Monograph on

Endemism in the Highlands and Escarpments of Angola and Namibia

Angola Cave-Chat *Xenocopsychus ansorgei*
Photo: M Mills

Editors:

John M Mendelsohn
Brian J Huntley
Pedro Vaz Pinto

Published with support and funding from:

Ongava Research Centre (ORC)
Namibian Chamber of Environment (NCE)
Centro de Investigação em Biodiversidade e Recursos Genéticos (CIBIO)
B2Gold Namibia
TotalEnergies

Language editor: Carole Roberts
Design and layout: Alice Jarvis

NJE Namibian Journal of Environment

2023: Volume 8 www.nje.org.na

ISSN: 2026-8327 (online)

» DOWNLOAD THE MONOGRAPH

CONTENTS

Geography of the highlands and escarpments

Diversity and endemism

Caves and their fauna in the highlands and escarpments of Angola and Namibia

D de Matos[1,2,3], J Zastrow[1], A Val[4,5], JM Mendelsohn[6]

URL: https://www.nje.org.na/index.php/nje/article/view/volume8-dematos
Published online: 15th December 2023

[1] Institute for Archaeological Sciences, Department of Geosciences, Eberhard-Karls-Universität Tübingen, Tübingen, Germany; daniela.de-matos@uni-tuebingen.de
[2] Centro de Geociências da Universidade de Coimbra, Universidade de Coimbra, Coimbra, Portugal
[3] Instituto Terra e Memória, Largo Infante Dom Henrique, Museu de Arte Pré-Histórica, Mação, Portugal
[4] CNRS, UMR 7269, Laboratoire Méditerranéen de Préhistoire Europe Afrique (LAMPEA), Aix-en-Provence, France
[5] Interdisciplinary Center for Archaeology and the Evolution of Human Behaviour, Universidade do Algarve, Faro, Portugal
[6] Research & Information Services of Namibia (RAISON), Windhoek, Namibia

ABSTRACT
Several landscapes in the highlands and escarpments of Angola and Namibia (HEAN) have karstic regions with caves. Within the Northern Escarpment in Angola there are two main karstic regions. The first one includes the northern caves associated with a tropical climate and mostly concentrated in Ambuíla, Uíge Province. The second region comprises caves near the Atlantic coast, which are linked to underground flows of the Cambongo-Negunza River. An additional cluster of caves is on the Humpata Plateau and its edges within Angola's Marginal Mountain Chain landscape. Most caves in Namibia are in the Karstveld and Khomas Hochland Plateau landscapes in karstic areas of relatively high rainfall. In this paper, we provide a brief overview of the history of cave exploration, sites and fauna documented in them. We report on the fauna recorded during surveys in 2010 and 2018–2021 in the southern karst around Humpata, Huíla Province; and summarise information available on fauna from Namibia. Most species recorded in Angolan caves are trogloxene taxa observed or collected in cave sediments. Namibian caves house a diversity of invertebrates, many of which are endemic or likely to be endemic to Namibia and the HEAN. Two endemic fish in underground lakes in Namibia are critically endangered. This study emphasises the need for further field research and for strategies to conserve caves and their faunas in both countries.

Keywords: Angola, caves, escarpments, fauna, highlands, Namibia

CAVES IN ANGOLA: INTRODUCTION AND HISTORY

Few studies of Angolan caves and karstic systems have been published. Documented cave explorations are rare, and studies of the biodiversity and microenvironments of these sites are even scarcer. Most information comes from geological surveys and quarrying in the early 1900s. Mining exploration and the development of roads motivated more serious scientific inquiry in the decades prior to independence in 1975. Early studies focused on sedimentary questions, but also highlighted particular landscapes or fossil findings (Mouta & Borges 1926, Mouta & O'Donnell 1933). Caves and crevices of the highlands and escarpments received particular attention in the 1950s due to their Quaternary palaeontological fossils. The main cave sites were discovered during mining operations in the 1940s and 1950s, and their fossil contents were analysed subsequently (Arambourg & Mouta 1952, Delson *et al.* 2000, Gilbert *et al.* 2009). More recent palaeontological surveys directed by Martin Pickford and Brigitte Senut between 1989 and 1991 discovered many more sinkholes, tufa and fissures with Plio-Pleistocene to Holocene fossil-bearing sediments (Pickford *et al.* 1992, 1994, David & Pickford 1999). A few direct but brief references about the biospeleology of Angola from the work of António de Barros Machado were reported by Regala (2014); these focus largely on the ecology of Arachnida and Diptera.

The key publications about the geomorphology of the Angolan karst are from Ilídio do Amaral, a prominent Angolan geographer at the University of Lisbon. He described three main areas with caves and karst features: (i) Nova Caimpemba, Ambuíla Uíge Province (do Amaral 1973a); (ii) Cambongo-Negunza, Cuanza-Sul Province (do Amaral 2006); and (iii) Leba, Humpata, Huíla Province (do Amaral 1973b). Other small caves and crevices occur along the coast, for instance near Cabo Ledo, Lobito and Moçâmedes, but these remain mostly unstudied.

