site (Olson 1985a). Such a diverse marine avifauna is striking and comparable only to the present situation on certain Subantarctic islands (Olson 1983). Not a single species of tubenoses breeds on any African continental island today (Olson 1983), and only the African Penguin breeds along the Southern African coast with its small offshore islands, alongside with Cape Gannet (*Morus capensis*) and three cormorant species (*Phalacrocorax capensis*, *Miocarbo coronatus*, and *M. neglectus*) (Harrison *et al.* 1997).

One explanation for the past diversity in seabirds is the greater number of potential nest sites for these taxa at that time. At the beginning of the Pliocene, sea levels were about 50 m above present-day conditions turning the West Coast Peninsula as well as Table Mountain and other peaks of the Cape Peninsula into large islands and thus providing suitable breeding sites for marine birds (Olson 1983; Ksepka & Thomas 2012).

Furthermore, it was assumed that the past seabird diversity provides strong evidence that the Benguela Upwelling System off the southwest coast of Africa was both colder and richer in nutrients than today (Olson 1983: p. 400). Recent estimates of past sea surface and subsurface temperatures indicate, however, that the Benguela Current was in fact much warmer than today during a period between 6.5 and 5 Ma, because the exchange between Antarctic deep water mass and North Atlantic Deep Water was reduced and consequently the heat export from the South Atlantic decreased (Rommerskirchen *et al.* 2011). Water temperatures remained warmer than today – although began decreasing at the beginning of the Pliocene (Diester-Haass *et al.* 2002; Rommerskirchen *et al.* 2011). Marine productivity was nevertheless high and kept rising during this period (Rommerskirchen *et al.* 2011), and was obviously sufficient for sustaining large seabird colonies.

The Terrestrial Avifauna

Woodland species

Recent studies of several evidently woodland dwelling bird taxa such as a true woodpeckers (Picinae, Picidae), honeyguides (Indicatoridae), parrots (Psittacoidea), and several species of songbirds (Oscines, Passeriformes) strongly support current hypotheses that woodlands were more extensive at Langebaanweg than previously thought.

The recently described (Manegold & Louchart 2012) true woodpecker from Langebaanweg, *Australopicus nelsonmandelai* (Fig. 3A–F) was comparable in size with the Greater Spotted, *Dendrocopos major*, or Red-bellied Woodpecker, *Melanerpes carolinus*. A phylogenetic analysis of 50 morphological characters shows that the fossil species is not closely related to any of the extant African woodpecker taxa such as *Campethera*, *Geocolaptes* or *Dendropicos*, but to a clade that comprises woodpeckers that are primarily characteristic of dense woodlands or forests in the tropics of the Old and New World, such as *Celeus* and *Dryocopus* (Fig. 4). Furthermore, the tarsometatarsus of the fossil woodpecker is short and stout (Fig. 3D–E), which is characteristic of the more arboreal woodpecker species, whereas more terrestrial woodpeckers such as *Campethera* or *Geocolaptes* have more elongated tarsometatarsi. Thus, the fossil woodpecker represents a previously unknown lineage of Eurasian origin with a strong association to woodlands. *Australopicus* probably became separated from its relatives in Eurasia during the period of general expansion of grasslands at the expense of forests and woodlands in the Late Miocene (Manegold & Louchart 2012) that also led to the separation of other picine lineages (Fuchs *et al.* 2007), *Sasia*-piculets (Fuchs *et al.* 2006) and many other 'forest relicts' (Louchart 2003; Louchart *et al.* 2005a, 2008).

Extant honeyguides (Indicatoridae) also inhabit forests and various kinds of woodland, but avoid open savannah. Thus, evidence for Indicatoridae in the fossil record clearly indicates presence of wooded areas at or close to the fossil site. Langebaanweg honeyguides were first noticed by Olson (1985d), but only recently

