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Message from the Chair

Andrew Taylor
Chair, IUCN SSC Afrotheria Specialist Group

Dear Afrotherian colleagues,

In our last newsletter we remembered Galen Rathbun, our group's founder and long-time Chair. He is still greatly missed, and it seems incredible that it is almost 18 months since he died. Since then we have lost two more long-standing members of the group, both of whom had made substantial contributions to our knowledge of the Afrotheria. Hendrik Hoeck passed in November 2019 and Martin Nicoll on the first day in January, 2020. Both have been remembered elsewhere, but we include some memories of them in the current issue. Condolences to their families and friends.

Although Galen can never be replaced, the gaping hole he left in sengi research and conservation needs to be filled, so we have been looking for someone to take over from him and guide our sengi section into the future. Fortunately, we have found such a person in Steven Heritage, a research scientist at the Lemur Center, Duke University. Steven worked closely with Galen during his final few years and is well placed to take over the mantle of sengi coordinator. Steven wrote the sengi section in the 2018 Handbook of the Mammals of the World and I look forward to working with him in the future.

During October 2019, PJ Stephenson and I attended the IUCN SSC Leaders Meeting in Abu Dhabi. This gathering, which takes place every four years and is funded by the Abu Dhabi Environment Agency, is an opportunity for Chairs, Red List coordinators and others in the species conservation community to build connections and strengthen relationships. Some of the issues covered during the meeting included discussions on how best to measure the effectiveness of SSC's actions on biodiversity conservation, identification of major new initiatives needed to address critical conservation issues, consultations on developing policies, guidelines and standards, and increasing visibility and public awareness of the work of SSC, its network and key partners.

Remarkably, 2020 marks the end of the current IUCN quadrennium, which means we will be dissolving the membership once again in early 2021, then reassembling it based on feedback from our members. I will be in touch with all members at the relevant time to find out who wishes to remain a member and whether there are any people you feel should be added to our group. No one is automatically re-admitted, however, so you will all need to actively inform me of your wishes.

We will very likely need to reassess the conservation status of all our species during the next quadrennium, so get ready for another round of Red Listing starting sometime in the not too distant future. This can be a slightly protracted process, especially for the section coordinators, but it is vital for the ongoing conservation support of our species.

Thanks again to PJ Stephenson for returning as the newsletter editor after the Stuarts stepped down last year.

INSIDE THIS ISSUE

PJ has done this job before, and I am grateful for his willingness to give time to this task. As we say every year, the newsletter is one of the few ways we have to keep our group relevant and on the radar under the current difficult funding climate. Funding our species was difficult enough before COVID-19, and now it is likely to become harder. The newsletter is one small way to keep public interest going. It is also one of the targets we set ourselves in our strategic plan that is manageable without financial resources. Please consider submitting articles to the next newsletter in 2021, even if they are only short essays or paper reviews relevant to your study species, as these help our members (and the general public) keep up to date with what research is going on.

Our group's other major contribution to educating the public about the smaller Afrotheres is our website. We will be revising some aspects of the website later this year and into 2021.

I hope you are all well and coping under the stresses of the pandemic, and I wish you well for the remainder of 2020.

Andrew

Andrew Taylor, Gauteng, South Africa
23 August 2020

Articles

Using applied research to conserve secretive Afrotheria: species distribution modelling to inform Environmental Impact Assessments in South Africa

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Introduction

South Africa is home to 30 species within the Afrotheria clade, of which 18 are endemic and 17 are categorized as either Data Deficient, Near Threatened, Vulnerable, Endangered, or Critically Endangered according to the Red List of Mammals of South Africa, Swaziland and Lesotho (Child et al., 2016). As such, improving the conservation of Afrotheria within the country is vital in safeguarding this ancient radiation of African mammals from the persistent pressures of the Anthropocene.

Of particular importance in South Africa are the golden moles (Chrysochloridae). Of the 21 species currently described, 17 are found within the country and 16 are endemic. The golden moles consist of some of the most endangered mammals in South Africa with conservation efforts hampered by a poor understanding of their distribution and ecology, and a failure to protect natural habitat from further degradation and destruction. The primary direct threats facing golden moles are sand mining, agricultural practices, urbanization, and predation by urban cats and dogs.

A further Afrotherian species of conservation concern in South Africa is the southern tree hyrax (*Dendrohyrax arboreus*), regionally listed as Endangered. Similar to its golden mole relatives, the tree hyrax depends on intact forest habitat which is increasingly under threat from degradation, fragmentation, and the direct loss of den and forage trees (Gaylard et al., 2016).

Ever-expanding development is transforming the remnant intact habitat where these species occur. A review of Environmental Impact Assessments (EIAs - legislation put in place to protect biodiversity and ensure responsible development) has shown, in most cases, that reports overlook these secretive and cryptic species. Golden moles are particularly susceptible to being overlooked during the EIA process as the majority of species live almost exclusively below ground at low population densities (Bronner, 2013). Similarly, tree hyraxes occur at low population densities and are arboreal, nocturnal, and can be inactive for long periods of time, avoiding detection in the high canopies or tree holes. This failure to detect species may be compounded either through a lack of adequate expertise from the environmental assessment practitioner or appointed specialist, ineffective fieldwork during the site assessment, or for more nefarious reasons whereby species are deliberately ignored to increase the likelihood of the development becoming authorised.

Many, if not all, species of conservation concern in South Africa would benefit from a more rigorous EIA process. In light of this, the Endangered Wildlife Trust (EWT) has been collaborating with the South African National Biodiversity Institute (SANBI), and the Department of Environment, Forestry and Fisheries (DEFF) to establish an online, open-access national Environmental Screening Tool (EST) which, by law (since October 2019), must be incorporated into the scoping phase of all EIAs to ensure that no species are overlooked and, additionally, removes some of the subjectivity inherent in previous assessment procedures.

Methods

We used occurrence data to ensure that Afrotherian species of conservation concern were as comprehensively represented in the terrestrial animal theme of the EST as possible. The primary source of occurrence records was the EWT mammal database (EWT & SANBI, 2020). However, these records were supplemented by searching the literature, contacting maintainers of provincial biodiversity and museum databases, and data from the citizen science app iNaturalist (iNaturalist, 2020). Two "layers" of sensitivity were used to indicate the potential presence of Afrotheria species on the EST. All occurrence records post-2000 were intersected with a high-resolution land-use layer and included as "high sensitivity". For species with sufficient occurrence records, Species Distribution Models (SDMs) were used to inform a "medium sensitivity" layer. SDMs use the environmental data of known species occurrence locations to predict suitable habitat in the surrounding landscape. Furthermore, for the species with no records post-2000, and insufficient overall records to perform SDMs, pre-2000 occurrence records were included in the "medium sensitivity" layer by intersecting the locations with the aforementioned high-resolution land-use layer.

Results and Discussion

A total of 11 Afrotheria species were included in the current iteration of the environmental screening tool (Table 1). Of these, five species (*Amblysomus marleyi, Chrysospalax trevelyani, Cryptochloris wintoni, Eremitalpa granti granti, Neamblysomus gunningi*) did not have any confirmed occurrence records post-2000. From the remaining six species, five had sufficient records to model their distributions, although in the case of *Neamblysomus julianae* this was limited to the Bronberg Ridge subpopulation. An SDM was also successfully performed for *Chrysospalax trevelyani* as sufficient pre-2000 occurrence records existed. *Cryptochloris zyli* was the only species with post-2000 records with insufficient data points to model its distribution.

Table 1. Details of the Afrotheria species of conservation concern included in the mammal layer of the EST. Status is the regional Red List category: VU = Vulnerable, EN = Endangered, CR = Critically Endangered. SDM shows if a species distribution model is present or not. All species except the hyrax are endemic to South Africa.

Species	Status	Pre-2002 records	Post-2002 records	SDM
Amblysomus marleyi Marley's golden mole	EN	2	0	x
Amblysomus robustus Robust golden mole	VU	8	3	✓
Chlorotalpa duthieae Duthie's golden mole	VU	23	1	✓
Chrysospalax trevelyani Giant golden mole	EN	42	0	✓
Chrysospalax villosus Rough-haired golden mole	VU	15	9	✓
Cryptochloris wintoni De Winton's golden mole	CR	2	0	x
Cryptochloris zyli Van Zyl's golden mole	EN	2	1	x
Eremitalpa granti granti Grant's golden mole	VU	10	0	x
Neamblysomus gunningi Gunning's golden mole	EN	8	0	x
Neamblysomus julianae Juliana's golden mole	EN	699	640	✓
Dendrohyrax arboreus Southern tree hyrax	EN	6	21	✓

Due to the large number of Afrotheria species which occur in South Africa, especially the 16 endemic golden mole species, improving conservation efforts within the country is of the utmost importance in protecting this clade of ancient mammals. Previous conservation efforts have been constrained by a lack of detailed ecological knowledge for many of the species, and a lack of stringent protocols within the EIA framework which failed to sufficiently protect their habitat from development.

