PALÆO VERTEBRATA

A new *Desmodillus* (Gerbillinae, Rodentia) species from the early Pliocene site of Langebaanweg (South-western Cape, South Africa)

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Abstract: Situated in the Cape region of the Republic of South Africa (RSA), the paleontological site of Langebaanweg is dated to 5.1 Myr and is famous for having yielded an abundant vertebrate assemblage, including numerous rodent species from the Mio-Pliocene transition. Based on molar morphology and skull anatomy, the single Gerbillinae taxon identified at Langebaanweg and described in this paper is allocated to *Desmodillus*, which is a modern monotypic South African endemic genus. It is significant in being the oldest representative of the genus in Africa. We describe here a new species of this genus which is larger than the modern *D. auricularis*, but nevertheless retains some of its main characteristics, namely the shape of the maxilla and mandible, the presence of poorly fused alternating cusps, and no longitudinal crest. This taxon differs from modern South African *Gerbilliscus* representatives in some mandibular and maxillary characters, in the m1 prelobe cusp, and in having less fused cusps. Two fossil Gerbillinae discovered in the Upper Miocene of Africa and Asia, *Abudhabia* and *Protatera*, have been compared with the new species. We discuss their relationships with modern and Plio-pleistocene Gerbillinae and conclude that *Abudhabia* could be the sister taxon of *Desmodillus* and that around 6-5 Myr a vicariance event allowed Gerbillinae to diversify into modern *Desmodillus* in South Africa, and *Gerbilliscus* in East Africa. The murine/gerbilline ratio, which is a good indicator of rainfall, supports other proxies which suggest that at 5.1 Myr the climate in the Langebaanweg region was more humid than today.

Keywords: Rodentia, Muridae, RSA, Lower Pliocene

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INTRODUCTION

The fossil site of Langebaanweg (LBW) (32°57'23.8"S 18°06'58.2"E) is situated in the south-western Cape region of South Africa and is world-renowned for having yielded very rich faunal assemblages of both marine and terrestrial vertebrates dating to the early Pliocene (~5.1 Myr). Micromammals (Muridae (rats and mice) and Soricidae (shrews)) have been collected in abundance at this site during phosphate mining operations in the area which began in 1943 and ceased in 1992, and also during subsequent formal palaeontological excavations at the fossil site which began in 1995. LBW is now the seat of the West Coast Fossil Park and was recently declared a National Heritage Site.

LBW is the only fossil micromammal site in the south-western Cape representing the early Pliocene, a period of time when both palaeontological and molecular phylogeny studies indicate that modern micromammal genera were emerging (Denys 1996, 1999). At LBW several modern micromammal genera make a first appearance in the South African fossil record, namely, *Aethomys, Mystromys,* and *Acomys,* and are found together with extinct taxa such as *Euryotomys* and *Stenodontomys* (Matthews *et al.*, 2007). This paper focuses on a new and undescribed species of gerbil (Family: Muridae, Subfamily: Gerbillinae) from the site. The Langebaanweg gerbil represents the earliest record of the genus *Desmodillus*

in Africa and thus requires investigation. Gerbillinae are important palaeoenvironmental indicators as they occur in greater abundance and diversity in the dry and open, more arid areas of Africa. In this article we describe the Gerbillinae from Langebaanweg and assess their taxonomic affinities through a revision of skull and dental characters of both modern and fossil specimens from the sub-family. The Langebaanweg Gerbillinae contribute to understanding the evolution of southern African gerbils, and also contribute to elucidating the palaeoenvironment for the site, and the Cape region.

Geological setting

The gerbillines reported on in this paper came from the two main fossil-bearing members of the Varswater formation, namely the Muishond Fontein Phosphatic Sand Member (MPPM), and the Langeberg Quarz Sand Member (LQSM). These members date to approximately 5.1 Myr. See Roberts *et al.* (2011) for a full report on the geology and fossil accumulations. The age difference between the two members is uncertain although the LQSM is purportedly slightly older as it underlies the MPPM in most areas. The fossil evidence suggests that they are very close in age (Roberts *et al.,* 2011).

The LQSM represents a variety of depositional environments including floodplain deposits, a tidal mud flat deposit, and an

extensive peat bed (Hendey, 1981a, 1981b). The MPPM is composed of ephemeral river channel lag deposits and the microfauna recovered from it probably represents a variety of depositional environments. The river appears to have shifted course several times and the MPPM has been divided into the fossiliferous bed 3a, which consisted of a northerly and southerly part, namely bed 3aS and bed 3aN, which represent separate shifts northwards in the course of the river. Detailed information as to the geology of the site is available in Hendey (1981a, 1981b) and Roberts *et al.* (2011).

Evolutionary history and fossil record of Gerbillinae in Africa

Currently Gerbillinae (Family Muridae, Subfamily Gerbillinae) are represented by nine genera in Africa among which two of them are found in South Africa, namely *Desmodillus* and *Gerbilliscus* (formerly *Tatera*) (Monadjem *et al.,* 2015). Different morphological and molecular phylogenies have been proposed for the classification of the subfamily and there is still some debate over the taxonomic position of some genera (Wilson & Reeder, 2005).

Gerbilliscus has a broad distribution over sub-Saharan Africa and includes some eighteen species, including four which were previously attributed to the genus *Gerbillurus* (Qumsiyeh *et al.,* 1991). *Gerbillurus* is now considered synonymous with *Gerbilliscus,* as indicated by chromosomal, mitochondrial and nuclear molecular DNA (Monadjem *et al.*, 2015). Because *Gerbillurus* is characterized by some unique morphological characters, has a southern African distribution, and forms a monophyletic clade within *Gerbilliscus* (Granjon *et al.*, 2012) we consider it here as a subgenus.

The southern African endemic rodent *Desmodillus auricularis* (Smith, 1834) (Cape short-eared gerbil) is the only extant representative of this genus and has a broad distribution from southwestern Angola, through large parts of Namibia and Botswana, into western, central and north-eastern South Africa, and may possibly also occur in Zimbabwe (IUCN 2014.3). Colangelo *et al.* (2007) suggested that the *Gerbillurus* and *Gerbilliscus* lineages diverged from a common ancestor in eastern Africa around 8.5 Myr. All *Gerbilliscus* taxa are considered monophyletic and are grouped in three main clades, namely an eastern, western and southern clade. The *Gerbillurus* and western–southern *Gerbilliscus* lineages split around 7.5 Myr according to Colangelo *et al.* (2007). The eastern clade of the *Gerbilliscus* split is set at 5.47 (5.16–5.7) Myr, the western clade of *Gerbilliscu*s at 3.89 (3.58–4.17) Myr, and the southern clade in the late Pliocene at 2.83 (2.60–3.07) Myr, with *G. brantsii* (Smith, 1836) and *G. afra* (Gray, 1830) splitting at 2.08 (2.87–2.31) Myr (Colangelo *et al.,* 2007).

Desmodillus has been placed in Tribe Taterillini and (together with *Gerbillurus*) in the Subtribe Gerbillurina (Pavlinov *et al.*, 1990; Musser & Carleton, 2005; Pavlinov, 2008). Knight *et al.* (2013) note that *Desmodillus* and *Gerbilliscus* (formerly *Tatera*) comprise a monophyletic group of gerbils which last shared a common ancestor approximately 8 million years ago. Phylogenetic analysis of morphological, chromosomal and molecular data have however not confidently resolved the

phylogenetic position of *Desmodillus* but recent molecular studies show it to be a basal lineage in the Taterillini, a conclusion supported by its retention of the primitive protoconulid cusp found also in the Miocene genus *Protatera* (Qumsiyeh *et al.*, 1987; Pavlinov *et al.,* 1990; Chevret & Dobigny, 2005; Colangelo *et al.,* 2007; Pavlinov, 2008; Granjon *et al.*, 2012).

Some authors consider the Myocricetodontinae an early representative of the Gerbillinae (Jaeger, 1977; Tong, 1989), however, others do not support this and have indicated their paraphyly (Flynn *et al.*, 2003; Denys & Winkler, 2015). There is a consensus that the fossil genus *Abudhabia* be considered an early representative of Taterillini, with *A. baheensis* as the earliest representative occurring at 10 Mya in China (Qiu *et al.*, 2004; Wessels, 2009). A second extinct genus, *Protatera*, is not yet clearly assigned to one or the other modern taxon.