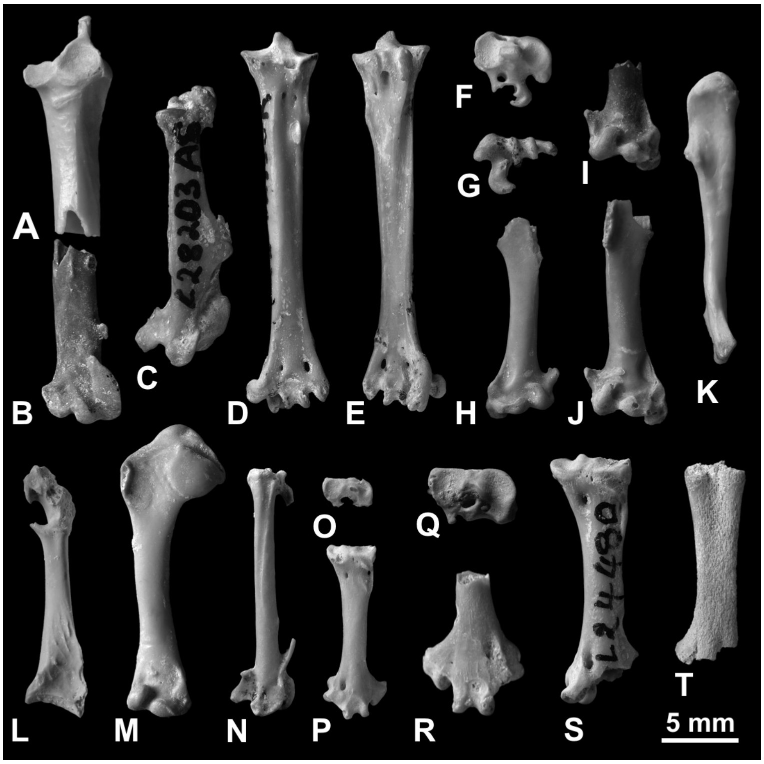

FIGURE 3. Recently described bird fossils from the Upper Varswater Formation, Langebaanweg (Early Pliocene, South Africa). (**A–F**) *Australopicus nelsonmandelai* (Picinae, Picidae): (**A**) right proximal ulna SAM PQ-L70284 in cranial view; (**B**) right distal ulna SAM PQ-L28428V in ventral view; (**C**) right carpometacarpus SAM PQ-L28203AS in dorsal view; (**D–E, G**) right tarsometatarsus L25293GR (holotype) in dorsal (**D**), plantar (**E**), and distal view (**G**); (**F**) right tarsometatarsus SAM PQ-L28199EE in proximal view. (**H–J**) Humeri of medium sized (**H**) and large (**I–J**) swallow species (Hirundinidae, Passeriformes) in cranial view: (**H**) left distal humerus SAM PQ-L 70289; (**I**) right distal humerus SAM PQ-L 70406; (**J**) right distal humerus SAM−PQ L 70288. (**K**) Left coracoid SAM PQ-L 20733N2 of a nightjar (Caprimulgidae) in medial view. (**L-P**) Lovebird *Agapornis attenboroughi* (Agapornithinae, Psittacoidea): (L) right coracoid SAM PQ-L704543 in dorsal view; (**M**) right humerus SAM PQ-L70432 in cranial view; (**N**) right carpometacarpus SAM PQ-L70451 in dorsal view; (**O–P**) right tarsometatarsus SAM-PQ-L70448 in proximal (**O**) and dorsal view (P). (**Q–T**) Psittacine parrot *Khwenena leopoldinae*: (**Q, S**) Right tarsometatarsus SAM PQ-L24480 in proximal (**Q**) and dorsal view (**S**); (**R**) left distal tarsometatarsus SAM PQ-L70432 in dorsal view; (**T**) left tarsometatarsus SAM PQ-L70441 of nestling parrot in dorsal view (Manegold 2010a, b, 2013; Manegold & Louchart 2012).

discovered material shows that in fact two species can be distinguished, which are tentatively referable to the genus *Indicator*. Both species were very small, but comparable to the tiny Least Honeyguide *I. exilis* and the only slightly larger Lesser Honeyguide *I. minor*, respectively. Although the biology and ecology of modern Indicatoridae are still insufficiently known, it seems evident that the last common ancestor of Indicatoridae was a brood parasite, and that the stem species of *Indicator* already had a strong preference for cavity nesting foster species, especially barbets (Short & Horne 2002). Thus, the fossil honeyguides could have benefited from the excavating activities of *Australopicus*. Surprisingly, barbets are as yet not evident in the fossil record of Langebaanweg, and probable foster species for the two indicatorids remain to be identified. The co-occurrence of two species of *Indicator* and the honey badger *Mellivora benfieldi* at Langebaanweg (Hendey 1978) is worth mentioning, although the alleged symbiotic relationship between the extant Greater Honeyguide *I. indicator* and Honey Badger *Mellivora capensis* is only a myth (Dean *et al.* 1990).

