Tiny Tenrecomorpha (Mammalia) from the Eocene of Black Crow, Namibia

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Abstract: The 2019 campaign of acid treatment of Eocene freshwater limestone from Black Crow, Namibia, resulted in the recovery of a minuscule mandible of an insectivoran-grade mammal representing a new genus and species of Tenrecomorpha. The specimen is the smallest mammal described from the fossil record from Africa. From the incisor alveoli to the rear end of the angle, the jaw measures a mere 8.6 mm. The jaw is relatively complete, but has lost the incisors, canine and p/2. It shows several characters that link it to the suborder Tenrecomorpha. In some morphological features it recalls Tenrecidae, in others Potamogalidae. The new genus and species throws doubt on the homogeneity of the order Afroinsectiphilia, which in its turn renders doubtful the concept of Afrotheria as currently understood.

Key words: Tenrec, Ypresian/Lutetian, Mandible, Namibia

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Introduction

This paper is devoted to the description and interpretation of a minuscule mammalian mandible from the middle Eocene limestones at Black Crow, Namibia. The freshwater limestone at Black Crow in the Sperrgebiet, Namibia, first yielded vertebrate fossils a decade ago (Pickford et al. 2008a, 2008b). The primitive aspect of the arsinoithere (*Namatherium*) and the hyracoid (*Namahyrax*) from the site suggested an age significantly older than any of the Fayum, Egypt, deposits (Pickford et al. 2014; Pickford, 2015a) an inference borne out by subsequent studies of the small and medium-sized mammals (Mein & Pickford, 2018; Morales & Pickford, 2018; Pickford, 2018b, c, d, e, f).

Each year the Namibia Palaeontology Expedition has visited the locality to search for blocks of limestone showing the presence of bones and teeth on their surfaces and these have been developed in the laboratory to extract the fossils. During 2019, as a blind test, the NPE decided to treat 150 kg of limestone that showed no signs of fossils on the surfaces of the blocks. The exercise was a success, with the recovery of several significant fossils including an adult mandible of Namahyrax corvus, several maxillae and mandible fragments of tenrecoids and chrysochlorids, along with over 110 crocodile teeth, several scincid jaws and vertebrae, bird postcranial bones, gastropod steinkerns and fruits of the Hackberry, Celtis (Pickford, 2018g).

Geological context

The geological context and age of the freshwater limestone at Black Crow have been mentioned on several occasions (Pickford *et al.* 2008a, 2014, 2015a). In brief, the locality comprises a small, shallow basin eroded into PreCambrian dolomites and infilled by a series of well-bedded limestone layers (probably of carbonatitic ash origin) overlain by freshwater limestone that accumulated in a low-energy aquatic environment in which plants were growing, probably a shallow swamp or a

sluggish backwater in a slow-flowing river (Fig. 1). The dominant gastropods in the limestone are landsnails of the genus *Dorcasia* (an indicator of a summer rainfall climatic regime, contrasting with the present day winter rainfall regime of the Sperrgebiet) and an elongated small subuliniform snail. No freshwater snails are known from this site. There are many small crocodile teeth in the deposits and freshwater fish teeth are quite common, although none were found in the 2019 sample.



Figure 1. Geological sketch map of the freshwater limestone outcrops at Black Crow, Sperrgebiet, Namibia, showing the locality from which the limestone blocks discussed in this paper were collected (large black arrow).

Material and methods

150 kg of limestone were collected from Black Crow (Fig. 1) and delivered to the laboratory in Paris for acid treatment. The blocks were bathed in formic acid (7%) without buffer (previous attempts to use calcium triphosphate buffer resulted in a precipitate covering the fossils which rendered it difficult to pick out from the insoluble residue and almost impossible to clean without damaging the fossils). Once the fossils had been released from the limestone they were washed in fresh water for 24 hours, dried and then consolidated with a solution of plexigum dissolved in acetone. Images were obtained using a Sony Cybershot camera by placing the lense over the eyepieces of a stereo microscope and treating the images with Photoshop Elements15 to increase contrast and remove unwanted background. Scales were added manually.

Abbreviations

BC - Black Crow
DPC - Duke Primate Center
GSN - Geological Survey of Namibia, Windhoek
TM - Transvaal Museum (now the Ditsong National Museum of Natural History), Pretoria

Systematic Palaeontology

Suborder Tenrecomorpha Butler, 1972

Genus Nanogale nov.

