

Small birds (Psittaculidae, Galliformes and Passeri) from the Early Miocene of Namibia

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Abstract :- Several post-cranial bones of small birds collected from Early Miocene deposits at Grillental in the Sperrgebiet, Namibia, are attributed to three groups, a small parrot-like species (Psittaculidae), a songbird (Passeriformes) and a gamebird (Galliformes). All three are among the earliest records of their respective groups in Africa. The lovebird specimens, in particular, greatly extend the fossil record of the family in the continent from the previous earliest record at Langebaanweg, South Africa (ca 6-5 Ma) to the Early Miocene (ca 20-19 Ma). The material is an interesting source of information about palaeoenvironments and palaeoclimate and, as an assemblage, it indicates that the locality was more humid than it is today, and that it lay within the summer rainfall belt, in contrast to the hyper-arid conditions with winter rainfall that prevail in this part of the continent at present.

Key Words :- Aves, Early Miocene, Namibia, Palaeoecology, Palaeoclimate

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Introduction

Fossilised bones of small birds collected from the Early Miocene (ca 19-20 Ma) green silts at Grillental VI, Sperrgebiet, Namibia, represent three different groups, Psittaculidae (lovebirds), Galliformes (gamebirds) and Passeriformes (song-birds). The lovebird from Grillental is by far the oldest known from Africa, the passerine from the site is one of the oldest known from the continent, the other record being from similar aged deposits at Napak, Uganda, (Riamon, pers.

comm.) while the galliform is also one of the earliest records of the group in Africa, only a record from Elisabethfeld, Sperrgebiet, Namibia, being slightly older than it (ca 21-20 Ma) (Mourer-Chauviré, 2008).

For these reasons, it is interesting to describe the avian material from Grillental VI and to use it for throwing light on aspects of the Early Miocene palaeoenvironment and palaeoclimate of southern Namibia.

Material and Methods

The fossils described herein are curated at the Earth Science Museum, Geological Survey of Namibia, Windhoek. They are registered with the abbreviation GSN GT followed by a field number and the year of collection (e.g. GSN GT 39'23).

Images of the fossils were captured with a Sony Cybershot Digital Camera, and were treated with Photoshop Elements15 to increase contrast, reduce tremor and clean away unwanted background. Scale bars were added following measurements of the fossils with sliding calipers.

Locality and Age

The locality from which these bones were collected is a small knoll (26°58'10.04"S : 15°19'26.50"E) in the broad area of sediment exposures known as Grillental VI in the northern Sperrgebiet, Namibia (Pickford,

2008a) (Figs 1-2). The deposits have yielded mammalian fossils that indicate an Early Miocene correlation (Aquitanian-Burdigalian). The strata are considered to date from 20-19 Ma.