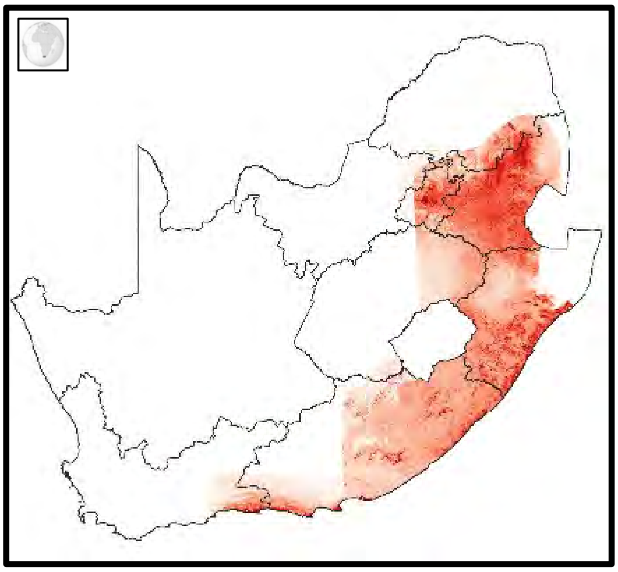

Figure 1. A map showing the overall coverage of combined Afrotheria species distribution models with South Africa. Darker shading shows regions with higher probability of species occurrence.

The inclusion of the "medium" sensitivity layer, utilising species distribution model outputs and pre-2000 occurrence records in the national screening tool, is a critically important consideration in a country with very high levels of biodiversity where most areas have not recently or, in some areas, have never been thoroughly surveyed. Thus, if the report generated by the EST flags for medium sensitivity of a golden mole species of conservation concern (as predicted by the SDM), then a qualified, registered ecologist/mammologist with experience working with the taxa is, by law, required to conduct site surveys to assess its presence or absence.

Surveying for golden moles is no easy task, but the Endangered Wildlife Trust is hoping to leverage its wide range of field staff to assist. For example, EWT's Dryland Conservation Programme has concrete plans in place to attempt to re-locate De Winton's golden mole (*Cryptochloris wintoni*) on the west coast of the country. This elusive species is listed as Critically Endangered and feared extinct, so confirming it is still extant would be a significant achievement. There are also some preliminary studies looking at the possibility of using eDNA (environmental DNA) as a method of confirming golden mole presence at specific sites. Environmental DNA is genetic material obtained directly from environmental samples (soil, sediment, water, etc.) without any obvious signs of biological source material, and is an efficient, non-invasive and easy-to-standardize sampling approach with important implications for the monitoring of cryptic species (see e.g. Deiner et al., 2017). Although very much in its infancy in South Africa, if the method proves viable it will greatly improve the ability to confirm the presence of fossorial golden moles, and the arboreal southern tree hyrax, without the need to observe them with the human eye.

Looking forward it is important that we do not let complacency set in with regards to Afrotheria conservation in South Africa, but rather actively increase our efforts. This can be done through lobbying for the inclusion of Near Threatened and Data Deficient species in the EST, confirming the presence of species with no post-2000 records, and ensuring that the data used for mapping species locations is kept up to date.

Acknowledgments

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Demystifying aardvark tracks and how (not) to determine aardvark sex

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Introduction

The ability to easily differentiate males and females is useful for many purposes ranging from studying animal behaviour and reproduction to monitoring and managing populations. In aardvarks (*Orycteropus afer*), telling males and females apart is not straightforward. In this article, we summarise the knowledge available about the aardvark's reproductive organs and scent glands with the aim of improving the identification of aardvark sexes. We also explain how to interpret scent gland imprints in aardvark spoor to help eliminate misidentification of aardvark sex in the field.

Lack of sexual dimorphism in aardvarks and the challenges this poses

Scientists and animal caretakers alike prefer simple ways of determining an animal's sex. In many mammal species, sexual dimorphism allows distinguishing males from females based on external characteristics, such as differences in body size between the sexes or the presence of horns or tusks in males but not females. When sexual dimorphism is less obvious, close examination of genitals can prove to be the most suitable diagnostic characteristic.

Older field guides have suggested differences in colouration between male and female aardvarks, such that females supposedly have lighter faces and tails (Skinner & Smithers, 1990). However, these suggestions have not been confirmed, and published field studies on tagged aardvarks have not reported any apparent sexual dimorphism (Taylor, 1998; Weyer, 2018; Weyer et al., 2020). It is also virtually impossible to distinguish males from females in the field by trying to observe their genitalia for two reasons. Firstly, free-roaming aardvarks are often only seen from a distance, at night, and only briefly, and do not allow a clear view of their groin region. Secondly, even a clear line of sight on an aardvark's groin region would not provide clarity on its sex, because both males and females have prominent scent glands that look much like scrota (Fig. 1). The presence of these large scent glands in both sexes is not widely known and still causes confusion, because they are often misinterpreted as a male's testicles. This common misinterpretation, combined with the difficult sexing of aardvarks, contributes to the challenges in monitoring wild populations (with likely bias towards more males), hindering our ability to determine necessary conservation actions.

Figure 1. Male and female aardvark resting in a zoo. Note the prominent scent glands in the groin regions of both aardvarks. Photo taken by L. Hautier at ZSL London Zoo.

Anatomy and evolution of testes and scent glands in aardvarks and other Afrotheria

In many mammal taxa, the testes descend from the abdominal cavity during ontogeny and are located in a scrotum outside of the body, allowing them to circumvent high abdominal temperatures. This setup is important because mammalian sperm production is temperature-sensitive, and temperatures above 38 °C can inhibit the production of normal, healthy sperm without defects (e.g., Cowles, 1965; Short, 1997). Examples of scrotal mammals include Primates, Scandentia, Dermoptera, most Rodentia, Lagomorpha, Microchiroptera, most Carnivora, most terrestrial Artiodactyla, and Equidae (Kleisner et al., 2010). Yet about 1500 mammal species are ascrotal (lacking a scrotum), with the males' testes being located inside the body, usually in the lower abdomen (Werdelin & Nilsonne, 1999).

The males of all Afrotheria (elephants, hyraxes, sirenians, sengis, golden moles, tenrecs, otter shrews and aardvarks) are ascrotal, and most also have non-descended testes that are located high (dorsally) within the abdomen, close to the kidneys (Fig. 2: elephant). This lack of testicular descent, termed testicondy, was long considered to be the ancestral condition of mammalian testes. However, a recent genomic analysis revealed that testicular descent is the ancestral condition in placental mammals, and that testicondy derived from this ancestral condition and occurred independently and asynchronously in elephants, hyraxes, sirenians, and sengis (Sharma et al., 2018). Importantly, this testicondy did not occur in Orycteropodidae, making the aardvark the only non-testicond Afrotherian. Instead, the male aardvark's testes partially descend during ontogeny and are located lower in the abdomen compared to other Afrotheria (Wojick et al., 2018; Fig. 2: aardvark). Yet despite the partial descent, their testes remained inside the body, and hence male aardvarks do not have a scrotum.

Sex determination in aardvarks

In zoos, female aardvarks can be identified by detection of pregnancies using ultrasound or once they have given birth. A non-invasive method to determine aardvark sex might possibly be derived from endocrinological analyses of aardvark faeces developed by Ganswindt et al. (2011) but would rely heavily on laboratory analyses of fresh faecal samples, which are difficult to obtain (Weyer, 2018). Therefore, the simplest way for determining the sex of an aardvark still depends on close examination and palpation of the genitals (Fig. 3), which in studies of free-living aardvarks requires their capture.

Palpation shows that the male aardvark's penis is conical and small (Sonntag, 1925), compared to the clitoris of female aardvarks, which is a large, heart-shaped, flexible plate (Pocock, 1924) (Fig. 3).

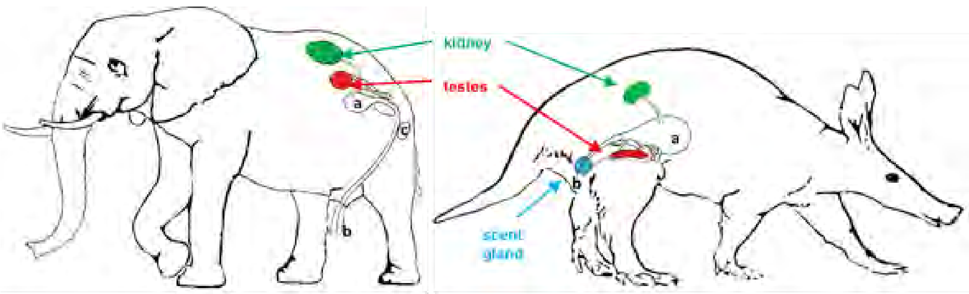

Figure 2. Comparison of the approximate position of testes (red), kidneys (green) and scent glands (blue) and other organs (a = bladder, b = penis, c = bulbourethral gland) in the abdominal cavities of male elephants (left) and aardvarks (right). Note that the prominent scent glands in the aardvark's groin region are also present in female aardvarks, but are absent from elephants. Not to scale.

