Reithroparamyine rodent from the Eocene of Namibia

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Abstract: The freshwater limestone deposits at Black Crow, Tsau//Khaeb National Park (Sperrgebiet) Namibia, have yielded a diverse fauna of invertebrates and vertebrates. Rodents are relatively rare and of low diversity, but include two taxa of Zegdoumyidae and a brachyodont form close to Reithroparamyinae, in particular the genus *Reithroparamys*. If the identification is valid, then this would be the first record of the subfamily Reithroparamyinae (family Paramyidae) in Africa, and would indicate that Black Crow could be older (Ypresian-Early Lutetian) than previously thought (Middle Lutetian). The brachyodont rodent molar is the subject of this paper and an isolated P3/ and a calcaneum from the same lot of limestone is included to complete the description.

Key words: Rodentia; Ypresian/Lutetian; Namibia; Reithroparamyinae; Palaeobiogeography.

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Introduction

The freshwater limestone deposit at Black Crow, Namibia (Pickford *et al*. 2008a, 2008b) has yielded a variety of exquisitely fossilised continental invertebrates and vertebrates. Initial studies of the mammals from the locality indicated a mid-Lutetian age (Pickford *et al*. 2008b), but the possibility exists that the sediments could be older, either Early Lutetian or even Ypresian.

In order to resolve the uncertainties following debate about the age of the deposits (Coster *et al*. 2015; Marivaux *et al*. 2011, 2015, 2017; Seiffert 2010) additional blocks of limestone were collected from *in situ* outcrops. Many fossils were found, including over a hundred and seventy small crocodile teeth, a few characiform fish teeth, many amphisbaenian vertebrae and jaws, a few snake vertebrae, some vertebrae and jaws of Scincidae and a variety of small and medium-sized mammals including the isolated molar, premolar and calcaneum described herein, which were recovered in 2009.

Material and Methods

Limestone blocks were treated in 7% formic acid to digest out the fossils. Initially a calcium triphosphate buffer was used to limit degradation of bones and teeth, but it soon became evident that this led to the formation of an insoluble product that coated fossils and was extremely difficult to remove without damaging them. Tests without buffer led to much better results with little or no matrix left on the fossils, a consequence of which was that picking through the residue was much less time consuming. Once the fossils were free of matrix they were consolidated in glyptol dissolved in acetone, or were treated with cyano-acrylate (super glue).

Two isolated rodent teeth of primitive bunodont aspect were found in the insoluble residue and are labelled GSN BC Ni 1’09 and GSN BC Ni 2’09 respectively (GSN - Geological Survey of Namibia, BC - Black Crow). A calcaneum from the same lot of limestone is catalogued GSN BC Ni 3’09.

Images were taken with a Sony Cybershot camera placed over the lenses of a binocular microscope. By this means stereo images were obtained, which were then enhanced and prepared for publication using Photoshop Elements3.

Measurements were made with sliding calipers. The Black Crow fossils were compared with the following genera (Table 1) which have at one time or another been attributed to Reithroparamyidae (or Reithroparamyinae) by Wood 1962, Korth 1984 and Escarguel 1999.

Table 1. Genera of Reithroparamyinae (Paramyidae auct.) compared with the Namibian fossil, arranged in order of naming.

Genus	Author
Reithroparamys	Matthew 1920
Rapamys	Wilson 1940
Microparamys	Wood 1959
Tapomys	Wood 1962
Franimys	Wood 1962
Lophiparamys	Wood 1962
Sparnacomys	Hartenberger 1971
Pantrogna	Hartenberger 1971
Birbalomys	Sahni & Khare 1973
Acritoparamys	Korth 1984
Apatisciuravus	Korth 1984
Hartenbergeromys	Escarguel 1999

Geological and faunal context

The geological context of the Black Crow Carbonate has been described on several occasions (Pickford 2015; Pickford *et al*. 2008a, 2008b) and it is not necessary to repeat it here.

The fauna from the limestone comprises the following taxa (Table 2).

Table 2. Faunal list of the Black Crow limestones, Namibia.

