New Zegdoumyidae (Rodentia, Mammalia) from the Middle Eocene of Black Crow, Namibia : taxonomy, dental formula

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Abstract: Continued acid treatment of blocks of Eocene freshwater limestone from Black Crow, Namibia (Ypresian/Lutetian) has yielded additional faunal remains, including an almost complete young adult mandible, several isolated teeth and some post-cranial elements of a zegdoumyid rodent, a family previously represented at the site by a single upper molar. A new genus and species is named and its locomotor repertoire is examined. A discussion of rodent deciduous teeth is undertaken.

Key words: Ypresian/Lutetian; Dentition; Southern Africa; Evolution; Zegdoumyidae; Rodentia.

To cite this paper: Pickford, M. 2018. New Zegdoumyidae (Rodentia, Mammalia) from the Middle Eocene of Black Crow, Namibia : taxonomy, dental formula. *Communications of the Geological Survey of Namibia*. **18**, 48-63.

Introduction

Black Crow is an Eocene locality in the Sperrgebiet, Namibia. The fossiliferous rocks are comprised of limestones which accumulated in a palustral basin about 15 km from an active Carbonatite Volcano (Ystervark) (Pickford 2015). One layer of limestone at Black Crow consists of carbonatitic volcanic breccia, but most of the deposit is freshwater limestone deposited in a swamp or shallow pond. The limestone is rich in plant root systems (rhizoliths, pedotubules) and also shows some layers with algal mats and similar structures. The clastic fraction in the limestone is minimal, comprising dust-sized particles and occasional quartz pellets and very few small pebbles or other rock particles derived from the underlying Proterozoic basement (Gariep Group dolomites, schists and other rock types). A few fish and many crocodile teeth have been identified, but most of the faunal remains comprise terrestrial elements, including gastropods (principally *Dorcasia* and subulinoids) other reptiles including Scincidae, Amphisbaenians and snakes (Rage *et al*. 2013) rare birds and mammals (Pickford *et al*. 2008b).

Geological context, age and associated fauna

The Black Crow limestone occupies a shallow, oval depression ca 700 x 300 metres in extent, in dolomitic rocks of the Gariep Group (Pickford *et al*. 2008a). The succession is about 16 metres thick. The calcareous deposits were previosuly correlated to the Middle Eocene, but could be older (Late Ypresian-Early Lutetian) than previously thought (Middle Lutetian) but are unlikely to be as young as Bartonian as estimated by Seiffert (2010). For an up-to-date faunal list for Black Crow, see Mein & Pickford (2018).

The Black Crow Limestone is radically different in age from the bedded limestones at Silica North and Silica South. Initially considered to represent diverse outcrops of a single widespread carbonate depositional phase 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 Black Crow, which is Lutetian, if not older. The younger suite of freshwater limestone deposits includes the immensely rich occurrences at Eocliff and Eoridge which were discovered in 2013 which yield similar rodents 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 nomeclature

The cheek teeth of zegdoumyids are relatively simple within a rodent context, showing a clear tribosphenic basic morphology accompanied by a well-developed hypocone(id) (Fig. 1, 2). As in many other mammalian groups there are generally three cristae(ids) descending from the apices of the main cusps, called the pre-, endo- and post-crista(ids) (numbered 1, 2 and 3 respectively in the figures). Marivaux *et al*. (2014) refer to these cristae as arms, e.g. anterior arm of protocone = pre-protocrista, anterior arm of hypocone = prehypocrista etc. Styles (anterostyle, parastyle, metastyle) are weakly developed in the upper molars and stylids are poorly developed or absent in the lower teeth (mesostylid). There are mesial and distal cingula(ids). In addition there are accessory cusplets between the main cusps (anteroconid, mesoconid, hypoconulid in lower molars : protoconule, metaconule in upper molars). The endocristae of the paracone and protocone cross the tooth to form the protoloph (protolophid in lower teeth), while those of the hypocone and metacone form the metaloph in upper molars (hypolophid in lower molars). The distal cingulum joins the metacone and hypocone, and is called the posteroloph by Marivaux *et al*. (2014).

The cingula(ids) and lophs(ids) wall off three basins in the occlusal surface of the teeth : the mesial fovea, the trigon basin and the distal fovea in the upper teeth, the mesial foveid (trigonid basin), talonid basin and distal foveid in the lower teeth. In the floor of the basins in the upper cheek teeth of zegdoumyids, there is sometimes a low mesio-distally oriented ridge, known as a «mur» or «mure» (French for wall) associated with the mesoconule. The Namibian fossils either do not possess this structure or, when developed, it is rudimentary and indistinguishable from the mesoconule.

On the buccal and lingual surfaces of the teeth, there are shallow depressions between the main cusps called sinuses (upper teeth) or sinusids (lower teeth) (also known as flexus, flexids or notches). The low points in the margins of the occlusal basins and foveae are sometimes spout-like, but most are sill-like.