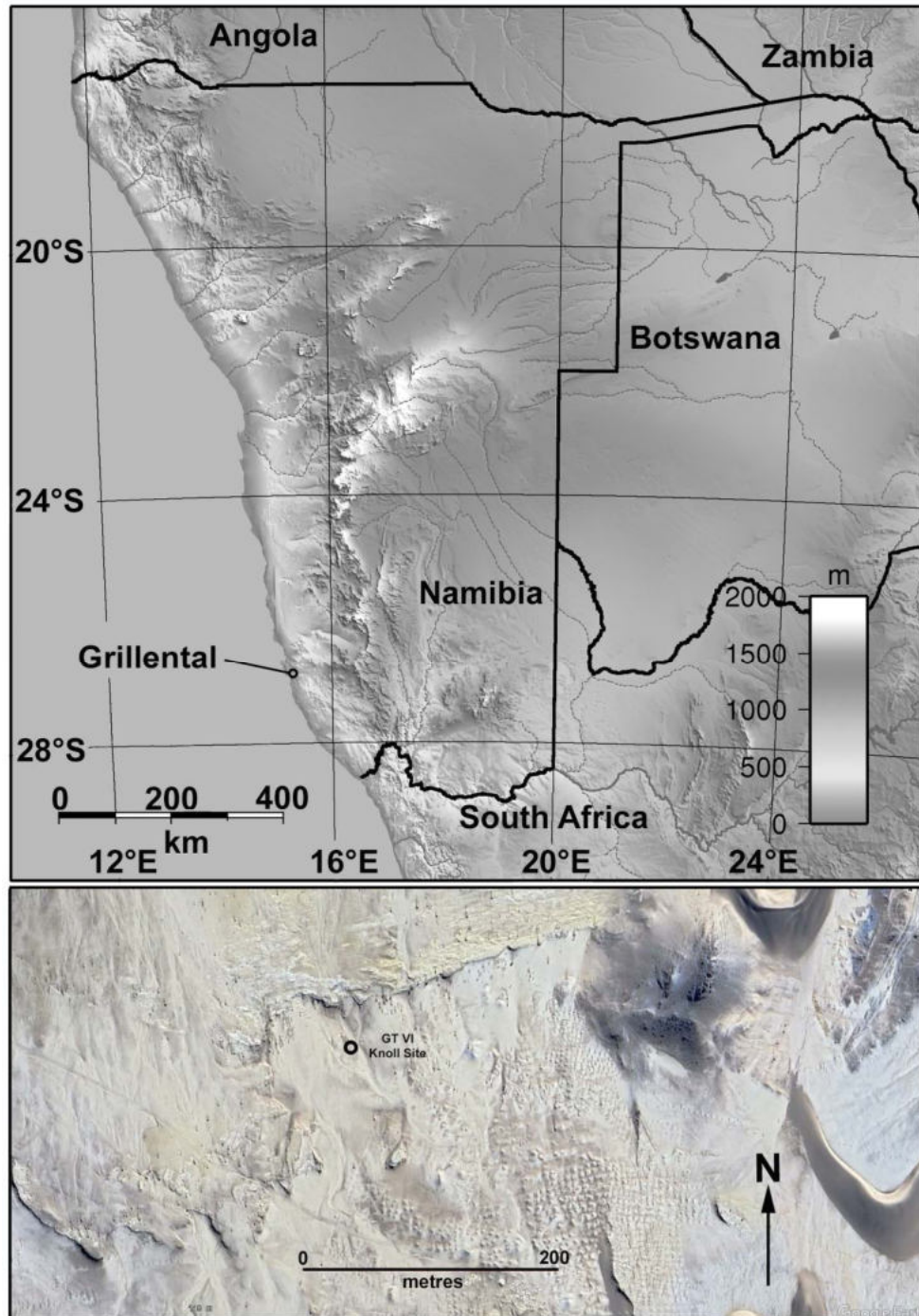


Figure 1. Digital elevation map of Namibia (upper frame) showing the location of Grillental in the Sperrgebiet. The Knoll Site is in the Grillental VI complex of fossiliferous deposits (lower frame: image modified from Google Earth). Note the regular pattern in the floor of the depression formed by trommel screen heaps resulting from diamond mining during the 1920's.



Figure 2. View of the Knoll Site at Grillental VI. In the foreground is a fossilised hive (*Namajenga mwichwa* Pickford, 2008b) a bioconstruction (fungus garden) made by a species of the termite, *Hodotermes*.

Systematic study

Order Psittaciformes Wagler 1830

Superfamily Psittacoidea Rafinesque-Schmaltz 1815 (sensu Joseph *et al.* 2012)

Family Psittaculidae Vigors 1825

Subfamily Agapornithinae Salvin 1882

Genus *Agapornis* Selby 1836

Type species :- *Agapornis swindernianus* Kuhl
1820

Species *Agapornis* incertae sedis

Locality :- Grillental VI, Sperrgebiet, Namibia.

Material :- GSN GT 39'23, left humerus, distal part (Fig. 3), GSN GT 38'23, left carpometacarpus (Fig. 4).

Age :- Early Miocene, ca 20-19 Ma.

