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Author: Manegold, Albrecht

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Brief report

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Two swallow species from the early Pliocene of Langebaanweg (South Africa)

ALBRECHT MANEGOLD

The Varswater Formation of Langebaanweg at the west coast of South Africa is one of the few fossil sites in Africa dating from the early Pliocene (approx. 5 Mya) (Hendey 1981) and excels in being especially rich in well preserved, though generally isolated, bird remains. Rich (1980: 166) regarded this site as richest pre-Pleistocene bird bone accumulation in the world with at least 60 bird species representing among them penguins, tubenoses, parrots and mousebirds. Studies on seabirds, ibises and other taxa (Olson 1985a, b, 1994) indicated that the Pliocene avifauna is even more diverse than initially thought. Passerines are represented by at least nine species (Rich 1980), but no attempts have been made so far to identify these specimens below the subordinal level. The screening of previously unsorted and unidentified material excavated during the 1960s and 1970s at "E" Quarry, Langebaanweg, yielded several hundred remains of passerines. This sample included five fragmentary humeri that show the characteristics of swallows and martins (Hirundinidae), which are described herein.

Material and methods

The fossil specimens were compared with specimens of 18 extant swallow and martin species representing ten out of 19 hirundinid genera (Turner 2004; Sheldon et al. 2005) from Africa, Australia, Eurasia, and North America (Appendix 1). This taxon sampling included *Cheramoeca*, *Psalidoprocne*, and *Pseudhirundo*, that are regarded as basal lineages within Hirundinidae (Sheldon et al. 2005). Unfortunately, no specimens of river martins (*Pseudochelidon*), sister taxon of all the remaining hirundinids (the Hirundininae; see Lowe 1938; Gaunt 1969; Sheldon et al. 2005), were available for comparison. Thus, characters described in the following as diagnostic features for swallows and martins might actually apply to Hirundininae only. Also unavailable were specimens of the rare, but apparently phylogenetically crucial, African genus *Phedina* (Sheldon et al. 2005). Lack of comparative material further prevents comparisons with most of the genera restricted to the New World.

Nomenclature of osteological terms follows Baumel and Witmer (1993), unless stated otherwise.

Measurements up to a length of 16 mm were taken by means of a WILD stereo microscope equipped with a camera lucida and an adjustable eyepiece measure (Leica MOK-93) calibrated to an object reference measure accurate to 0.1 mm. Sections >16 mm were measured with vernier callipers accurate to 0.1 mm. Measurements were taken in accordance with the descriptions by von den Driesch (1976).

Institutional abbreviations.—SAM-PQ, Cenozoic Collections of Iziko the South African Museum, Cape Town.

Other abbreviations.—M., Musculus; PPM, Pellatal Phosphorite Member; QSM, Quartzose Sand Member.

Systematic paleontology

Order Passeriformes (Linnaeus, 1758)
Family Hirundinidae Vigors, 1825
Hirundinidae gen. et sp. indet.

Figs. 1, 2.

Material.—Large species: SAM-PQ L 24915T, left humerus; SAM-PQ L 70288, right distal humerus; SAM-PQ L 70406 right distal humerus (Fig. 1). Medium-sized species: SAM-PQ L 70289, left distal humerus; SAM-PQ L 70290, right distal humerus (Fig. 2).

Remarks.—All five humeri show the following characters diagnostic for hirundinids (Figs. 1, 2). The humeri are short with stout shafts; their dorso-caudal part, including processus supracondylaris dorsalis and sulcus scapulotricipitalis, is well developed, reaching far proximally and ventrally; the processus flexorius is large and extends far distally (note, however, that the distal end is not preserved in SAM-PQ L 24915T). The proximal end of the humerus is heavily damaged in all five specimens; only in SAM-PQ L 24915T it is sufficiently well preserved so two additional features of hirundinids are discernable (Fig. 1A$_2$). The dorsal, secondary fossa pneumotricipitalis is a distinct oval depression just distal of the head of the humerus. The ventral fossa pneumotricipitalis is very deep, but not pneumatic as it is the case with most hirundinids studied. African saw-wings (*Psalidoprocne*) and the Banded Martin (*Riparia cincta*) are exceptional in having a pneumatic ventral fossa pneumotricipitalis.