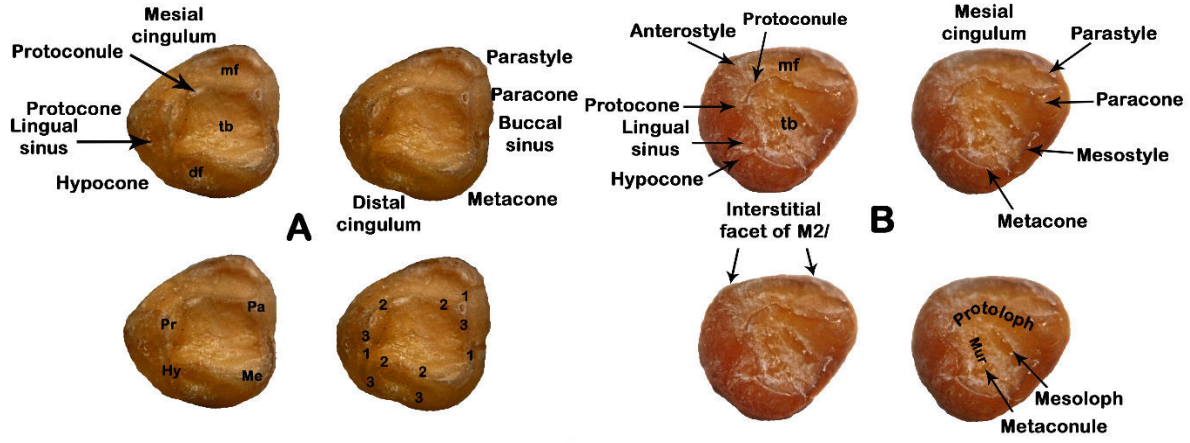

Figure 1. Nomenclature of upper cheek teeth of *Tsaukhaebmys calcareus*. Stereo occlusal views of A) left P4/, B) left M3/. Mesial is towards the top of the page ; lingual to the left (1 : pre-, 2 : endo-, 3 : post-crista of respective cusps ; df : distal fovea, mf : mesial fovea, tb : trigon basin ; Hy : hypocone, Me : metacone, Pa : paracone, Pr : protocone).

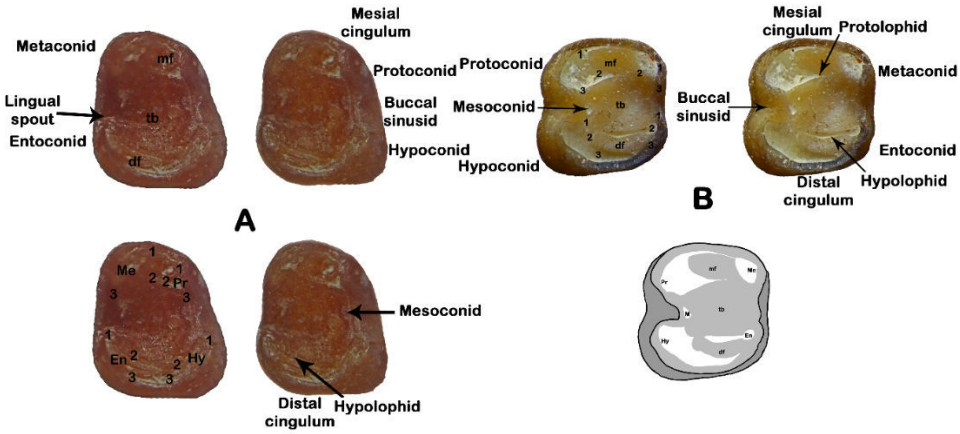

Figure 2. Nomenclature of lower cheek teeth of *Tsaukhaebmys calcareus*. Stereo occlusal views of A) right p/4 and B) left m/2. Mesial is towards the top of the page ; lingual to the left in 'A', and to the right in 'B' (1 : pre-, 2 : endo-, 3 : post-cristid of respective cusps ; df : distal foveid, mf : mesial foveid (= trigonid basin), tb : talonid basin ; En : entoconid, Hy : hypoconid, Me : metaconid, Pr : protoconid).

Systematic Palaeontology

Order Rodentia Bowdich 1821

Family Zegdoumyidae Vianey-Liaud, Jaeger, Hartenberger & Mahboubi 1994

Genus *Tsaukhaebmys* nov.