Diagnosis: Minute tenrecomorph with mandibular foramen in a very posterior position close to the termination of the angle of the jaw. Clear separation between the lingual and buccal parts of the alveolar process distal to the tooth row, the coronoid part rising at an angle of ca 70° , the lingual part (endocoronoid crest) extending horizontally and forming a strong lingual wall for a deep coronoid fossa. Mandibular condyle low down, in line with the cheek teeth. Mental foramen beneath the p/3.

Etymology: The genus name is a combination of the Greek word 'nano' in reference to the its tiny dimensions, linked to the word 'gale' Lower permanent dental formula 3-1-3-3. Smaller than *Eochrysochloris* Seiffert *et al.* 2007, *Dilambdogale* Seiffert (2010), *Jawharia* Seiffert *et al.* (2007), *Qatranilestes* Seiffert (2010), *Widanelfarasia* Seiffert & Simons (2000), *Namagale* Pickford, (2015b), *Sperrgale* Pickford (2015b), *Arenagale* Pickford (2015b); *Protenrec* Butler & Hopwood (1957), *Erythrozootes* Butler & Hopwood (1957) and *Promicrogale* Pickford (2018a).

meaning 'weasel', a suffix commonly used when naming potamogalids, tenrecids, other insectivorans and small carnivores.

Type species Nanogale fragilis nov.

Diagnosis: As for genus. Length of mandible from incisor alveoli to angle ca 8.6 mm; length m/1+m/2+m/3 = 2.29 mm.

Etymology: The species name refers to the extremely fragile nature of the specimen referred to it.

Holotype: GSN BC 3'19, left mandible containing p/3-m/3 and alveoli of i/1-i/3, c/1 and two alveoli of p/2.

Description

The mandible of Nonogale fragilis possesss some peculiar characteristics, among which figures a deeply concave coronoid fossa bordered lingually by a strong mandibular buttress, the endocoronoid crest (Seiffert et al. 2007). The sheet of bone between the coronoid process and the condylar process is reduced to a low wall on the lateral side of the coronoid fossa, expanding slightly as it approaches the condyle. This part of the mandible superficially resembles the morphology in *Dasypus hybridus* (Abba & Superina, 2016) but the rest of the jaw and the teeth of the two genera are completely different. The mandibular foramen is positioned close to the posterior end of the jaw and lower than the tooth row. Unlike most mammals, the lingual and buccal parts of the alveolar process do not coalesce distal to the m/3, but the buccal

part rises at an angle of ca 70° to form the coronoid process, while the lingual part extends directly distally as a strong ridge, the endocoronoid crest, which forms the lingual wall of the deep coronoid fossa and terminating distally as the condylar process.

The ramus is long, slender and shallow. In lingual view, the ventral margin of the ramus is observed to be gently curved, deepest beneath the molars and rising gently anteriorly and posteriorly where it flexes gently ventrally towards the posterior end of the angle (Fig. 2, 3). The symphysis is unfused and short, ending beneath the canine alveolus. It has an elongated central depression. The alveolar margin is straight from m/3 to p/3 then rises gently towards the incisors. The endocoronoid crest is a straight horizontal bony ridge behind the m/3 which extends posteriorly towards the condyle, forming the lingual wall at the base of the coronoid fossa. The condyle is at the same level as the occlusal surface of the cheek teeth. The mandibular foramen opens far back in the reentrant between the condylar process above and the posterior end of the angle below (Fig. 4). As such it is well beneath the level of the alveolar process and the mandibular canal courses in almost a straight line from its origin at the foramen to the level of the p/3. The angle of the jaw itself is short and slightly recurved medially.



Figure 2. Stereo lingual view of GSN BC 3'19, mandible of *Nanogale fragilis*, after repair. The coronoid process is slightly out of position. Note the groove in the symphyseal surface and the extremely low and posterior position of the mandibular foramen (scale : 5 mm).

In lateral view, the coronoid process is seen to rise well behind the m/3 at an angle of about 70° (Fig. 3, 5, 6). Posterior to the coronoid process there is a large space bordered ventrally by the thin lateral margin of the coronoid fossa. The edge of the thin bone forming the lateral margin of the coronoid fossa descends gently from the base of the coronoid process then rises gently as it approaches the condyle to form a lamina of bone which then curves in the opposite sense before blending into the condylar process near the distal end of the jaw. There is a single mental foramen, opening at mid-height of the ramus between the roots of the p/3.