Osteology

Humerus

Measurement :- distal width, 4.0 mm.

On the cranial side of the humerus, the *condylus ventralis* projects weakly and the

condylus dorsalis is almost vertical. On the caudal side the *fossa olecrani* is wide and shallow, and the *epicondylus ventralis* projects strongly ventrally.



Figure 3. *Agapornis* sp. from Grillental VI (A - distal left humerus, GSN GT 39'23), *Agapornis attenboroughi* Langebaanweg (B - right humerus,) and extant *Agapornis roseicollis* (C - right humerus). Images B and C are modified from Manegold (2013) (A1-C1 : cranial views, A2-C2 : caudal views) (scale bars : 5 mm).

Carpometacarpus

Measurement :- total length, 14.4 mm.

On the carpometacarpus the *processus extensorius* and the *os metacarpale minus* are missing. The *processus pisiformis*, below the

trochlea carpalis, on the medial side, is well developed

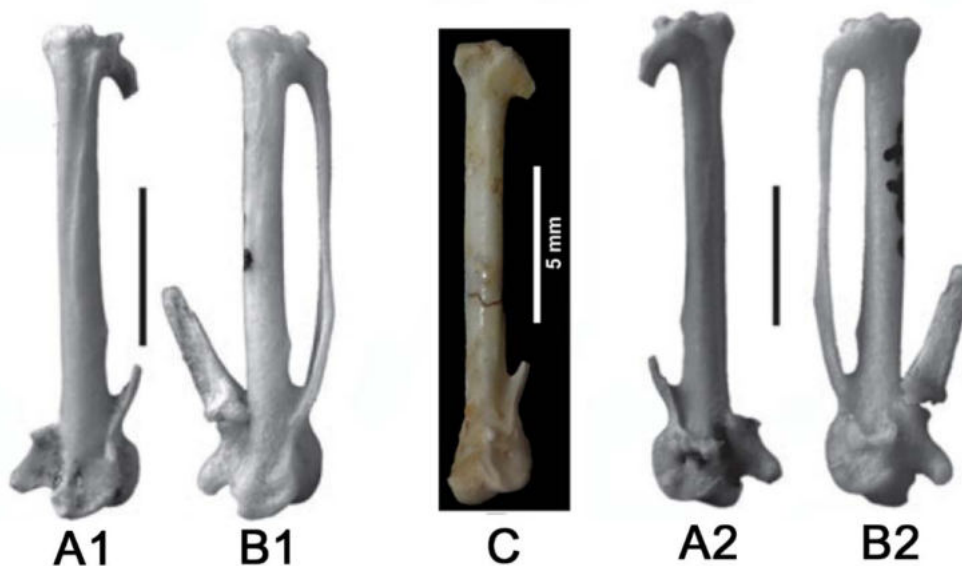


Figure 4. *Agapornis attenboroughi* from Langebaanweg (A - right carpometacarpus) extant *Agapornis roseicollis* (B - right carpometacarpus) and *Agapornis* sp. from Grillental (C - GSN GT 38'23, left carpometacarpus). Images A and B are modified from Manegold (2013) (A1-B1 : dorsal views, A2, B2 and C : ventral views) (scale bars : 5 mm).

The dimensions of these fossil bones from Grillental are comparable to those of the

smallest extant species of the genus *Agapornis* (Manegold, 2013).

Fossil Record of *Agapornis*

Fossil remains of *Agapornis* have been reported from seven areas in Africa, most of which are far from the extant distribution of the genus (Fig. 5). The Moroccan occurrence (Mourer-Chauviré & Geraads, 2010) is close to the Mediterranean more than 2,500 km north of the present day range of the genus and the localities of Langebaanweg (Manegold, 2013;

Stidham, 2006) and Gauteng (Pocock, 1969; Stidham, 2009) are well south of the closest extant occurrences.

Until the material from Grillental VI was found, the oldest record of the genus was from Langebaanweg, South Africa (ca 6-5 Ma) (Fig. 5, 6).