The most recent field studies have focused on the karstic features of the Leba dolomites in Humpata and Chibia *municípios* in Huíla Province. This work produced a preliminary map of 45 caves on and around the plateau, photographic records of ethnographical and biospeleological features and identified the first evidence of so-called "pseudo-karst" in the eastern flanks of the Humpata Plateau (Pinto *et al.* 2017).

The northern karst of Angola
Only a few patches of carbonate rocks occur in northern Angola and karstic areas are consequently

rare (Figure 1). Precambrian rocks of the Xisto-Calcário/Schisto-Calcaire of Congo (de Carvalho *et al.* 2000) occur in the highlands of Zaire Province. The limestone there is heavily weathered and its residual formations show many of the characteristics of tropical karst.

In Zaire Province, karst features are mostly superficial and found in the upper M'bridge River basin. One cave is located at Nzau Evua hills in the Vamba River valley, about 80 km southwest of M'banza Congo city. It is locally called the *Gruta da Igreja* (Church Cave), as it once served as an improvised chapel. The cave has a cold spring with a wide dry chamber with many speleothem formations. The site has been heavily altered by recent human activities and is frequently visited by tourists. The walls of the cave are painted and local tales assign the authorship of the paintings to people of the Kongo Kingdom, who found refuge from slavery in the cave in the 15th century. Other chambers and shafts remain unexplored.

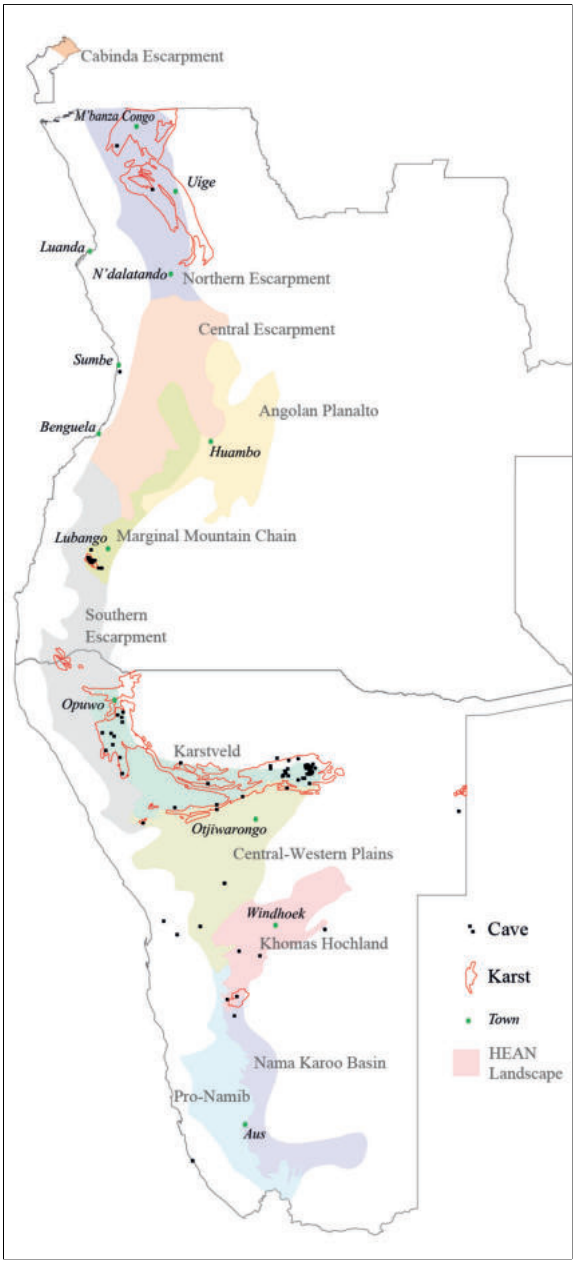

***Figure 1:** Areas of karst and locations of caves in Namibia and Angola, the boundaries of the zone of highlands and escarpments of Angola and Namibia (HEAN) and their landscapes (adapted from Mendelsohn & Huntley 2023).*

Further south in Uíge Province, approximately 200 km from the coast, a tropical karst is found in the *município* of Ambuíla in the upper Loge River basin. The area is hilly with elevations between 1,100 and 1,200 masl, in mountains locally known as Serra da Mucaba, Planalto do Cau, Serra da Buela and Serra da Inga. The topography is characterised by long, dissected valleys, alternating with ridges oriented NNW–SSE and a dense dendritic network of the Loge River tributaries (see Lautenschläger *et al.* 2023).

The regional geology of the Northern Escarpment is dominated by the Upper Precambrian rocks of the Shale-Limestone Series of Sansícua and Alto Chiloango (Mouta 1954). Karstic features occur in a bedrock of dark dolomites and dolostones with cherts, oolites and stromatolites. The tropical conditions have contributed to an accelerated corrosion of the dolomites along the major fracture zones. The intense karstification in the region is expressed in a variety of depressions, dolines, uvalas and poljes, as well as many residual forms. Isolated columns and septum windows remain in the valleys as relicts of collapsed caves.

Some karst forms are overshadowed by the dense gallery forest covering the mountains, contrasting with the savanna-like vegetation of the plains. At the foothills of these poljes there are solution chambers and labyrinths. Nzenzo Cave is located in the southern flank of the Buela hills, where a limestone tower with a chamber about 10 m wide partially collapsed when the slope retreated. A waterfall drops into the cave forming a spring and a thick stalagmitic base. Most caves at Ambuíla remain unmapped but local people mentioned Kinivavua, Kulo and Nsala caves as meeting points during the first liberation movements in the 1960s.