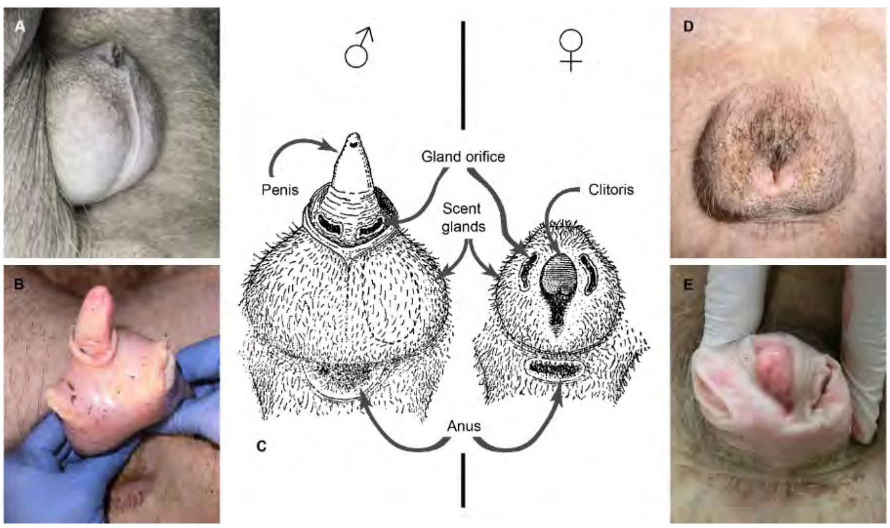

Figure 3. Genitals and scent gland in the groin region of the aardvark. A male zoo aardvark's prominent scent glands and penis (**A**) within the preputial sheath and (**B**) during palpation, showing the orifices of the glandular sacs to both sides of the penis. Drawings of the genitals of a male (**C, left**) and female (**C, right**) aardvark (not to scale; modified after Pocock, 1924). The outline of one of the scent glands is suggested by a dotted line (C, left). The prominent scent glands and vulva in female zoo aardvark unpalpated (**D**) and during palpation (**E**), showing the large heart-shaped clitoris and orifices of the glandular sacs on each side of the vulva. Photos shared by A. Parys, taken at Frankfurt Zoological Garden.

The scent-glands in the groin region of aardvarks are situated underneath skin elevations at the sides of the penis (in males) or of the vulva (in females), giving the appearance of a scrotum with testes (Sonntag, 1925). The short, wide glandular sacs contain a yellow secretion smelling as pungent as the anal gland discharge of the European polecat (*Mustela putorius;* Pocock, 1924). A strong constrictor muscle around the thick lower part of the wall of the glandular sac (Pocock, 1916) probably plays a role in discharging the gland secretion. Scent gland obstruction and abscessation can occur, as has been reported in zoo aardvarks (Wojick et al., 2018).

Male and female aardvarks use their scent glands to leave scent marks

Observations of habituated aardvarks in the Nama-Karoo (WAT, personal observation) and non-habituated ones in the Kalahari (NMW, personal observation) of South Africa revealed that females and males alike use their scent glands to leave scent marks within their home ranges. They often leave scent marks on the ground by pressing their scent glands down onto freshly excavated soil with an exaggerated downward hip movement during feeding bouts or after defecating.

The tracks (or "spoor") aardvarks leave behind during feeding are quite distinctive (Fig. 4). Aardvarks usually bury their faecal deposits in shallow, heart-shaped scrapes. When feeding, they dig a shallow pit to access prey ants and termites in the soil, thereby extracting a small mound of soil from the feeding pit. On this soil mound, the aardvark often leaves an imprint from placing weight on its tail during digging, and a small, round impression from leaving a scent mark using its scent gland. Importantly, this round impression is commonly mistaken to be an imprint of a male's testicles, although the imprint might well stem from a female aardvark's scent glands. This misinterpretation often leads to the false assumption that a male aardvark was present, whereas it just as likely could have been a female aardvark.

Fresh scent marks of female and male aardvarks are characterised by an intense and pungent odour that lingers for several hours. Aardvarks almost always mark their defecation sites with scent, whereas the marking of soil during feeding is less frequent (WAT & NMW, personal observations). Interestingly, aardvarks often release a similar odour when startled or running away or while walking , and may even release drops of liquid from the scent gland while feeding (WAT & NMW, personal observations), although it is unclear whether these are intentional scent-mark releases.

Possible uses of scent glands for aardvarks

The reasons for scent-marking behaviour or the presence of scent glands in aardvarks have not been formally investigated, but we present some hypotheses.

Pocock (1916) suggested that the aardvark's scent gland might be a protective feature, like that of the anal glands of skunks and mustelids to make up for their apparent lack of means of self-defence. However, we suggest that the scent-marking behaviour of aardvarks is more likely to be a means of olfactory communication. Communication is an essential part of animal behaviour that can affect population structure, fitness of and interactions between individuals. Olfactory communication is based on detection of chemicals, which is considered the oldest of all communication forms in the animal kingdom (e.g., Wyatt, 2003). In mammals, a common form of olfactory communication is scent-marking. The olfactory cues from scent marks allow individuals to get indirect clues about their conspecifics in an area after these cues are produced and placed. Scent-marking can serve for advertising to and selection of potential mates, establishing or asserting dominance within an area, and territory maintenance (e.g., Johnson, 1973; Gosling & Roberts, 2001). It may even be used by an animal as a means of orientation within an area (Johnson, 1973). Scent-marking is especially important for solitary species that are widely dispersed and need to communicate through indirect, lasting means (e.g., David Smith et al., 1989).

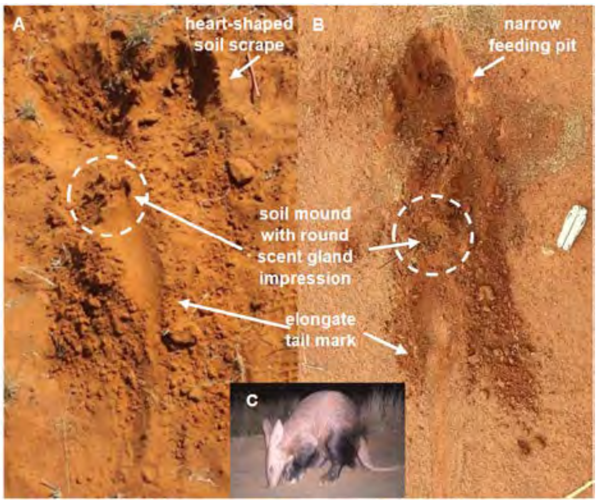

Figure 4 Characteristic aardvark tracks or "spoor" showing scent glands impressions (white circles) on the soil mounds, at the base of the tail imprint. **A**: A female aardvark's defecation site with the characteristic heart-shaped soil scrape to cover the faeces underneath a soil mound (pencil for scale). Photo taken by N. Weyer at Tswalu, South Africa. **B**: An unidentified aardvark's feeding site (multi-tool for scale). Photo taken by B. de Klerk at Grensplaas Private Game Reserve, South Africa. **C:** During digging, the aardvark frees its forelimbs by placing its weight on its tail and hindlimbs. Photo taken by A. Taylor at Tussen die Riviere Nature Reserve, Free State.

Aardvarks are solitary animals and thus scent-marking could be a practical means of communication for them. The aardvark has more turbinate bones and olfactory bulbs in its nose than any other mammal and a strongly developed olfactory lobe in its brain, providing it with an excellent sense of smell (Rahm, 1990; Shoshani, 2002). However, to date, it is not known what messages aardvarks might convey through their scent marks. Aardvarks show a strong degree of home range fidelity (Taylor & Skinner, 2003; van Aarde et al., 1992), but the home ranges of different individuals can overlap. Other than that, the extent of aardvarks' territoriality is unknown, including the strictness of their territorial boundaries and whether they would detect intruders based on scent cues and defend their home range against these. It is also unknown whether territoriality differs between male and female aardvarks. Considering the likely inability of aardvarks to use visual cues due to their poor eyesight, it is also possible, but unconfirmed, that aardvarks use scent marks to orientate themselves within their home ranges.

Knowledge is further lacking about aardvarks use of scent-marking to communicate clues on their sexual status, such as information on their readiness to mate, male sexual prowess or female oestrus signals. The chemical composition of their scent marks has not been analysed in detail yet.

Conclusion

The knowledge gap is vast on why aardvarks deploy scent-marking and what signals they are communicating. What we do know is that both male and female aardvarks have, and frequently use, scent glands to leave scent marks in their environment. Applying this knowledge in aardvark observations, and filling the existing knowledge gaps, might be key to future studies on aardvark populations that could support conservation management decisions.