The fossil record indicates that *Protatera* and *Abudhabia* make an appearance during the upper Miocene (probably before 6.1 Myr) in Africa (Tong, 1989, Winkler *et al.*, 2010), and also in Pakistan, Arabia, Afghanistan, and India as early as 8.6 Myr (Flynn & Jacobs, 1999; Flynn *et al.*, 2003; Wessels, 2009). *Protatera* is known only in North Africa (Libya, Morocco, and Algeria) and Spain (Jaeger, 1977; Munthe, 1987; Agusti, 1990; Geraads, 1998) while *Abudhabia* was described in East Africa (Winkler, 2003; Mein & Pickford, 2006), see Table 1. Some fossils have been attributed to modern genera, and the earliest *Gerbilliscus* (ex *Tatera*) is from Kenya from the sites of Kanapoi (4 Myr) and Laetoli (3.7 Myr) (Denys, 2011). Pocock's (1987) paper on South African Pliocene rodents notes the presence of a *Desmodillus* sp. at both Langebaanweg and Makapsangat but does not provide any descriptions of the fossils. Sénégas (2000) confirms the presence of both *Desmodillus* and *Gerbilliscus* (formerly *Tatera*) at Border Cave and Gladysvale, and an indeterminate Gerbillinae from the Waypoint 160 deposits (~4 Myr). Other South African sites containing *Desmodillus* include Kromdraai B and Swartkrans (Members 1, 2 and 3).

MATERIAL AND METHODS

Teeth were studied using a light microscope and variable magnification. Drawings were made of fossil and modern upper first molars (M1) and lower first molars (m1) using a *camera lucida*, and maximum length and width of molars was measured either using the MTV software program, or by hand. Classical univariate and bivariate statistics were then performed on modern and fossil molar dimensions. For each molar and taxon the mean, standard-deviation and the variation coefficient were calculated. SEM pictures of the dental rows were taken using a Hitachi SU3500 at the PMEM (*Plateau technique de microscopie électronique et de microanalyse*, Dr C. Rausch) in the Muséum National d'Histoire Naturelle, Paris MNHN.

The length and breadth of some 196 molars from the LQSM, and the MPPM, Bed 3AN and Bed 3AS have been measured (Table 2, S1). Data has been compared with other measurements either made by one of the authors (CD), or extracted from the literature. For the purposes of comparison, using the same techniques, the molars of modern *Desmodillus auricularis*

Table 1. List of the gerbilline species found in Miocene, Pliocene and Pleistocene fossil sites in north, east and southern Africa. Note that this list is comprehensive, but not exhaustive. Abbreviations: COH = Cradle of Humankind. Please note that in this table we have replaced the defunct genus *Tatera* with the current classification of '*Gerbilliscus*'.

Site name	Age	Species	Reference
North Africa			
Sahabi, Libya	Pliocene	*Protatera yardangi*	Munthe (1987) = Abudhabia ? Flynn & Jacobs (1999)
Amama 2, Algeria	Late Miocene	*Protatera algeriensis*	Jaeger (1977)
Spain, Morocco	Late Miocene	*Protatera almenarensis*	Agusti (1990) Geraads (1998)
Lissasfsa, Morocco	5.5 Ma	*Protatera davidi*	Geraads (1998)
Ahl al Oughlam, Morocco	2.5 Ma	*Gerbillus bibersoni*	Geraads (1995)
East Africa			
Lemudong'o, Kenya	6 Ma	*Gerbilliscus* sp.	Manthi *et al.* (2007)
Lothagham, upper Nawata, Kenya	5.23 Ma	*Abudhabia* sp.	Winkler (2003)
Kapsomin, Lukeino, Kenya	6.1-5.8 Ma	*Abudhabia tateroides*	Mein & Pickford (2006)
Adu-Asa, Ethiopia	5-6 Ma	*Gerbilliscus* sp.	Wesselman *et al.* (2009)
Aramis, Ethiopia	4,4 Ma	*Gerbilliscus* sp.	Louchart *et al.* (2009)
Laetoli Upper Ndolanya Beds, Tanzania	2.8-2.4 Ma	*Gerbilliscus* cf. *inclusus* *Gerbilliscus winkleri*	Denys (2011)
Laetoli, Laetolil beds, Tanzania	3.7-3.5 Ma	*Gerbilliscus satimani*	Denys (2011)
Kanapoi, Kenya	~ 4 Ma	*Gerbillus* sp. *Gerbilliscus* sp.	Behrensmeyer (1976)
Omo, Ethiopia	3.3-1.7 Ma	*Gerbillus* and *Gerbilliscus* (both indet. sp).	Wesselman (1984)
Olduvai Bed I, Tanzania	Pleistocene (1.8-1.75 Ma)	*Gerbilliscus gentryi* *Gerbillus* sp.	Denys (1989)
Hadar, Ethiopia	Early-middle Pliocene	*Gerbilliscus* sp. = *Gerbilliscus winkleri*	Sabatier (1982) Denys (2011)
Hadar, AL 894	2.4 Ma	*Gerbilliscus* sp. cf. *Gerbillus*	Reed & Geraads (2012)
East Turkana, Kenya	1,6 Ma	*Gerbilliscus* sp.	Black & Krishtalka (1986)
Southern Africa			
Otavi mountains, Berg Aukas I, Namibia	Post-Miocene	*Gerbilliscus* sp.	Senut *et al.* (1992)
Aigamas, Namibia	Plio-Pleistocene	*Desmodillus* sp.	Senut *et al.* (1992)
Humpata Plateau breccias, Angola	Late Pliocene/Early Pleistocene	*Gerbilliscus* sp.	Pickford *et al.* (1994)
Kaokoland breccias, Namibia	Late Pliocene/Early Pleistocene	*Gerbilliscus* sp.	Pickford *et al.* (1994)
Aukuas, Aigamas and Nosib, Namibia	Plio-Pleistocene	*Gerbillurus* sp. *Gerbilliscus* sp.	Senut *et al.* (1992)
Uisib and Jägersquelle, Namibia	Plio-Pleistocene	*Gerbillurus* sp.	Senut *et al.* (1992)
Ngamiland, Botswana	Plio-Pleistocene	*Gerbilliscus* and *Taterillus* (three indet. species)	Pickford & Mein (1988)
Twin Rivers and the Mumba Caves, Zambia	Early and middle Pleistocene	*Gerbilliscus leucogaster* *Gerbilliscus valida*	Avery (2003)
South Africa			
Wonderwerk Cave	Pleistocene	*Desmodillus* sp.	Avery (2007)
Gladysvale cave, COH*	200 kyr to. 1.3 Ma	*Desmodillus auricularis*	Avery (1995) Hall *et al.* (2006)
Swartkrans (Members 2 and 3), COH	1 - 1.5 Ma	*Desmodillus auricularis*	Avery (1998, 2001)
Swartkrans Member 1	From 1.5 to 2.5 Ma	*Desmodillus auricularis*	Cooke (1990)
Drimolen, COH	1 - 1.5 Ma	*Gerbilliscus* sp.	Sénégas *et al.* (2005)
Bridge Cave, Gladysvale 3,5	1 - 1.5 Ma	*Desmodillus* aff. *auricularis*	Sénégas (2000)
Bolt's Farm, COH Waypoint 160, COH	~4 Ma	Gerbillinae indet. *Gerbilliscus* sp.	Sénégas (2000) Davis & Meester (unpublished)
Kromdraai B, COH	2.0 - 1.6 Ma	*Desmodillus* sp.	Pocock (1987)
Makapansgat, Rodent corner, COH	~4 Ma	Gerbillinae indet *Gerbilliscus* sp.	Lavocat (1956) De Graaff (1960) Cooke (1990)
Sterkfontein, STS4, COH	2.0 - 1.6 Ma From ~2.0 Ma to 100 000 BP	*Desmodillus* sp. *Gerbilliscus* cf. *leucogaster* *G.* cf. *brantsii*	Pocock (1987) Avery (2000) Cooke (1990)
Taung	3.3-2.5 Ma	*Gerbilliscus* sp. *Gerbilliscus* cf. *brantsii*	Lavocat (1956) De Graaff (1960) Cooke (1990)
Taung	2.8 Ma	*Desmodillus auricularis*	Cooke (1963) Davis & Meester (unpublished)
Hoedjiespunt 1, west coast,	200 000 - 300 000 BP	*Gerbilliscus afra*	Matthews *et al.* (2005)
Saldhana Bay Yacht Club, west coast	~15540 BP	*Gerbillurus paeba* *Gerbilliscus afra*	Manthi (2002)
Elands Bay cave, west coast	Terminal Pleistocene and Holocene	*Gerbillurus paeba* *Gerbilliscus afra*	Matthews *et al.* (2007)
Cave PP13B and Cave PP9C Mossel Bay, south coast	MIS 5, early MIS 6	*Gerbilliscus afra*	Matthews *et al.* (2009, 2011)
Blombos cave, south coast	~70 000 BP	*Gerbilliscus afra*	Hillestad (pers. comm.)

and *Gerbilliscus* spp. have been measured. All comparative material came from the Natural History Museum (London), the Ditsong Museum (South Africa), The Museum of Namibia (Windhoek) or the MNHN collections.

The nomenclature used here (Fig. 1) follows Tong (1989), Flynn *et al.* (2003) and Pavlinov (2008).