Diagnosis: *Tsaukhaebmys* is a genus of zegdoumyid rodent with permanent dental formula 2/0/2/3 (upper) and 2/0/1/3 (lower), mandible sciurognath, low coronoid process, mandibular condyle slightly above cheek tooth occlusal plane, lower incisor section with flat labial and lingual sides and rounded labio-distal corner, diastemal ridge not depressed, mental foramen beneath the diastema at mid-height of jaw. Upper fourth premolars with clear mesial fovea, large, almost smooth-floored trigon basin and distal fovea separated from each other by low transverse lophs (protoloph, hypoloph) and with prominent mesial and distal cingula; prominent parastyle, anterostyle obsolete, weak lingual sinus. Upper molars with large main cusps and prominent mesostyle and metaconule, protoconule not well differentiated, strong protoloph and hypoloph, prominent lingual sinus, clear parastyle and anterostyle joined by the mesial cingulum. M3/ with almost obsolete hypocone and distally positioned metacone, prominent parastyle and anterostyle, protoloph anteriorly bent, very obliquely oriented mesoloph, extensive mesostylar ridge blocking trigon basin buccally but with spouts at either end, small metaconule and associated mur, large mesial fovea and trigon basin, obsolete distal fovea, prominent lingual sinus. Lower p/4 with four main cusps (protoconid reduced in dimensions), mesial foveid small, talonid basin large without ridges but lightly rugose enamel surface, distal fovea mesio-distally short but bucco-lingually broad. Mesoconid low and sharp-edged separating the trigon basin from the buccal notch (sinusid), lingual spout open to trigon basin. Lower m/2 with clear mesial and distal foveids, large talonid basin, strong protoloph, weaker hypoloph, strong mesial and distal cingulids. Mesoconid low and small, lingually positioned relative to protoconid and hypoconid, deep buccal sinusid. Lower third molar with four main cusps, expansive trigonid basin with low oblique ridge in the floor, otherwise smooth-floored, prominent but low protolophid and hypolophid, well formed mesial cingulum.

Differential diagnosis: *Tsaukhaebmys* differs from *Zegdoumys* Vianey-Liaud *et al*. (1994) by the following features :- The P4/ (i.e. dP4/ of Marivaux *et al*. 2014) *Tsaukhaebmys* differs

from that of *Zegdoumys* by the reduction of the relative size of the hypocone and its position close to the protocone (larger and well separated from protocone in *Zegdoumys*) and shallower lingual sinus (broader and deeper in *Zegdoumys*). The M3/ protoloph is markedly bent in *Tsaukhaebmys*, almost straight in *Zegdoumys*, the hypocone complex has no endo-hypocrista (present in *Zegdoumys*), it possesses an oblique mesoloph (absent in *Zegdoumys*) a small metaconule and mur (absent in *Zegdoumys*). The p/4 (i.e. dp/4 of Marivaux *et al*. 2014) of *Tsaukhaebmys* differs from that of *Zegdoumys* by the following characters :- absence of cusplets between the metaconid and entoconid (present in *Zegdoumys*), protolophid obliquely oriented (more transverse in *Zegdoumys*), small mesoconid (stronger in *Zegdoumys* with endocristid).

Tsaukhaebmys differs from *Glibia* Vianey-Liaud *et al. (*1994) by the presence of lophs and lophids in the molars which are lower, narrower and, when unworn, sharper. The mesoconid in *Tsaukhaebmys calcareus* is more continuous between the protoconid and hypoconid than it is in *Glibia* and there is no transverse ridge nor mur in the floor of the talonid basin, unlike *Glibia* where there is a ridge and often a mur.

Tsaukhaebmys differs from *Glibemys* Vianey-Liaud *et al*. (1994) by the absence of a transverse lophid in the floor of the talonid basin of the lower molars (present in *Glibemys*), by a mesio-distally compressed but bucco-lingually broad mesial foveid (almost as long mesio-distally as it is bucco-lingually in *Glibemys*), by the smaller mesoconid (large with a transverse lophid in *Glibemys*), shallower buccal sinusid (deep with a low-level spout in *Glibemys*) and a greater separation between the ends of the post-metacristid and pre-entocristid (close together in *Glibemys*, making for a narrow lingual spout).

Tsaukhaebmys differs from *Lazibemys* Marivaux *et al*. (2011) by the absence of, or only feeble corrugations, in the floors of the trigonid basin in the upper molars and the talonid basin of the lower molars and p/4 (clear corrugations and ridges in *Lazibemys*) by a less obvious mesoconid in the p/4 (large with transverse lophid in *Lazibemys*) and an M3/ with rudimentary hypocone (large and well-differentiated in *Lazibemys*).

Derivatio nominis.: Tsau//Khaeb National Park is the replacement name for the Sperrgebiet National Park. Tsau//Khaeb means «*Deep sandy soils*» in the Nama Language, here abbreviated to «*Tsaukhaeb*» to which the suffix «*mys*» has been added, signifying «*mouse*» in Greek.

Species *Tsaukhaebmys calcareus* nov.

Holotype: GSN BC Tc 1'17, right mandible containing i/1, p/4, empty alveoli of m/1 and m/2, and m/3 in crypt.