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Afrotheria News

Obituary: Dr Hendrik N. Hoeck

18 January 1944 - 13 November 2019

Many people were deeply saddened when Hendrik Hoeck succumbed to cancer last November. He was a passionate hyrax researcher and member of the IUCN SSC Afrotheria Specialist Group, a former director of the Charles Darwin Research Station in the Galápagos, and a tireless proponent of the conservation of nature.

© *Vinzenz Bickel*

Hendrik Hoeck in 2014.

Enrique, as he was known in the Spanish-speaking world, was born and raised in Bogotá, Colombia. He spent most of his adult life in Germany and Switzerland, but he remained Colombian at heart, was most at home speaking Spanish, and never got used to the cold, dark winters of Europe. Hendrik started a degree in biology in Bogotá and then moved to Germany – his parents' country of origin – to study aircraft engineering. After a while he decided to switch back to biology. Flying remained a lifelong passion, however, and he later became an accomplished bush pilot in Africa.

Hendrik's dream was to return to Colombia as a marine biologist to study the ocean environment on the two coasts of Colombia. He finished his degree at the University of Munich and contacted the future Nobel prize winner Konrad Lorenz with the idea of doing a PhD on tropical marine fishes. Lorenz passed him on to Wolfgang Wickler who was starting a project on fish in the Rift Valley lakes in Kenya. While not a research project in a marine environment, it was a project on the ecology of fishes that live in very saline water, and so Hendrik decided to start that PhD project.

He was about to leave for Africa when Wolfgang Wickler informed him that the funding for the fish project had fallen through but that he did have funding for a project in Tanzania on hyrax. Hendrik was fascinated by how little was known about these animals and was keen to experience Africa, so he started this project on the ecology and behaviour of hyrax. It was to become a life-long passion and led to the nickname by which he became known to many: Pimbi – Swahili for hyrax.

Hendrik moved to Serengeti National Park in Tanzania in January 1971. Surrounded by park officials and scientists focusing on lions, cheetahs, buffalos, elephants, and other large and charismatic mammals, his study on the small and unassuming hyrax sometimes met with ridicule. Hendrik met this challenge with the aplomb, tenacity, and perseverance typical of him. Not allowed to carry a gun in case of an encounter with dangerous animals, Hendrik used the behavioural concepts he had learned in Konrad Lorenz's lectures: he used an umbrella and painted large eyes on it. This gave him the appearance of a very large animal and he successfully chased away lions, hyenas, leopards, rhinos, and buffaloes, which he encountered on foot while working in the rocky outcrops where hyrax live.

© Pia Hoeck.

Hendrik in Serengeti with his tame rock hyrax, Pole Pole, and one of her friends.

In Serengeti Pimbi also met the love of his life, Pia. Mama Pimbi as she was soon to be known, had heard about Hendrik through a mutual contact, and asked about possibilities to volunteer. Undeterred by the unfavourable reply, Pia traveled to Serengeti by bus, and the rest is history: Pia spent as much time with Hendrik in Serengeti as her job teaching French and Italian in Switzerland allowed. They married a few years later.

Hendrik returned to Germany to complete his PhD after three years of field work in Tanzania. The papers that resulted from his PhD still make up some of the core ecological literature on hyrax. One of the most broadly influential publications to appear from Pimbi's work in Tanzania compared the microwear on teeth of rock and bush hyrax. Published in *Science* in 1978 together with two anthropologists interested in the diets of early hominids, it compared the microwear patterns that different diets left on the teeth of rock and bush hyrax. The method enables others to reconstruct the diets of species only known from the fossil record and is still widely used today. The publication highlights Hendrik's broad interests but also the collaborative spirit among researchers in East Africa at the time. The idea for the paper was born when Hendrik was flying from Nairobi to Serengeti one day and stopped over at Mary Leaky's camp at Olduvai Gorge to drop off some strawberries, a rare delicacy out in the field. There he met Alan Walker, an anthropologist who was looking for a way to determine the diets of extinct hominoid species from tooth microwear patterns. Hendrik suggested his hyrax as an ideal study system, since both species lived on the same kopjes, experiencing the same climate and soils, but differing in diet. This was the basis for the paper in *Science*. It gave Hendrik great joy that his unassuming hyrax had provided the crucial evidence in the development of a technique essential to the study of human origins and evolution.

Hendrik, in collaboration with the German Institute for Scientific Films (IWF Göttingen), also created films summarizing his insights into the ecology and behaviour of rock and bush hyrax using fascinating footage from the Serengeti. His 1980 film "Feeding Ecology in the Bush and Rock Hyraxes – Living Sympatrically" remains an excellent teaching resource outlining the anatomical, physiological, and behavioural differences that allow these two related species to coexist sympatrically on larger kopjes.

After another brief period of hyrax research in Tanzania, Hendrik was offered the position as director of the Charles Darwin Research Station in the Galápagos. Keen to work in one of the most unique national parks in South America, Hendrik moved to the islands in 1978 with Pia and their young daughter, Paquita.

Back then, Puerto Ayora was a very small town with only three cars and few connections to the outside world. News travelled slowly, causing Hendrik some of the worst days of his life. Pia had returned to Switzerland to give birth to their son, Tobias, and informed Hendrik of the imminent birth. The telegram with the news of the birth of a healthy baby, however, did not reach Hendrik for many days, leaving him to believe that both mother and son had died. He never forgot the agony of this long wait.

© Hans Kruuk

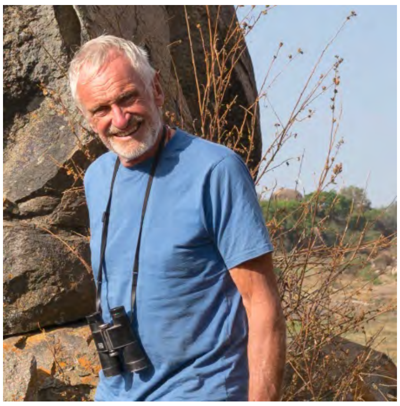
Hendrik with his daughter Paquita in Galápagos in 1978.

The family spent three years in the Galápagos. It was an important time for the conservation of the islands. In

Hendrik's first year, UNESCO declared the Galápagos islands its first natural World Heritage site. It was also a time when the impact of introduced species received increased attention. Having worked on mammals in Africa, Hendrik was keenly aware that introduced mammals on islands with very few native, terrestrial mammals pose a great risk to island ecosystems. Hence, in collaboration with Hans Kruuk, his friend who had studied carnivores in Serengeti, Hendrik started a programme to eradicate the introduced feral dogs from Isabela island, also enlisting the help of Hernán Vargas and Felipe Cruz, two young Galápageños with whom he remained in close contact for the rest of his life. Stimulating, promoting and supporting young people in the long-term were a hallmark of Hendrik's work everywhere. Through this network of enthusiastic, young people he multiplied his impact on the protection of nature he loved so much.

After their time in the Galápagos, Hendrik and his family moved to Switzerland where he joined the University of Konstanz, just across the border in Germany, as a fellow of the Alexander von Humboldt Foundation. There he continued his interests in small mammals. He started a new research project on hedgehogs and worked on maternal investment in house mice and yellow-toothed cavies. He also continued his work on hyrax in Serengeti, focusing on interspecific competition between rock hyrax and bush hyrax and the metapopulation dynamics and its genetic consequences. Hendrik never stopped his research on hyrax. In 2016 he travelled to Namibia and in 2018 back to the Serengeti to continue his study of hyrax. Had he not felt the beginning of his illness, he would have spent another field season in the Serengeti in the summer of 2019. It was important to Pimbi that his research project on hyrax would continue, and he passed his hyrax data on to research groups in Israel and Switzerland. Thus, Pimbi's hyrax research lives on.

After several years at the University of Konstanz, Hendrik left and started a biological consulting company, BiCon. This gave him the flexibility to look after the family business in Colombia after his father's death, and it allowed him to be more closely involved with applied conservation projects. Hendrik realized that ecotourism would be key to the protection of conservation areas in Africa and South America, and so he began to guide tourists to both the Galápagos and Africa. Through these trips, longer and more in-depth than most others on offer, he managed to pass on his passion for nature and his concern for the protection of our planet with a lasting impact to a large number of people.



Hendrik in the Serengeti in 2018.

For Hendrik, solid research was a prerequisite for the successful protection and long-term conservation of nature, but it was not enough. Effective conservation measures needed to be put in place. To this end, he joined in the founding and running of several conservation organizations, such as the Fundación Humedales in Colombia and the Friends of Galápagos Association in Switzerland. With the land of his parents in Colombia, he and his sister created a nature reserve, La Reserva Biológica Encenillo, which he donated to the Fundación Natura. True to Hendrik's vision, it now not only serves to protect nature but also as a study site for field research.

With Hendrik Hoeck we have lost a passionate Afrotheria researcher, and a persistent and effective champion for the conservation of the natural world. He was an inspiring colleague and friend, whose insights, generosity, and friendship we will miss more than words can express.