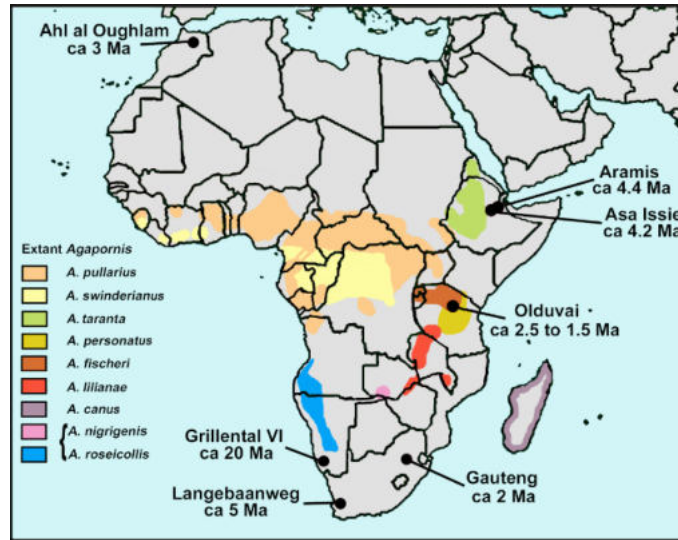


Figure 5. Distribution of fossil and extant species of *Agapornis*. Extant distribution is based on <https://www.zoochat.com/community/media/lovebirds-distribution-maps.564221/>, downloaded 28/10/2023. Note that only one of the palaeontological sites (Olduvai) that have yielded fossils of *Agapornis* falls within the present-day distribution range of the genus. Two extant species (bracketed) occur in Namibia.

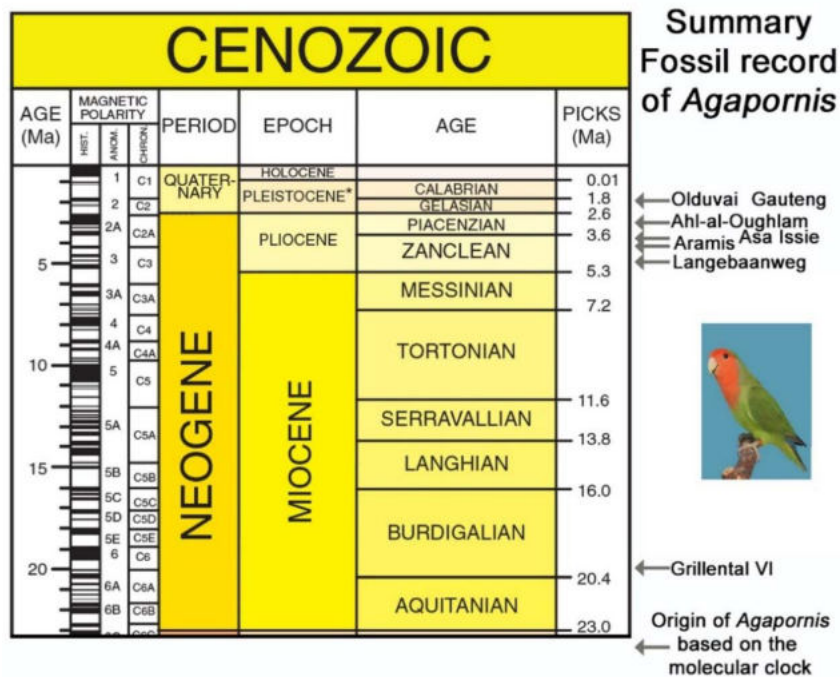


Figure 6. Stratigraphic position of fossils attributed to *Agapornis* species. Data from Manegold (2013), Louchart *et al.* (2009), White *et al.* (2006) and this paper.