Diagnosis: as for the genus.

Derivatio nominis: The species name '*calcareus*' refers to the limestone deposits in which the fossils at Black Crow are preserved.

Additional material: See Table 1.

Table 1. Material of *Tsaukhaebmys calcareus* from Black Crow, Namibia.

Catalogue	Specimen
GSN BC Tc 1'17	right mandible with incisor, fully erupted p/4 and m/3 in crypt
GSN BC Tc 2'17	right p/4
GSN BC Tc 3'17	left P4/
GSN BC Tc 4'17	left m/2
GSN BC Tc 5'17	right m/2 fragment
GSN BC Tc 6'17	left M3/
GSN BC Tc 7'17	right p/4
GSN BC Tc 8'17	second phalanx
GSN BC Tc 9'17	second phalanx
GSN BC Tc 10'17	second phalanx
GSN BC Tc 11'17	second phalanx
GSN BC Tc 12'17	third phalanx
GSN BC Tc 13'17	third phalanx
GSN BC Tc 14'17	third phalanx

Type locality and Age: Black Crow, Namibia, Ypresian/Lutetian (Pickford *et al*. 2008b; Pickford 2015).

Description

The right mandible GSN BC Tc 1'17 contains the incisor and p/4 in occlusion and the m/3 in its crypt (Fig. 3-6). The jaw is sciurognathous, remarkably slender, with the mental foramen at mid-height of the jaw mesial to the apex of the anterior root of the p/4 and immediately above the incisor. The coronid process is abraded but was in any case very low, not projecting above the mandibular condyle. The leading edge of the masseteric fossa forms a strong, curved ridge which reaches as far anteriorly as the rear of the m/1. The mandibular foramen on the lingual side of the jaw, is far back, slightly above the occlusal plane of the cheek teeth and at the same height as the mandibular condyle. The condyle is immediately behind the mandibular foramen and it lies only slightly above the level of the cheek tooth occlusal surface. This is a remarkably low position for the mandibular condyle. The angle of the jaw descends postero-ventrally at a relatively shallow angle. Above and behind it there is a capacious fossa, entirely distal to the tooth row. The diastema does not descend below the gingival level of the cheek teeth but, in lateral view, it does have a shallowly concave dorsal profile.

Figure 3. GSN BC Tc 1'17, holotype right mandible of *Tsaukhaebmys calcareus*, stereo views, A) lingual and B) buccal (scale : 10 mm).