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Obituary: Dr Martin E. Nicoll

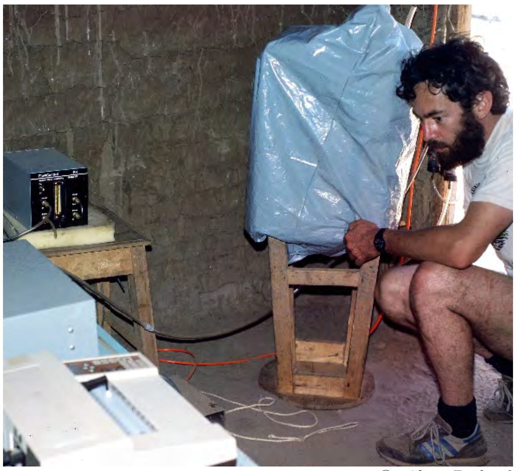
17 April 1954 - 1 January 2020

© *PJ Stephenson*

It was a terrible start to the year for the Afrotheria Specialist Group when we were shocked and saddened to hear of the loss of our long-standing friend and colleague Martin E. Nicoll. Martin died from pancreatic cancer in Tulear, Madagascar. He was just 65.

Martin and I first met in 1985 in the Tsimbazaza Botanical and Zoological Gardens in Antananarivo when I had just returned from surveying mammals in Zahemena and he was conducting a research fellowship with Smithsonian. We hit it off immediately and his passion, knowledge and enthusiasm for nature in general, and tenrecs in particular, helped inspire me to go back to Madagascar a year later. He had an immense impact on my early research and career path, helping me plan my undergraduate project on Malagasy small mammal ecology (even inviting me to his father-in-law's farm in the UK to practice small mammal trapping and habitat measurements) and providing support and advice throughout my PhD on tenrecs. We went on to work together in the WWF Africa & Madagascar Programme, and our paths crossed again in Switzerland, Kenya and Tanzania, as well as back in Madagascar. He was a joy to work with and to spend time with.

Martin was born in Devizes, Wiltshire in the UK on 17 April 1954. He showed an early interest in wildlife as a schoolboy, keeping terrapins, birds and small mammals. He went on to study zoology at the University of Aberdeen for his Bachelor of Science degree. During his undergraduate years, he participated in a student expedition to the Seychelles to study fruit bats (Nicoll & Suttie, 1982) and tenrecs, which inspired him to go back later and study the tailless tenrec (*Tenrec ecaudatus*) for his PhD under Professor Paul Racey at Aberdeen. Martin's work provided some invaluable insights into the reproductive biology and physiology of a mammal that was very poorly known at the time (see, e.g., Nicoll, 1982, 1985, 1986, 2003, 2009; Nicoll & Racey, 1985). Martin received his PhD in 1982 and went on to be awarded a prestigious Harkness Fellowship for a post-doctoral programme with the National Zoological Park, Smithsonian Institution, Washington DC, where he got to work with one of the fathers of tenrec biology, Dr Edwin Gould. Martin conducted field work in Madagascar on the ecology and reproductive energetics of tenrecs (Thompson & Nicoll, 1986), as well as some work on lemurs.



© Alison Richard

Martin measuring the metabolic rate of a lemur in Beza Mahafaly Reserve, Madagascar, in 1985.

After a spell at the Durrell Institute of Conservation Ecology, University of Kent, UK, he went back to Madagascar from 1986 to 1992 to set up, with Olivier Langrand, the WWF Protected Areas Programme. During this time Martin helped assess and conserve the country's protected areas network (see Nicoll & Langrand, 1989) and establish the "*Association Nationale pour la Gestion des Aires Protégées*" (ANGAP), which later became Madagascar National Parks. Throughout this time he continued to help Malagasy and foreign students and set up the WWF Ecology Training Programme.

In 1992, Martin moved to Nairobi, Kenya to work as senior conservation advisor for the WWF Africa & Madagascar Programme under John Newby, where he developed and supported projects across west, central and east Africa. Five years later he returned to his beloved Madagascar where he would work in the country, and the broader Western Indian Ocean region, for almost a quarter of a century, primarily for WWF, and often focused on protected areas (see Nicoll & Ratsifandrihamanana, 2014; Gardner et al., 2018).

Martin's work made him one of the pioneers of tenrec biology and from 1986 to 1994 he was appointed as Chair of the IUCN Species Survival Commission Insectivore, Tree-shrew, and Elephant-shrew Specialist Group. He produced the first ever conservation action plan for tenrecs in 1990 (in Nicoll & Rathbun, 1990), and shortly before his death co-authored an update on the status and conservation priorities of these mammals (Stephenson et al., 2019). Martin was also a member of the IUCN SSC specialist groups for bats, viverrids and mustelids, and, of course, the Afrotheria.

I saw less of Martin in recent years after my move to Switzerland, but, whenever I visited Madagascar, our friendship continued where it had left off. I was very pleased that on my last trip we had a chance to look for tenrecs and lemurs together again in our old stomping ground of Perinet, rekindling memories of many memorable field trips over the years.

© PJ Stephenson

Martin celebrating Christmas Day with friends in Morondava in 1988.

Martin was a passionate and knowledgeable scientist and conservationist, inspiring many he worked with, advised and mentored. His strategic thinking was a great asset in planning and evaluating conservation projects. He was erudite, humorous, generous and sympathetic. While on one hand he was very sociable and gregarious, on the other he was a very private person. He was notoriously difficult to pin down for a meal, and hopeless at personal correspondence. Martin treated everyone the same, whatever their circumstances or level of education, and all the people who spent any length of time working with Martin considered him a friend, which is a testament to his character. Few Malagasy conservationists and visiting biologists in the last 30 years would not have known Martin and recognized his distinctive sartorial style of jeans and striped shirts – a fashion from the 1980's he kept going longer than most (before eventually moving on to T-shirts)!

Martin touched and enriched the lives of many people from many places and walks of life. WWF-Madagascar set up a memorial page online where you will find many more messages and tributes from friends and colleagues: https://tributetomartin.natiora.mg/

Madagascar has lost one of its finest environmentalists, the conservation world has lost a skilled and potent advocate, and many of us have lost a dear friend. But Martin Nicoll's legacy lives on in the many protected areas and young conservation professionals he supported.

© PJ Stephenson

Martin talking to a colleague in Madagascar in 2015.

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Somali sengi found in Djibouti after eluding scientists for half a century

The Somali sengi (*Galegeeska revoilii*) is a poorly known Afrotherian previously recorded from only 39 specimens from northern Somalia and considered Data Deficient in the IUCN Red List of Threatened Species (Rathbun, 2015). It had not been documented by scientists since the early 1970s. However, an expedition to the Horn of Africa last year found this elusive species in Djibouti. In total, the team (which included Afrotheria Specialist Group members Galen Rathbun and Steven Heritage) recorded 12 sengis during their expedition and published the first-ever photos and video of live Somali sengis. A paper was published on 18 August 2020 in PeerJ (Heritage et al., 2020) along with a story on the Global Wildlife Conservation website, the organisation that considers the Somali sengi one of the top 25 most wanted lost animals.

© Steven Heritage, Duke University Lemur Center

The first-ever published photo of a live Somali sengi.

It has been exciting to see so many media outlets pick up the story, with news items appearing on numerous websites, including the BBC, CNN, Earth.org, Global News, LiveScience, South China Morning Post, The Guardian and USA Today, to name but a few. It was also shared across social media platforms such as Twitter. This surely confirms that sengis represent one of the flagship groups within the Afrotheria.

Heritage, S., Rayaleh, H., Awaleh, D.G. & Rathbun, G.B. (2020). New records of a lost species and a geographic range expansion for sengis in the Horn of Africa. *PeerJ*, 8, e9652.

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PJ Stephenson & Steven Heritage
IUCN SSC Afrotheria Specialist Group

Research Updates

Surveys and morphological studies of the Nimba Otter Shrew

The Nimba otter shrew (*Micropotamogale lamottei*) has recently been categorized as Vulnerable on the IUCN Red List of Threatened Species (Stephenson et al., 2018b), yet there is urgent need for more information on the distribution of this threatened afrothere, especially of the Putu sub-population (Decher et al., 2016; Stephenson et al. 2018a). The species is the western-most member of the Potamogalidae (following Everson et al., 2016 and Monadjem, 2018), with its distribution centred on Mount Nimba on the border of Côte d'Ivoire, Guinea and Liberia. There are two disjunct satellite distributions in the Ziama Forest Reserve near Sérédou in Guinea to the north-west and in the Putu Mountains almost 200 km to the south-east in Liberia (Kuhn, 1971). Only two specimens exist from the Putu Mountains. The first is an adult female captured on 5 December 1970 "in a mountain near the camp of the Bong Mining Company near Peloken" (Kuhn, 1971:477) and preserved under the number LIB 2273 in the Liberia Collection Kuhn housed at the Senckenberg Museum, Frankfurt. The second is a young female (ZFMK MAM 2011.0044; Fig. 1) captured almost 40 years later by Jan Decher and team on 10 November 2010 in the context of an environmental impact study at what is most likely the same location in the creek. The location is next to the "Slabertsville Mining Camp" of the Putu Iron Ore Mining Company.