The preservation of the fossil specimens does not allow their assignment to any particular extant genus or species of hirundinids. However, the specimens differ from each other in respect to size and morphological features, indicating that at least

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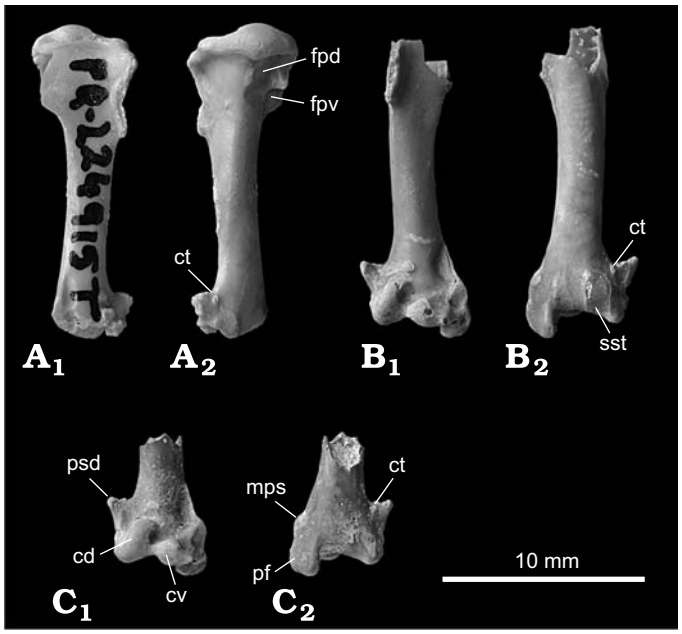

Fig. 1. Fragmentary humeri of a large swallow species from the early Pliocene Varswater Formation at Langebaanweg, South Africa in cranial (A_1, B_1, C_1) and caudal (A_2, B_2, C_2) view. **A**. Left humerus SAM-PQ L 24915T. **B**. Right distal humerus SAM-PQ L 70288. **C**. Right distal humerus SAM-PQ L 70406. Abbreviations: cd, condylus dorsalis; ct, caudal tubercle; cv, condylus ventralis; fpd, fossa pneumotricipitalis dorsalis; fpv, fossa pneumotricipitalis ventralis; mps, attachment site for tendon of M. pronator superficialis; pf, processus flexorius; psd, processus supracondylaris dorsalis; sst, sulcus scapulotricipitalis.

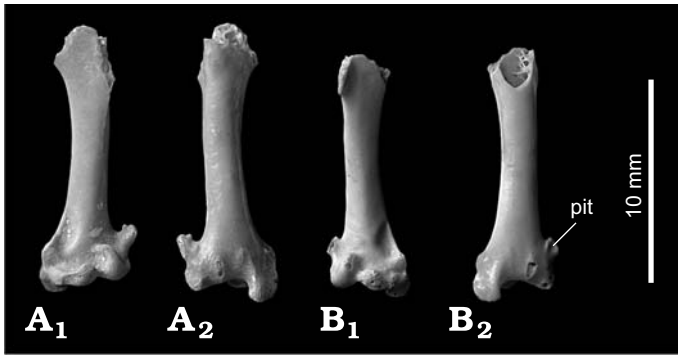

Fig. 2. Fragmentary humeri of a medium-sized swallow species from the early Pliocene Varswater Formation at Langebaanweg, South Africa in cranial (A_1, B_1) and caudal (A_2, B_2) view. **A**. Left distal humerus SAM-PQ L 70289. **B**. Right distal humerus SAM-PQ L 70290. Abbreviation: pit, small depression on caudal surface of processus supracondylaris dorsalis.

two distinct hirundinid species, a large and a medium-sized species, are present in the fossil record of Langebaanweg.

Specimens SAM-PQ L 24915T, L 70288, and L 70406 are comparable in size to the humerus of the Red-breasted Swallow (*Cecropis semirufa*) (Table 2). Their processus supracondylaris dorsalis is triangular in outline, bears a proximal process and its cranial surface is slightly concave in all three specimens, although this process is damaged in SAM-PQ L 24915T (Fig. 1). These characters are shared with *Cheramoeca*, *Riparia*, *Petrochelidon*, and *Psalidoprocne*, whereas the processus supracondylaris dorsalis is more prong-like in *Delichon*, *Hirundo*, *Pseudhirundo*, *Ptyonoprogne*, and *Tachycineta*. In the fossil specimens the processus supracondylaris also bears a small but distinct tubercle on its caudal surface (Fig. $1A_2$, B_2, C_2), and the attachment site for M. pronator superficialis is conspicuously large (Fig. $1B_2$, C_2). Both features were not recognized in any extant swallow species studied.

Table 1. Locality and horizon of four specimens of large (L) and medium-sized (M) swallow species from the Varswater Formation at "E" Quarry, Langebaanweg, South Africa. No supplemental information is available for the fifth specimen, SAM-PQ L 24915T.