In dorsal view the entire jaw is remarkably straight (Fig. 6, 7).



Figure 3. Stereo image of the buccal side of GSN 3'19, left mandible of *Nanogale fragilis* with the coronoid process in position prior to breaking off (scale : 5 mm).



Figure 4. Stereo images of the posterior part of GSN BC 3'19, holotype left mandible of *Nanogale fragilis* gen. et sp. nov. from Black Crow, Namibia. A) buccal view, B) occlusal view, C) lingual view to show details of the condylar process, the angle and the posteriorly situated mandibular foramen. 1 - base of the coronoid process, 2 - coronoid fossa, 3 - mandibular foramen (scale : 1 mm).

There are three procumbent incisor alveoli but they are damaged ventrally, the one for the second incisor is seemingly slightly bigger than those for the i/1 and the i/3. The canine alveolus is close behind that of the i/3 and is ovoid in outline with a slight undulation on the lingual side suggesting that the root of the tooth possessed a shallow longitudinal groove. This alveolus slants disto-ventrally. There is a short diastema behind the canine alveolus followed by two alveoli close together which slope distoventrally, sub-parallel to the alveolus of the canine. These alveoli are interpreted to correspond to a two-rooted p/2 rather than representing alveoli for single-rooted p/1 and p/2. The diastema behind the alveolus for the p/2 is somewhat longer than the one in front of it. The two roots of the p/3 are splayed apart, the anterior one slanting slightly antero-ventrally, the posterior one slightly disto-ventrally. The roots of the p/4 and the three molars are almost vertical.



Figure 5. Close-up stereo images of the anterior part of the ramus of GSN BC 3'19, the holotype mandible of *Nanogale fragilis* gen. et sp. nov. from Black Crow, Namibia, to show details of incisor and post-incisor alveoli. A) and B) buccal views (scale : 1 mm).

Table 1. Measurements (in mm) of GSN BC 3'19, the holotype mandible of *Nanogale fragilis* gen. et sp. nov. from Black Crow, Namibia.

Length of mandible from incisor alveoli to posterior end of angle	8.6
Greatest depth of ramus beneath m/2	0.8
Depth of ramus beneath p/3	0.6
Distance from rear of m/3 to posterior end of angle	2.63
Length p/3 to m/3	3.45
Length p/4	0.70
Length m/1	0.73
Length m/2	0.78
Length m/3	0.78

There are three incisor alveoli, but the teeth are missing. Judging from the remnants of the alveoli, the i/2 was probably slightly larger than the i/1 and i/3.

The canine is single-rooted and much larger than the incisors. Its root and the two roots of the p/2 descend disto-ventrally into the ramus.

The p/2 was a two-rooted tooth with the roots sub-parallel to each other and close together, but not coalescent. The p/3 is damaged by corrosion, but it is possible to infer that it was significantly smaller than the p/4.



Figure 6. Close-up stereo images of the cheek teeth of GSN BC 3'19, the holotype mandible of *Nanogale fragilis* gen. et sp. nov. from Black Crow, Namibia. A) occlusal view, B) lingual view, C) buccal view (scale : 1 mm).

The crown of the p/3 is too corroded to provide any useful details of crown morphology, but it is possible to surmise that it was appreciably smaller than the p/4 and that it has two roots. It is separated from the p/4 by a short gap, but this could be due to the loss of the talonid of the tooth rather than signifying the presence of a diastema between the two teeth.

The p/4 is molariform, but with the trigonid less well-defined and more bucco-lingually compressed than in the molars. The paraconid is low and projects anteriorly, the metaconid is tall, being only slightly lower than the protoconid and slightly behind it. The precingulid slopes downwards gently towards the buccal side of the tooth. The talonid is very low and positioned more towards the buccal side of the midline of the tooth.

The m/1 is a larger version of the p/4, but with the trigonid more inflated bucco-lingually. The postprotocristid is slightly oblique extending disto-lingually at a small angle towards the premetacristid. The paraconid is about half the height of the protoconid and the metaconid is slightly lower than the protoconid and is positioned slightly behind it. There is a low-relief precingulid. The talonid is low and its hypoflexid is tilted slightly buccally.