Previous studies supposed that two or three parrot species can be distinguished in the fossil record of Langebaanweg (Rich 1980; Stidham

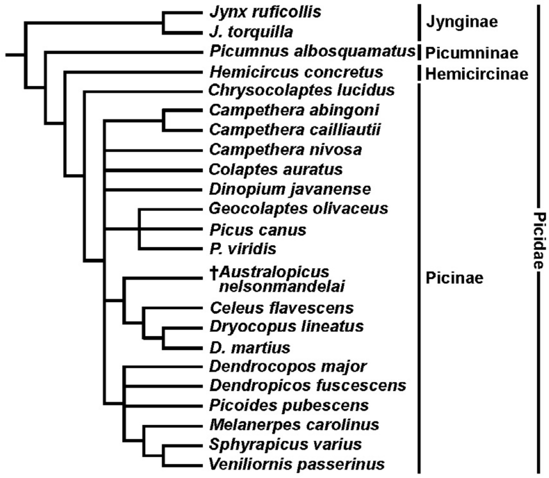

FIGURE 4. Simplified cladogram of woodpeckers (Picidae) based on a cladistic analysis of 50 morphological characters. *Australopicus nelsonmandelai* is sister taxon to a clade that comprises malarpicine woodpeckers primarily characteristic for tropical and subtropical forests (Manegold & Louchart 2012).

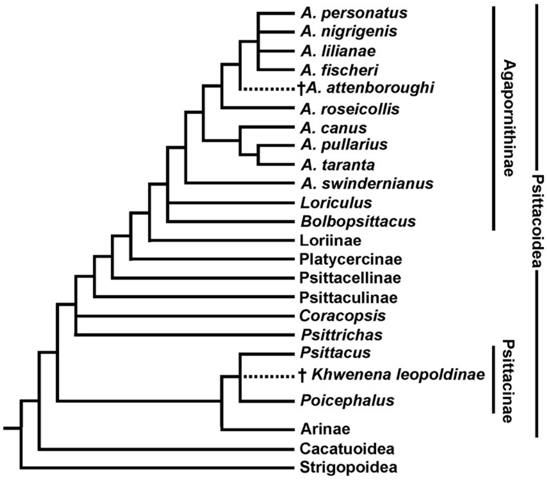

FIGURE 5. Simplified cladogram of parrots (Psittaciformes) after Joseph *et al*. (2012) indicating the phylogenetic position of the newly described lovebird and psittacine parrot from the Upper Varswater Formation, Langebaanweg (Manegold 2013). Phylogenetic position of *A. swindernianus* is only tentative and awaits further study.

2006). Stidham (2006) identified a species of lovebird (*Agapornis* sp.) and two other parrot species of uncertain affinities. Based on additional specimens (Fig. 3L–P), a new species of lovebird, *A. attenboroughi*, was described (Manegold 2013), which is comparable in size to the small species of the *A. personatus*-group and which probably is a stem lineage representative of this taxon (Fig. 5). Except for the Black-collared Lovebird *A. swindernianus*, all lovebirds avoid primary forest, but prefer different kinds of woodlands (Moreau 1948), and such habitat preferences might also apply to the fossil species. Although seeds of C_4 grasses play an important role in the diet of *A. roseicollis* and *A. nigrigenis* (Warburton & Perrin 2005; Ndithia & Perrin 2006) it would be premature to take the new species of lovebird as an indicator of C_4 grasslands.

Khwenena leopoldinae is the second, recently described species of fossil parrot from Langebaanweg (Fig. 3Q–T; Manegold 2013). It is of the size of the extant Ring-necked Parakeet *Psittacula krameri*, but is more closely related to the African Grey Parrot *Psittacus erithacus* and the genus *Poicephalus* (Fig. 4). Similarly to extant *Poicephalus* species, *K. leopoldinae* probably preferred woodlands with tall trees bearing suitable nest cavities – often provided by the Amethyst Starling *Cinnyricinclus leucogaster* and two additional species of Sturnidae, which are among the most common songbirds in the fossil record of Langebaanweg. *Cinnyricinclus leucogaster* is no longer part of the Western Cape avifauna, but common in different kinds of African woodlands, where it breeds in tree cavities like most sturnids. It seems likely that this breeding behaviour also applied for all three fossil starling species, although building of exposed globular or domed nests evolved independently in several, only distantly related lineages of Sturnidae (Lovette & Rubenstein 2007; Craig & Feare 2009).