Specimen	Species	Previous No.	Locality and horizon
SAM-PQ L 70288	L	SAM-PQ L 28469T	Dump 9, East Stream collection area, Quartzose Sand Member (QSM), possibly contains also some fossils from Pelletal Phosphorite Member (PPM)
SAM-PQ L 70406	L	–	Dump 3, East Stream, QSM
SAM-PQ L 70289	M	–	Dump 3, East Stream, QSM
SAM-PQ L 70290	M	SAM-PQ L 43148	Pelletal Phosphorite Member (PPM) bed 3aN III (= Bed C West Wall (BCWW) Cut 5), sieve concentrate, grey sand

Specimens SAM-PQ L 70289 and L 70290 fall within the size range of the humeri of House Martin (*Delichon urbicum*), Barn Swallow (*Hirundo rustica*) and Tree Swallow (*Tachycineta bicolor*) (Table 2). Compared to extant species, the distal ends of the fossil humeri are apparently broader, although SAM-PQ L 70290 is slightly damaged distally (Table 2). This difference results from the fact that the condylus ventralis is much more elongated dorsoventrally in the fossil specimens as compared to other hirundinids (Fig. $2A_1$, B_1). The condylus dorsalis of the fossil specimens appears to be more slender than in any swallow species studied. In SAM-PQ L 70289 and L 70290 the processus flexorius is large, but does not extend as far distally as in extant hirundinids or the large swallow species from Langebaanweg (Fig. 2). In SAM-PQ L 70289, the processus supracondylaris dorsalis is cranially convex and rather blunt (Fig. $2A_1$), but not pointed and prong-like as it is the case in *Delichon*, *Hirundo*, or *Ptyonoprogne*. The tip of processus supracondylaris dorsalis is damaged in SAM-PQ L 70290 and it bears a distinct pit on its caudal surface (Fig. $2B_2$), but otherwise it resembles strongly the corresponding process of SAM-PQ L 70289.

Geographic and stratigraphic range.—"E" Quarry, Varswater Formation, Langebaanweg (18°9' E, 32°58' S), South Africa, approximately 110 km NNW of Cape Town (Hendey 1981), early Pliocene (Hendey 1981). Information regarding locality and horizon for each of the specimens is given in Table 1.

Discussion

Today, Africa shows the greatest diversity of swallows and martins (Mayr and Bond 1943), and the latest phylogenetic studies imply that at least the major groups within hirundinids are of African origin (Sheldon et al. 2005). Therefore, evidence for two hirundi-

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Table 2. Measurements (in mm) of humeri of a large (SAM-PQ L 24915T, L 70288, L 70406) and a medium-sized swallow species (SAM-PQ L 70289, L 70290) from Langebaanweg in comparison with extant species. Abbreviations: Bd, greatest width of distal end; GL, greatest length; Sc, smallest width of shaft. Square brackets indicate maximum dimension of an incompletely preserved bone.

Specimen	SAM-PQ L 24915T	SAM-PQ L 70288	SAM-PQ L 70406	*Cecropis semirufa* n =1	SAM-PQ L 70289	SAM-PQ L 70290	*Delichon urbicum* n = 3	*Hirundo rustica* n = 5	*Tachycineta bicolor* n = 1
GL	[15.3]	[14.8]	[7.3]	18.2	[13.5]	[12.1]	14.2 (13.6–14.7)	14.9 (14.3–15.3)	15.2
Bd	[4.4]	5.3	5.1	5.2	4.8	[4.0]	4.5 (4.4–4.7)	4.5 (4.3–4.7)	4.3
Sc	2.1	2.3	2.3	2.2	1.9	1.7	1.8 (1.7–1.9)	1.9 (1.7–2.0)	1.9

nid species in the fossil record of Africa is not unexpected. However, much younger swallow remains probably referable to extant species from the lower Pleistocene at Kromdraai, South Africa (Pocock 1970), were the only previously published fossil evidence for this taxon on the entire continent.

The fossils described above are apparently slightly older than the only other pre-Pleistocene record for Hirundinidae in the world, an isolated humerus from Fox Canyon, Kansas (Feduccia 1967), now supposed to be of early Pliocene age (4.3–4.8 Mya) (Emslie 2007). The latter specimen, described as *Hirundo aprica* Feduccia, 1967, is comparable in size to a Barn Swallow, but is more robust and apparently distinct from the similar-sized swallow species from Langebaanweg. Its description is mainly based on characters of the proximal end of the humerus, so detailed comparisons with the Langebaanweg specimens are not possible.

Hirundinids are the third group of aerial insectivores in the fossil record of Langebaanweg. Before, this ecological guild was represented by an as yet undescribed swift (Apodidae, Rich 1980; depicted in Hendey 1982: 26), and a nightjar (Caprimulgidae, Manegold 2010). Both species are known only from a single bone.

