Fossiliferous Neogene karst fillings in Angola, Botswana and Namibia

Martin Pickford,* Pierre Mein[1] and Brigitte Senut[2]

*Collège de France, 11 Place Marcellin Berthelot, 75005 Paris, France and Geological Survey of Namibia, P.O. Box 2168, Windhoek, Namibia 9000; [1]Departement de Sciences de la Terre, Université Claude Bernard, 27–43 Boulevard 11 Novembre, 69621 Villeurbanne, France; and [2]Institut de Paléontologie, 8 rue Buffon, 75005 Paris, France.

During the past eight years, palaeontologists participating in a programme of research called Paléokarst Afrique, have been examining karst fillings in Botswana, Angola and Namibia. Numerous richly fossiliferous occurrences have been discovered in all three countries, ranging in age from middle Miocene to Holocene. Preliminary analyses of the fossils indicates that the southern portion of Africa was home to primates throughout this time period, as well as to a host of micromammals and other vertebrates, many of which are new to science.

Since 1988, palaeontological expeditions to Botswana, Angola and Namibia have led to the discovery of numerous Neogene fossiliferous deposits in karstified dolomites, some of which have yielded evidence concerning the evolution of primates. Micromammals are extremely common in these karst-fill breccias, while large mammals tend to be rare in most localities. Where macrofaunal remains do occur, primates, especially cercopithecids, predominate. The breccias range in age from middle Miocene (13 ± 1 Myr ago) to Holocene, the majority of sites being of post-Miocene age. Hominoids have been found in middle and upper Miocene deposits, cercopithecids and lorisids in upper Miocene breccias and papionines in late Pliocene to Pleistocene sediments. Hominid remains are scarce: early stone tools have been identified in a lower Pleistocene deposit in Botswana and a ?Holocene human femur is reported to have been found in a cave in Namibia.

Recent scientific literature on ancient human origins is dominated by publications which highlight fossil discoveries in eastern — and to a lesser extent southern — Africa. Partly as a result of this geographic bias, some authors have proposed Zinj-centred hypotheses of hominid origins,[1] the assumption being that successive hominid taxa evolved in restricted parts of Africa, such as the East African Rift Valley, from which they subsequently spread outwards in waves to occupy the entire continent. The attitude is succinctly summarized for the general public in *Time* magazine, of 3 February 1992, 'Paleohistorians agree that intelligent human life began in the Rift Valley of Africa'. Under such a model, southern Africa is viewed as having had only a minor role to play in the evolution of new genera and species of hominids — the bulk of evolutionary innovations are viewed as having occurred in the tropics. Whilst it is true that the diversity of most groups of organisms is greatest at the equator and minimal at high latitudes — Wallace's Rule[2] — which in turn provides evidence that more new species evolve in the tropics than at higher latitudes, this generalization tends to break down when one examines eurytopic organisms, such as baboons and hominids.

One way of overcoming the Zinj bias is to search in other African countries for evidence concerning human evolution. Many parts of Africa lack conventional sedimentary basins of appropriate ages and for this reason large areas of the continent have not been prospected palaeontologically. However, many parts of Africa are endowed with extensive bodies of carbonate rocks — dolomites and limestones — which have undergone karstic processes and therefore have the potential for containing fossiliferous breccias. The authors have organized a project entitled 'Paléokarst Afrique' with a view to studying systematically areas known to contain karstified carbonate rocks (Fig. 1).

Countries visited so far include Tunisia,[3] Gabon, Botswana,[4,5] Angola[6] and Namibia,[7] all of which have proved to be fossiliferous. In the last three countries, extensive, richly fossiliferous karst-fill deposits have been discovered (Fig. 2), which promise to close many of the geographic and temporal gaps that existed in our knowledge of African Neogene palaeontology. This paper provides a summary of progress made during the past five years, the focus being on the biostratigraphy of the deposits (Table 1) and their contained faunas (see faunal lists, Table 2). Many of the micromammals are new to science. For this reason, the faunal lists do not include many specific names, but generally remain at the generic level. Descriptions of hominoids and other primates are in print[8–11] or are in preparation (Senut *et al.* in prep.).