A fragmentary tarsometatarsus of a tiny songbird shows all the features characteristic for the closely related Old World warblers and babblers (Sylviidae and Timaliidae *sensu* Gelang *et al.* 2009). Extant Sylviidae with African and Eurasian distribution are regarded as typical for drier habitats, but Timaliidae are in general more characteristic for different types of forest, woodland, and thickets (Gelang *et al.* 2009).

Non-marine aquatic and semi-aquatic birds

About one third of all bird species were typical for freshwater habitats. They comprise approximately 10–15% of all bird remains known from Langebaanweg and include predominantly members of the Charadriidae (ca. 15 species), and Anatidae (at least 4 species mainly by size groups). The latter family includes a large species, which probably represents the swan genus *Afrocygnus* Louchart *et al.*, 2005b (Louchart unpubl. data), based on the morphology of the humerus (Louchart *et al.* 2005b). This extinct endemic African swan was hitherto known from northern Africa only, and today swans are absent from sub-Saharan Africa (Louchart *et al.* 2005b).

Species of dry open grasslands, savannah and/or arid habitats

Taxa characteristic for open habitats are the already mentioned ibis *Geronticus apelex* and stork *Ciconia kahli* (Olson 1985c; Haarhoff 1988), but also the as yet not described species of sandgrouse (Pteroclidae), bustards (Otididae), and thick-knees (Burhinidae) (Rich 1980; Louchart unpubl. data). Presence of fossil sandgrouse (Pteroclidae) and bustards (Otididae) at Langebaanweg was already mentioned by Rich (1980). More recent studies show that at least two species of *Pterocles* can be distinguished, which makes them the earliest record for crown group sandgrouse in the world (Louchart unpubl. data). Both *Pterocles* species differ in size, with the larger one being comparable to the extant Crowned Sandgrouse, *P. coronatus,* and the smaller species being even smaller than the modern Namaqua Sandgrouse, *P. namaqua* (Louchart unpubl. data). Today sandgrouse are among the most characteristic bird species of arid and semi-arid regions throughout Africa and Asia. Such preference for arid conditions might have been already present in stem-lineage representatives of modern Pteroclidae from the Palaeogene and Early Miocene of France (Mourer-Chauviré 1992). A thick-knee and two species of bustards, one of them as large as the huge Denham's Bustard, *Ardeotis denhami*, but the second smaller and of the size of extant *Afrotis* bustards (Louchart unpubl. data), are represented by a handful of fossil remains each. The bustards in particular (less clearly so the thick-knee as some today favour rather humid habitats) also indicate arid to semi-arid environments, i.e. deserts to semi-wooded savannah, at or quite close to Langebaanweg five million years ago (Louchart unpubl. data).

Ostriches are among the most characteristic bird species of open habitats. The extant *Struthio camelus*, with four living and one recently extinct subspecies, prefers open short-grass plains and semi-deserts, and avoids areas with tall grass as well as dense woodlands, although open mopane woodland seems to be suitable for *S. camelus australis* (Brown *et al.* 1982: p. 33). Fossil ostriches from SE Europe and the Middle East are characteristic elements of the *Hipparion*-fauna (Boev & Spassov 2009). The presence of fossil ostriches in the Langebaanweg Varswater Formation has long been known (Rich 1980; Hendey 1982: p. 70) but no study of this material has been undertaken before.