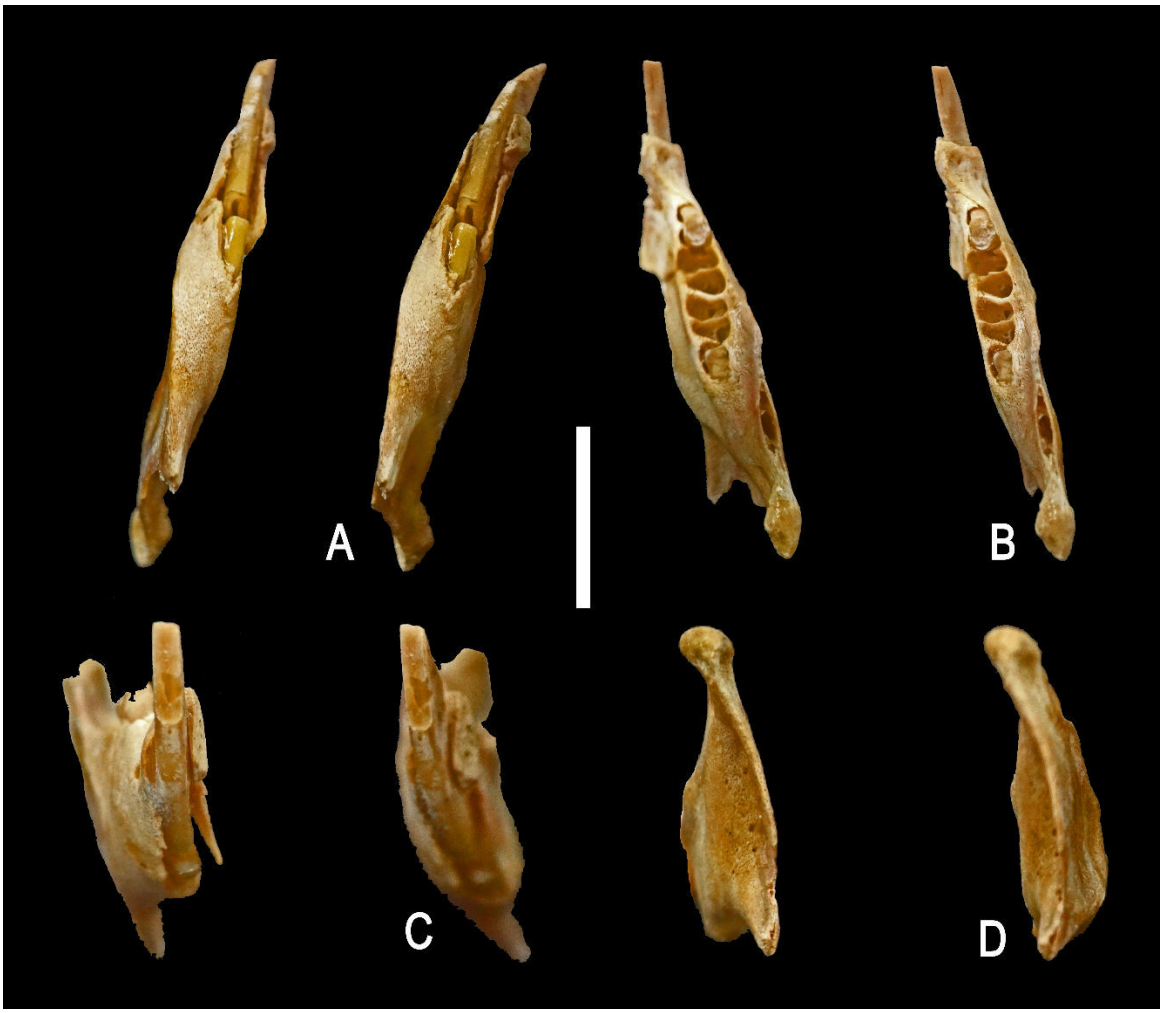

Figure 4. GSN BC Tc 1’17, holotype right mandible of *Tsaukhaebmys calcareus*, stereo views, A) ventral, B) occlusal, C) anterior and D) posterior (scale : 10 mm).

The lower incisor is moderately broad, with a flat labial surface lying at right angles to the mesial surface and sloping round to the distal side. Where unworn, the lingual side of the lower incisor is rounded.

The p/4 in GSN BC Tc 1’17 has two robust roots, the anterior one slanting markedly forwards beneath the diastema, the posterior one vertical. The anterior root is almost circular in section, the posterior one mesiodistally compressed into an oval section. The crown is noticeably narrower than the length, especially narrow at its mesial end.

Figure 5. GSN BC Tc 1’17, right p/4 in mandible of *Tsaukhaebmys calcareus*, stereo occlusal view and interpretive drawing of occlusal crests and basins (1, 2, 3 = pre-, endo- and post-cristids, df - distal foveid, mf - mesial foveid, tb - talonid basin) (scale : 2 mm).

There are three p/4s in the collection (GSN BC Tc 1'17, Tc 2'17, Tc 7'17). It has four main cusps : subequal metaconid, hypoconid and entoconid, and a diminutive protoconid. The protoconid has three cristids descending from its apex, one anteriorly, one posteriorly and one medially. The metaconid also has three cristids, one directed antero-buccally where it descends to the end of the pre-cristid of the protoconid, thereby delimiting a mesial foveid on the mesio-buccal end of the crown. The post-cristid of the metaconid is robust and extends towards the short pre-cristid of the entoconid, forming a low spout to the central basin. Finally, the endo-metacristid extends across the tooth towards the base of the endo-protocristid, walling off the rear of the mesial foveid. The entoconid has a short pre-cristid, a long and robust endo-cristid which extends straight across the tooth, ending at the lingual wall of the post-hypocristid. The post-cristid of the entoconid is thin near the cusp, but broadens distally before curving buccally to blend into the post-hypocristid, thereby closing off a distal foveid. The hypoconid has three crests, a large post-hypocristid, a short and weak endo-hypocristid which descends mesially towards the post-protocristid, leaving a spout-like opening on the buccal side of the central basin, and there is a short pre-hypocristid which descends down the buccal aspect of the crown as a fold of enamel walling off the shallow buccal notch or sinusid.

The m/1 and m/2 are missing from the Black Crow mandible, but it is clear that each tooth possessed two robust roots, both of which are sub-ovoid in section and mesio-distally compressed. The anterior root is mesio-distally longer on the lingual side than on the buccal side, whereas the posterior root shows the opposite conformation, longer buccally than lingually. In addition, the posterior root is slightly more buccally positioned than the mesial one and it leans buccally at a slightly greater angle than the almost vertical mesial root. The same conformation applies to the alveoli of the m/2.

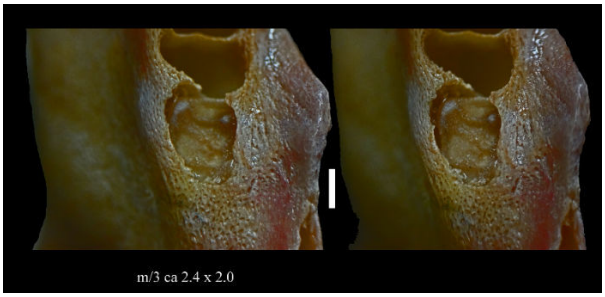

Figure 6. GSN BC Tc 1'17, part of right mandible of *Tsaukhaebmys calcareus* showing the m/3 in crypto, stereo occlusal view (scale : 1 mm).