Near Sumbe, along the coast of Cuanza-Sul Province, there is an active karstic system associated with the underground drainage of the Cambongo-Negunza river system. There, the Negunza River has carved a subterranean canyon for about 600 m with an E–W orientation, abruptly changing its direction to S–N, controlled by a fault and forming a waterfall into a circular depression, like a funnel. The waterfall has a drop of about 135 m and leads into a wide channel. The site of Furnas, also known as Sassa Caves, is a collapsed doline with two levels. In the top level, a large chamber and adjacent solution chambers are frequently visited by tourists for their scenic views of the waterfall dropping into the interior canyon, and its speleothems which include drapes, stalactites and stalagmites. Below, the channel may only be accessed during dry seasons when the phreatic level drops.

The southern karst of Leba, Humpata

The karst features in the Southern Escarpment are mostly concentrated in Huíla Province between the municipalities of Humpata and Chibia, around 30 km west of Lubango. Caves are found on the Humpata Plateau where a combination of lithology, tectonics and climate conditions allowed the development of karst features in dolomites, as well as of a pseudo-karst in quartzite-sandstone bedrocks of the Chela Group.

The Humpata Plateau is a pediplain of polygonal shape located in a sector of the Marginal Mountain Chain (Mendelsohn & Huntley 2023) that is structurally organised by systems of crossed fractures, faults and fissures (Lopes *et al.* 2016). Severe erosion shaped the hydrographic basin and formed deep valleys and canyons. At the edges, abrupt scarps and ravines over 1,200 m high (such as Fenda do Bimbe and Fenda da Tundavala) become waterfalls during torrential storms. Impressive crests of bare rock face both east and west.

In the eastern flank of the plateau, facing Lubango city, there are small fissures (fendas) in the quartzitic crests, for instance Fenda da Mapunda. At the top of the crest, many pseudo-karst forms are present at the surface. Small circular depressions, narrow chimneys and fissures give access to underground galleries. These formations are associated with the spring of Senhora do Monte which supplies water to part of the city of Lubango. Galleries with vertical development have maximum drops of 60 m. Bat populations of the genus *Rhinolophus* occupy the fissures. Other solution chambers should be present at the phreatic level.

The southwestern flank of the Humpata Plateau where the dolomites crop out is crossed by numerous fractures and faults. There are many karstic forms with subterranean development in the extensive fault of Bentiaba–Leba–Caholo–Cangalongue orientated NW–SE, which splits the plateau almost in half between Leba and Cangalongue villages. Another less extensive fault follows a NNW–SSE axis from Molo–Muange–Nuinge–Numbalo, and is partially filled by norite sills of post-Permian Age intrusive into the Chela sequence. These two main faults are structurally connected by other smaller EEN–WSW fractures and fissures at different locations, such as Leba, Bruco, Tchivinguiro, Bata-Bata and Cangalongue (Lopes *et al.* 2016).

In locations such as Leba, Bruco and M'basso, a dendritic drainage facing east follows the fractures of the Chela quartzites at the contact with the dolomites. Waterfalls can be found at the western edge of the Humpata Plateau; some are only active during wet periods, when ground saturation allows the reactivation of *mulolas* (ephemeral rivers) and interior lakes such as Nuantchite and Catende located about 20 km south of Humpata town.

Most of the known caves at Humpata are located close to the foot of the valley walls, usually 6–15 m above the talwegs. The hills usually have labyrinths of chimneys and tubules connecting the main chambers and adjacent solution chambers. Breccias and tufa deposits infill these fissures. Most of the cave entrances were exposed during the Quaternary by erosional retreat of the slopes, for instance at Leba or Malola. Others, for instance the solution chambers of Tchaticuca or Cangalongue, were connected to the surface through chimneys and were exposed only after horizontal entrances were created by quarrying. Columns and pinnacles are evident from a distance but are covered by dense shrubs.

In the upper stream of the Cudeje River (Bruco) in the Malola-Ufefua area, the dolomite hills are mostly residual and have been heavily explored for hydraulic lime until the present day. Nonetheless, important development of endokarst has been observed here. For instance, Malola II Cave is in a blind valley and has a cave mouth about 4 m wide. A vertical entrance with a talus cone of guano and silts leads to a large chamber in which the floor is covered by boulders of roof spall and guano. A few stalagmites are visible and boulders possibly cover more. The walls have travertines and speleothem drapes but the environment is dry and dusty. The chamber connects with a labyrinth of other galleries upward where eccentric flowstones and dripstones cover the walls.

Many of the solution chambers and fractures are infilled with Plio-Pleistocene breccias or younger unconsolidated deposits that yield the remains of species that lived in or near the karst habitats during prehistoric times (Pickford *et al.* 1994, Gautier 1995, Gilbert *et al.* 2009, Sen & Pickford 2022).

In the area of Tchivinguiro, several springs are tourist hotspots and support freshwater hypogean fauna. An active endorkarst developed underground is controlled by a structural faulting system with a main fault and a series of radial fractures. This geomorphology shaped the weathering of the Tchivinguiro Depression and the development of an underground network of chambers.