Taxon	Fossils
Dorcasia	Many shells
Subulinoid	Poorly preserved shells
Pisces (Cichlidae)	Button-shaped teeth
Pisces (*Hydrocynus*)	Tooth
Pisces (Alestidae ?)	Tricuspid tooth
Amphibia (Pipidae)	Radio-ulna
Scincidae	Mandibles and post-cranial elements
Amphisbaenia	Vertebrae, mandibles, premaxilla, maxilla
Ophidea	Fang, vertebrae
Crocodylia	Maxilla fragment, teeth and vertebra
Aves	Indeterminate post-cranial elements
Namalestes gheerbranti	Isolated teeth and maxilla
Tiny zalambdodont	Mandible
Diamantochloris inconcessus	Lower molars, maxillary fragments with premolars and molars
Erinaceomorph	Isolated tooth
Pterodon sp.	Mandible
Proviverrinae	Deciduous tooth
Xenarthra ?	Phalanx
Namahyrax corvus	Skull, mandible, isolated teeth
Namatherium blackcrowense	Skull
Namaparamys inexpectatus	Isolated molar, premolar, calcaneum
Zegdoumys namibiensis	Upper molar
Tsaukhaebmys calcareus	Isolated teeth, mandible, post-cranial bones
Notnamaia bogenfelsi	Maxilla
Adapidae	Mandible, isolated teeth

The Black Crow Limestone is significantly older than the limestones at Silica North and Silica South, all of which were originally thought to represent diverse outcrops of a single widespread carbonate depositional phase that occurred during the Middle Eocene (Pickford *et al*. 2008a, 2008b). The Silica North and Silica South and some of the other freshwater limestones in the Sperrgebiet are now known to be considerably younger than the Black Crow deposit which is Lutetian, if not older (Ypresian/Lutetian). The younger suite of freshwater limestone deposits includes the rich occurrences at Eocliff and Eoridge which were discovered in 2013 and which have yielded rodents similar to those known from the Silica sites. Large mammals from Eoridge indicate a late Bartonian or early Priabonian correlation for this ensemble (Pickford 2015). The rodents from the younger set of limestone deposits is totally different from the Black Crow fauna, not only because it lacks zegdoumyids but also because it is dominated by ctenohystricans and phiomyids of which there are about a dozen taxa.

Dental nomenclature

The crown of the rodent molar (GSN BC Ni 1'09) described in this paper has four main cusps, considered to be the protoconid, metaconid, entoconid and hypoconid. It possesses transverse lophids and a longitudinal crest, two large occlusal basins (confluent trigonid + talonid basin and a posterior basin) and a deep buccal sinusid. Nomenclature is depicted in Fig. 1.