Iron ore mining at Putu is currently suspended, creating an opportunity to search for further specimens of the otter shrew in the creeks and rivers of the Putu watershed and to define more clearly the species' range. We have been fund-raising to conduct surveys using the well-tested commercial and locally made fish traps (Monadjem et al., 2019), and to test environmental DNA monitoring, which has already been used to detect other water-dwelling mammals like the North American river otters (Padgett-Stewart et al., 2016).

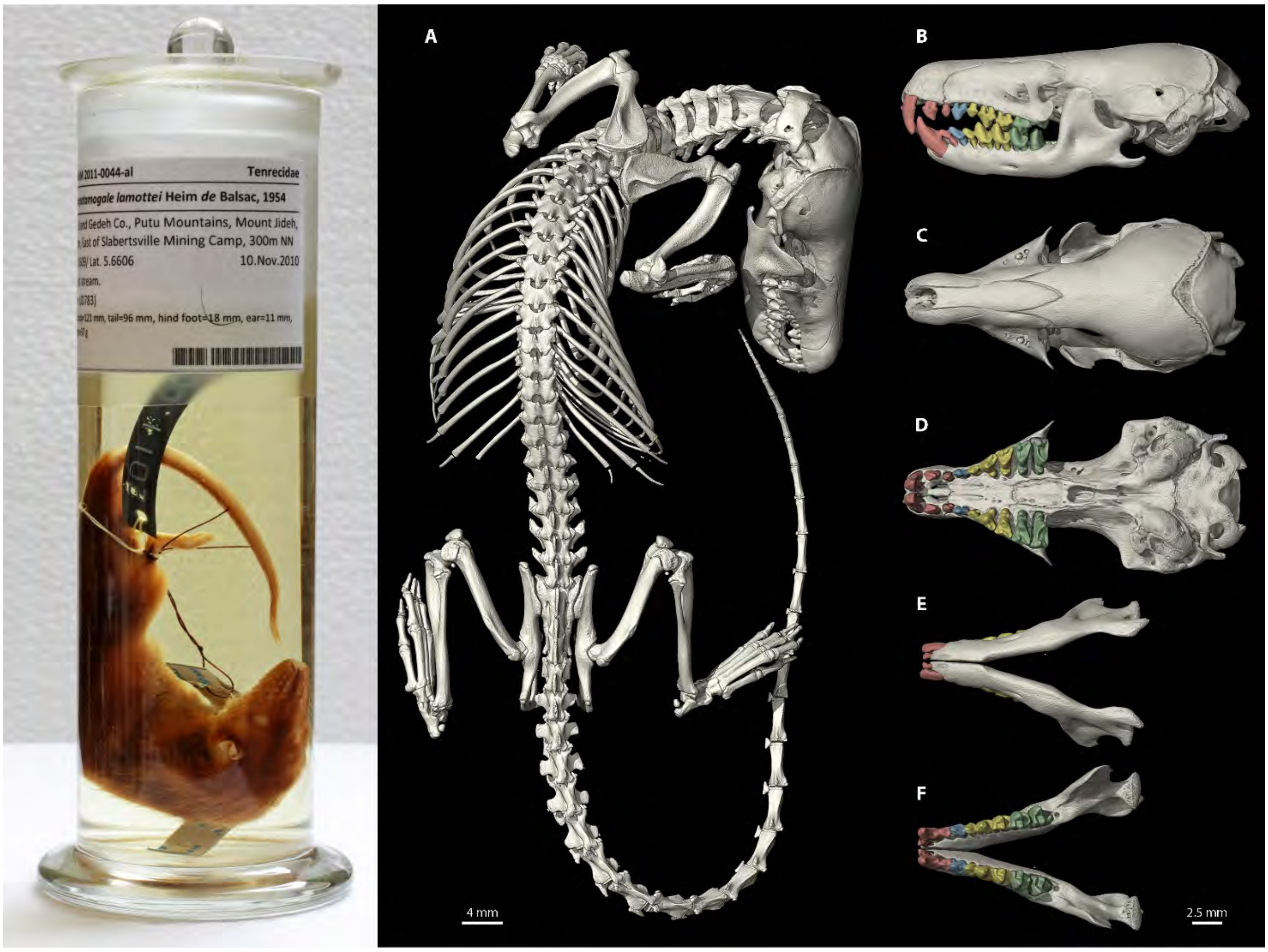

Figure 1. Left side: Ethanol-preserved 2010 specimen from the Putu Mountains in Liberia (ZFMK, MAM 2011.0044). **Right side: (A)** µCT-Scan of the entire skeleton of the Nimba otter shrew, Micropotamogale lamottei ZFMK MAM 2011.0044 in its current fluid-preserved position. (**B**) Lateral view of cranium and mandible, (**C+D**) dorsal and ventral (occlusal) view of the cranium; (**E+F**) ventral and occlusal view of the mandible.

While we continue to search for funds for surveys, we conducted a non-destructive anatomical study of our 2010 specimen, the first morphological study of this species for more than 60 years (Guth et al. 1959, 1960).

The method of choice to study internal anatomy is the µCT-scan, retaining the specimen's integrity for other investigations. The specimen of *M. lamottei* was braced firmly in a small plastic tube to prevent it shifting position or being damaged during the scan rotation. The entire skeleton was scanned at Museum Koenig (ZFMK) in Bonn with a SkyScan 1173 scanner (Bruker) using the following parameters: 2 connected scans; 0.3° rotation steps over 180°; spatial resolution of 25.907723 µm; 43 kV; 114 µA; no filter; frame averaging of 5; random movement of 15; 500 ms exposure time. The scan was reconstructed with the software package N-recon (Bruker) into tif stacks. Subsequently these data were imported into Amira v.6.5.0 (Thermo Fisher) where the relevant structures were segmented and isolated using the "arithmetic" function of the programme. The resulting data were imported into VG Studio v.3.3.4 (Volume Graphics) where volume rendering (Phong) was performed. The created images were adjusted and assembled to plates with Photoshop CS6 and Illustrator CS6 (Adobe). The scan was transferred to the digital collection of the ZFMK (for access, please contact BW).

The µCT-Scan of the complete skeleton and different views of the cranium and mandible are shown on the right side of Figure 1. The skeleton demonstrates the robust skull and neck vertebrae proportions evolved for crushing freshwater crabs. Skull sutures are still quite visible in this young female specimen and the dentition still deviates from the adult potamogalid dental formula of $\frac{3.1.3.3.}{3.1.3.3.} = 40$, by having 3 incisors, 1 canine, 3 premolars but just 2 molars. Striking are the massive upper first and lower second incisors for holding large prey items but relatively small canines.

A more detailed paper with an "exploded view" of the entire skeleton and a discussion of more morphological detail is in preparation. µCT-scanning and subsequent 3D-reconstruction are powerful non-destructive tools for rendering skeletons and other internal structures of small and rare specimens in perfect 3-D imagery, without the limitation of the narrow depth-of-focus of macro photography. The technique is also suitable for taking standard measurements and conducting more advanced analyses including geometric morphometrics.

We hope that enhancing our anatomical knowledge of the Nimba otter shrew will enable us to detect potential morphological subpopulation differences and stimulate more interest in its conservation and the survey work needed to confirm the distribution of this poorly-known species.

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The collection of subfossil tenrecs at Duke University: the TenRecord at Duke

As the name implies, the Duke Lemur Center (DLC) at Duke University (Durham, North Carolina, USA), is an important field station for the non-invasive study of strepsirrhine primates. Less obvious – based on the name – is that the DLC is responsible for an extensive and publicly accessible fossil collection that documents many major transitions in African mammal evolution during the Cenozoic. The DLC's "Division of Fossil Primates" was founded by Dr. Elwyn Simons in 1977, but since its inception, the collection has strained this title with significant holdings that are neither fossils nor primates. Especially relevant to the Afrothere research community is a large collection of subfossil tenrec specimens from the Holocene of Madagascar.

One of Simons' innovations was to position the DLC as a genetic safety-net for several lemur species. In collaboration with the Malagasy government, the DLC conducted multiple expeditions to Madagascar where wild lemurs were located and exported to the United States. Descendants of those lineages now roam the DLC's free-range forests. In addition to these conservation efforts, the DLC field-teams searched for fossils in an attempt to build a better understanding of the natural history of Madagascar and its unique fauna. The University of Antananarivo (then the University of Madagascar) and Duke University agreed that half of the fossils recovered during these expeditions (1983-2008) would be exported for permanent accession at the DLC. The other half were kept at the University of Antananarivo. The intent was to make redundant Duke and Antananarivo collections to ensure that if either one is ever damaged, there will still be material from the expeditions preserved at the other institution.