The m/3 lies in its crypt which is open occlusally, revealing about three quarters of the surface of the crown, including the apices of the metaconid, protoconid and hypoconid. The protolophid is low and narrow and the floor of the talonid basin shows an oblique ridge running from the base of the metaconid towards the hypoconid. The hypolophid is transversely oriented walling off the rear of the talonid basin between the bases of the hypoconid and entoconid. The mesial and distal foveids are mesio-distally narrow, but bucco-lingually broad.

GSN BC Tc 4'17 is a heavily worn left m/2 retaining both its roots. The crown has four main cusps and a mesoconid. The protoconid has a prominent pre-cristid which curves anteriorly and lingually forming the mesial border of the mesial foveid. It links to the pre-cristid of the metaconid which curves antero-buccally. The endo-cristids of the protoconid and metaconid descend into the trigonid basin, forming a low distal wall to the mesial foveid (the protolophid). The post-protocristid is short and is directed towards the low endoconid. The entoconid is small and has three cristids, the pre-cristid directed towards the post-cristid of the metaconid but not fusing with it, leaving a low lingual spout for the trigonid basin. The endo-cristid of the entoconid descends into the central basin, forming a low ridge in its floor (hypolophid). This ridge runs towards the short endo-cristid of the hypoconid, but does not join it. The post-entocristid curves distally and buccally to join the distal cingulum and the post-hypocristid. The distal foveid is separated

from the trigonid basin by the low endo-cristid of the entoconid, but the ridge separating them is low. Finally, the mesoconid is small and low, positioned to the lingual side of the line between the protoconid and the hypoconid. This makes for a well-marked buccal sinusid or notch.

GSN BC Tc 5'17, is an unworn right m/2 missing the anterior half. The hypoconid is large and has thick but short pre- and post-cristids which are obliquely oriented, the latter cristid blending into the distal cingulum. The entoconid is partly preserved and it has a low but sharp ridge (hypolophid) directed across the trigonid basin, ending before it reaches the base of the hypoconid, and walling off a distal foveid. The post-entocristid blends into the distal cingulum.

Upper dentition

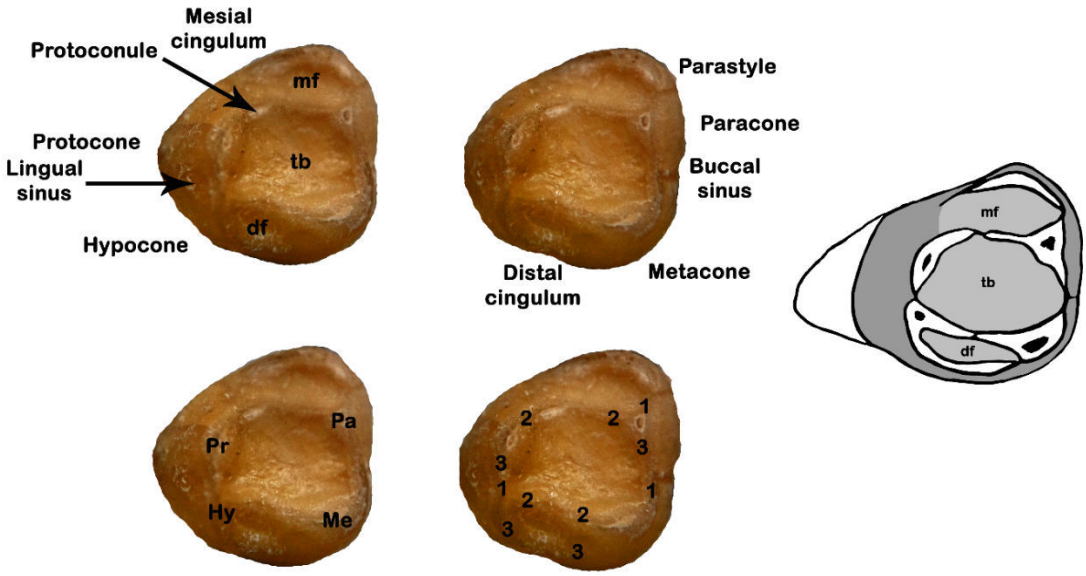

Figure 7. GSN BC Tc 3'17, left P4/, stereo occlusal images and interpretive drawing (df : distal fovea, mf : mesial fovea, tb : trigon basin, Hy : hypocone Me : metacone, Pa : paracone, Pr : protocone ; 1, 2, 3, = pre-, endo- and post-crista of respective cusps).