RESULTS

Revision of characters: Attributes of the Langebaanweg gerbilline

The fossils from Langebaanweg indisputably belong to the Gerbillinae, but genus allocation is complicated by the absence of complete skulls. Figures 2, 3, and 4 provide some morphological dental and skull characters derived from the literature, and this research.

Compared to modern genera occurring in South Africa, the Langebaanweg molars with their high crowns and semi-lophodont pattern fall closer to *Gerbilliscus* (*Gerbillurus*) and *Desmodillus* rather than *Gerbilliscus* (*Tatera*). The molars have an "advanced lophodont" pattern in *Gerbilliscus* (*Tatera*), and lack longitudinal connections between laminae. The horseshoe-shaped appearance of the anteroconid of m1 is present from an early age but is highly variable. A "semi-lophodont" pattern has been described for the molar crown of *Gerbillurus*, which also has the horseshoe-shaped anteroconid on m1 which becomes more circular ("rhomboid") with age (as in other *Gerbilliscus*). Cusps are round and high and do not fuse together in transverse laminae in *Gerbillurus* whereas they fuse more easily, and earlier, in other *Gerbilliscus* (*Tatera*) species. In the fossils, *Protatera* and *Abudhabia* cusps are fused and the absence of vestigial longitudinal crests resembles *Abudhabia* which is more derived in this aspect. The absence of the horsehoe pattern of the prelobe on m1 distinguishes the

Langebaanweg specimens from *Gerbilliscus* sp. (excluding *Gerbillurus*) (Fig. 2).

According to Pavlinov (2008), *Desmodillus* posesses a separate protoconulid on the m1 (Pavlinov, 1984, 1985). Pavlinov (1985) notes that such an anteroconid pattern is also visible in *Protatera,* indicating the ancient origin of *Desmodillus* (Pavlinov, 1985, 2008). In *Desmodillus*, the molar crowns are advanced compared to *Gerbilliscus* (*Gerbillurus*) in that they are semi-lophodont, with symmetrical cusps tending to fuse early in the transverse laminae.

The mandibular shape of the Langebaanweg gerbil more closely resembles *Desmodillus* than *Gerbilliscus sensu lato*. In lateral external view the mandibles of modern *Desmodillus* are characterized by a small oblique coronoid process situated at the same level as the condyloid process, separated by a horizontal mandibular notch. In *Gerbillurus* the coronoid process is smaller than in *Desmodillus* and lies below the level of the condyle. In *Gerbilliscus s.s.* the coronoid process is small and is situated below the level of the condyle, and the notch is small and oblique (Fig. 3).

Desmodillus is characterized by a prominent capsular process below the masseteric fossa, which ends in a relatively deep gutter, as well as the presence of a mental foramen and an oblique marked masseteric crest (Fig. 1). *Abudhabia* has a mental foramen and oblique marked masseteric crest, and a marked capsular process. There is a small bump in *G. brantsi*, *G. paeba* (A. Smith, 1836)*,* and *G. tytonis* (Bauer & Niethammer, 1960) but no gutter as seen in *A. radinskyi* (Flynn *et al.,* 2003 (Fig. 3). The mental foramen is absent in *G. brantsii*. The lack of complete fossil skulls prevents characterisation of the tympanic bullae and the keel of the masseteric (Pavlinov, 2008). These two characters are thus unknown in the fossil genera.

Because we have only a partial zygomatic plate region and palate we focused our comparisons on these two parts of the

Molar/site	N	Length	Width
M1 LQSM			
Mean (Min-Max)	56	3.06 (2.75-3.46)	2.12 (1.77-2.46)
Standard deviation		0.13	0.14
M1 LPPM	28	3.59 (3-4.1)	2.38 (1.83-2.9)
Standard deviation		0.27	0.23
M2 LQSM	16	1.85 (1.67-2.08)	1.84 (1.79-2.08)
		0.12	0.09
M2 LPPM	5	1.97 (1.83-2.08)	2.05 (2-2.08)
		0.09	0.04
M3 LQSM	9	0.96 (0.83-1.08)	1.3 (1.25-1.42)
		0.09	0.06
M3 LPPM	3	1.06 (0.92-1.17)	1.29 (1.08-1.42)
		0.13	0.18
m1 LQSM+LPPM	34	2.95 (2.75-3.2)	1.91 (1.74-2.08)
Standard deviation		0.11	0.08
m2 LQSM	26	1.94 (1.67-2.12)	1.88 (1.67-2)
		0.1	0.09
m2 LPPM	14	2.04 (1.83-2.33)	2.01 (1.83-2.17)
		0.13	0.12
m3 LQSM	10	0.92 (0.58-1.17)	1.22 (1.08-1.33)
		0.25	0.09
m3 LPPM	4	0.65 (0.5-0.83)	1.17 (1.08-1.25)
		0.14	0.07

Table 2. Upper and lower molars dimensions of Langebaanweg *Desmodillus magnus* sp. nov. in millimetres. N= number of molars measured; Min= minimum value; Max=maximum value.
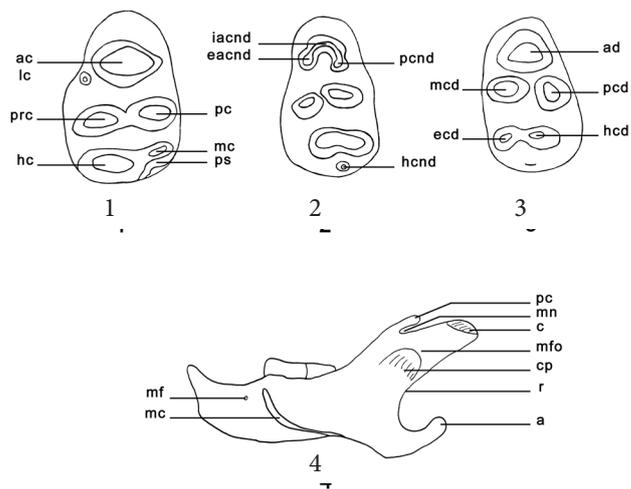
Figure 1. Dental nomenclature (after Jacobs, 1978, Pavlinov, 2008). **1.** Left M1; ac: anterocone; lc:lingual cusplet; prc: protocone; hc: hypocone; pc: paracone; mc: metacone; ps: posterior sinus; **2 and 3.** Right m1 with different wear stages; iacnd: internal anteroconid; eacnd: external anteroconid; pcnd: protoconulid; hcnd: hypoconulid (or posterior cingulum); ad: anteroconid; mcd: metaconid; pcd: protoconid; ecd: entoconid; hcd: hypoconid; **4.** Mandible nomenclature (*D. auricularis* DM3313); pc: coronoid process; mn: mandibular notch; c: condyloid process; r: ramus; a: angular process; cp: capsular process; mfo: masseteric fossa; mf: mental foramen; mc: masseteric crest.

skull, which may be observed in ventral view in fossil and modern comparative taxa in Figure 4.

The zygomatic plate is very broad in *Gerbilliscus s.s.* and has a convex anterior edge and evenly curved dorsal angle. In *Gerbilliscus* the plate is narrower, forward sloping, and cut away above. In the Langebaanweg gerbil the zygomatic plate is broad and flat as seen in *Desmodillus*.

Based upon molar cusp and mandibular morphology and zygomatic plate shape, the new species of Langebaanweg gerbil most closely resembles the genus *Desmodillus* and it is to this genus that we thus assign the fossil species.

Description of the new Langebaanweg species

Order RODENTIA Bowdich,1821

Family MURIDAE Illiger, 1811

Subfamily GERBILLINAE Alston, 1876

Genus *Desmodillus* Thomas & Schwann, 1904

Modern *Desmodillus* are different from other gerbils in their skull anatomy and are characterized by the peculiar and marked development of the tympanic bullae. This feature is not preserved in the Langebaanweg material but the fossils share several characters with this genus, namely the short and flat zygomatic plate, the narrow, short anterior palatal foramina, relatively long palatal foramen, relatively narrow upper molars, absence of longitudinal crests between high cusps rows, presence of a protoconulid on poorly worn m1s, and the presence of a strong capsular process and a gutter on the mandible. It is distinguished from modern *Gerbilliscus s. l.* (including sub-genera *Tatera* and *Gerbillurus*) by its zygomatic plate and mandibular morphology. It differs to *Abudhabia* in the disposition of the cusps on the M1 prelobe, and differs from all species of *Protatera* by the absence of well developed longitudinal crests connecting the cusp rows. In size, the *Gerbilliscus* taxa of the sub-genus *Gerbillurus* are smaller (greatest length of the skull (GLS): ca. 27-33 mm) compared to those of the subgenus *Tatera* (GSL ca. 35-45 mm) (Monadjem *et al.*, 2015). *Desmodillus* is intermediate in size (GLS ca. 30-38 mm).

Desmodillus magnus sp. nov.
(Figs. 4-7)
lsid:zoobank.org:act:00EC0C7C-BBE9-44DF-B1FC-F1AE63BE7794

Named after the large molars and mandibles of this taxon whose teeth are larger than any other known *Desmodillus* species.