The subfossil lemur specimens from these expeditions have received most of the published research attention (e.g. Simons et al., 1992; Godfrey & Jungers, 2003; Jungers et al., 2008). However, the DLC field-teams also recovered thousands of other fossils (e.g., bats, rodents, fossae, lizards, birds) which allow for checklist-reconstructions of ancient communities. Of course, among these are many tenrecs. Notably, recent research has suggested that lemurs may have migrated to Madagascar much later than was previously thought (Gunnell et al., 2018), potentially leaving tenrecs as the oldest Cenozoic mammal radiation in Madagascar.

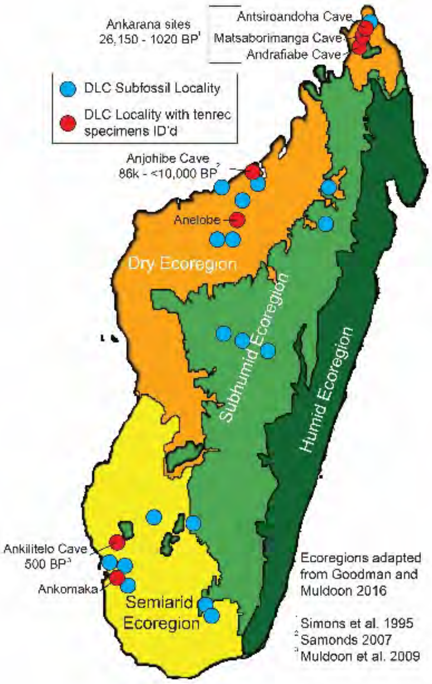

Figure 1. DLC subfossil localities.

A caver/excavator repels into Ankilitelo Cave down the 145 meter entry shaft

Radiocarbon dates place the Ankilitelo remains around 500 years BP

Simons sorts microvertebrate at Ankilitelo Cave, one of the youngest giant lemur sites

Photos courtesy of Prithijit Chatrath taken in 1998

Figure 2. Photos from Ankilitelo Cave.

Subfossil tenrecs in the DLC collection are from sites across the island including Anjohibe Cave and others in the north-west, The Cave of the Lone Barefoot Stranger (at Ankarana) and others in the north, and Ankilitelo Cave and others in the south-west (Fig. 1). Major analyses of the microfossil record at Ankilitelo (~500 years old) found at least 34 mammalian species, making this site the most diverse Holocene assemblage in Madagascar (Muldoon & Simons, 2007; Muldoon et al., 2009; Muldoon 2010; Goodman et al., 2013) (Fig. 2). This fauna includes multiple species that are rare or extinct in the island's south-west, including the shrew tenrecs *Microgale brevicaudata* and *M. nasoloi* (Fig. 3). These studies demonstrate that the currently observed geographic distributions and densities of mammalian species on Madagascar are different than they were in the recent past, and that studies that attempt to explain the adaptive radiation of tenrecs or their biogeography should do so through the lens of Madagascar's Holocene paleontological record.

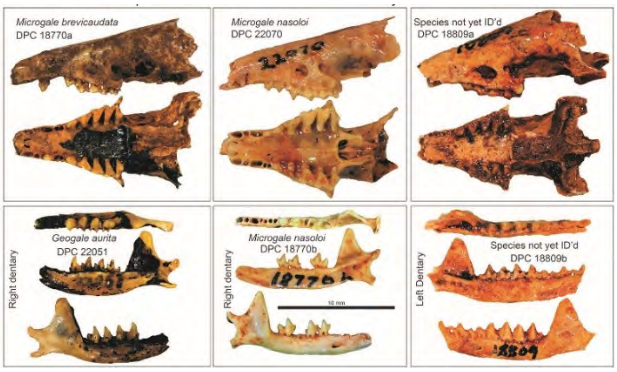

Figure 3. Tenrec specimens from Ankilitelo Cave identified by Muldoon et al. (2009).

Unfortunately, before researchers can use the subfossil record to inform conservation initiatives and evolutionary studies, we must continue the labour-intensive effort of identifying the tenrec species that are part of the DLC collection. While these efforts are ongoing for the micromammals from Ankilitelo, there is also plenty of room for other specialists interested in the archaic biological record of Madagascar (e.g., ancient DNA studies, paleo-ecological niche modelling, geometric morphometric change through time, etc.) (Fig. 4).

Figure 4. Unsorted and unidentified tenrec specimen lot that is typical of the tenrec collection at the DLC and which is in need of specialist attention.

This article is primarily intended to alert Afrothere researchers to the existence of the DLC's Madagascar collection, which may be more easily accessible than other subfossil Madagascar collections, or may offer opportunities for significant contributions to the field. Also of interest are the Eocene-Oligocene specimens at the DLC from the Fayum Depression of Egypt, which includes some of the oldest afrosoricids known, 37 million year old *Dilambdogale* and 34 million year old *Widanelfarasia*.

In addition to DLC access via traditional collection visits (and specimen loans), researchers can now download high-resolution micro-CT scan data of many specimens via the online repository at Morphosource.org (Fig. 5). The expanding digitization of the DLC's fossils, subfossils, and osteological specimens provides web-based open access to morphological information about tenrecs (past and present) and many other extant and extinct afrotherian mammals from mainland Africa.

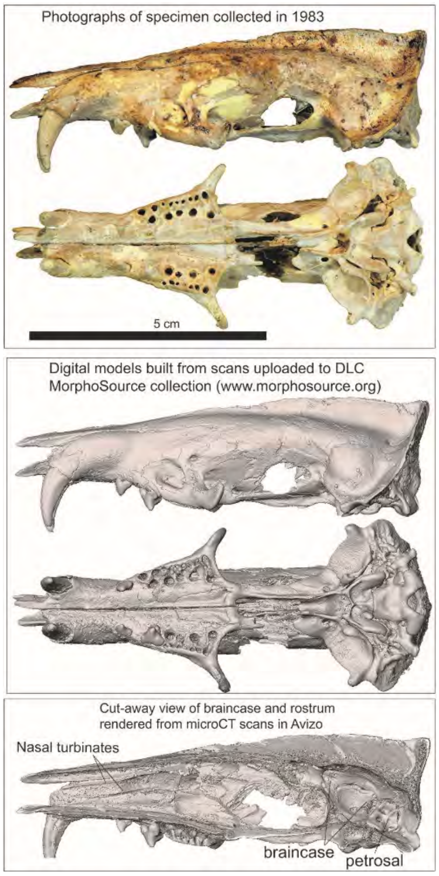

Figure 5. Undescribed Tenrec ecaudatus cranium (DPC 3784) from Anjohibe Cave.

With over 35,000 specimens in the physical collection, the DLC is soon to launch a publicly accessible online database. Until then, if you are interested in learning more about the tenrecs available for study, or any other taxa in the collection, please contact DLC Fossil Curator Matthew Borths.

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Genome-wide markers shed light on differentiation in the Hottentot golden mole species complex

The Hottentot golden mole (*Amblysomus hottentotus*; A. Smith, 1829) belongs to the highly threatened golden mole family, Chrysochloridae, of which ten of the 21 species are listed as threatened (Critically Endangered, Endangered, or Vulnerable) on the IUCN Red List of Threatened Species (IUCN, 2020). The taxonomy of many taxa within the family is largely unresolved, and a deeper understanding of the phylogenetic and phylogeographic relationships within the Chrysochloridae is imperative for informing conservation efforts for the taxa under threat.

Three years ago I reported here on cryptic diversity in the Hottentot golden mole from the Greater-Maputaland-Pondoland-Albany (GMPA) region of southern Africa (Mynhardt, 2017). In this article I provide an update on our ongoing research concerning this fascinating species complex.

The subdivision into 5 subspecies of the relatively widespread and abundant *A. hottentotus* is generally in line with the distribution of localized populations in South Africa (Fig. 1). *Amblysomus h. hottentotus* and *A. h. pondoliae* (Thomas & Schwann, 1905) were recognised as distinct subspecies on the basis of phenetics, and *A. h. iris* (Thomas & Schwann, 1905) on the basis of colourimetric and craniometric comparisons. *Amblysomus h. longiceps* (Broom, 1907) was afforded subspecific rank based on its markedly larger body size and does not differ significantly from coastal populations in cranial shape. *Amblysomus h. meesteri* (Bronner, 2000) closely resembles the coastal populations in craniometric properties, but was recognised as a subspecies on the basis of colourimetric differences, with a mid-dorsal band of reddish-black fur distinguishing it from all other forms (Bronner, 1996a). Thus, the current classification is primarily based on subtle morphological distinctions, but many of these characteristics have proven to be ambiguous and inconclusive (Bronner, 1996b).

Since a comprehensive karyotypic study revealed that *A. h. meesteri* might represent a distinct species (Gilbert et al., 2008), and our previous phylogeographic study supported this and uncovered additional cryptic diversity within the species (Mynhardt et al., 2015), we consider *A. hottentotus* to be a species complex, although we have refrained from revising the taxonomy until further evidence is obtained. From a phylogenetic standpoint, our study provided evidence from two mtDNA genes (NADH dehydrogenase subunit 2, *MT-ND2*, and cytochrome *b*, cyt *b*) and one nuclear intron (Growth Hormone Receptor, GHR, intron 9) in support of *A. h. meesteri* as a distinct species. There are two additional cryptic lineages, one tentatively referred to as "Umtata", based on the type locality, and the other as the "central coastal clade", based on its geographic distribution between the northern coastal *A. h. iris*, and southern coastal *A. h. pondoliae*.