Tchivinguiro Cave is located at the foothills of Nandimba, a dolomite cupula with a spring fed by an underground lake. The hill has a low gradient, and

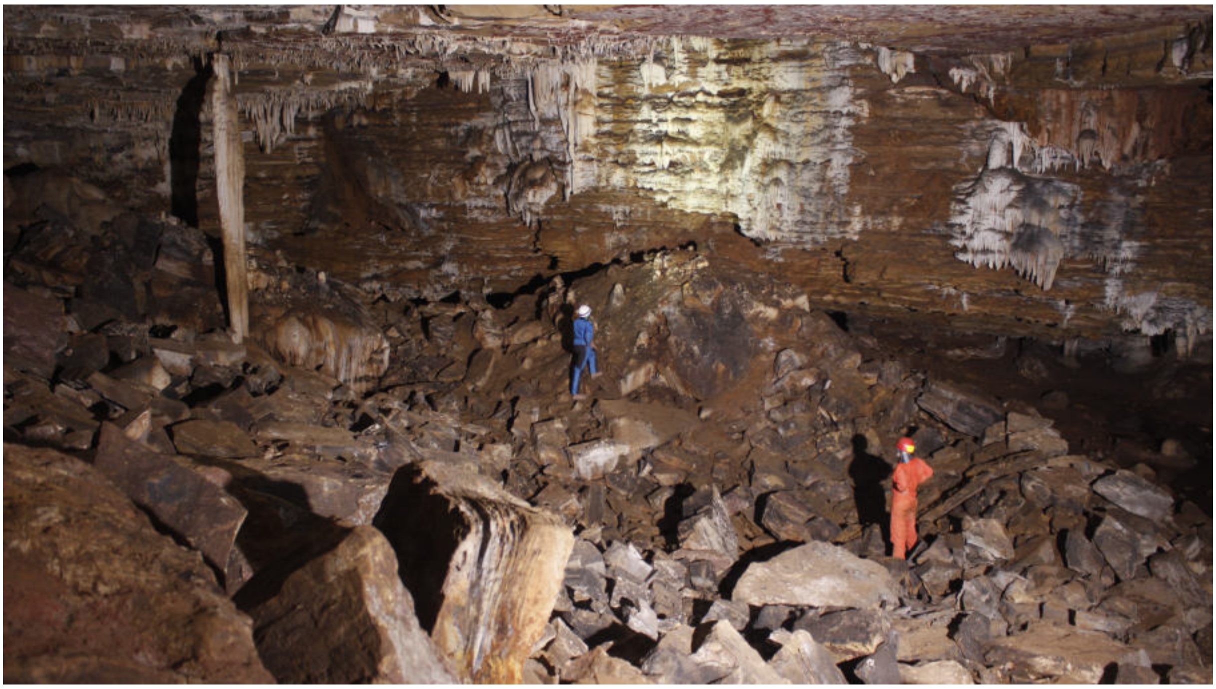

Figure 2: *The main chamber of Tchivinguiro Cave, with a column on the left. Photo: Rui Francisco, 2019.*

many chimneys and narrow sinkholes give access to the subterranean chambers. These chimneys are frequently obscured by thick thorn bushes and the channels are choked by pink–red muds and bedrock debris. Inside the cave, the environment is warm with temperatures ranging 25–28ºC, with relative humidity over 90%. The chambers are covered with the boulders of roof spall. Many stalagmites cover the upper surface of these blocks. A few speleothem columns are also present, some exceeding 4 m in height (Figure 2). The underground network surveyed at Tchivinguiro extends for about 1 km but it is likely to be longer, with a few shafts connecting to the outside. The freshwater reservoir emerges at Nandimba spring along the western foothills of the escarpment where it is used to irrigate crops. Crabs and catfish are commonly observed inside the cave pools but the aquatic fauna of Tchivinguiro cannot be regarded as stygobiotic because the pools are connected to surface pools. Areas of suction were detected and indicate pipes and chimneys to other lower bodies of water which suggest that different microenvironments and biota may be present at deeper levels.

Fauna in Angolan caves

The list of subterranean fauna presented here includes species documented during speleological surveys in 2010, and between 2018 and 2021, of the Leba caves in Humpata. The list is based on observations and skeletons collected in archaeological excavations of recent natural accumulations. Most of the species identified are trogloxene taxa. The list is notably poor in invertebrate taxa and reptiles. This should not be perceived as proof of absence but rather as an opportunity for more intensive biospeleological studies. A selection of animals found in caves is shown in Figure 3.

CRUSTACEA: Brachyuran, pigmented aquatic crab, lives in the pools of the cold spring Nandimba-Tchivinguiro.

INSECTA: Scarabaeoidea, Scarabaeinae, can be found close to the entrance of the fissures of Senhora do Monte, Malola and Cangalongue caves where there are bat roosts. *Heliocopris* sp. dung beetles have been observed in the floors of caves recently used by cattle. Orthoptera, Gryllidae, have been observed in all of the caves surveyed. They are macrophthalmic, pigmented, apterous crickets. At Leba and Cangalongue they frequent the humid shade in crevices adjacent to the main cave channels. They are typically found between large boulders coated with guano.