Holotype. Right mandible with m1-3 (SAM-PQL-69673) from MPPM Langebaanweg (Fig. 6.1).

Paratypes. Maxillary fragment with M-3 (SAM-PQL-67865); Maxillary fragment with M1-3 (SAM-PQL-67838). Housed in the Iziko South African Museum in Cape Town (Iziko Museums of South Africa).

Diagnosis. A large *Desmodillus* which closely resembles *D. auricularis* in terms of dentition and shape of the zygomatic plate. The LBW specimens appear, from the size of the available skull fragments and molars, to have been approximately the same size as large South African *Gerbilliscus* spp. and considerably larger than the relatively small, extant *D. auricularis*. The new species is different from *Gerbilliscus s.l.* by the shape of the zygomatic plate in ventral view. In *D. magnus* the plate is flat and broad, and some bone is visible on the labial side of the molars. In *Gerbilliscus* the plate is
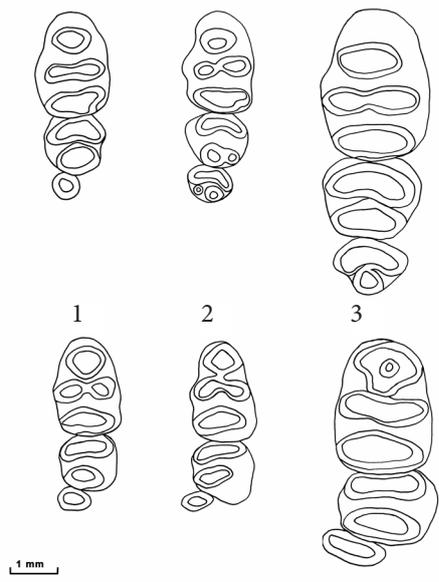
Figure 2. Modern South African Gerbillinae dental patterns, top: upper left molars, bottom: lower right molars. **1.** *Desmodillus auricularis* BMNH 28.911.227 Gohinduo, Namibia; **2.** *Gerbilliscus paeba* BMNH 49.345 Middleburg Cape Province, RSA; **3.** *Gerbilliscus afra* BMNH 29.10.1.19 Muhango, Angola.

Figure 3. Lateral view of right mandibles of modern and fossil Gerbillinae. **1.** modern *Desmodillus auricularis* MNHN ZM-AC 1983-814; **2.** fossil *D. magnus* sp. nov. L40201 SAM-PQL-68603, Langebaanweg; **3.** modern *Gerbilliscus leucogaster* MNHN ZM-MO 2007-1134 Tanzania; **4.** modern *Gerbilliscus paeba* MNHN-ZM-MO-1969-66, Botswana.

more convex and no maxillary bone is visible along the labial side of the upper molars. The depth of the mandible (below the m1) is larger in *D. magnus* than in the mandibles of modern *Desmodillus* and *Gerbilliscus*. *Desmodillus magnus* differs from *Abudhabia*, *Protatera,* and *Gerbilliscus s.s.* by having less fused cusps in the first lobe of upper and lower first molars. *Desmodillus magnus* differs from *Gerbilliscus* (ex *Gerbillurus*) by its larger molar size, and a longer palatal foramen beginning at the level of the second lamina of the M1 instead of the first. Compared to *Protatera*, the cusps of *D. magnus* are less alternating and there is no trace of a longitudinal crest. It differs from all *Abudhabia* representatives by the absence of an isolated posterior cingulum on the m1, and by the absence of an anterior cingulum on the M2. It differs from *Abudhabia* sp. from Lothagam by the prelobe of the m1 (not horsehoe shaped in *D. magnus*). Compared to *Abudhabia tateroides* (Mein & Pickford, 2006) from Lukeino it differs in a narrower prelobe on the M1, the reduced or absent posteroconid, and the more lophodont teeth.

Type series.

Upper Maxillaries with M1-3

LQSM: L67688 – L67756 – L67815 – L67816 – L67824 – L67838 – L67853 – L67883 – L67886 – L67888 – L68598 – L69681 – L67684 – L67691 – L67813 – L67814 – L67832

MPPM: L69626 – L69741 – L69671 – L69629 – L69659 – L69763 – L69782 – L69603 – L69604 – L69745.

Lower Mandibles with m1-3

LQSM: L67633 – L67624 – L67636 – L67812 – L67823 – L67826 – L67841 – L67846 – L67863 – L67865 – L67880 – L68599 – L68603.

MPPM: L69772 – L69667 – L69598 - L69773 – L69665 – L69608 – L69614 – L69616 – L69621 – L69747.

Distribution. LQSM and MPPM in Langebaanweg.

Description

Maxillary bone

Maxillae were fragmented and retained only a small portion of the zygomatic process in even the best preserved specimens (Fig. 4). The incisive foramen stops slightly before, or at, the level of the first root of the M1. The palatal foramen starts at the second M1 lobe and ends past the M2 to the level of M3 at least, but the palate is generally broken in that region so the ending point is uncertain. The zygomatic plate is flat in ventral view and there is some visible maxillary bone on the labial side of the upper molars. A small, round foramen is visible in front of the M1. No upper incisors were preserved *in situ*.

Upper molars

The M1 is trilaminate, the M2 bilaminate, and the M3 uni or bilaminate. The M3 is reduced in size (Figs. 4.1-2; Figs 5.1-2, Fig. 7, Supplementary Table S1).

M1: the prelobe is generally composed of one high laminate cusp (anterocone) which never divides into two distinct, separate cusps. This feature is however highly variable, and the shape of the prelobe changes with the degree of wear of the molars. Generally, it is round in shape and becomes larger and more oval with wear. No longitudinal crest is visible between lobes of the molar and the prelobe, and the first lobe is always well separated from the other cusps. The first lamina is divided into two round conjoined cusps transversally aligned, with the protocone being slightly larger than the paracone. In worn specimens the latter cusps fuse together so that the dentine forms a continuous surface and the enamel differentiating the two cusps is completely worn away. The second lobe is composed of two well fused cusps which remain individualized and not well aligned transversally. The hypocone is larger and situated posteriorly as compared to the metacone, which is smaller and roundish in shape (when teeth are less worn in 44 % of cases, S1). The shift between the hypocone and metacone is marked by an inflexion in the enamel (the posterior sinus of Tong, 1989). This molar has one large anterior and posterior root, plus one internal median one (lingual side).

M2: two laminae comprise this molar with the first one generally convex in its anterior border, and concave in the posterior one. On slightly worn specimens there is the trace of two cusps forming a chevron. The second lamina is narrower

Figure 4. Maxillary shape and upper right molar rows of fossil and modern South African Gerbillinae. **1.** *Desmodillus magnus* sp. nov. M1 SAM-PQL L50230; **2.** *Desmodillus magnus* sp. nov. M1-3 (L24052 SAM-PQL-67886); **3.** Modern *Desmodillus auricularis* M1-3 (MNHN ZM-MO 1983-814); **4.** modern *Gerbilliscus kempi* M1-3 (MNHN ZM-MO- 1973-695); **5.** modern *Gerbilliscus paeba* M1-3 (MNHN ZM-MO 1969-66).
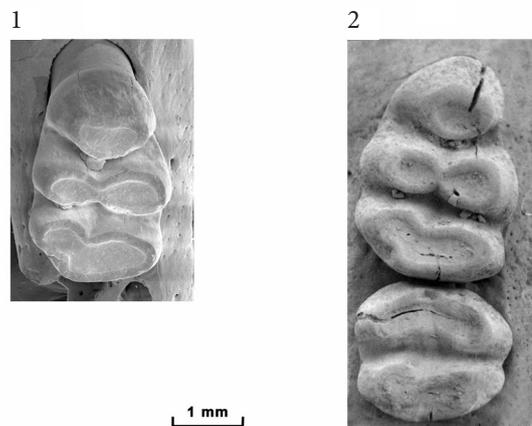
Figure 5. *Desmodillus* magnus sp. nov. from Langebaanweg upper molars. **1.** right maxilla with M1 (SAM-PQL L24850); **2.** right maxilla with M1-2 (SAM-PQL L50230).

and composed of two round cusps that are separated by an enamel border only in very young specimens. Generally the two cusps form a rectilinear lamina, but in some cases (43 % of cases, see S1) the posterior sinus may be observed. There is no cingulum but some specimens have a slight posterior sinus in the middle of the posterior border of the lobe. This molar has two roots situated anteriorly and posteriorly, and a third on the lingual side.

M3: this molar is triangular when worn and no cusps can be observed, but in unworn specimens it exhibits an anterior lamina linked to a small posterior cusp. Most of the M3s exhibit a trace of three cusps (71.5 %), but when worn only one cusp may be visible (14 %), and in rare cases (14%) there is only a trace of two cusps. There is one large root.