The m/2 and m/3 are similar to each other and both are slightly larger than the m/1. The

precingulid is low down on the mesial edge of the tooth, well beneath the paraconid and protoconid. The paraconid and metaconid are subequal in dimensions and are 2/3rds the height of the protoconid and are well separated at their apices with a deep gulley between them on the lingual aspect of the crown representing the lingual opening of the trigonid basin. The postprotocristid and premetacristid form a transverse wall to the trigonid basin. The talonid is bucco-lingually narrow and the hypoflexid is relatively expansive comprising about half the occlusal area of the talonid. The hypoconulid is 1/3rd the height of the protoconid and the cristid obliqua slopes forwards and downwards towards the base of the metaconid and, as a result, the talonid basin is small and shallow.

Discussion

The mandible of *Nanogale fragilis* shows some peculiar features concentrated in the posterior part of the jaw. The coronoid fossa is deeply excavated and has a robust lingual wall and a thin, low lateral wall. The condylar process is low down, such that the condyle is at about the same level as the occlusal surface of the cheek teeth. The angular process is short and medially recurved and bends ventrally and between it and the condyle there is a prominent mandibular foramen which is located below the level of the tooth row. The mandibular canal runs directly anteriorly, emerging at a mental foramen between the roots of the p/3.



Figure 7. Interpretive sketch of GSN BC 3'19, the holotype left mandible of *Nanogale fragilis* from the Eocene limestone at Black Crow, Namibia. A) buccal, B) occlusal, C) lingual views (scale : 5 mm).

There are three procumbent incisors, a slanting canine, the p/1 is absent and the p/2 has two sub-parallel roots which are inclined ventro-distally in the ramus. The canine is separated from the incisors and the p/2 by short diastemata and there is another diastema between the p/2 and p/3.

The molars of *Nanogale fragilis* have prominent trigonids and somewhat reduced and low talonids, which are slightly bucco-lingually compressed.

Comparison of this jaw with those of various mammals is a challenge. Many of the fossil afrosoricid mandibles described do not preserve the distal parts of the jaw. The post-dental part of the jaw of *Nanogale* differs from the corresponding part of mandibles of many tenrecoids and potamogalids, as well as those of most other mammals. The dentition, however, most closely recalls those of tenrecomorphs.

For this reason, *Nanogale* is included in the Tenrecomorpha, but with the understanding that it is a peculiar member of the suborder. Whether it is closer to Tenrecidae or to Potamogalidae is a moot point, with the balance slightly in favour of it being a tenrecid.

Nanogale differs from *Todralestes* Gheerbrant (1991) by the short retromolar space and the steeper coronoid process in the latter genus. It is also smaller (length m/1-m/3 in *Todralestes variabilis* is 3.9 mm, in *Nanogale fragilis* it is 2.9 mm).

There are some dental similarities between *Eochrysochloris* Seiffert *et al.* (2007) and *Nanogale fragilis* but the latter genus is considerably smaller and the talonids of the molars are more bucco-lingually compressed such that the cristid obliqua is positioned lingual to the midline of the crown, unlike the situation in *Eochrysochloris* in which it is largely buccal of the midline of the tooth. The distal part of the jaw is unknown in *Eochrysochloris*, so no comparisons can be made.

Dilambdogale Seiffert (2010) from the Fayum, Egypt, is much larger than *Nanogale*. The morphology of the jaw in the vicinty of the coronoid process is different, in particular concerning the presence of a deep masseteric fossa in *Dilambdogale* (only the base is preserved in DPC 23783B, from BQ-2, Birket Qarun Formation, Fayum, Egypt). Both the Namibian and Egyptian jaws have long retromolar spaces between the m/3 and the base of the coronoid process. The talonids of the m/2 and m/3 in *Dilambdogale* appear to be taller

relative to trigonid height than they are in *Nanogale*.

Jawharia Seiffert et al. (2007) from Quarry E, Jebel Qatrani Formation, Egypt, is larger than Nanogale. The rear of the mandible of Jawharia is almost complete and it reveals major differences from that of Nanogale. In Jawharia there is a sheet of bone between the coronoid process and the condylar process on the lateral surface of which is a well-developed masseter fossa. The corresponding area is devoid of a sheet of bone in Nanogale. The mandibular condyle is slightly above the level of the tooth row in Jawharia but is lower in Nanogale. Finally, the coronoid fossa in Jawharia is shallow, whereas in Nanogale it is deep and is bordered by a robust lingual ridge, the endocoronoid crest.