ARACHNIDA: Amblypygid *Damon variegatus* (whip spider) is found in dry and humid caves, and in the shade of smaller crevices. It has been observed in most of the caves of the southwestern system. Chernetidae: Chernetid pseudoscorpions have been observed in most of the Humpata caves.

GASTROPODA: *Achatina tincta*, a land gastropod, has been observed at Leba and Malola.

MYRIAPODA: Diplopoda, *Archispirostreptus gigas*, the giant African millipede, has been observed in fissures and subsurface features at Senhora do Monte, Leba and Tchivinguiro where they were probably trapped.

AVES: The remains of small owls from the genera *Glaucidium* (pygmy owls) and/or *Otus* (scops owls) spp., as well Columbiformes, Passeriformes and Piciformes have been found in caves; probably from human or carnivore prey.

REPTILIA: Testudines, Pelomedusidae: *Pelusios* spp. (turtles) have been observed in caves near water bodies or associated springs. Colubridae: *Boaedon angolensis,* the Angolan house snake, has been observed inside and in the vicinity of the caves. Agamidae: *Agama planiceps* is found in rocky areas and cliffs in the vicinity of caves. Scincidae:

Figure 3: *A selection of animals found in caves in Namibia and Angola. a) Nycteribiidae sp., bat fly found near horseshoe bat roosting deep in the caves of Senhora do Monte (photo: Renato Serôdio, 2010); b)* Amietia angolensis *observed at Algar do Tchivinguiro (photo: Renato Serôdio, 2010); c) Chernetid pseudoscorpions found at the Humpata caves (photo: Renato Serôdio, 2010); d) Groups of horseshoe bats roosting in the pseudo-karst fissures Senhora do Monte (photo: Renato Serôdio, 2010); e) Giant African millipede, Cangalongue Cave (photo: Rui Francisco, 2010); f) Amblypigi at Sumidouro Candimba Cocufima, Tchivinguiro (photo: Rui Francisco, 2010); g) Cricket (Grillidae) at Sumidouro Nandimba Cocufima (photo: Rui Francisco, 2010); h)* Clarias cavernicola *cave catfish in Aigamas cave, Namibia (photo: Francois Jacobs).*

Trachylepis sulcata ansorgii, the Ansorge's rock skink, has been seen in the fissures adjacent to most caves in the southwest.

PISCES: Ictaluridae: pigmented catfish have been observed in the Nandimba-Tchivinguiro cold spring.

AMPHIBIA: Cacosterninae, *Amietia angolensis*, the Angolan river frog, was found in springs and ponds associated with the Tchivinguiro cave system, and in crevices near rivers, ponds and lakes around Humpata, and the cold springs of Umbutu and Mewó (de Matos 2021, Robakiewicz *et al.* 2021).

MAMMALIA: Chiroptera, *Rhinolophidae* spp., horseshoe bats roost in several caves at Humpata and are the most common mammals seen inside the Humpata caves, with populations in the caves of the dolomite karst at Leba, Malola and Cangalongue, and in the fissures of the pseudo-karst of Senhora do Monte. Hystricidae: Porcupines *Hystrix africaeaustralis* are trogloxene animals; they are often found sheltering deep into many caves. Abundant Muridae (e.g., mice and rats) and Macroscelidae (e.g., elephant shrews) remains were found in prehistoric and modern sediments in caves of the Humpata Plateau (Pickford *et al.* 1992, de Matos 2022). Skeletal material originates from both the natural deaths of animals burrowing inside the cave and from skeletal fragments in regurgitated pellets produced by barn owls *Tyto alba*. Hyracoidea (the rock hyrax *Procavia capensis* and the bush hyrax *Heterohyrax brucei)* have been sighted at Leba. Remains and ichnofossils of lion (*Panthera leo*) and leopard (*P. pardus*) were collected deep inside caves before the 1950s. Spotted hyaena *Crocuta crocuta* ichnofossils have been found in cave sediments at Leba and Cangalongue. Papionini fossils were found at Leba, Malola and Cangalongue. Small groups of *Papio* spp. (baboons) can be found in the vicinity of the main caves, particularly along the western cliffs between Bimbe and Leba. They also inhabit the humid forest surrounding the spring of Senhora do Monte.

CAVES IN NAMIBIA: INTRODUCTION AND HISTORY

The first geological and hydrological survey of karst in Namibia was by Jaeger (1921), while the earliest scientific explorations and surveys of Namibian caves were by Jordan (1936), Strinati (1977) and Churchill *et al.* (1997). The South African Speleological Association undertook several expeditions to Namibia between 1968 and 1988. John Irish and colleagues established the Suid Wes Afrika Karst Navorsing Organisasie (SWAKNO) in Namibia in 1988 with the aim to promote biospeleological research. They surveyed many caves and collected biological specimens, as well as collating information on karst features and cave fauna (Irish *et al.* 2001). Pickford and Senut (2010) provide a substantial review on the geology of karst and its palaeobiology in Namibia.