Discussion

Interpretations of molecular data obtained from extant parrots suggest that *Agapornis* dispersed from Australia to Africa at the end of the Oligocene or the beginning of the Miocene (Manegold, 2013). If the timing of this trans-oceanic dispersal is correct, then it would imply that the Grillental VI fossils were

preserved relatively soon after the arrival of the genus in Africa. This dispersal took place a long time after a previous dispersal of parrots to Africa during the Palaeogene, represented by *Namapsitta praeruptorum* from the Late Eocene of Eocliff, also in the Sperrgebiet (Mourer-Chauviré *et al.* 2014, 2017).

Palaeobiogeography

Lovebirds (*Agapornis*, Psittaculidae) currently occur in many parts of Namibia including Mopane Woodland and slightly more humid environments (Miombo Woodlands, Savannah) but are not often encountered in the Namib Desert or in winter rainfall areas of the country. Fossils of this family of small parrot-like birds, also known as parakeets, have been described from the late Miocene of South Africa (Langebaanweg, ca 5-6 Ma - Stidham, 2006; Manegold, 2013) and the Pliocene of Morocco (Ahl-al-Oughlam, ca 3 Ma - Mourer-Chauviré & Geraads, 2010) among other younger sites in Ethiopia (Louchart *et al.* 2009; White *et al.* 2006), South Africa (Pocock, 1969; Stidham, 2009) and Tanzania (Brodkorb, 1985; Prassack, 2010) (Fig. 5).

The distribution of fossils of *Agapornis*, even though limited to seven areas in the

continent (Fig. 5, 6) is intriguing, in that six of the seven occurrences fall outside the distribution ranges of extant species of the genus. The locality of Ahl Al Oughlam, Morocco, is north of the Sahara, some 2,500 km from the nearest present-day occurrence of the genus. Two of the three fossiliferous areas in southern Africa that have yielded *Agapornis* (Fig. 7) are also far from the ranges of extant species, Gauteng (Plover's Lake, Kromdraai and Sterkfontein) being some 400 km south of the nearest occurrence, and Langebaanweg, ca 1,000 km south. Grillental VI falls outside the distribution range of extant *Agapornis*, but the distance is not great (ca 100 km) although its winter rainfall regime differs from the summer rainfall regime that today characterises the places where *Agapornis* survives.

Palaeoecology and Palaeoclimatology

Extant species of lovebirds nest in tall trees or crevices in high cliffs or in arboreal termite hives, and the staple diet of most species consists of grass seeds while only one species (forest-dwelling *Agapornis swinderianus*) feeds on figs (Manegold, 2013). The macrofaunal and microfaunal remains from Grillental VI include several vertebrate lineages (crocodiles, large tortoises, anthracotheres, rhinocerotids, proboscideans, hyracoids, ruminants, suids, carnivorans, rodents, macroscelideans, erinaceids, etc.) (Pickford, 2008c) which indicate that, during the Early Miocene, the region was relatively humid and well vegetated, with an important tree cover, radically different from the treeless hyper-arid conditions that prevail there today. The termites (hives of the polycalate genus *Hodotermes*) and the large species of the land snail genus *Dorcasia*, indicate that the area was probably within the summer rainfall zone, although the presence of

the land snail *Trigonephrus* at Grillental VI suggests that the winter rainfall zone was not far away.

The presence of *Agapornis* in the Early Miocene sediments at Grillental reinforces these palaeoenvironmental and palaeoclimatic reconstructions. Considering all the evidence, it is concluded that the hyper-arid conditions that prevail in the Namib Desert today, were established sometime after the deposition of the Grillental green silts, hyper-aridity probably starting about 17 Ma.

The birds previously described from Grillental (Mourer-Chauviré, 2008) were not from the Knoll Site, but were found nearby. They comprise several waterbirds, *Megapalaelodus* (Family Palaelodidae, a primitive flamingo), and four Anseriformes, two in the subfamily Oxyurinae (stiff-tailed ducks) and two in the Anserinae (swans and geese). It is generally considered that Palaelodidae were

fully aquatic. Taken together, the waterfowl from Grillental indicate the presence of significant bodies of water.