Mandible

A feature of the mandible of the fossil gerbil, in medial view, is the greater depth of the mandible as measured from the distal edge of the mandible to the top of the mandible, under the prelobe of the m1 (see Table 3 for measurements). This is markedly deeper than the mandibles of modern *Desmodillus, Gerbilliscus* and *Gerbillurus* taxa. The mental foramen is large in *D. magnus*, as in *D. auricularis*, and the masseteric crest, a prominent capsular process and a gutter are well developed in both species. The upper and lower molars of the LBW gerbilline are slightly smaller, and considerably narrower in aspect when compared to *Gerbilliscus afra*. The fossil species is considerably larger and more robust in all aspects of the teeth and mandibles than *Gerbillurus paeba* and *Desmodillus auricularis*. Lower incisors are ungrooved and narrow.

Lower Molars

The m1 is trilaminate, the m2 bilaminate, and the m3 unilaminate and reduced in size (Figs. 6.1-6, Figs. 7-8, Supplementary Table S1).

m1: the prelobe constitutes one large cusp which is situated slightly obliquely on the labial side relative to the next lobe. In a few cases the trace of two (23.3 %) or three cusps (0.3 %) was observed and in two cases (0.3 %) the prelobe opens distally (Figs. 5 and 7 and Supplementary Table S1). In some specimens, a little swelling situated in the middle of the distal border of this cusp is reminiscent of a longitudinal crest (11 %). When the traces of three cusps are visible (external, internal and protoconulids) on the prelobe the lingual side is constituted by two round equal cusps, and the labial side by a single round one. There is no isolated protoconulid as in some *D. auricularis* (Fig. 9). Pavlinov (2008) notes that the presence of a protoconulid is a primitive condition for gerbils. The valley separating the prelobe from the first lobe is deep and the cusps generally remain well differentiated although a longitudinal link may develop when teeth are worn, but this feature is very variable and the prelobe may remain well-differentiated until the teeth show advanced stages of wear. The second lamina is composed of two poorly alternating cusps of roughly equal size. The lingual cusps (metaconid) is slightly anteriorly situated. The posterior lobe is in shape of a lamina and the two posterior cusps have a continuous dentine surface with no dividing enamel, except in very young specimens. A small swelling of the distal wall of the molar may be visible in posterior view (possibly a trace of a posterior cingulum or hypoconulid) and occurs in 15 % of the cases (S1). This tooth has a large anterior and posterior root. Some specimens appear to have a small extra rootlet on the lingual and/or labial side but the alveoli for these roots is shallow and ill-defined.
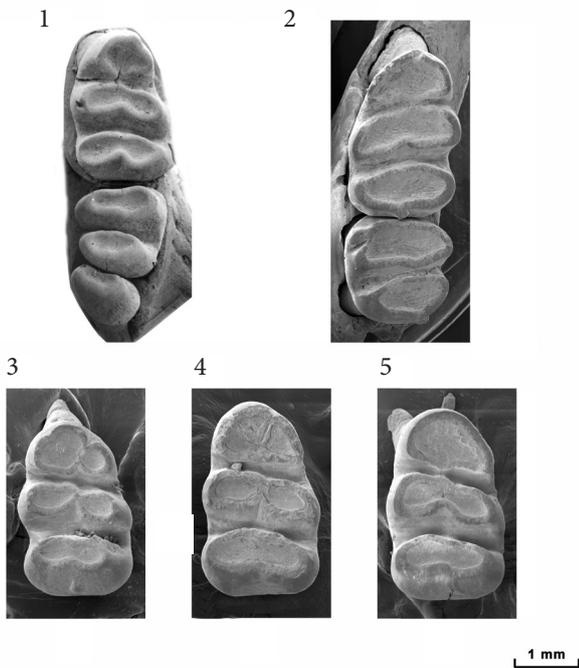
Figure 6. *Desmodillus magnus* sp. nov. from Langebaanweg - lower molars. **1.** right mandible with m1-3 (SAM-PQL 69673 25900); **2.** left mandible with m1-2 (SAM-PQL 50230); **3:** isolated m1 (SAM-PQL 24850); **4.** isolated m1 (SAM-PQL 24850); **5.** isolated m1 (SAM-PQL 24850). NB: for convenience pictures have been mirrored in the same side to facilitate observation.
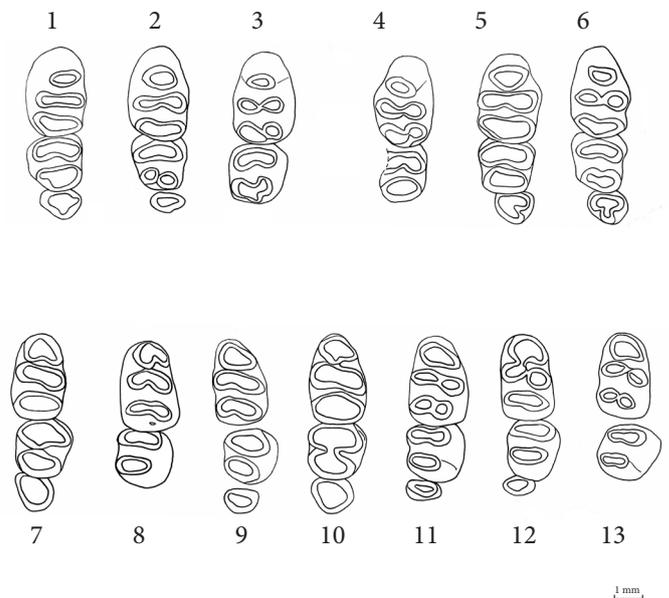
Figure 7. Molar variability among different *Desmodillus magnus* sp. nov. of Langebaanweg (x8). **1-6.** upper molars rows SAM-PQL 25891 (LQSM); **7-9.** lower molar rows from SAM-PQL 25891 (LQSM); **10.** right mandible with m1-3 (SAM-PQL 24012-LQSM); **11.** Right mandible with m1-3 (SAM-PQL 24570-LQSM); **12.** left mandible with m1-3 (SAM-PQL24031-LQSM); **13.** right mandible with m1-2 (SAM-PQL L24131-LQSM). NB: for convenience pictures have been mirrored in the same side to facilitate observation.
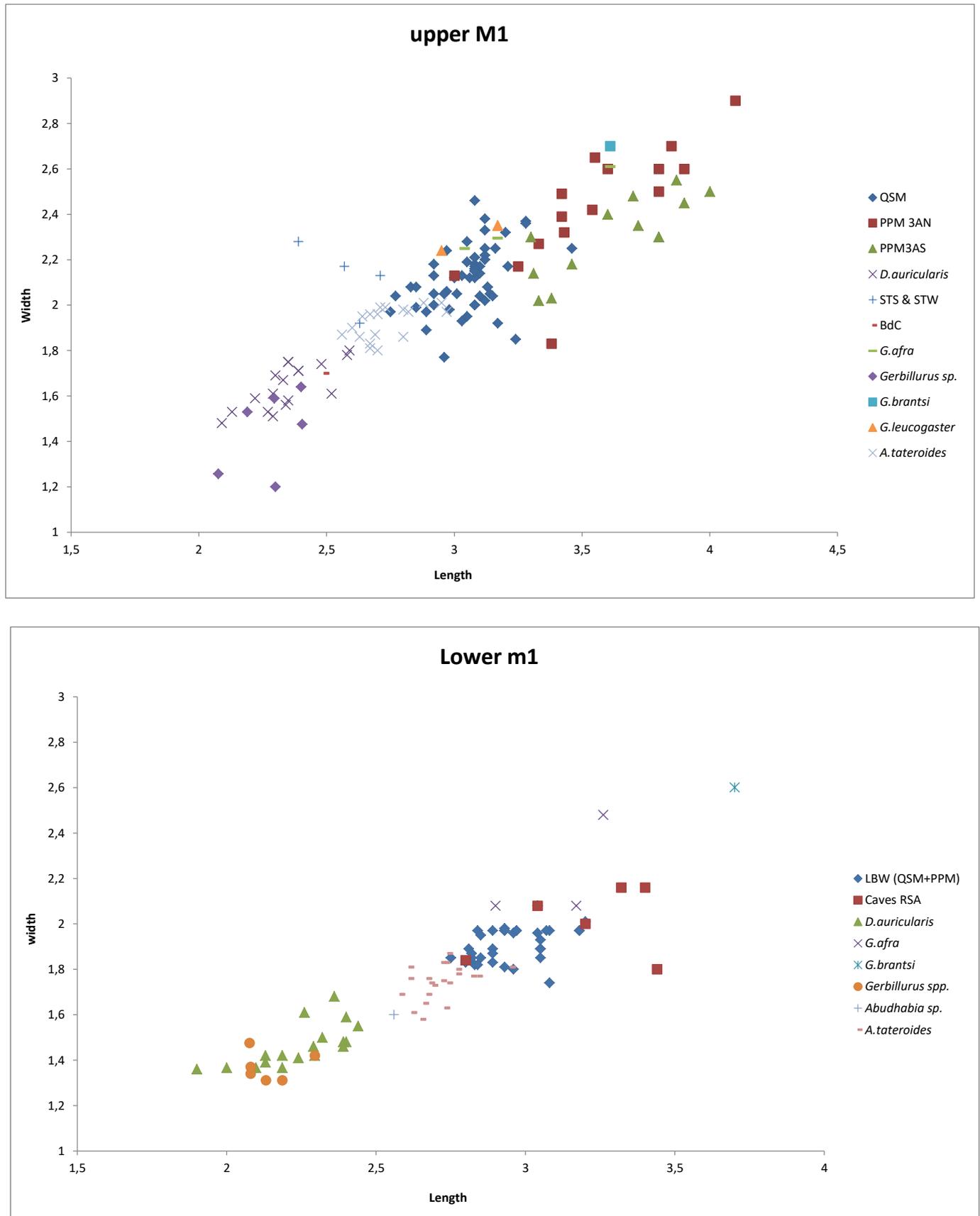
Figure 8. Scatterplots of the M1 and m1 proportions. Top: upper M1 length x width in mm, bottom: lower m1. Abbreviations: QSM, PPM 3AN, PPM 3AS *Desmodillus magnus* sp. nov. Langebaanweg; modern *D. auricularis*; STS & STW: *Gerbilliscus* sp. Sterkfontein type site and Swartkrans; BdC: *D.* aff. *auricularis* (after Sénégas 2000) Border Cave; Modern *Gerbilliscus afra*; *Gerbillurus* spp. modern; modern *Gerbilliscus brantsi*; modern *Gerbilliscus leucogaster*; *A. tateroides* Lukeino (after Mein & Pickford 2006), *Abudhabia* sp. Lothagam (Winkler, 2003).