Botswana

The Botswana Palaeontology Expedition discovered five major fossiliferous sites in ancient caves in north-western Botswana in 1988 and 1989.[4,5] All are of late Pliocene to early Pleistocene age, but only one (Koanaka North) has yielded cercopithecids [*Parapapio* sp. (Senut in prep.)] similar to material from Makapansgat. A nearby site (Koanaka South) yielded *in situ* quartzite flakes, suggesting that humans inhabited the area

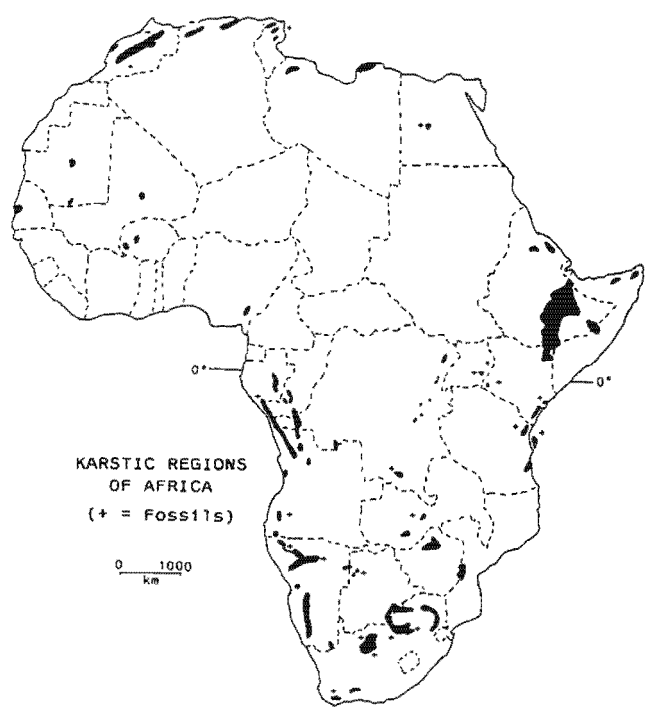

Fig. 1. Carbonate rocks of Africa known to, or likely to, contain karst-fill breccias. + = fossil occurrences.

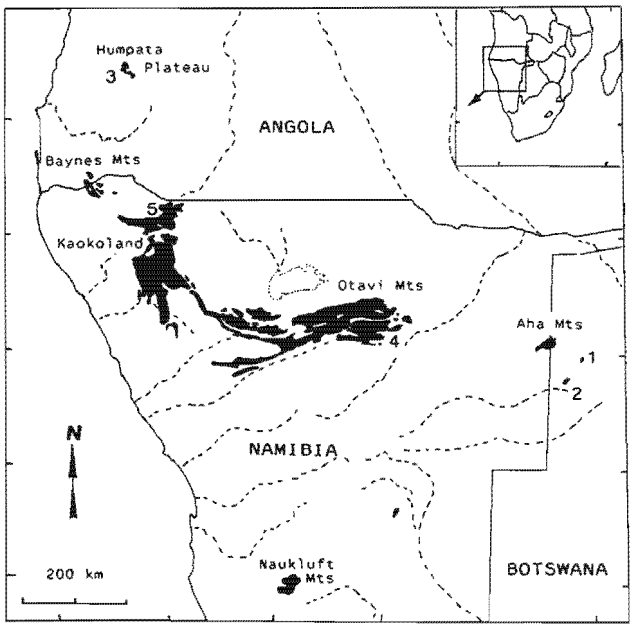

Fig. 2. Dolomite outcrops in western Botswana, southern Angola and northern Namibia. 1–5: areas in which fossiliferous breccias have been mapped. 1, Gcwihaba (three occurrences: Gcw A, Gcw C north, Gcw C south). 2, Koanaka (two occurrences: Koa N, Koa S). 3, Humpata (15 occurrences: Cangalongue (1–4, north), Malola (kiln, 2, 2S), Tchiua (grey, pink), Ufefua (1, 2, S, 8/9), Molo, Tchivinguiro). 4, Otavi (12 occurrences: Berg Aukas (I, II), Jägersquelle, Aigamas (I, II) Nosib (I, II), Harasib 3a, Gabus, Uisib, Asis Ost, Elefantenberg Nord). 5, Kaokoland (six occurrences: Rocky (I-IV), Ondera, Tim's Cave).

during the lower Pleistocene, but no hominid remains were located. The microfaunas which are dominated by nocturnal species indicate that the palaeoenvironment was semi-arid to arid during the period of fossil accumulation, but that the climate fluctuated around this 'mean', sometimes being more humid, at other times more arid.