Qatranilestes Seiffert (2010) from Quarry L, Jebel Qatrani Formation, Egypt, is larger than *Nanogale*. Poorly known due to the fragmentary nature of the available sample, it is difficult to make detailed comparisons, but it is noted that it also has a long retromolar space.

Widanelfarasia Seiffert & Simons (2000) from the Jebel Qatrani Formation, Egypt, is larger than *Nanogale* and the trigonids in the lower molars are more mesio-distally compressed, with the paraconid closer to the metaconid than in *Nanogale*. The protoconid of p/4 is appreciably taller relative to tooth length in *Widanelfarasia* than it is in *Nanogale*.

Nanogale differs from Namagale Pickford (2015b) by its considerably smaller dimensions. The rear of the jaws are morphologically divergent, with Namagale from Eocliff possessing a well-developed sheet of bone between the coronoid process and the condylar process with a shallow masseteric fossa on its lateral aspect. Namagale has an exceedingly shallow coronoid fossa, unlike the deep and capacious fossa that occurs in Nanogale. The mandibular condyle is missing in the *Namagale* sample but it was at about the same level as the occlusal surface of the cheek teeth and thus higher than it is in Nanogale. The molar talonids of *Namagale* are broader bucco-lingually than those of Nanogale.

Sperrgale Pickford (2015b) is slightly larger than *Nanogale*. The rear of the jaw in *Sperrgale* is well-represented and it shows a number of differences from that of *Nanogale*. The mandibular condyle is above the level of the cheek teeth in *Sperrgale*, below it in *Nanogale*. There is a clear masseteric fossa and a shallow

coronoid fossa in *Sperrgale* and interestingly, the sheet of bone between the coronoid process and the condylar process is quite small, but not nearly as reduced as it is in *Nanogale*. There is a strong bony margin to the coronoid fossa in *Sperrgale*, as in *Nanogale*, but the fossa is not as deeply excavated. Like *Sperrgale*, there is no p/1 in *Nanogale*, but the mental foramen is beneath the p/2 rather than the p/3. The mandibular foramen is at the same level as the cheek teeth in *Sperrgale*, but is lower than them in *Nanogale*. However, of all the fossil tenrecomorphs described, *Sperrgale* is closest morphologically to *Nanogale*.

The mandible of *Arenagale* Pickford (2015b) is rather poorly represented, so comparisons with *Nanogale* are limited to the lower dentition. The talonids of the lower molars of *Arenagale* are almost as broad bucco-lingually as the trigonids unlike the narrower talonids in *Nanogale*. *Arenagale* is the smallest of the Eocliff tenrecomorphs, but it is larger than *Nanogale*, which is currently the smallest known fossil representative of the suborder Tenrecomorpha.

Protenrec Butler & Hopwood (1957) from the early Miocene of Songhor, Kenya, is appreciably larger than Nanogale (length m/1m/3 is 4.9 mm in Protenrec versus 2.9 mm in Nanogale). Protenrec resembles Nanogale in the low position of the mandibular foramen and the presence of an endocoronoid crest (albeit much weaker) but it differs from it by the somewhat more anteriorly positioned mandibular foramen, by the presence of a welldeveloped sheet of bone between the coronoid process and the condylar process, by the shallow coronoid fossa and by the presence of a mental foramen beneath the m/1 (Butler & Hopwood, 1957; Butler, 1984). The lower molars of Protenrec are comparable in morphology to those of Nanogale with the talonid somewhat narrower bucco-lingually than the trigonid.

Erythrozootzes Butler & Hopwood (1957) from the early Miocene of Kenya and Uganda, is much larger than *Nanogale*. The retromolar space is relatively short in *Erythrozootes* and the coronoid process rises at a steeper angle than in *Nanogale*.