GSN BC Tc 3'17 is an upper left P4/. (Fig. 7). The specimen is lightly worn, and at cervix level in the middle of the mesial side of the tooth it shows a contact facet for a P3/. Indeed the mesial surface of the tooth is slightly concave where the crown of the P3/ would have been positioned. The roots have broken off, save for a small sliver of the root associated with the protocone and hypocone. The crown is composed of four main cusps with prominent crista and there is a well-developed parastyle and a mesial cingulum which extends between the parastyle and the mesial base of the protocone. The pre-protocrista is obsolete to exceedingly weakly expressed. In contrast the well-developed endo-protocrista curves antero-buccally to join the protoconule which terminates in the centre-line of the crown, leaving a small gap between it and the endo-paracrista, the two cristae forming the protoloph which walls off the rear of the mesial fovea. The post-crista of the protocone and paracone are short and directed distally where they join the pre-crista of the hypocone and metacone respectively. The endo-hypocrista and endo-metacrista join each other in the centre-line of the crown, thereby forming a hypoloph which comprises the transverse wall separating the trigon basin from the distal fovea. The latter fovea is bordered by the elongated transversely oriented post-hypocrista and the short post-metacrista forming the distal cingular structure.

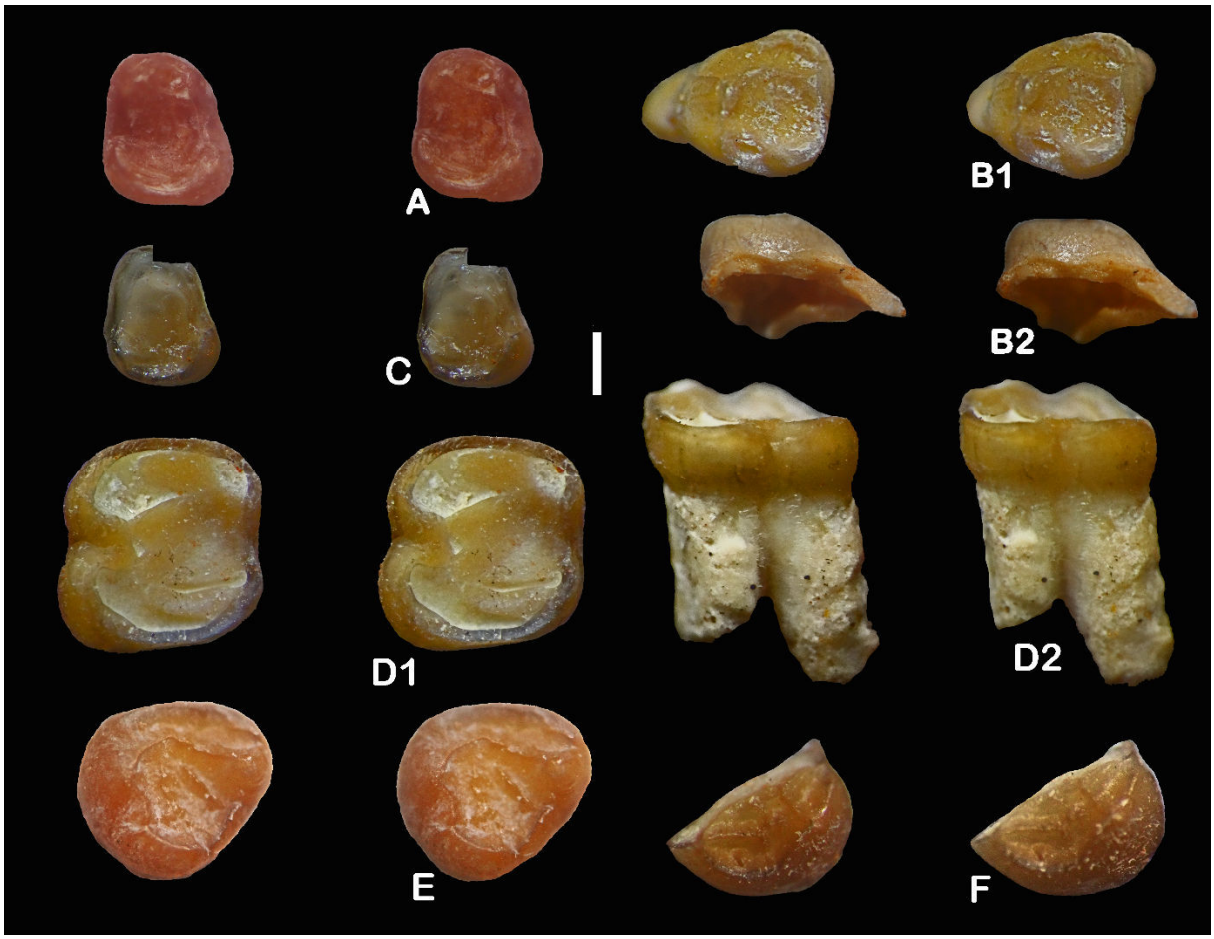

Figure 8. Stereo images of isolated teeth of *Tsaukhaebmys calcareus* from Black Crow, Namibia. A) GSN BC Tc 2'17, right p/4 (occlusal view), B) GSN BC Tc 3'17, left P4/ (B1 : occlusal view, B2 : anterior view to show contact facet of P3/), C) GSN BC Tc 7'17, right p/4, D) GSN BC Tc 4'17, left m/2 (D1 : occlusal view : D2 : buccal view), E) GSN BC Tc 6'17, left M3/ (occlusal view), F) GSN BC Tc 5'17, distal part of right m/2 (occlusal view) (scale : 1 mm).

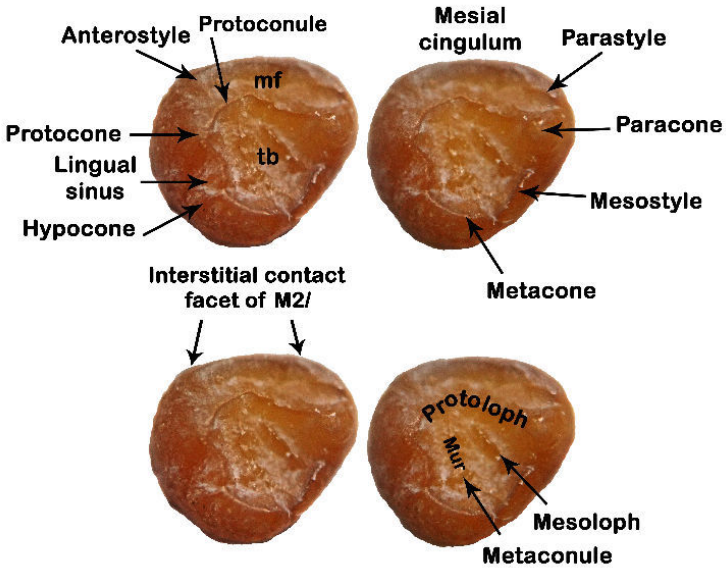

Figure 9. GSN BC Tc 6'17, left M3/ of *Tsaukhaebmys calcareus*, stereo occlusal views and nomenclature of cusps, crests and basins (mf : mesial fovea, tb : trigon basin).