Angola

Fossil cercopithecids have been known to occur in southern Angola since 1950.[12–14] Until recently, these fossils had received only cursory attention and description, but Delson and Dean[15] have provided illustrations, descriptions and measurements of specimens. The Angola Palaeontology Expedition spent three weeks in southern Angola in 1989 and 1990 and discovered numerous new localities and abundant fossil remains, especially of cercopithecids[6,16] which are being described by Jablonski (in prep.). Previous studies have suggested that three species of cercopithecids occur in the Humpata breccias (the papionines *Dinopithecus* and *Parapapio*, and the colobine *Cercopithecoides*) but recent work by Jablonski (in prep.) suggests that the new collections from Tchiua, Malola and Cangalongue contain only one species of *Theropithecus*.

The main interest in the fossiliferous breccias of the Humpata Plateau, apart from the cercopithecids, is the abundant microfauna, which yields information concerning the age and palaeoecology of the deposits.[16] All the Humpata sites are of late Pliocene to early Pleistocene age. Cangalongue, for example, is estimated to be between 1.3 and 1.8 Myr, while Malola may be about the same age as Makapansgat.

The rodent fauna is dominated by nocturnal species, probably because their remains were carried into the caves by owls. Nevertheless, the fauna suggests that during the period of deposition, the environment in the Humpata Plateau was rather similar to what it is today, but that it fluctuated, sometimes being more humid (with forest-adapted genera such as *Uranomys*) and at other times more arid than at present.

Table 1. Provisional age determinations of karst-fill deposits in Botswana, Angola and Namibia.

Myr	Angola	Namibia	Botswana
0		Berg Aukas II(*?)	
		Asis Ost	
1		Berg Aukas I	
		Tim's Cave	
	Cangalongue*	Uisib,* Aigamas	
2	Tchiua*	Nosib*	Gcwihaba
	Malola*	Jägersquelle,*	Koanaka*
	Ufefua	Rocky II	
3		Berg Aukas I	
4			
5		Berg Aukas I	
6			
7			
8			
9		Berg Aukas I	
		Berg Aukas I*	
10		Harasib 3a*	
11			
12			
13		Berg Aukas I*	
		Berg Aukas I	
14			

*Primate fossils.

Namibia

Fossiliferous breccias have been discovered in two main areas of northern Namibia, the Otavi Mountain Land[7] and the Kaokoland.[17] In the former area 14 sites have been found, ranging in age from middle Miocene to Holocene, while in the latter, half a dozen are now known, all of which are of late Pliocene to early Pleistocene age.

The Otavi Mountain Land. Whilst it is clear that most of the Otavi sites yield faunas of restricted age ranges, Berg Aukas is an exception: it contains breccias ranging in age from middle Miocene to Holocene. Because of the risk of mixing faunas of diverse ages during acid digestion, the Berg Aukas breccias are treated on a block-by-block basis, each block representing one sample. By this means we have observed that there were at least six separate episodes of fissure infillings at Berg Aukas. Hominoid remains have been found in breccias of late Middle Miocene (13 ± 1 Myr) and upper Miocene age (9–10 Myr)[8–11,18] (Senut *et al.* in prep.).

The site at Harasib 3a has yielded abundant fossils of upper Miocene age (*c.* 10 Myr), including galagids[10] and cercopithecids. Cercopithecids have been found at several of the Plio–Pleistocene localities such as Jägersquelle, Nosib and Uisib but they are yet to be studied. Preliminary examination indicates that the genus *Dinopithecus* is probably represented at Jägersquelle.

The only hominid known from the Otavi Mountain Land is a proximal femur reportedly found at a depth of 500 feet (180 m) in Berg Aukas mine.[8,11,19] Some doubt surrounds this specimen in view of the lack of geological, chronological and detailed discovery context.