Most karst in Namibia is in areas of relatively high rainfall, and the majority of underground solution features is in the form of sinkholes (Irish *et al.* 2001). Much of eastern Namibia (and Angola) is covered by young aeolian and alluvial sediments which conceal older karst features. The majority of the 76 surveyed caves (Irish *et al.* 2001) are therefore in central and northwestern Namibia (Figure 1). These 76 caves exclude small or short caves (less than 10 m in depth).

The longest caves are Arnhem (4,494 m in length) approximately 110 km ESE of Windhoek, and Pofaddergrot (2,812 m) and Ghaub (2,700 m) in the Otavi–Grootfontein–Tsumeb hills of dolomites and limestones. In the same area, Lakes Otjikoto and Guinas are open cenotes, the latter reaching a depth of 132 m. Several other large underground lakes have been found and reached through small openings on the surface, notably Aikab, Harasib, Gamkarab and Dragon's Breath. Dragon's Breath Cave contains the largest underground lake on Earth, with a surface area of about 2 ha.

Fauna in Namibian caves

The list of subterranean fauna presented here is based on the literature about Namibian biospeleology and information kindly provided by John Irish (in litt.).

CRUSTACEA: Terrestrial Isopoda, anophthalmic and pigmented, are found on the beach in the Dragon's Breath Cave and are likely to occur in areas with higher moisture in the Otavi Mountains, such as Pofadder, Ghaub, Aigamas and Johann's caves (Irish *et al.* 2001). Ostracoda, Candonidae: *Namibcypris costata,* an endemic ostracod crustacean can be found at the springs of Sesfontein. Protojaniroidea: four endemic species of depigmented crustacean isopode, stygobitic species: *Namibianira aigamensis* in Aigamas Cave; *N. aikabensis* in Aikab Cave; *N. arnhemensis* in Arnhem Cave; and *N. dracohalitus* in Dragon's Breath Cave. Amphipoda include six species of Ingolfiellidae: *Trogloleleupia dracospiritus* in Dragon's Breath Cave; *T. gobabis* in Arnhem Cave; *T. eggerti* in a borehole near Tsumeb; *T. nudicarpus* in Wondergat Cave; *T. opisthodorus* in Dragon's Breath Cave; and *Stygobarnardia caprellinoides* in groundwater in the Tsumeb area. Sternophysingidae: *Sternophysinx hibernic* was reported at Naos Cave.

ARACHNIDA: Cyatholipidae: *Cyatholipus* spp. has been recorded in Johann's Caves in the Otavi mountains. Hahniidae: *Hahnia* sp. at Scorpion's Maze. Loxoscelidae: four species of *Loxosceles* have been reported where there is low humidity. These are depigmented and troglophile species which build ground webs to entangle guanobian prey (Irish *et al.* 2001). *Loxosceles bergeri* and *L. pilosa* are reported from Arnhem Cave; *L. simillima* Lawrence, reported at Ludwig's and Kimberlite caves; and *L. vonwredei* Newlands, reported at Uhlenhorst, Otavi and Märchen Cave. Many diverse groups of Pseudoscorpiones (Cheiridiidae, Cheliferidae, Withiidae); Araneae (Cyatholipidae, Hahniidae, Loxoscelidae, Palpimanidae, Pholcidae, Prodidomidae, Segestriidae, Selenopidae, Sicariidae, Theridiidae); Opiliones (Assamidae); Amblypygi; Scorpiones (Bothriuridae); and Acari (Argasidae) have been reported at Aigamas, Nosib, Dragon's Breath, Pofadder, Obab, Ghaub, Arnhem, De Valle and Nooitgedacht caves by Irish *et al.* (2001).

MYRIAPODA: Diplopod, *Juliformia*, and other millipedes, are found mostly trapped in vertical entrances.

INSECTA: Nicoletiidae, *Lepidospora* sp., in Dragon's Breath Cave and Pofaddergat. *Katacamilla cavernicola*, at Nosib, Arnhem and De Valle caves.

ORTHOPTERA: Gryllidae are reported from caves where there are bat roosts. These macrophthalmic, pigmented, apterous crickets are typically found between large boulders coated with guano.

PISCES: The fish *Tilapia guinasana* which is endemic to Lake Guinas, and the cave catfish *Clarias cavernicola* (Figure 3h; Jacobs *et al.* 2019, 2021) which is restricted to Aigamas Cave, are both listed by IUCN as Critically Endangered (Bills 2007a, 2007b).

MAMMALIA: Soricidae: *Crocidura cyanea*, permanent troglobitic populations reported at Arhem Cave and Nooitgedacht Cave (Irish *et al.* 2001). These shrews inhabit dark zones and reportedly feed on bat carcasses and invertebrates (Irish *et al.* 2001). Chiroptera: Insectivorous bats have been recorded in Namibian caves, including *Hipposideros commersoni* at Arnhem, Aigamas and Aikab caves; *Sauromys petrophilus* at De Valle Cave; *Tadarida aegyptica* in Arnhem, De Valle and Nooitgedacht caves; and *Nycteris thebaica* in Arnhem, Gcwihaba and Nooitgedacht caves. Five species of horseshoe bats are known to roost in Namibian caves: *Rhinolophus denti* in Arnhem, Naos, Nooitgedacht and Tsumeb caves; *R. darlingi* in Arnhem and Dante caves; *R. capensis* in Arnhem Cave; *R. clivosus* in Arnhem and Nooitgedacht caves; and *R. fumigatus* in Nooitgedacht and Otgrot caves. In addition, *Miniopterus inflatus* and *M. schreibersi* roost in Arnhem, De Valle, Gifgat and Nooitgedacht caves. Medium-sized mammals such as porcupines and rock hyraxes have been found in crevices and deep caves. Leopards can be found sheltering in deep caves.