Thirteen among 17 leg bone fragments proved measurable in some dimensions except for the length of femur, tibiotarsus and tarsometatarsus as these bones are preserved only as proximal, distal or shaft fragments, which makes straightforward body size estimations impossible. However, all available measurement values of these bones are substantially higher than those of any *S. camelus*, indicating a larger body size. The tibiotarsal shaft depth is 107.1%–127.1% and the distal end measurements 105.6% (width) and 116.6% (lateral depth) of the mean values for extant ostriches. The values for the fibular shaft are 105% (width) and 122% (diameter), and those of the tarsometatarsal shaft about 114% (depth) and 123% (width) of the mean for *S. camelus*. These ranges (especially in shaft depth) exceed the adult variation between the extant ostrich subspecies (SD = 4.3%) and thus call for an explanation. Bone texture is not obviously unfinished in any of the five Langebaanweg tibiotarsi, which makes age-related variation unlikely to be responsible for the observed size ranges. The shaft depth reveals an indication of bimodality with two specimens measuring exactly 35.6 mm and two about 32 mm, which suggests either two (sub)species or sexual dimorphism. Except for size there is no evidence for two species and both larger and smaller specimens share the lateral trochlear crest that is more oblique than in Pleistocene and extant ostriches. Therefore, the observed size differences seem to be better accounted for by sexual dimorphism. In the extant ostriches the tibiotarsus (as well as femur and tarsometatarsus) tends to be wider and/or deeper in females (Elzanowski *et al.*, unpubl. data). In addition to the four discussed tibiotarsi, the smallest Langebaanweg tibiotarsus (SAM PQ-L50093A) has the shaft depth (30 mm, 107.1 % of the average for *S. camelus*) as in *S. barbarus* Arambourg, 1979 from the Villafranchian of North Africa thus leaving a possibility of a second, smaller ostrich (sub)species being represented at Langebaanweg.

In contrast to the other leg bones, the Langebaanweg phalanges are essentially of the same length as those of the largest *S. camelus*. Since the Langebaanweg ostriches were larger, their phalanges were shorter relative to body size than they are in the extant ostriches. The Langebaanweg III/1 phalanges are similar in proportions to those of *S. camelus* and differ from the prevailing type of Pleistocene phalanges that are much less waisted and thus more cylindrical or rod-shaped than the Langebaanweg and extant *S. camelus* specimens.

In both size and shape of the phalanges as well as the body size (as approximated form the measurements of other leg bones), the large Langebaanweg ostriches are comparable to *S. asiaticus* as described from the latest Pliocene of North Africa (Morocco) by Mourer-Chauviré & Geraads (2008). *Struthio asiaticus* is about 20 % larger than large *S. camelus* specimens and so are the shaft measurements of larger tibiotarsi, fibula, and tarsometatarsus from Langebaanweg. Growing larger (especially taller) is a common defence adaptation that is easiest to achieve developmentally. The Early Pliocene fauna of Langebaanweg abounded in large mammalian predators such as sabre-toothed felids, hyaenas, and giant civets (Hendey 1982; Werdelin 2006). However, the size dynamics of fossil ostriches needs to be discussed in a broader geographic and stratigraphic context. While in the post-Pliocene southern Africa the ostriches consistently decrease in size, even larger ostriches appeared in the Early Pleistocene of Kenya (Leakey 1965) and elsewhere. This suggests a role of local ecological factors that need to be analysed and compared against a paleogeographic background.

A guild of aerial insect hunters

Aerial insect hunters such as nightjars (Caprimulgidae) (Fig. 3K), swifts (Apodidae) and swallows (Hirundinidae) (Fig. 3H–J) are rarely described from pre-Pleistocene fossil localities, and evidence for all three taxa at Langebaanweg represents their first occurrence in the fossil record of Africa. Unfortunately, their use for palaeoenvironmental reconstructions is only limited. Habitat preferences of the Langebaanweg's nightjar cannot be deduced from the isolated coracoid referred to this species (Manegold 2010a), and although open woodlands might have been the ancestral habitat of Caprimulgidae, few more forest adapted nightjars occur in Central Africa (*Caprimulgus batesi*, *Veles binotatus*) and Madagascar (*Gactornis enarratus*) (Cleere & Nurney 1998, Han *et al.* 2010). The swift, known from a single humerus only and with strong resemblance to extant Alpine Swift *Tachymarptis melba* and Mottled Swift *T. aequatorialis* (Louchart unpubl. data) probably exploited food resources at Langebaanweg, but might have relied on the presence of rock crevices for nest building like most of the extant Apodidae (Chantler 1999). The rocky escarpments of the Piketberg massif, 50 km E of Langebaanweg, were already proposed as possible breeding site for the putative cliff nesting ibis *Geronticus apelex* (Olson 1985c), but might also have been used by swifts. The same might also apply for the two unidentified species of Hirundinidae (Manegold 2010b), because many extant swallows and martins breed in rock crevices or attach their mud nests to rock surfaces, but based on the limited fossil material it cannot be ruled out that the fossils retained the ancestral behaviour of Hirundinidae of excavating burrows in riverbanks (Winkler & Sheldon 1993; Manegold 2010b).