The fragmentary nature of the fossil specimens arguments against the erection of new taxa and further does not allow hypotheses regarding their phylogenetic position within Hirundinidae. Thus, conclusions regarding the paleoecology of the fossil swallows are rather limited. A few assumptions can, however, be deduced from previous reconstructions of the paleoenvironment at Langebaanweg (Hendey 1981; Olson 1985b). Two of the five swallow specimens representing both species were excavated in the so called Quartzose Sand Member (QSM) of "E" Quarry within the "East Stream" collection area, and a third specimen might be also from the same horizon, although the sample wherein it was found was apparently mixed with a probe of the so-called Pellatal Phosphorite Member (PPM), which overlies QSM and also yielded a fourth hirundinid humerus (Table 1; no further information is available for the fifth specimen). The depositional environments of the East Stream collection area and the particular section of PPM, where specimen SAM-PQ L 70290 was found, are described as floodplain with adjoining ponds, drainage channels and similar microenvironments (Hendey 1981: 31), and as a mixture of river channel, marsh and pond deposits, respectively (Hendey 1981: 26). The accumulation of bird, frog, and micromammal remains in QSM could have been the result of predation by mongooses (Herpestidae) and other small to medium-sized carnivores (Hendey 1981), whereas the majority of the fossils in PPM was "washed into the area by the river, but at least some [fossils] must represent animals that were resident locally" (Hendey 1981: 33).

The watercourses and ponds at Langebaanweg were probably lined with reeds that provided roosting sites for large flocks of swallows, as it is the case with almost every hirundinid species outside their breeding season (Turner and Rose 1989). With its river banks, gallery forests, adjacent grasslands and open woodlands (Hendey 1981), Langebaanweg certainly could have provided suitable nesting sites for those hirundinid species either capable of burrowing nest tunnels in the soil or of adopting tree cavities as breeding sites. The burrowing behavior, today shared by *Cheramoeca*, *Phedina*, *Psalidoprocne*, *Pseudochelidon*, and *Riparia*, is an ancestral character for Hirundinidae, whereas cavity adopting is characteristic for the clade comprising exclusively New World hirundinids, for example, *Progne* and *Tachycineta* (Winkler and Sheldon 1993; Sheldon et al. 2005). The behavior of building mud-nests evolved only once within Hirundinidae, namely in the ancestral lineage of a clade comprising *Cecropis*, *Delichon*, *Hirundo*, *Petrochelidon*, and *Ptyonoprogne* (Winkler and Sheldon 1993; Sheldon et al. 2005). It seems unlikely that representatives of this clade could have found suitable places for constructing their nests in the flat Langebaanweg area; although today mud nests are occasionally built in hollow tree stems by several extant swallow species (Turner and Rose 1989). More typical nesting sites would have been the mountain ranges less than 100 km to the west and northwest. However, additional fossil specimens and more comparative material are necessary before nest-building behavior of hirundinids can be deduced on the basis of osteological characters.

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Albrecht Manegold [albrecht.manegold@senckenberg.de], Forschungsinstitut Senckenberg, Sektion Ornithologie, Senckenberganlage 25, D-60325 Frankfurt am Main, Germany.

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Appendix 1

List of specimens of extant hirundinid species studied. Abbreviations: IRSN, Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; NMB, National Museum Bloemfontein, South Africa; SAM, Iziko South African Museum, Cape Town, South Africa; SAuM, South Australian Museum, Adelaide, Australia; SMF, Forschungsinstitut Senckenberg, Frankfurt/Main, Germany; TM, Transvaal Museum/Northern Flagship Institute, Pretoria, South Africa; ZMB, Museum für Naturkunde der Humboldt-Universität, Berlin, Germany.

Species	Common name	Specimen
Cheramoeca leucosterna	White-backed Swallow	SAuM B38515, 48893
Delichon urbicum	House Martin	NMB 00817; SMF 2559; ZMB 2000.10719, 1983.82
Cecropis abyssinica	Lesser Striped Swallow	NMB 00770
Cecropis cucullata	Greater Striped Swallow	SAM ZO 58555
Cecropis semirufa	Red-breasted Swallow	SAM ZO T464; SMF 181
Petrochelidon ariel	Fairy Martin	SAuM B30876, B49310
Petrochelidon nigricans	Australian Tree Martin	SAuM B37437, B37535
Petrochelidon spilodera	South African Cliff-swallow	NMB 02077; SAM ZO 57543
Petrochelidon pyrrhonota	American Cliff-swallow	SMF 6461
Ptyonoprogne fuligula	Rock Martin	SAM ZO T1292
Hirundo rustica	Barn Swallow	SAM ZO 58223; SMF 2834; ZMB 1980.34, 1996.96, 1996.97
Psalidoprocne albiceps	White-headed Saw-wing	IRSN B51380
Psalidoprocne pristoptera holomelas	Black Saw-wing	NMB 00767, SAM ZO T856
Pseudhirundo griseopyga	Grey-rumped Swallow	TM 61455
Riparia cincta	Banded Martin	SAM ZO T137
Riparia paludicola	Brown-throated Martin	NMB 2123, SAM ZO 57197
Riparia riparia	Sand Martin	SMF 325, 5024
Tachycineta bicolor	Tree Swallow	ZMB 2000.10329

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