CONCLUSIONS

The diversity of cave-dwelling animals is relatively understudied in Angola and Namibia. The karst of the Northern Escarpment in Angola, in particular, has very few records as most surveys have been informal and not specialised in this field. Large areas of the northern and coastal karsts of Angola are unexplored, and it is likely that many more endemic species will be found. Understanding the processes that guide the distribution of caves and their fauna requires a complex and multidisciplinary approach with fieldwork and the involvement of local populations and stakeholders in risk assessments and conservation.

A more comprehensive spatial assessment within one or more caves in a regional context can unveil subtle variations between biotic and abiotic parameters. The remarkable connection observed between faunal groups and distinct microhabitats, as opposed to the broader range of substrate diversity, highlights the profound reliance of cave-dwelling communities on external resources. In most cases, bat guano is the main source of nutrients for cave fauna, the great majority of which are invertebrates and likely to be endemic to specific caves or karstic areas. Relative humidity is the key factor influencing the development of the underground environment, and moisture availability is therefore directly correlated to the frequency of endemic hypogean fauna. We encourage and emphasise the need for much more research on caves and their fauna in Namibia and Angola.

ACKNOWLEDGEMENTS

Fieldwork in Angola was funded by grants to D Matos by the Fundação para Ciência e Tecnologia (SFRH/BD/11716 2/2016), the Leakey Foundation Dissertation, and the National Geographic Society (USA). Studies were developed in partnership with the Department of Geology and Mining, the Instituto Superior Politécnico da Huíla, the Reitoria Universidade Mandume Ya Ndemufayo, Governo Provincial da Huíla, and the Humpata and Chibia Administration Offices. Thanks are due to Rui Francisco and Renato Serôdio for photographs and preliminary documentation during the 2010 Humpata Caves Survey, and to Carlos Bumba for information about the northern karst. We thank Mariana Marques and Luís Ceríaco for identification of reptiles, and Fernanda Lages and Adjany Costa for identification of fish. Special thanks to Martin Pickford for comments and corrections. John Irish kindly provided advice, and the information and geographic coordinates of caves in Namibia.

REFERENCES

Arambourg A, Mouta F (1952) Les grottes et fentes a ossements du sud de l'Angola. In: *Actes du IIème Congrès Panafricain de Préhistoire d'Alger*. Presented at the 2nd PanAfricanist Archaeological Association, Algiers, Algeria.

Bills, R. 2007a. *Tilapia guinasana*. The IUCN Red List of Threatened Species 2007: e.T63354A12662434. https://dx.doi.org/10.2305/IUCN.UK.2007.RLTS.T63354A12662434.en. Accessed on 07 July 2023.

Bills, R. 2007b. *Clarias cavernicola*. The IUCN Red List of Threatened Species 2007: e.T63363A12662977. https://dx.doi.org/10.2305/IUCN.UK.2007.RLTS.T63363A12662977.en. Accessed on 07 July 2023.

Churchill S, Draper R, Marais E (1997) Cave utilization by Namibian bats. *South African Journal Wildlife Research* 27(2): 44–50.

David H, Pickford M (1999) Composition en acides aminés d'os de mammifères fossiles de deux sites du Plio-Pléistocène d'Angola. Comparaison. *Geodiversitas* 1(2): 215–227.

De Carvalho H, Tassinari C, Alves PM, Guimarães F, Simões MC (2000) Geochronological review of the Precambrian in western Angola: Links with Brazil. *Journal of African Earth Sciences* 31(2): 383–402. https://doi.org/10.1016/S0899-5362(00)00095-6.

Delson E, Terranova CJ, Jungers WL, Sargis EJ, Jablonski NG, Dechow PC (2000) *Body mass in Cercopithecidae (Primates, Mammalia): estimation and scaling in extinct and extant taxa*. American Museum of Natural History, Washington. http://hdl.handle.net/2246/282.

De Matos D (2021) A paisagem cársica do sudoeste de Angola. *Revista Angolana de Geociências* 2(1): 127–143.

De Matos D (2022) *Geoarchaeological investigations in Southwestern Angola: macro- and micro-scale approaches to the Middle and Late Pleistocene of Leba Cave.* (Dr.rer.natdissertation). Eberhard–Karls–Universität Tübingen.

Do Amaral I (1973a) Contribuição para o Estudo do karst ou carso de Nova Caimpemba, no Noroeste de Angola. *Garcia de Orta* 1(2).

Do Amaral I (1973b) Nota sobre o karst ou carso do planalto do Planalto da Humpata (Huíla) no Sudoeste de Angola. *Garcia de Orta* Série de G(2): 29–36.

Do Amaral I (2006) O Rio Cambongo-Negunza e os seus afluentes: um exemplo da complexidade de padrões de drenagem em Angola. *Finisterra* XLI(82): 15–48. https://doi.org/10.18055/finis1447.