Discussion

A palaeoecological analysis of the highly diverse fossil avifauna indicates that the Early Pliocene Langebaanweg area was characterized by a mosaic of many fairly diversified habitats ranging from almost arid regions and open grasslands to floodplains, marshes, and woodlands. Evidence for typical inhabitants of tropical and subtropical forests such as pittas (Pittidae), broadbills (Eurylaimidae) and trogons (Trogonidae) is missing. This is in line with the lack of other key indicators of tropical or subtropical climate such as crocodiles (Crocodylia) (HENDEY 1973), and the general temperate character of the rest of the fauna and flora. Other groups of primarily forest taxa with a few secondarily dwellers of well-wooded savannah such as turacos (Musophagidae) and hornbills (Bucerotidae) are also missing. Apparently, precipitation at Langebaanweg was too low during the early Pliocene for sustaining forests that are suitable for these bird species. Surprisingly, there is still no evidence of barbets (Ramphastidae) and cuckoos (Cuculidae), which today are found in various habitats throughout sub-Saharan Africa. Even more remarkable is the absence of many aquatic taxa such as anhingas (Anhingidae), flamingos (Phoenicopteridae), herons (Ardeidae), or pelicans (Pelecanidae), which are known from the Miocene and Pliocene of sub-Saharan Africa (OLSON 1985c; LOUCHART *et al.* 2008). None of these taxa are strongly linked to tropical or subtropical climates, and it is hard to believe that they did not reach southern Africa in the early Pliocene. On the other hand, there is no obvious taphonomic phenomenon that might explain their absence from the fossil record. OLSON & ELLER (1989) supposed that the absence of these taxa could be explained by too small size and ephemeral nature of suitable aquatic habitats. However, the record of a hippopotamine, numerous anatids, charadriiforms, and rallids strongly suggests that fresh water habitats were present in the early Pliocene Langebaanweg area. The absence of flamingos alone (but not other missing groups) could be explained by the absence of alkaline or saline lakes that these birds require for feeding, and brackish lagoons or estuaries for their breeding colonies.

Birds continue to provide unique cues to the reconstruction of the Early Pliocene environment and local climate at Langebaanweg. Ongoing and future studies of certain bird groups will add more lines of evidence and help refine the present interpretations.

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Appendix

TABLE 1. Bird taxa of the Upper Varswater Formation at Langebaanweg, earliest Pliocene of South Africa, and their likely preferential habitat types. As far as possible, the number of specimens (n) followed by the estimated minimum number of individuals (mni) is given for each species. Only rough estimates are given for certain taxa such as ducks, geese and swans (Anatidae), cormorants (Phalacrocoracidae), and birds of prey (Accipitridae). No hypotheses on the probable habitat types of the fossil representatives of birds of prey, doves and pigeons (Columbidae), owls (Strigidae), swallows (Hirundinidae), and swifts (Apodidae) are given because of their diverse habitat preferences.