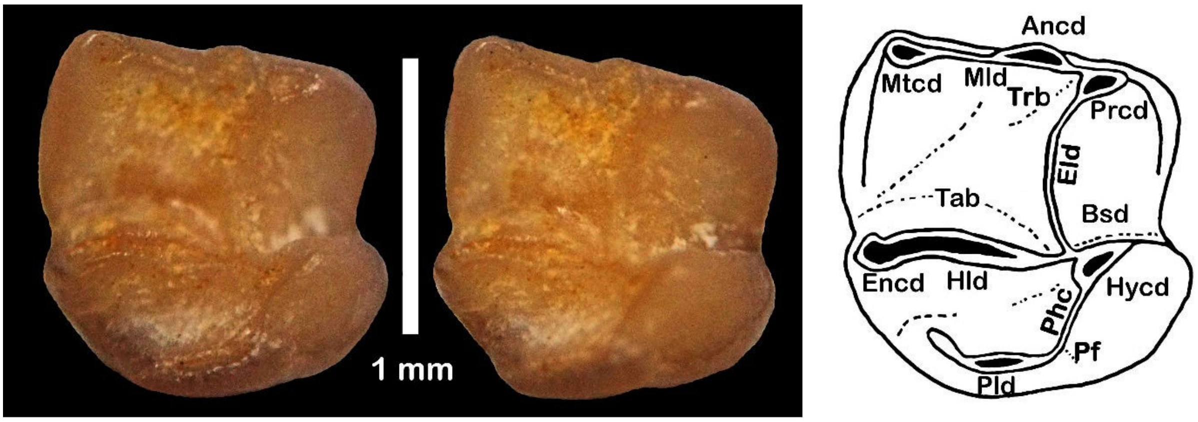

Figure 1. GSN BC Ni 1'09, right m/2, holotype of *Namaparamys inexpectatus*, gen. et sp. nov. from Black Crow, Namibia. Ancd - anteroconid, Bsd - buccal sinusid, Eld - ectolophid, Encd - entoconid, Hld - hypolophid, Hycd - hypoconid, Mld - metalophid, Mtcd - metaconid, Pf - posterior flexid, Phc – Post-hypoconidcristid, Pld - posterolophid, Prcd - protoconid, Tab - talonid basin, Trb - trigonid basin (scale : 1 mm).

Systematic Palaeontology

Order Rodentia Bowdich 1821

Family Paramyidae Miller & Gidley 1918

Subfamily Reithroparamyinae Wood 1962

Genus *Namaparamys* nov.

Diagnosis: Lower molar with four cuspids arranged in two lophids. The anterior lophid (metalophid) is straight and comprises the margin of the tooth which overhangs the anterior cingulum, but is not connected to it by cristids (visible in mesial view); the posterior lophid is bucco-lingually short and extends well to the rear of the lingual margin. A broad transverse valley separates the trigonid from the talonid. The molar has large cuspids, and relatively shallow valleys and weakly marked crests. Root of P3/ extremely tall. Three roots in m/2, small compared to the dimensions of the crown. Calcaneum «squirrel-like». *Namaparamys* resembles Reithroparamyinae but differs from other Paramyidae by the following characters :- the bunodont aspect of the cusps which occupy almost all the crown save for the broad horizontal valley, and the large size of the metaconid relative to the other main cusps.

Differential diagnosis: *Namaparamys* differs from most reithroparamyines (and ischyromyids) by its diminutive dimensions and by the metalophid in the m/2 overhanging the mesial cingulum but not connected to it by cristids.

Type species: *Namaparamys inexpectatus* nov.

Derivatio nominis: '*Nama*' for the Namib, meaning deserted waste land, '*Paramys*' a genus of paramyid rodent from North America ('*para*' close, '*mys*' mouse).

Species *Namaparamys inexpectatus* nov.

Diagnosis: as for the genus.

Holotype: GSN BC Ni 1'09, right m/2.

Other material: GSN BC Ni 2'09, P3/, and GSN BC Ni 3'09, left calcaneum, attributed to this genus on the basis that they were found in the same lot of limestone as the holotype.

Type locality: Black Crow, Namibia.

Age: Ypresian/Lutetian (Middle Eocene).

Derivatio nominis: '*inexpectatus'* Latin for '*unexpected'*.

Description

GSN BC Ni 1'09 is a lightly worn right m/2 (Fig. 1, 2). The crown is brachyodont, with prominent metaconid, protoconid, entoconid and hypoconid arranged in two lophids, the metaconid being joined to the protoconid by the metalophid, and the entoconid and hypoconid being joined by the hypolophid. In addition there is a weak anteroconid mesial to the metalophid, and there is a prominent postero-lophid linked to the hypoconid on its buccal end via the post-hypocristid, but not reaching the entoconid on the lingual side, leaving the posterior basin open lingually. Furthermore there is a mesio-distally oriented lophid, the ectolophid, which separates the buccal sinusid from the trigonid-talonid basin. The ectolophid links the protoconid to the hypoconid. The trigonid-talonid basin is large and opens lingually via a mesio-distally broad transverse valley.

The buccal surface of the post-hypocristid is slightly concave forming a shallow flexid.

The tooth measures 1.28 x 1.22 x 1.25 mm (mesio-distal length x breadth of anterior lophid x breadth of posterior lophid).

There are three roots, a small one beneath the protoconid, a slightly larger one beneath the metaconid, both of which are circular in section, whilst the third root is a compressed transversely broad column which supports the entoconid and hypoconid. The distal root slants distally.