m2: this molar has two parallel laminae which are slightly bifurcated into two cusps. Bifurcation of the cusps is much less marked than in the m1. The anterior cusp is larger than the posterior. In very worn specimens the enamel border between the two cusps disappears and the dentine forms one single surface. On some specimens (5.3 %, S1) a little antero-labial cingulum takes the form of either a cusplet, or a swelling at the base of the crown (Fig. 6). This molar is two-rooted with the roots situated anteriorly and posteriorly.

m3: this is a small, two-rooted molar, with the roots situated anteriorly and posteriorly on the tooth. It is composed of a small single lamina with no visible lobes.

Comparisons with modern and fossil Gerbillinae

Size. Comparison with modern gerbil species and Plio-Pleistocene fossils

The Gerbillinae molars from Langebaanweg most closely resemble those of *Desmodillus auricularis* in morphology, but not size. The molars of the fossil *D. magnus* are significantly larger than modern *Desmodillus auricularis* from South Africa and Namibia in terms of both mandible depth and molar rows size, but the general proportions and aspect of the teeth is very similar (Fig. 8, Table 3, Supplementary material S2, S3 and S4).

Desmodillus magnus also has larger molars than modern representatives of the smaller *Gerbilliscus* species (*Gerbillurus*). They are close in size to the medium sized South African *Gerbilliscus* taxa like *G. (Tatera) leucogaster* (Peters, 1852), but slightly smaller than the largest modern *Gerbilliscus brantsi* and *Gerbilliscus afra*. *Desmodillus magnus* thus fits within the variability of large fossils like *Gerbilliscus* sp. of the Adu-Asa formation (Ethiopia) and *G. winkleri* (Denys, 2011) from Hadar and Laetoli. Compared to *A. tateroides* M1 and m1 size is similar to *D. magnus* (Fig. 8, S4) but the M2 and m2 of *A. tateroides* are significantly smaller than those of *D. magnus* and the width of m3 of *A. tateroides* is significantly larger (S2,S3,S4).

Shape. Comparison with modern Desmodillus auricularis

In *D. auricularis* the incisive foramen stops at the beginning of the alveolus of the first molar root, or slightly before, while in *D. magnus* it stops at the level of the prelobe of M1. The palatal foramen is long and starts at the level of the M1 second lobe in *D. magnus* as in *D.auricularis* (Fig. 4). The prelobe of the M1 of *D. magnus* and *D. auricularis* have a similar shape and are both composed of one cusp when worn (Fig. 9). In some young *D. auricularis* one can observe two or three small cusps in the anteroconid. Two (9.5 %, S1) or three (19 % of cases, S1) cusps are also visible in the anteroconid in some m1 of *D. magnus*. We never observed more than one cusp in the anterocone of all M1 molars of *D. magnus* and *D. auricularis*. In both modern and fossil *Desmodillus* we always find two visible cusps in the first lobe of the M1 but in *D. auricularis* they look more transversally aligned and seem be of a more equal size in M1 than in *D. magnus*. The posterior sinus is visible on 68 % of all M1s of *D. auricularis* examined (S1). The M3 in *D. auricularis* is small with generally (58 % of specimens) one anterior lamina (1 or 2 visible cusps) and small posterior cusps which is also visible in some *D. magnus* specimens. But, like in Langebaanweg specimens, the M3 of *D. auricularis* may be constituted of a single lamina with only traces of two cusps (42 %, S1). In *D. auricularis*, the first lobe of the M2 is convex in shape and the molar is as wide as the M1 and, in some slightly worn specimens, there is the trace of three cusps analogous to those of murine molars (Fig. 9). In the m1, both some Langebaanweg fossils and some modern *D. auricularis* show the trace of a longitudinal link between the anteroconid and the first lobe either in the middle, or joining the anteroconid to the metaconid on lingual side. Like in *D. magnus*, the m3 of *D. auricularis* of worn specimens is reduced to a single small lamina with no visible cusps.

Modern *D. auricularis* display a high variability in their molar cusps patterns and some specimens exhibit primitive characters such as the presence of small anterior cusps (either labial or central) in the first lobe of the M2, or may retain a tricuspid prelobe on a poorly worn m1, or present a small hypoconulid in 9.5 % of the specimens (S1). The number of laminae (1 or 2) in both M3/m3 may vary (Fig. 9, S1).

Comparison with Plio-Pleistocene Desmodillus *from South African cave sites*

The occurrence of *Desmodillus* in South African sites is detailed in Table 1. The length and breadth measurements of the single M1 from Bridge Cave (*D.* aff. *auricularis*) is 2.49 x 1.7 mm, which fits in with modern *D. auricularis* values, as does the tooth morphology. The measurements of the Waypoint 160 molars according to Sénégas (2000) are larger (mean M1: 3.35 x 2.4 mm; mean m1: 3.33 x 2.21 mm) and fits in the upper part of *D. magnus* variability. Based upon drawings, the morphology of the M1 shows well aligned transversal cusps becoming fused early, the presence of a posterior sinus on the M1, and a bilaminate prelobe. The prelobe of the m1 is composed of 2 to 3 cusps and an anterior and posterior sinus is distinguishable – a characteristic of *Gerbilliscus* rather than *Desmodillus*. The cusps of the first lobe of m1 are poorly fused and slightly oblique in their alignment. These characters suggest that the indeterminate gerbil found at Waypoint 160 may be an old *Gerbilliscus* representative, rather than *Desmodillus*.

Comparison with Protatera

Based upon isolated fossil molars found in North Africa and Spain three species of *Protatera* have been described: *P. algeriensis* (Jaeger, 1977) (type species of the genus), *P. almeriensis* (Agusti, 1990) and *P. davidi* (Geraads, 1998). They all have transverse, fused cusps in M1 and M2, with oblique lobes which form a continuous occlusal surface. The

Taxon	UTR	LTR	MD
Desmodillus magnus sp. nov. N=10	6.05 (5.8-6.5)	5.88 (5.8-6.1)	N=30 ; 4.73 (3.96-5.66)
Desmodillus auricularis N=72	4.3 (3.84-4.75)	4.05 (4.13-4.52)	N=3 ; 4.64 (4.59-4.73)
Gerbilliscus (*Gerbillurus*) spp. N=42	4.14 (3.47-4.54)	4.06 (3.34-4.69)	N=5 ; 3.67 (3.27-3.99)
Gerbilliscus (*Gerbilliscus*) spp. N=26	5.61 (5.02-6.73)	5.39 (4.88-6.6)	N=7 ; 5.66 (4.99-6.23)