Nanogale differs from *Promicrogale* Pickford (2018a) from the basal Miocene of Elisabethfeld, Namibia, by its slightly smaller dimensions (the length of m/1-m/3 in *Promicrogale* is 3.2 mm) by the lack of diastemata between the canine, the p/2 and p/3. The symphysis in *Promicrogale* is elongated, terminating posteriorly at the level of the anterior root of the p/4, and its surface is corrugated, unlike the short, relatively smooth symphyseal surface in Nanogale which ends beneath the root of the canine (indistinctly it must be admitted). The posterior part of the jaw of *Promicrogale* curves more steeply upwards behind the m/3 but the distal part is broken off. However, what remains suggests that the condyle would have been at about the level of the occlusal surface of the cheek teeth or slightly above it, because the entocoronoid crest rises dorso-posteriorly rather than running horizontally as in Nanogale. The paraconid and metaconid in the molars of Promicrogale are taller relative to the protoconid than in Nanogale.

Comparisons with extant tenrecs reveals several similarities in the dentition to forms such as Microgale, but few in details of the rear of the mandible. Like Nanogale, in Microgale the mental foramen lies beneath the p/3, there is no p/1, the p/2 has two roots that are inclined in the jaw and the symphysis is unfused. Microgale has a coronoid fossa bordered lingually by a ridge of bone that terminates distally as the condylar process, but the fossa is shallower than in Nanogale, and there is a sheet of bone between the coronoid process and the condylar process. Furthermore, in Microgale, the posterior part of the jaw bends upwards at the level of the m/3 which makes the coronoid process steeper, and lifts the mandibular condyle upwards so that it is above the occlusal surface of the cheek teeth. Thus, even though Nanogale has some dental resemblances to *Microgale*, its mandible is divergent, especially the posterior part.

Comparisons between the mandibles of potamogalids and *Nanogale* reveal few similarities except in the low positions of the condyle, the mandibular foramen and the angle. In *Potamogale* the coronoid process is almost vertical, the distal part of the jaw has a well-developed sheet of bone between the coronoid process and the condylar process, the condyle is at the same level as the occlusal surface of the cheek teeth, and there is a greater distance between the condyle and the angle, all of which are different from the condition in *Nanogale*. Furthermore, in *Potamogale* there is a mental foramen beneath the p/2 in addition to the ones beneath the p/3 and m/1.

An almost complete micromammalian mandible from the middle Eocene Black Crow limestone, Namibia, is interpeted to belong to a new genus and species of Tenrecomorpha, herein named *Nanogale fragilis*. The fossil jaw shows several peculiar features including a large and deep coronoid fossa bordered lingually by a well-developed endocoronoid crest but the sheet of bone between the coronoid process and the condylar process is low, only increasing in height as it approaches the condyle. The condyle is low down, below the level of the occlusal surface of the cheek teeth and the mandibular foramen is far back.

Despite these differences from mandibles of Tenrecomorpha, the dentition of *Nanogale* shows affinities with some members of this suborder, especially *Microgale* and to some extent *Protenrec*. The permanent lower dental formula is the same as that of *Microgale* (3, 1, 3, 3) and the p/2 is two-rooted, with the roots sub-parallel to each other and inclined in the jaw.

The most striking aspect of *Nanogale*, as its name implies, is its minuscule size. The entire jaw is a mere 8.6 mm long. This is as small as the lower jaw of a female *Suncus orangiae orangiae* (T.M. 2564 from Bothaville, Orange

Free State, in Roberts, 1951) one of the smallest extant non-chiropteran African mammals.

No attempt is made to discuss the phylogenetic relationships of the new genus, *Nanogale*, partly because only the mandible is currently known and partly because many recent phylogenetic analyses of Afrotheria seem to be incompatible with each other (Asher, 2001; Seiffert *et al.* 2007). Most of them are heavily biassed towards molecular evidence and the few analyses that include fossils rely on fragmentary specimens which yield only a few characters, some of which are of doubtful value for phylogeny reconstruction.

The focus needs to be on the recovery of additional fossil material in an effort to obtain improved evidence of Palaeogene mammalian diversity rather than producing phenograms that obscure relationships rather than clarifying them.

The lower jaw of *Nanogale fragilis* is morphologically remote from those of Paenaungulata and many Tenrecomorpha (Afroinsectiphilia) to the extent of throwing doubt on the hypothesised homogeneity of the Superorder Afrotheria (Stanhope *et al.* 1998). This conclusion agrees with the results of the analysis by Averianov & Lopatin (2016).

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