Recently emerging, rigorous methods of species delimitation typically employ genome-wide data and therefore we investigated the use of restriction-site associated DNA sequencing (RADseq; Miller et al., 2007; Baird et al., 2008), a reduced-representation sequencing approach which enables single nucleotide polymorphism (SNP) marker discovery and simultaneous genotyping in non-model species such as golden moles. We conducted a pilot RADseq study in a carefully selected panel of 18 *A. hottentotus* individuals to test our cryptic diversity hypotheses for (1) *A. h. meesteri*, (2) the central coastal clade, and (3) Umtata, and with the hope of incorporating these results, along with additional RADseq data in future species delimitation.

Our methods for DNA extraction, library preparation, sequencing and bioinformatics are outlined in Mynhardt et al. (2020). Phylogenetic relationships were estimated using the SNAPP template implemented in BEAST v. 2.5.1 (results not shown here; Bouckaert et al., 2014) and population differentiation was assessed using STRUCTURE v. 2.3 (Pritchard et al., 2000) and FineRADStructure (results not shown here; Malinsky et al., 2018).

The STRUCTURE analysis identified four major clusters in the data (Fig. 1), corresponding to: (1) *A. h. meesteri* (Sabie), (2) *A. h. longiceps* (Cedarville, Drakensberg Gardens, Sani Pass), (3) *A. h. pondoliae* (Margate, Port Edward, San Lameer, Umtamvuna, Umtata), (4) central coastal clade (Illovo, Umkomaas and Umhlali). The two *A. h. meesteri* individuals from Sabie consistently assigned to a unique cluster, indicating that they represent a population that is genetically isolated from other *A. hottentotus* populations. These results support our previous findings, based on mtDNA and limited nuclear intron data, that *A. h. meesteri* is a monophyletic lineage that diverged from the remainder of its extant genus, along with sister species *A. marleyi* from the Lebombo mountains just southeast of Swaziland, approximately 4.42 million years ago (Ma), and later diverged from *A. marleyi*, approximately 1.9 Ma (Mynhardt et al., 2015). *Amblysomus h. meesteri* is geographically isolated and morphologically and cytogenetically distinct from other *A. hottentotus* (Bronner, 1996a; Gilbert et al., 2008), and may thus be worthy of specific status, as previously recommended (Gilbert et al., 2008; Mynhardt et al., 2015).

Individuals from Illovo, Umkomaas and Umhlali represent the recently discovered cryptic central coastal clade, which is thought to have diverged from a shared common ancestor with *A. h. longiceps* and *A. h. pondoliae* approximately 2.53 Ma (Mynhardt et al., 2015). These individuals were fairly confidently assigned to a unique cluster at $K = 4$ (Fig. 1), however there is a possibility of some admixture in this population. It is clear that these individuals are different to *A. h. pondoliae* farther south, and we have already demonstrated that this lineage is divergent from northern coastal *A. h. iris* (Mynhardt et al., 2015), and may therefore represent a unique (sub)species, as previously recommended (Mynhardt et al., 2015).

Our previous phylogenetic study, based on mtDNA and limited nuclear intron data, placed Umtata as a unique lineage sister to *A. h. longiceps*, but with support from only mtDNA (Mynhardt et al., 2015). Although our current STRUCTURE analysis provided some support for an additional cluster to which Umtata is strongly assigned (see $K = 5$, Fig. 1), clustering at $K = 4$ supports the placement of Umtata within *A. h. pondoliae*, as currently classified based on predicted distribution of the subspecies.

This study thus succeeded in providing evidence in support of our cryptic diversity hypotheses, as well as some additional insights (Mynhardt et al., 2020). We provide support for the recognition of *A. h. meesteri* as a separate species to *A. hottentotus* and for the recognition of a fourth coastal *Amblysomus* lineage (the central coastal clade). Although our previous study indicated that Umtata may represent a unique lineage sister to *A. h. longiceps* (Mynhardt et al., 2015), whole-genome representative RADseq SNP data revealed that this lineage is instead more closely related to *A. h. pondoliae*. However, since only one Umtata sample was included in our RADseq dataset, we cannot say whether this mito-nuclear discordance is representative of the entire lineage. This has raised further questions about the evolutionary history of this unique lineage, which highlights the need for additional sampling from the largely under-sampled Transkei region of the Eastern Cape.

Over and above the phylogeographic findings, our study presents a high-quality filtered SNP dataset, comprising well over 100 000 SNPs, which may serve as a useful resource for future golden mole studies. The full dataset was filtered to retain 805 informative SNPs for downstream analysis However the full set of SNPs can easily be re-filtered to obtain alternative SNP sets in order to address more specific questions pertaining to population structure in *A. hottentotus*. For example, in order to investigate population structure more thoroughly within a particular (sub)species, the data can be filtered specifically for SNPs that are polymorphic within that (sub)species. Moreover, mapped sequences can be used to facilitate downstream assay design, potentially also for application in other species of golden moles. It is our hope that the genomic resources provided by this study will continue to assist us and others in understanding the genomic diversity and genetic differentiation among populations of golden moles in South Africa.

Although we have provided molecular support for the recognition of various *A. hottentotus* cryptic taxa, we have refrained from formal taxonomic revision until this hypo-

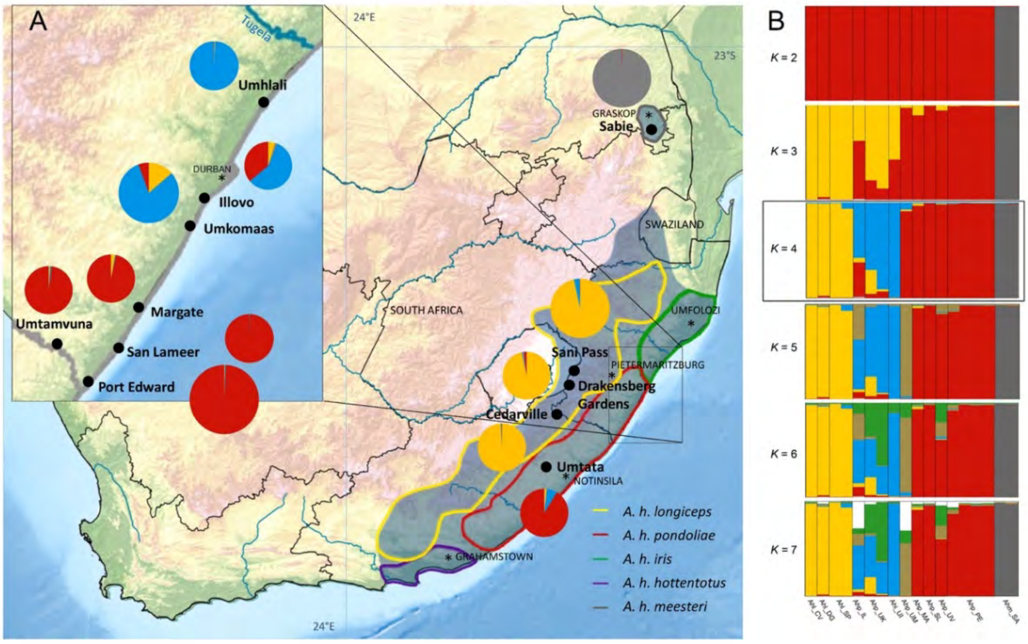

Figure 1. (**A**) Map of southern Africa indicating the distribution of *Amblysomus hottentotus* (shading) and its five subspecies, each subspecies type locality (asterisks) and the 12 sampling sites (black circles). Proportionate assignment to four putative populations is indicated in the associated pie charts. (**B**) STRUCTURE analysis for the full dataset, based on 805 SNPs, indicating the probability of each individual belonging to each of *K* clusters (Structure's Q). Results are shown for *K* = 2–7, with *K* = 4 being the most likely, based on delta *K* estimation. Vertical bars represent the 18 individuals, with the 12 sampling localities indicated below (Mynhardt et al., 2020).

-thesis can be further corroborated by more rigorous species delimitation. However, we recommend the recognition of these lineages as evolutionarily significant units (ESUs) for the purpose of potentially urgent conservation management. *Amblysomus hottentotus* is considered widespread and abundant (listed as Least Concern on the IUCN Red List; IUCN, 2020) and, as a result, is not under formal protection. The threats posed to the various *A. hottentotus* cryptic taxa remain to be determined and, consequently, the conservation status of the newly recognized ESUs will need separate evaluation until a formal taxonomic revision can be completed.

For more information see New insights from RADseq data on differentiation in the Hottentot golden mole species complex from South Africa. Results of this study were also disseminated at last year's Evolution meeting in Providence, Rhode Island, USA (Mynhardt et al., 2019).

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