Taxon	Abundance n/mni	Habitat type	References
Struthioniformes, Struthionidae			
Struthio cf. *asiaticus* Milne-Edwards, 1871	24/ <5	dry open grasslands, savannah and/or arid habitats, fynbos, marginally open woodlands	Rich (1980); Elzanowski *et al.* (unpubl. data)
possibly another *Struthio* sp.	1/1		
Galliformes, Phasianidae			
Francolinus sp.	– / > 500	open savannah and bushlands	Rich (1980);Crowe (1992)
Dendroperdix aff. *sephaena* (A. Smith, 1836)			
cf. *Coturnix* sp.	Rare	open grasslands, fynbos	Rich (1980); Hendey (1981)
Anseriformes, Anatidae			
Anatidae gen. et sp. indet., sp. A, small	– / > 40	various fresh water habitats	Rich (1980, unpubl. data); Louchart, (unpubl. data)
Anatidae gen. et sp. indet., sp. B, small/ medium			
Anatidae gen. et sp. indet., sp. C, medium/ large			
cf. *Afrocygnus* sp.			
Sphenisciformes, Spheniscidae			
Inguza predemersus (Simpson, 1971)	7/2	marine	Simpson (1971, 1973, 1979a, b); Olson (1983, 1985b); Ksepka & Thomas (2012)
Dege hendeyi Simpson, 1979a	14/3		
Nucleornis insolitus Simpson, 1979b	2/2		
Palaeospheniscus? *huxleyorum* Simpson, 1973	Few		
Procellariiformes, Diomedeidae			
Diomedea sp.	1/1	marine	Olson (1985a)
Procellariiformes, Oceanitidae (Oceanitinae)			
Oceanites zaloscarthmus Olson, 1985a	176/23	marine	Olson (1985a)
Procellariiformes, Procellariidae			
Pachyptila salax Olson, 1985a	203/20	marine	Olson (1985a)
Pachyptila sp. B	2/2		
Pachyptila sp. C	4/3		
Puffinus sp.	3/3		
Procellariidae gen. et sp. indet.	1/1		

Taxon	Abundance n/mni	Habitat type	References
Procellariiformes, Pelecanoididae			
Pelecanoides cymatotrypetes Olson, 1985a	3/2	marine	Olson (1985a)
Podicipediformes, Podicipedidae			
Podiceps? sp.	3/1	various fresh water habitats	Olson (1994)
Tachybaptus ruficollis (Pallas, 1764)	56/16	various fresh water habitats	Olson (1994)
Ciconiiformes, Ciconiidae			
Ciconia kahli Haarhoff, 1988	30/2	open savannah and bushlands, fynbos?	Haarhoff (1988)
Ciconiiformes, Threskiornithidae			
Geronticus apelex Olson, 1985c	15/2	grasslands, open savannah and bushlands	Olson (1985c)
Threskiornis aff. *aethiopicus* (Latham, 1790)	1/1	various fresh water habitats, grasslands	Olson (1985c)
Pelecaniformes, Scopidae			
Scopus xenopus Olson, 1984	2/2	various fresh water habitats	Olson (1984)
Pelecaniformes, Sulidae			
Sula sp.	4/4	marine	Olson (1983, 1985b)
Pelecaniformes, Phalacrocoracidae			
Phalacrocorax sp. A, small	– / >25	marine?	Olson (1983, 1985b)
Phalacrocorax sp. B, medium sized			
Phalacrocorax sp. C, medium sized			
Falconiformes, Falconidae			
Falconidae gen. et sp. indet.	– / ca. 5	–	Rich (1980)
Accipitriformes, Accipitridae		–	
Accipitridae, Aegypiinae gen. et. sp. indet., sp. A	– /10	–	Rich (1980)
Accipitridae gen. et. sp. indet., sp. B			
Accipitridae gen. et. sp. indet., sp. C			
Accipitridae gen. et. sp. indet., sp. D			
Accipitridae gen. et. sp. indet., sp. E			
Gruiformes, Otitidae			
Otitidae gen. et sp. indet., sp. A, small	16/ < 5	dry open grasslands, scrubland, fynbos, savannah and/or arid habitats, marginally open woodlands	Rich (1980); Louchart (unpubl. data)
Otitidae gen. et sp. indet., sp. B, larger			
Gruiformes, Rallidae			
several species; ranging from crake to *Porphyrio* size	– / <10	various fresh water habitats	Rich (1980); Olson (unpubl. data)
Gruiformes, Gruidae			
Gruidae gen et. sp. indet.	2/2	wetlands, open grasslands	Rich (1980); Louchart (unpubl. data)