In mesial view it is possible to discern a low mesial cingulum beneath the interstitial facet on the metalophid caused by wear against the m/1. This cingulum also shows interstitial wear against the m/1. The form of the interstitial facets, in which there are thin crests separated by broad depressions, indicates that chewing forces were predominantly in the vertical plane, with a minor medio-lateral component of movement. The relatively small vertical roots (Fig. 2 D) which are sensibly smaller than the crown indicate the same thing.

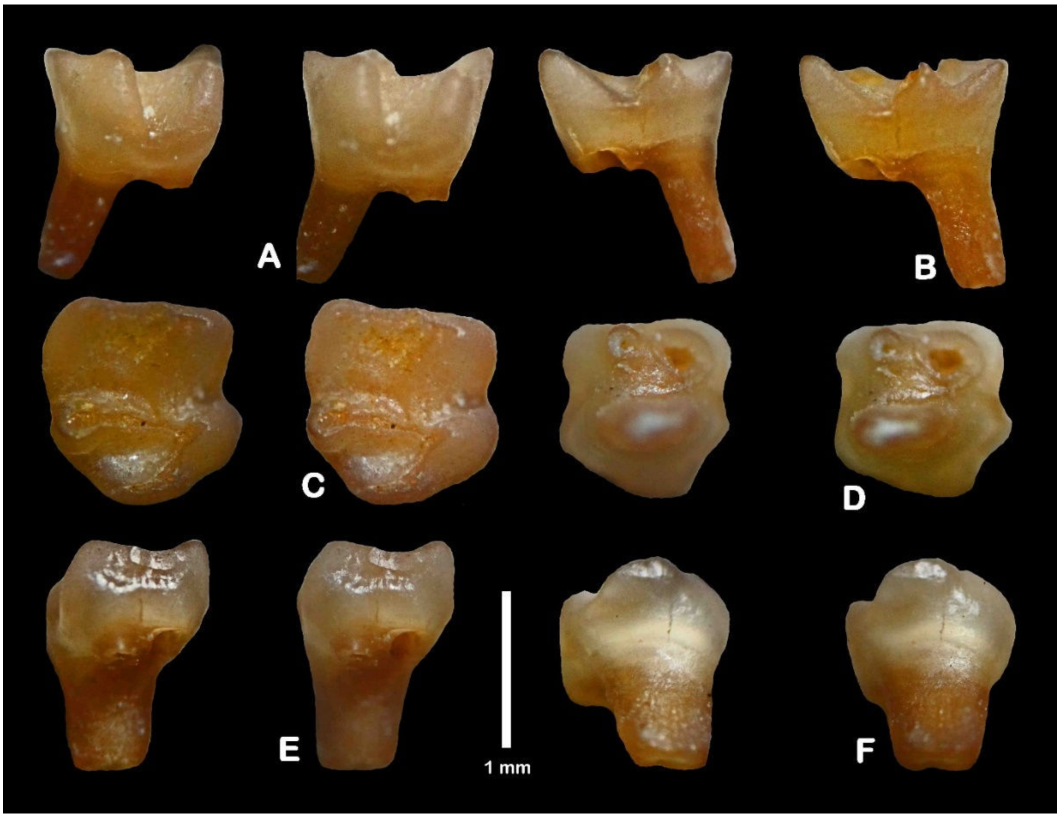

Figure 2. Stereo images of GSN BC Ni 1’09, holotype right m/2 of *Namaparamys inexpectatus* gen. et sp. nov. from Black Crow, Namibia. A) buccal, B) lingual, C) occlusal, D) radicular, E) mesial, and F) distal views (scale : 1 mm). Note the mesial and distal interstitial facets in E and F.

From the same lot of limestone as the molar described above, there is an isolated unicuspid premolar, which we interpret to be a P3/ (Fig. 3). The root is tall, slightly curved and has an apical bulge, suggesting the presence of a tall maxillary process above the gingival level. The crown is circular in occlusal outline, and almost hemispherical in shape with a large fossette (interpreted to be mesial) and accompanied by a smaller fovea near the apex. There is a clear wear facet caused by abrasion against its lower antagonist (Fig. 3-A1). The tooth is compatible in dimensions with the molar, but considering the presence of zegdoumyids at Black Crow, the specimen might belong to the latter family. We include it for the sake of completeness.