The Otavi microfaunas, which are dominated by nocturnal species, reveal that the climate changed dramatically over geological time. During the middle Miocene, the Otavi region appears to have been considerably more humid than it is now, with fruit trees producing crops more or less throughout the

Table 2. Recent faunal discoveries at karstified dolomite sites in Namibia, Botswana and Angola.

Middle Miocene fauna from Otavi breccias: Berg Aukas I, Namibia (Blocks BA 92-5, 15, 18, 24, 25, 30, 33, 38, 51, 52)	
Insectivora	Erinaceidae
	Tenrecoidea
Macroscelidea	Macroscelididae
Chiroptera	*Megaderma*
	Taphozous 1
	Taphozous 2
	Hipposideros
	?Coelops
	Rhinolophus
	Vespertilionidae
	Myotis
	Molossidae
	Tadarida
Primates	*Otavipithecus namibiensis*
Rodentia	*Apodecter*
	Parapedetes
	Vulcanisciurus
	Sciuridae indet.
	Cricetidae indet.
	Petromyscinae
	'*Steatomys*'
	Protarsomys small
	Protarsomys large
	Notocricetodon
	Myocricetodon large
	Myocricetodon small
	cf. *Democricetodon*
	Dakkamyoides 1
	Dakkamyoides 2
Carnivora	small indet.
Hyracoidea	*Parapliohyrax*
Upper Miocene fauna from Otavi breccias (Berg Aukas and Harasib 3a), Namibia (Blocks Ari, BA 92-9, 22, 26, 27, 29, 42, 57, 86)	
Insectivora	Soricidae
	Tenrecoidea
Macroscelidea	Macroscelididae
Megachiroptera	
Chiroptera	Vespertilionidae or *Myotis*
	Hipposideros
	? Coelops or small *Hipposideros*
	Rhinolophus
	Molossidae
Primates	Galagidae
	Cercopithecidae
Rodentia	Bathyergidae
	Paraulacodus
	cf *Apodecter*
	Nakalimys
	Vulcanisciurus
	Sciuridae indet.
	Cricetidae cf '*Brachyuromys*'
	Cricetidae cf '*Mystromys*'
	Gliridae
	Stenodontomys
	Myocricetodon small
	New genus myocricetodontine
	New genus Kabarsero large
	New genus Kabarsero small
	New genus Kabarsero sp. 3
	Dendromurinae
	'*Steatomys*'
	'*Dendromus*'
	'*Petromyscus*'
	'Archaic Muridae'
	Protarsomys
	Dakkamyoides
Hyracoidea	*Heterohyrax*
Artiodactyla	Bovidae
Post-Miocene faunas of the Otavi breccias, Namibia (Blocks BA 92-6/7, 11, 12, 14, 31, 35, 54)	
Insectivora	*Crocidura* 1
	Crocidura 2
Macroscelidea	Macroscelididae
Chiroptera	*Rhinolophus* 1
	Rhinolophus 2
	Hipposideros
	Molossidae
	Vespertilionidae
	? Coelops
Primates	*Dinopithecus*
Rodentia	New genus Myocricetodontine
	Cryptomys
	Graphiurus
	Mystromys
	Stenodontomys
	Tatera
	Gerbillurus
	Saccostomus
	Petromyscus
	Steatomys
	Malacothrix
	Dendromus
	Dendromuridae indet.
	Delanamys
	Petromus
	Mus
	Zelotomys
	Praomys
	Grammomys
	Rhabdomys large
	Rhabdomys small
	Thallomys?
	Micaelamys
	Aethomys
	Parotomys
	Otomys
	Acomys
	Muridae indet.
	Cricetidae large
	Dakkamyoides
	New genus Cricetomyidae
Faunal list: Holocene breccias, Otavi, Namibia	
Macroscelidea	Macroscelididae
Chiroptera	indet.
Primates	*?Homo*
Rodentia	*Tatera*
	Otomys
Hyracoidea	*Procavia*
Bovidae	*Tragelaphus strepsiceros*
	Antidorcas
	Alcelaphini
Faunal list: Humpata Plateau breccias, Angola	
Insectivora	*Crocidura* 1
	Crocidura 2
	Crocidura 3
	Crocidura 4
Macroscelidea	Macroscelididae
Chiroptera	*Rhinolophus*
	Miniopterus
	Nycteris
Primates	*Theropithecus*
Rodentia	*Uranomys*
	Acomys
	Dasymys
	Aethomys
	Thallomys
	Zelotomys
	Mus
	Pelomys
	Malacomys
	Praomys
	Grammomys
	Dendromus
	Steatomys
	Petromyscus
	Tatera
	Otomys
	Cryptomys
	Graphiurus
	Hystrix
Lagomorpha	*Serengetilagus*
Carnivora	Mustelidae
	Viverridae
	Canidae
	Hyaenidae cf *Chasmoporthetes*
Hyracoidea	*Gigantohyrax*
	Procavia
Rhinocerotidae	
Equidae	
Suidae	*Metridiochoerus andrewsi*
Bovidae	Hippotragini
	Connochaetes
Faunal list: Kaokoland breccias, Namibia	
Insectivora	*Crocidura*
Macroscelidea	Macroscelididae
Chiroptera	*Rhinolophus*
	Nycteris
	Myotis
Rodentia	*Thryonomys*
	Petromus
	Graphiurus
	Tatera
	Desmodillus
	Petromyscus
	Steatomys
	Dendromus
	Saccostomus
	Aethomys
	Mus
	Otomys
	Mastomys
	Zelotomys
	Thallomys
	Rhabdomys
Lagomorpha	*Lepus*
Hyracoidea	*Procavia*
Giraffidae	
Bovidae	
Faunal list: north-western Botswana	
Insectivora	*Myosorex*
	Suncus
Macroscelidea	Macroscelididae
Chiroptera	*Rhinolophus* 1
	Rhinolophus 2
	Vespertilionidae
Primates	*Parapapio*