Gautier A (1995) Restes animaux Holocènes et du Paléolithique Moyen (MSA) de la Grotte de Leba sur le Plateau de Humpata (Angola). *Archaeofauna* 4: 131–143.

Gilbert CC, McGraw WS, Delson E (2009) Brief communication: Plio-Pleistocene eagle predation on fossil cercopithecids from the Humpata Plateau, southern Angola. *American Journal of Physical Anthropology* 139(3): 421–429. https://doi.org/10.1002/ajpa.21004.

Irish J, Marais E, Juberthie C, Decu V (2001) Namibia. *Encyclopaedia Biospeologica*: 1639–1650.

Jacobs FJ, Hay CH, Jacobs PG (2019) A baseline study of the critically endangered cave-dwelling catfish (*Clarias cavernicola*). Unpublished report: Kamutjonga Inland Fisheries Institute (KIFI).

Jacobs FG, Jacobs PG, Hay CJ, Naesje TF (2021) Status update of the endemic and critically endangered cave catfish *Clarias cavernicola* Trewavas 1936, from the Aigamas Cave system, Namibia. *African Journal of Aquatic Science* 46(1): 18–21. https://doi.org/10.2989/16085914.2020.1787125.

Jaeger F (1921) Landschaften des nordlichen Südwestafrikas. In: Jaeger F, Waibel L (eds) *Beitrage wr Landeskunde von Südwestafrika. Band II.*E.S. Mittler & Sohn, Berlin.

Jordan K (1936) Dr. Karl Jordan's Expedition to South-West Africa and Angola. Narrative. *Novitates Zoologicae* 40: 17–62.

Lautenschläger T, Aime MC, Clausnitzer V, Langer L, Meller P, Müller F *et al*. (2023) Green gem of the Northern Escarpment: biodiversity and endemism of the Serra do Pingano Forest Ecosystem. In: Mendelsohn JM, Huntley BJ, Vaz Pinto P (eds) Monograph on endemism in the highlands and escarpments of Angola and Namibia. *Namibian Journal of Environment 8:* 161–172.

Lopes FC, Pereira AJ, Mantas VM, Mpengo HK (2016) Morphostructural characterization of the western edge of the Huila Plateau (SW Angola), based on remote sensing techniques. *Journal of African Earth Sciences* 117: 114–123. https://doi.org/10.1016/j.jafrearsci.2016.01.007.

Mendelsohn JM, Huntley BJ (2023) Introducing the highlands and escarpments of Angola and Namibia. In: Mendelsohn JM, Huntley BJ, Vaz Pinto P (eds) Monograph on endemism in the highlands and escarpments of Angola and Namibia. *Namibian Journal of Environment 8:* 7–22.

Mouta F (1954) *Notícia explicativa do esboço geológico de Angola (1:2.000.000)*. Serviços Geológicos de Angola, Lisboa.

Mouta F, Borges A (1926) Communication de la Mission Geologique de l'Angola Congrés Geologique International XIV session - Espagne. Sur le Crétace de la Mission Geólogique du litoral de l'Angola (Districts de Benguela et Mossamedes). *Boletim da Agência Geral das Colónias* 2(15): 100–118.

Mouta F, O'Donnell H (1933) *Carte géologique de l'Angola: notice explicative*. Ministério das Colónias, Lisboa.

Pickford M, Mein P, Senut B (1992) Primate bearing Plio-Pleistocene cave deposits of Humpata, southern Angola. *Human Evolution* 7(1): 17–33. https://doi.org/10.1007/BF02437475.

Pickford M, Mein P, Senut B (1994) Fossiliferous Neogene karst fillings in Angola, Botswana and Namibia. *South African Journal of Science* 90(4): 227–230.

Pickford M, Senut B (2010) *Karst geology and palaeobiology of northern Namibia*. Ministry of Mines and Energy, Geological Survey of Namibia, Windhoek, Namibia.

Pinto P, Freire M., Andrade R, Francisco R, Serôdio R (2017) Caving expedition to the Humpata Plateau, Angola. In: *Proceedings of the 17th International Congress of Speleology*. Presented at the International Congress of Speleology, Sydney.

Regala FT (2014) António de Barros Machado (01/10/1912 - 30/05/2002) - figura ímpar da Espeleologia Portuguesa. *Trogle. Boletim da Associação de Estudos Subterrâneos e Defesa do Ambiente* 6(October): 46–61.

Robakiewicz E, De Matos D, Stone JR, Junginger A (2021) Hydrochemistry and diatom assemblages on the Humpata Plateau, southwestern Angola. *Geosciences* 11(9): 359. https://doi.org/10.3390/geosciences11090359.

Sen S, Pickford M (2022) Red rock hares (Leporidae, Lagomorpha) past and present in southern African, and a new species of *Pronolagus* from the early Pleistocene of Angola. *Communications of the Geological Survey of Namibia* 24: 67–97.

Strinati P (1977) Recherches biospeologiques au sud-ouest Africain. In: *Comunicacions del 6è. Simposium d'Espeleologia. Bioespeleologia. Terrassa*. Presented at the 6th Speleology Symposium of Speleology, Escola Catalana d'espeleologia, Secció d'investigacions subterrànies, Barcelona, Spain.