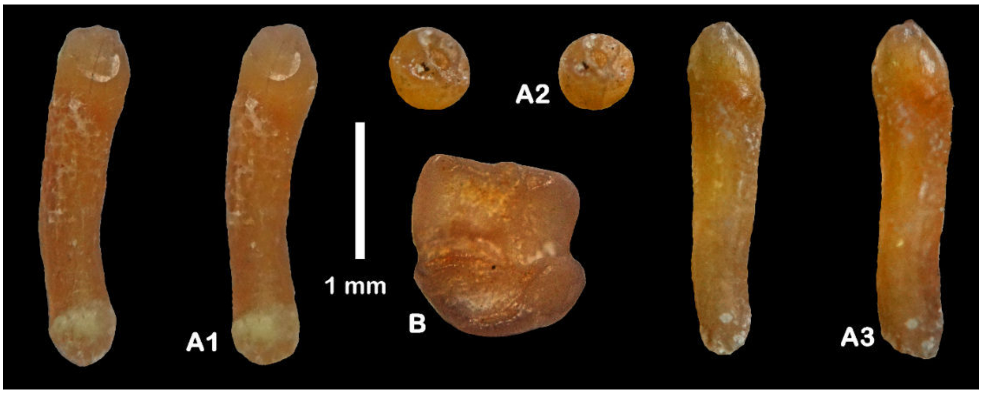

Figure 3. *Namaparamys inexpectatus* gen. et sp. nov. from Black Crow, Namibia. A) GSN Ni 2’09 isolated P3/ (A1 - stereo mesial, A2 - stereo occlusal and A3 - stereo distal views), B) GSN Ni 1’09, holotype right m/2, occlusal view at same scale as the P3/. Note the wear facet on the crown in image A1 caused by abrasion against its lower anatagonist (scale : 1 mm).

Post-cranial elements of Black Crow Reithroparamyinae

Calcaneum

A calcaneum was found in the same series of blocks that yielded the molar of *Namaparamys*, which is compatible in dimensions with this small rodent (Fig. 4, 5).

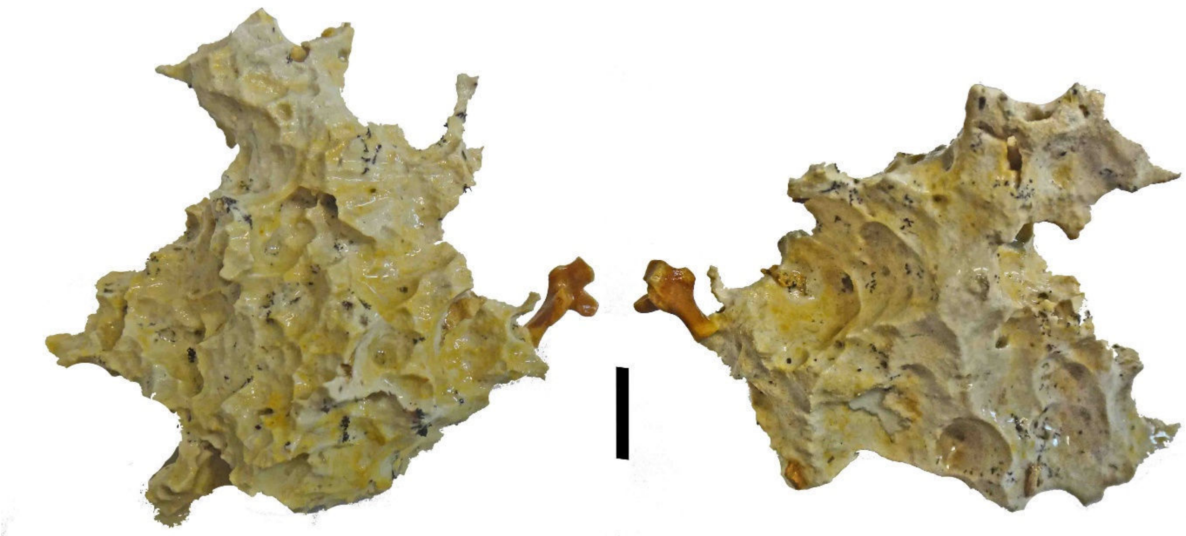

Figure 4. GSN BC Ni 3'09, 'squirrel-like' left calcaneum of a rodent in the process of being extracted from the Black Crow Limestone (scale : 10 mm).