The fossil ostriches from Grillental (Mourer-Chauviré *et al.* 2023) suggest that there was open country in the region. The

picture is emerging that during the Early Miocene, the Northern Sperrgebiet was considerably more humid than it is today, with savannah to woodland vegetation and substantial bodies of water in rivers and ponds.



Figure 7. The distribution of extant lovebirds in Southern Africa and the position of three fossiliferous areas that have yielded specimens of these small parrot-like birds (blue circles with red centre). Distribution of extant species is from Sinclair & Hockey (2005).

Order Galliformes Linnaeus 1758

Family Phasianidae Vigors 1825

cf Genus *Palaeortyx* Milne-Edwards 1869

Material :- Left tarsometatarsus, distal part, GSN GT 104'19 (Fig. 8)

Osteology

Tarsometatarsus

Measurements :- distal width, 11.0 mm; distal depth, 7.5 mm.

On the tarsometatarsus the *trochleae met. II* and *IV* are relatively far apart from the *tr. met. III*. In distal view, the three trochleae are arranged along a slightly curved line. The *tr. met. II* extends a short way beyond the base of the *tr. met. III*, and it is weakly displaced plantarly. The *tr. met. IV* reaches the middle of the *tr. met. III*. The *foramen vasculare distale* is wide open and is followed by a broad groove between the *tr. met. III* and *IV*. The *incisura intertrochlearis lateralis* is wide.

Above the *incisura intertrochlearis medialis*, on the dorsal surface, there is a very

small foramen. On the plantar surface this foramen opens by two very small orifices. This small foramen also exists in the genera *Pavo*, *Afropavo*, in some specimens of *Gallus*, and in several other phasianid genera (Mourer-Chauviré, 1989).

By the setting aside of the trochleae and the presence of a large *foramen vasculare distale*, this tarsometatarsus differs from those of the genera *Afropavo*, *Pavo*, *Gallus* and *Phasianus* and closely matches that of the genus *Palaeortyx* (Göhlich & Mourer-Chauviré, 2005).

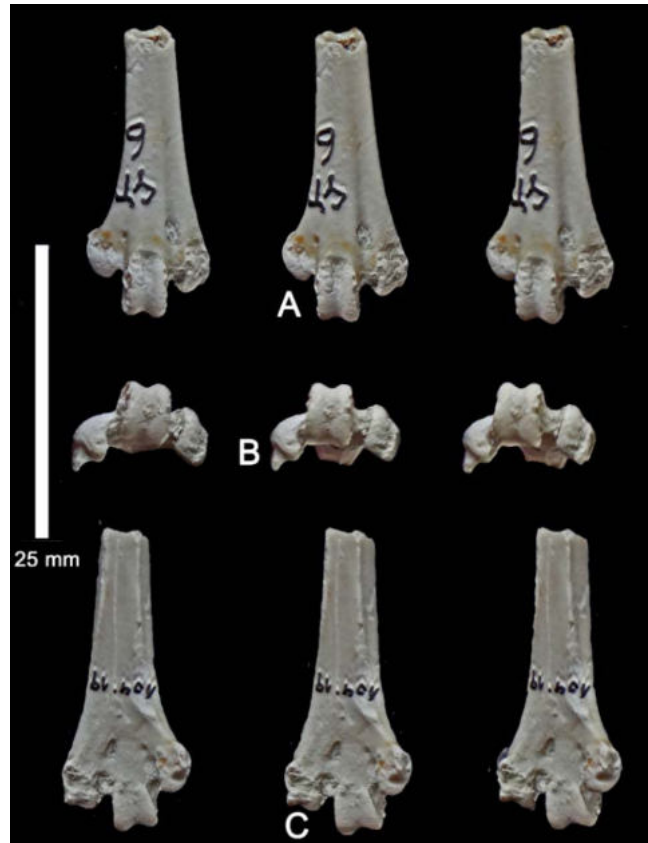


Figure 8. Stereo images of GSN GT 104'19, distal left tarsometatarsus of cf *Palaeortyx* sp. A) dorsal views, B) distal views, C) plantar views.