Taxon	Abundance n/mni	Habitat type	References
Charadriiformes, Turnicidae			
Turnix cf. *hottentottus* Temminck, 1815	1/1	short, moist grasslands	Olson (1994)
Charadriiformes, Burhinidae			
Burhinidae gen. et sp. indet.		dry open grasslands, fynbos, savannah and/or arid habitats	Rich (1980); Olson (unpubl. data), Louchart (unpubl. data.)
Charadriiformes, Recurvirostridae			
Himantopus sp.		wetlands	Rich (1980); Olson (unpubl. data)
Charadriiformes, Scolopacidae			
aff. *Gallinago* sp.		open wetlands, swamps, marshes	Rich (1980); Olson (unpubl. data)
Charadriiformes, Charadriidae			
Charadrius sp. A, similar in size to *C. pecuarius*	mni > 50	open wetlands, grasslands, seashores	Rich (1980); Olson (unpubl. data)
Charadrius sp. B, similar in size to *Pluvialis apricaria*			
Charadrius sp. C, smallest of all fossil *Charadrius*			
Charadrius sp. D, of the size of *C. marginatus*			
Charadrius sp. E, of the size of *C. placidus*			
Charadrius sp. F, of the size of *C. leschenaultii*			
Charadrius sp. H, of the size of *C. tricollaris*			
Charadrius sp. I, of the size of *C. mongolus*			
cf. *Vanellus senegallus* (Linneaus, 1766)			
cf. *Vanellus crassirostris* (Hartlaub, 1855)			
cf. *Vanellus albiceps* Gould, 1834			
cf. *Vanellus armatus* (Burchell, 1822)			
Charadriidae gen. et sp. indet., similar to *Vanellus* (*Stephanibyx*) spp.			
Charadriidae gen. et sp. indet., similar in size to *P. apricaria* or larger			
Charadriiformes, Rostratulidae			
Rostratula minator Olson & Eller, 1989	16/4	open wetlands, swamps, marshes	Olson & Eller (1989)
Charadriiformes, Laridae			
Larus sp. A, medium sized	Rare	marine?	Olson (1983, 1985b)
Larus sp. B, large sp.	1/1		
Sterna sp. A, medium sized	Few		
Sterna sp. B, larger	Few		

Taxon	Abundance n/mni	Habitat type	References
Columbiformes, Pteroclidae			
Pterocles sp. A	– / < 5	grasslands, open arid/ semiarid habitats	Rich (1980); Louchart (unpubl. data)
Pterocles sp. B			
Columbiformes, Columbidae			
Columbidae gen. et sp. indet., sp. A	– /10	–	Rich (1980)
Columbidae gen. et sp. indet., sp. B			
Psittaciformes, Psittacoidea			
Agapornis attenboroughi Manegold, 2013	30/4	woodlands	Rich (1980, unpubl. data); Stidham (2006); Manegold (2013),
Khwenena leopoldinae Manegold, 2013	6/5	woodland	Rich (1980, unpubl. data); Stidham (2006); Manegold (2013)
Psittacoidea gen. et sp. indet., large	1/1	woodlands	Stidham (2006); Louchart (unpubl. data)
Strigiformes, Strigidae			
Strigidae gen. et sp. indet., sp. A	– /10–15	–	Rich (1980)
Strigidae gen. et sp. indet., sp. B			
Coliiformes, Coliidae			
Colius hendeyi Rich & Haarhoff, 1985	124/26	open savannah and bushlands	Rich & Haarhoff (1985)
Alcediniformes, Alcedinidae			
Ceryle sp.	2/1	wetlands	Olson (1994)
Halcyon sp.	1/1	open savannah and bushlands	Olson (1994)
Piciformes, Picidae			
Australopicus nelsonmandelai Manegold & Louchart, 2012	14/4	woodlands, forest	Manegold & Louchart (2012)
Piciformes, Indicatoridae			
cf. *Indicator* sp. A	– /4	woodlands, forest	Olson (1985d); Louchart & Manegold (unpubl. data)
cf. *Indicator* sp. B			
Apodiformes, Apodidae			
cf. *Tachymarptis* sp.	1/1	–	Rich (1980); Louchart (unpubl. data)
Caprimulgiformes, Caprimulgidae			
Caprimulgidae gen. et sp. indet.	1/1	open woodlands?	Manegold (2010a)
Passeriformes	– / >100		
Hirundinidae gen. et sp. indet., sp. A	3/3	–	Manegold (2010b)
Hirundinidae gen. et sp. indet., sp. B	2/2	–	Manegold (2010b)
Sturnidae gen. et sp. indet., sp. A		woodlands?	
Sturnidae gen. et sp. indet., sp. B		woodlands?	
Sturnidae gen. et sp. indet., sp. C, aff. *Cinnyricinclus leucogaster*	1/1	woodlands	
Sylvioidea, gen. et sp. indet.	1/1	woodlands?	