Table 3. Length of upper (UTR) and lower teeth rows (LTR), mandibular depth (MD) in mm.
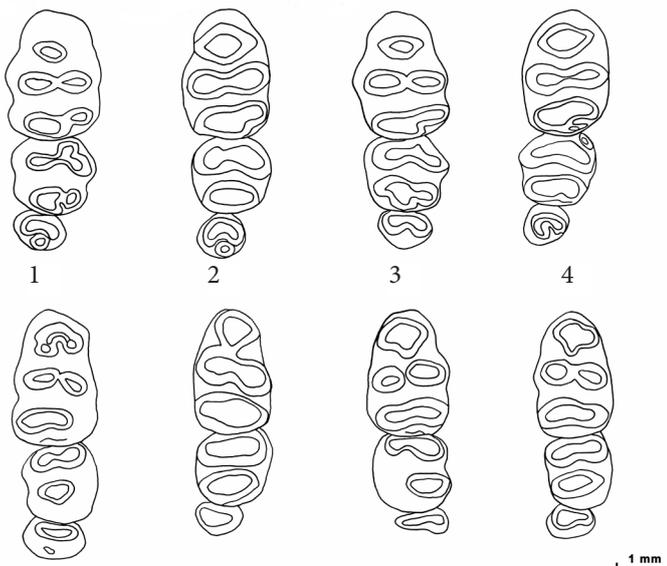
Figure 9. Variability in modern *Desmodillus auricularis* molars. Top row: upper molars, bottom row: lower molars. **1.** BMNH 34.10.10.66 Ondonga, Namibia; **2.** BMNH 25.1.2.78 Ongandjera, Namibia; **3.** 34.10.10.79 Windhoek, Namibia; **4.** BMNH 20.9.11.2. 29 Gohinduo, Namibia.

three hypsodont laminae are well separated by deep lingual and labial folds. On the m1 vestigial longitudinal crests are more or less developed, the M1 has a large anterocone, the anteroconid of the m1 is complex including an anterior sinus, a central fovea, a labial tubercle (protolophid?), and the m3 is reduced (Wessels, 2009). De Bruijn & Whybrow (1994) considered *Protatera* to have stronger longitudinal ridges and prismatic cusps than *Abudhabia*.

Compared to the three species of *Protatera*, the Langebaanweg *D. magnus* differs in the following features; *Protatera* has a more developed hypsodont crown which results in cusps which are very high and which become relatively well fused when worn. In *P. algeriensis, P. davidi*, and *P. almeriensis* there is no posterior sinus and the distal edge of the second lobe of the M1 is rectilinear or convex. In *Protatera* the anterocone of the M1 is either lozenge-shaped and related by a longitudinal link to the first lobe, or takes the form of a long lamina composed of two cusps. The prelobe of the m1 is composed of two alternate oblique cusps as well as the first lobe. This is not seen in *D. magnus* which has an anterior sinus.

Comparison with Abudhabia

Among the various species of *Abudhabia* De Bruijn & Whybrow (1994) described from Asia, Arabia and Africa, we observe a large variability. In his amended diagnosis of the genus, De Bruijn (1999) included the existence of a posterior cingulum isolated and developed as a cusp on m1; this is not observed in *D. magnus* where only a little swelling of the posterior wall of the m1 may be seen in some cases. The M2 and m2 have remnants of the anterior cingulum in *Abudhabia*. It is absent in the M2 of all *D. magnus* but may be found on some m2s. Cusps pairs of M1-2 of *Abudhabia* form transverse ridges and are high while they are well differentiated in *D. magnus*. The m1 has alternating cusps and an anteroconid with a posterolabially directed crest in *Abudhabia* while cusps are less alternated in *D. magnus* and there is no posterolabial crest. Flynn *et al.* (2003) in the revision of the genus added other characters found in the

type species such as the absence of longitudinal crests and the fact that the cusps of m1 are slightly oblique.

Desmodillus magnus are clearly different from *Abudhabia radinskyi, A. kabulense* (Sen, 1983), *A. baynunensis* (Bruijn & Whybrow, 1994) and *A.baheensis* (Qiu *et al.*, 2004) in that this taxa has less alternating and oblique cusps and also lacks the isolated cusp such as the posterior cingulum of the m1-2. The m3 is proportionally less reduced in *Abudhabia* than in *D. magnus*.

The comparison with African *Abudhabia* specimens of Lukeino and Lothagam (Kenya) shows that these specimens both display the posterior cingulum but have more transversally aligned cusp rows than in *D. magnus*. The prelobe of the M1 of *A. tateroides* is broad and displays an anterior sinus separating two cusps, a feature which is also seen in *A. radinskyi* and *A.baheensis*, but is not observed in *D. magnus* or *D. auricularis* and is rare in modern South African Gerbillinae. The prelobe of the m1 of *A. tateroides* is wide with a small cingulum, and there is a small posterior cingulum (see Mein & Pickford, 2006, plate 2, fig. 3: 222). In some specimens of *D. magnus* a little swelling of the distal wall of the m1 may be observed, reminiscent of this little cusp.

According to Mein & Pickford (2006), *A. tateroides* presents a small "anterocone" (antero-externe cusplet) in the M2 and a small "anteroconid" (antero-external cusplet in murinae terminology) in the majority of m2. In *D. magnus* this antero-external cusp is absent in M2 and a small cusp was observed only in 3 individuals in the m2 (5.3 % of cases, S1). In modern *D. auricularis* these features were not observed. *Abudhabia tateroides* was similar to Plio-pleistocene species of *Gerbilliscus* (*Tatera*) or *Taterillus* but differs in the anterior position of the metacone in the upper molars, a situation similar to *Desmodillus* or *Gerbilliscus* (*Gerbillurus*). According to Mein & Pickford (2006), the Langebaanweg gerbil could belong to the *Abudhabia - Gerbilliscus* (*Tatera*) group and represents an intermediate stage between those two genera. The Lothagam *Abudhabia* sp. m1 displays a three cusps anteroconid horsehoe shaped prelobe that was found once in modern *D. auricularis* and is common in modern *Gerbilliscus*. Both East African *Abudhabia* species are intermediate in size between modern *D. auricularis* and *Gerbilliscus* species. They are also slightly smaller than *D. magnus* (Fig. 8). Based upon the observations presented in this paper we do not support the suggestion that *D. magnus* represents an intermediate form between *Abudhabia* and *Gerbilliscus,* but, like Mein & Pickford (2006) and Flynn *et al.* (2003), we concur that *Abudhabia* is a Taterilline related to *Taterillus, Gerbilliscus* and *Tatera,* but not to *Desmodillus*.

Much revision remains to be done on the classification of fossil South African gerbils due to the high degree of variability observed, but, based upon skull and dental characters, the new Langebaanweg gerbil species shows affinities to the South African endemic genus *Desmodillus, Abudhabia* with the East and South African *Gerbilliscus* lineages, and *Protatera* with North African *Gerbillus*.

EVOLUTIONARY SCENARIO

Many researchers have shown that East and southern Africa faunas evolved independently from North Africa through the Miocene (Denys, 1999). Molecular research has indicated the monophyly of the Gerbillinae and their early occurrence in East Africa at around 8.5 Myr (Colangelo *et al.*, 2007, Knight *et al.*, 2013), which places their origin at the same time as the
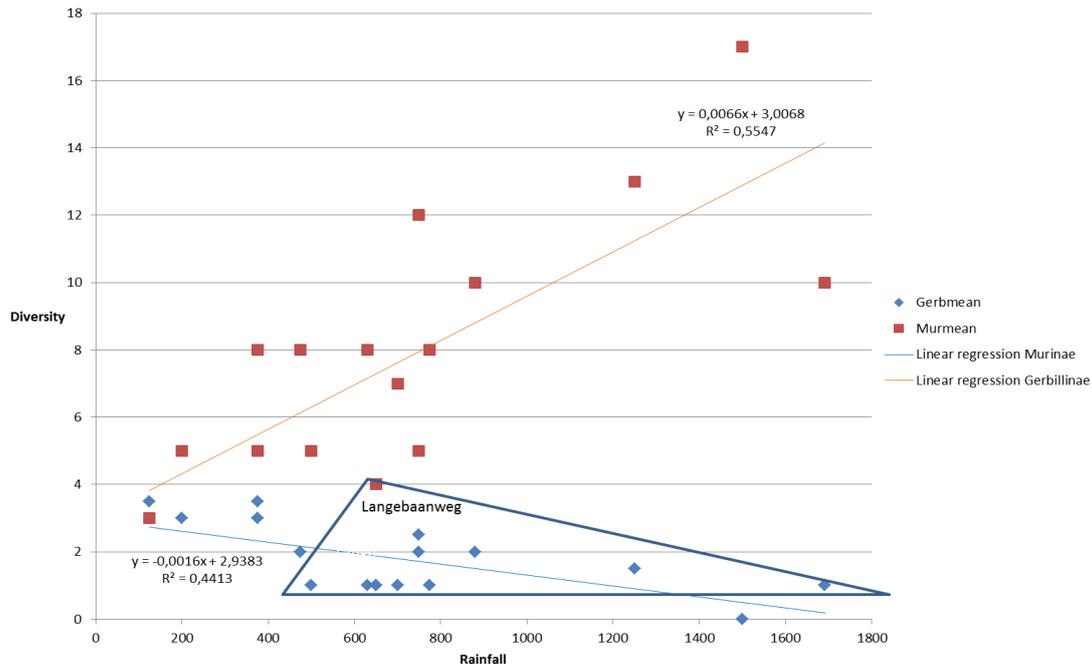
Figure 10. Correlations between rainfall and gerbillinae vs Murinae diversity in tropical Africa (after Denys, 1999). The blue triangle indicates the position of Langebaanweg on this graph. Gerbmean: Average value for number of Gerbillinae species for different sites in function of the level of pluviometry, Murmean: Average value for Murinae species per level of pluviometry from the literature.

earliest fossil appearance of a gerbil (*Abudhabia*) in China (10 Myr). Because it is now well supported by molecular analyses that Gerbillinae belong to Muridae, Denys & Winkler (2015) suggested that *Leakeymys ternani* (Lavocat, 1964), which is dated to around 14 Myr, could be an ancestor of modern Gerbillinae rather than Miocene Myocricetodontinae. *Leakeymys ternani* is very modern in appearance and exhibits none of the features of *Abudhabia*. *Leakeymys ternani* has no posterior cingulum on the m1, a small anteroconid, and well fused cusps on the upper first laminae of M1. It shows only an antero-external cusp on the m2. Its relationship with late Miocene gerbils still needs clarification.