Discussion

The genus *Palaeortyx* is known in Europe from the very beginning of the Late Oligocene to the Early Pliocene. It is widespread in France, Germany, Hungary, Spain and Italy (Mourer-Chauviré & Geraads, 2010). In Africa, a proximal carpometacarpus from the

early Miocene of Elisabethfeld has been referred to *Palaeortyx* (Mourer-Chauviré, 2008) and two proximal parts of humeri from the basal Middle Miocene of Arrisdrift also show the morphological features of this genus (Mourer-Chauviré, 2003).

Order Passeriformes Linnaeus 1758

Suborder Passeri Sibley *et al.* 1988

Genus *incertae sedis*

Material :- GSN GT 54'23, left tarsometatarsus, distal part (Fig. 9).

Osteology

Tarsometatarsus

Measurement :- distal width 2.1 mm.

On the dorsal side of the tarsometatarsus the trochleae are slightly damaged. They are better preserved on the plantar side but the tip of the *tr. met. II* is broken. This tarsometatarsus shows the characteristic shape of the Passeriformes, Passeri. In distal view, the three

trochleae are disposed in a straight line. The *tr. met. III* is larger and shows a groove, the *tr. met. II* and *IV* are narrow and ungrooved, the *tr. met. II* is directed slightly obliquely towards the medial side.



Figure 9. GSN GT 54'23, left tarsometatarsus of a small passerine bird from Grillental VI, Sperrgebiet, Namibia. A) dorsal view, B) plantar view.

Discussion

Apart from the Acanthisittidae of New Zealand, the Passeriformes are divided into two large groups, the Tyranni (or Suboscines), and the Passeri (or Oscines). The Tyranni are mainly present on the American continent and in the Old World tropics, while the Passeri are widespread over the entire globe, with the exceptions of South and Central America, and Antarctica.

The Tyranni were present in Europe from the Early Oligocene (Riamon *et al.* 2020),

while the crown-group Passeri were present in Europe only from the Late Oligocene (Mayr, 2022). The Tyranni and the Passeri coexisted in Europe until the Early Miocene (Manegold, 2008). Passeriformes are unknown from the Palaeogene of Africa, Asia, North and South America. Passeriformes are present in the Early Miocene of Grillental and also of Napak in Uganda (Riamon, pers. comm). These two localities have yielded the earliest evidence of Passeriformes in Africa.

General Discussion and Conclusions

The green silts at Grillental VI Knoll Site have yielded a rich and diverse assemblage of small and medium-sized mammals, as well as remains of frogs, snakes, lizards and small birds. The mammalian fauna indicates correlation to the Early Miocene, ca 20-19 Ma (Pickford, 2008a, 2008c).

Three groups of small birds are now known from the deposit, Psittaculidae (lovebirds), Galliformes (gamebirds) and Passeri (songbirds). The staple diets of two of these

groups comprise grass seeds, suggesting that, during the Early Miocene, the Northern Sperrgebiet was endowed with areas of grassland. Other fossils from the deposits such as termites, land snails and mammals, indicate a savannah to woodland environment, with annual rainfall of ca 750 mm which fell during the summer, contrasting with the hyper-arid conditions and winter rainfall that prevail in the region at present.

At 20-19 Ma, the Grillental representatives of the three avian groups described herein are among the earliest known from Africa. Previously, the oldest known lovebird from the continent was from Langebaanweg, South Africa (ca 6-5 Ma) (Manegold, 2013), the

oldest known passerine was from Napak, Uganda (ca 20-19 Ma) (Riamon, pers. comm.) while the oldest known *Palaeortyx* was from Elisabethfeld (21-20 Ma) with slightly younger fossils of this genus known from Arrisdrift (ca 17.5 Ma) (Mourer-Chauviré, 2003, 2008).

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