Figure 5. Left calcanea attributed to A) GSN BC Ni 3'09, *Namaparamys inexpectatus* from Black Crow, Namibia, and B) *Nonanomalurus soniae* from Napak, Uganda (Early Miocene). (A1 - stereo lateral view, A2 - stereo dorsal view, A3 - stereo plantar view, B1 - medial view, B2 - lateral view, B3 - stereo dorsal view, B4 - stereo plantar view) (scales : 10 mm).

GSN BC Ni 3'09 is a left calcaneum (Fig. 5). The overall morphology of the specimen is sciuroid (Ginot *et al*. 2016) with a short but robust tuber, a broad, flaring sustentaculum, a well-developed but posteriorly positioned peroneal process, a short calcaneocuboid process, a cuboid facet which is ovoid, almost circular, in outline and oriented at right angles to the long axis of the calcaneum, and an ectal facet that extends to about mid-height of the tuber, if not slighly more. On the plantar aspect there is a prominent groove over which the *M. flexor fibularis* and *M. flexor digiti* slide. Comparison with the calcaneum of *Nonanomalurus* (Pickford *et al*. 2013) reveals that the latter has a weaker peroneal process, the sustentaculum is further from the tuber (not overlapping the base of the ectal facet) and there is a much shallower groove for the *M. flexor fibularis* and *M. flexor digiti*. In other respects the calcanea of the two genera are generally similar apart from the obvious difference in dimensions.

Discussion

Reithroparamyinae are well represented in the Eocene of North America (Wood 1962; Korth 1984) Europe (Escarguel 1999) and Asia (Wood 1962; Sahni & Srivastava 1977) but have not previously been reported from Africa. Even though the representation at Black Crow is limited to two teeth, the morphology of the lower molar in particular suggests affinities with this subfamily (and more widely to Paramyidae *sensu* Wood 1962) rather than with Zegdoumyidae, Ctenohistrica or Phiomyidae.

Namaparamys inexpectatus is one of the smallest known species of the subfamily (as currently understood), the only species close to it in dimensions are *Microparamys reginensis* Korth 1984, which is slightly smaller (Fig. 6) and *Pantrogna russelli* (Michaux 1964) and *Sparnacomys chandoni* Hartenberger 1971, which are marginally larger. All the other taxa studied are appreciably larger than the Namibian species (Fig. 6).