Table 2. Continued.

Rodentia	*Zelotomys* aff *woosnami*
	Millardia aff *kathleenae*
	Mus
	Steatomys
	Malacothrix
	Dendromus
	Tatera cf *brantsi*
	Taterillus 1

Table 2. Continued.

	Taterillus 2
	Gerbillurus
	Palaeotomys gracilis
	Prototomys campbelli
	Graphiurus
	Georhycus/Cryptomys
	Hystrix
	Pedetes

Table 2. Continued.

Lagomorpha	*Lepus*
Hyracoidea	*Procavia*
Proboscidea	*?Mammuthus*
Suidae	Phacochoerini
Bovidae	Alcelaphini
	cf *Raphicerus* or *Cephalophus*

year. The upper Miocene faunas also appear to indicate a climatic regime more humid than that of today, but more xeric than that of the middle Miocene. By the Plio-Pleistocene, conditions broadly similar to those that occur in the region today appear to have been established, with fluctuations around a semi-arid 'mean'.

The Kaokoland. All six breccia occurrences found in the Kaokoland, north-west Namibia, are of Plio-Pleistocene to Recent age.[17] The microfauna, the bulk of which is of nocturnal affinities, and terrestrial gastropods indicate that during the period of breccia deposition, the climate in Kaokoland was consistently semi-arid to arid. No fossil primates have been found in Kaokoland.

Discussion

Paléokarst Afrique has already yielded important results in several countries. As concerns southern Africa, it has led to the discovery of numerous fossiliferous localities in what were previously enormous geographic areas from which no palaeontological information had ever been recorded. Several of these sites have yielded primates, but no hominids have yet been found, even though early stone tools have been observed in several places. Major advances in primate palaeobiogeography concern the discovery of galagids, cercopithecids and hominoids in the Miocene breccias of Namibia well south of their previously known distribution range in equatorial Africa. Such discoveries have already had an important impact on the way that researchers interpret the fossil record — the tendency to look exclusively towards Zinj and regions further north for early stages of hominoid and hominid evolution is no longer defensible. The research in Botswana, Angola and Namibia reveals that southern Africa was not a primate-poor backwater during the Miocene, just as it wasn't peripheral to hominid evolution during the Plio-Pleistocene.

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