Desmodillus magnus, *Abudhabia tateroides* and *Abudhabia* sp. all lived at approximately the same time intervals (6.1 to 5.8 Myr (Lukeino), 5.23 Myr (Lothagam), 5.1 Myr (Langebaanweg) and may be members of the same clade and represent sister taxa that diverged at around 8 Myr. Because it has been shown that East and South African faunas evolved in separate biogeographic regions during the lower Pliocene we can assume a vicariance event (occurring around 6-5 Myr during the Messinian salinity crisis which led to the evolution of *Gerbilliscus* and *Taterillus* in East Africa, and modern *Desmodillus* in South Africa (Denys, 1999). In Pakistan and Arabia, *Abudhabia radinksy* is probably the ancestor of the modern *Tatera indica* Hardwicke, 1807 (Flynn *et al.,* 2003) while in East Africa, *Abudhabia tateroides* may be the ancestor of *Gerbilliscus* in Africa. *Abudhabia* sp. from Lothagam probably belongs to *A. tateroides*. Further revisions of the genus *Abudhabia* are needed to test its paraphyly. In South Africa, *D. magnus* has some common, shared characters with *D. auricularis*, which include characteristics of the teeth and maxilla, molar prelobes, and the posterior sinus of the M1. *Desmodillus magnus* also exhibits some primitive characters such as alternating cusps, less individualised cusps of the first lobe of M1, and traces of a posterior cingulum incorporated

(not isolated) into the distal wall on the m1. Between *D. auricularis* and *D. magnus* a size reduction of the molars has occurred – an event which does not necessarily imply skull size reduction. In fact, in modern *D. auricularis* the development of large tympanic bullae which is probably an adaptation to an open arid environment (Yazdi *et al.*, 2015) may affect the size of the molars (Monadjem *et al.*, 2015). This hypothesis needs now to be tested by using a developmental approach. When looking at the ratio between upper tooth row length (LS13) and greatest length of the skull (GLS), *D. auricularis* has a low index value of LS13/GLS of 0.12 (0.11 - 0.14) against *Gerbilliscus* (*Gerbillurus*) (Mean=0.14; 0.122 - 0.156) or *Gerbilliscus* (*Tatera*) (Mean = 0.154; 0.14 - 0.172). *Desmodillus auricularis* is today classified as a microdont (see definition in Monadjem *et al.*, 2015). The adaptions of this taxon may be related to its particular ecological niche, or competition with other successful *Gerbilliscus* representatives that invaded South Africa later. No complete skull of *D. magnus* is available to compare the proportion of its molars respective to the skull length and the development of the tympanic bullae and cannot thus be commented on.

PALEOENVIRONMENTAL AND PALEOBIOGEOGRAPHICAL IMPLICATIONS

Today *D. auricularis* is associated with dry habitats. The IUCN (2014) describes its habitat as being arid gravel plains and areas of hardened sand; it is absent from high, soft dune sand areas (Stuart & Stuart, 2001; IUCN, 2014). It occurs throughout the South West Arid Zone, extending into the Southern Savanna and South West Cape biotic zones (Rautenbach, 1978; De Graaff, 1981; Monadjem *et al.*, 2015) where annual rainfall does not exceed 250mm/year. *Desmodillus auricularis* is graminivorous and its diet consists mainly of seeds, predominantly grass

seeds (Stuart & Stuart, 2001; Skinner & Chimimba, 2005). *Desmodillus auricularis* makes burrows in fine soils in sparse grass or shrub cover.

The majority of micromammals at Langebaanweg appear to have been deposited through the agency of a predator; Matthews (2004) found that 66-92 % of murid incisors in the larger LQSM micromammal units, and just over half of the incisors from the MPPM assemblages, showed signs of digestion, thereby indicating that they had been deposited in a scat or pellet. The spotted eagle ((*Bubo africanus*) (Temminck, 1821)) and barn owls ((*Tyto alba*) (Scopoli, 1769)) are among the most frequent agents responsible for fossil microfaunal accumulations, particularly in cave sites (Andrews, 1990; Matthews *et al.*, 2009, 2011). They hunt in open environments and have ranges which may vary from 400 m to 3 km (Andrews, 1990; Avery, 1992) from the roost site. In a study done in Namibia, *D. auricularis* made up ~14% of the micromammal taxa taken by *Tyto alba* (Avery, 1986), although this varies between sites. In another study a barn owl roost site from the Western Cape indicated that *G. (Tatera) afra* made up 60 % of prey items taken (Avery, 2005). Avery (1986) notes that there is some evidence that an owl hunting in an area will focus on one particular gerbil species, although other gerbillid taxa are available. *Desmodillus auricularis* is nocturnal and terrestrial in habits, and, as gerbillines are a favoured prey item of owls, would have been taken by these bird taxa which were present at Langebaanweg (Manegold *et al.,* 2013; Pavia *et al.,* 2015). It has also been demonstrated that some viverrids such as the small grey (*Galerella pulverenta* (Wagner, 1839)) or large grey (*Herpestes ichneumon* (Linnaeus, 1758)) mongoose, genet species such as *Genetta genetta* (Linnaeus, 1758) or *Genetta tigrina* (Schreber, 1776), and felid species such as *Caracal caracal* (Schreber, 1776) or *Felis lybica* (Forster 1780) include rodents in their diet (Stuart & Stuart, 2001). Ancestors of these taxa were also present at Langebaanweg and may have contributed to the micromammal fossil assemblages. *Desmodillus magnus* indicates the presence of open, dry areas at Langebaanweg. This is corroborated by the bird fauna which contains taxa indicative of dry open grasslands, savannah and/or arid habitats (Manegold *et al.,* 2013). Other rodent taxa found at Langebaanweg indicated the presence of swamps, wet environments, and some rocky areas and savanna woodland (Denys, 1990a, b, 1991, 1994, 1998; Matthews *et al.*, 2007).

Denys (1999) introduced the Gerbillinae/Murinae ratio as a palaeoecological index for quantifying vegetation cover and rainfall for tropical Africa. The ratio of Murinae to Gerbillinae has thus been used as an indicator of aridity by several authors as the number of gerbillines are known to increase, and the number of Murinae decrease, with an increase in aridity (Denys, 1997, 1999; Fernandez-Jalvo *et al.*, 1998). An update on the faunal list of Langebaanweg suggests one gerbilline for at least 4 murine species. Because there are linear relationships between diversity and rainfall we have calculated an estimate for Langebaanweg. Based upon the presence of a single gerbil, rainfall is indicated at between 500 and 1600 mm per year, which implies less aridity at 5 Myr than today (Fig. 10). This is corroborated by the frog fauna from Langebaanweg, which has provided the first direct proxy for rainfall at the site. Matthews *et al.* (2015) note that rainfall appears to have been substantially higher than today as approximately 18 fossil frog taxa have been identified to date at Langebaanweg. Such a high diversity of frog species is currently found in southern Africa only in areas of high rainfall (900 mm per year) (Du Preez & Carruthers, 2009), although it is obviously not possible to make a direct comparison between the number of taxa and rainfall given the many variables and factors involved. The frog fauna does however indicate a high rainfall, which concurs with the fact that only one gerbil species is found at Langebaanweg.

CONCLUSION

The new gerbil species from Langebaanweg is the oldest representative of the genus *Desmodillus* in Africa and retains some primitive characters. *Desmodillus magnus* resembles *D. auricularis* in terms of dentition and shape of the zygomatic plate, but is quite a bit larger than the relatively small, extant species. This gerbil contributes new information on the evolution of the subfamily during the early Pliocene. Contrary to previous claims the evidence presented here indicates that *Desmodillus magnus* cannot be considered as the ancestor of *Gerbilliscus*, but possibly represents the sister taxon of, and is very close to, *A. tateroides*. This suggests that they have both diverged subsequent to 6 Myr to give rise to the different modern Gerbillinae tribes.

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