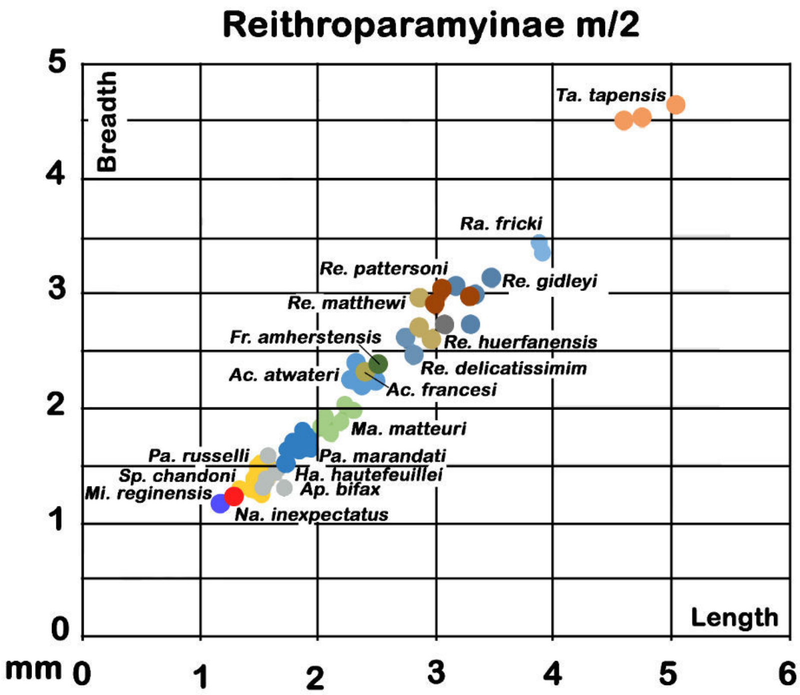

Figure 6. Scatter plot (length x breadth of anterior lophid) of the m/2 of various species of Reithroparamyinae. *Namaparamys inexpectatus* (red dot) is one of the smallest species recorded in the family. (*Ac - Acritoparamys, Ap - Apatisciuravus, Fr - Franimys, Ha - Hartenbergeromys, Ma – Masillamys, Mi - Microparamys, Na - Namaparamys, Pa - Pantrogna, Ra - Rapamys, Re - Reithroparamys, Sp - Sparnacomys, Ta - Tapomys*) (Data for European and North American species is from Wood 1962, Tobien 1954, Korth 1984, and Escarguel 1999). *Birbalomys woodi* from India is close in dimensions to *Acritoparamys atwateri* and *Acritoparamys francesi* (Sahni & Srivastava 1977).

The primitive morphology of the cheek teeth of Reithroparamyinae Wood 1962 (as well as those of Ischyromyidae Alston 1876, and Paramyidae Miller & Gidley 1918, in general) has been interpreted in various ways : a hypothesis commonly encountered in the literature is that they gave rise to most other families of rodents (Wood 1962; Korth 1984; Sahni & Srivastava 1977). It is interesting to note that the African family Zegdoumyidae could be descended from Reithroparamyinae (Marivaux, pers. comm. and this paper).

The extremely elongated root of the P3/ from Black Crow indicates that the maxilla was probably rather tall in the zone of the tooth. The P3/ commonly occurs in primitive rodents, but many later lineages lost it. However, the Miocene family Diamantomyidae retain a P3/ (Lavocat 1973).

The calcaneum attributed to *Namaparamys inexpectatus* is similar in overall morphology but is smaller than that of *Non-anomalurus soniae* from the Early Miocene of Uganda (Pickford *et al*. 2013). Morphologically it recalls the corresponding bone in the Palaeogene North American paramyid rodent *Notoparamys costilloi* (Rose & Von Koenigswald 2007) and to some extent *Protosciurus* (Emry & Thorington 1982). In contrast, the calcanea of Pedetidae and Anomaluridae are completely different from that of *Namaparamys*, as are the calcanea of Phiomyidae, Diamantomyidae and other hystricomorphs (Lavocat 1973) and Ctenohystrica in general (Ginot *et al*. 2016).

The calcaneum falls within the squirrel-like grouping of Ginot *et al.* (2016). It shows several morphological features that suggest that it was a climber, including a medially curved calcaneum (but not as markedly curved at the neck of the tuber as in *Sciurus vulgaris*), a well-developed peroneal process in a posterior position, a broad anterior part of the bone, and an approximately circular cuboid facet oriented perpendicular to the long axis of the calcaneum.

There appears to be no consensus concerning the contents of, or systematic rank of, Reithroparamyinae (see discussions in Wood 1962; Korth 1984 and Escarguel 1999). In this paper we adopt the view that the reithroparamyines merit subfamily rank within the family Paramyidae Miller & Gidley 1918, but given the limited nature of the African specimens described herein, we do not insist on this interpretation, and pending a full revision of all the material from North America, Asia and Europe, would be amenable either to including it in Ischyromyidae Alston 1876, or to raising the rank to family level as Reithroparamyidae Wood 1962.

Conclusions

The limestones at Black Crow in the Sperrgebiet, Namibia (now called Tsau//Khaeb National Park) have yielded three taxa of rodents - two zegdoumyids and a new genus of Reithroparamyinae, *Namaparamys inexpectatus*. The new genus and species is the first record of the subfamily Reithroparamyinae from Africa. The new discoveries indicate that Black Crow could be substantially older than previously thought (Middle Lutetian) and an age of either Early Lutetian or even Late Ypresian would not be out of order.

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