GSN BC Tc 6'17 is an unworn left M3/ (Fig. 8, 9). The protocone, paracone and metacone are large, but the hypocone is greatly reduced, being little more than a small bulge on the lingual side of the crown, so much so that this part of the tooth is difficult to interpret. There is a prominent mesial cingulum bordering the broad but short mesial fovea. The protocone has two cristae (the pre-crista is absent or represented by a low swelling) : the endo-crista joins the protoconule, from which there is a secondary crista leading to the anterostyle near the mesial cingulum, and the post-protocrista is thick and short and leads obliquely backwards towards the hypocone complex. The pre-paracrista is short and does not join the parastyle, leaving a spout at the buccal end of the mesial fovea. The post-paracrista is almost obsolete but descends towards the mesostyle which forms a low buccal wall to the trigon basin. The metacone has two cristae, the pre-metacrista directed towards the mesostyle, the post-metacrista extending towards the tiny hypocone. There is a long, straight, but low ridge (mesoloph) in the floor of the trigon basin running between the mesostyle and the lingual base of the protoconule but stopping short before reaching it. Finally, there is a small metaconule and mur in the floor of the trigon basin, the mur running sub-parallel to the mesoloph. The length and breadth of the tooth (2.3 x 2.4 mm) is compatible with the other zegdoumyid teeth from Black Crow (Table 2).

Table 2. Dimensions (in mm) of the teeth of *Tsaukhaebmys calcareus* gen. et sp. nov. from Black Crow, Namibia (e - estimated measurement).

Catalogue	Tooth	Mesio-distal length	Bucco-lingual breadth
GSN BC Tc 1'17	right i/1	1.2	2.3
GSN BC Tc 1'17	right p/4	2.1	1.6
GSN BC Tc 1'17	right m/3	2.8e	2.3e
GSN BC Tc 2'17	right p/4	2.0	1.7
GSN BC Tc 7'17	right p/4	2.2	1.55
GSN BC Tc 3'17	left P4/	1.9	1.9
GSN BC Tc 4'17	left m/2	2.6	2.5
GSN BC Tc 5'17	right m/2 fragment	--	--
GSN BC Tc 6'17	left M3/	2.3	2.4

Genus *Zegdoumys* Vianey-Liaud *et al*. 1994

Species *Zegdoumys namibiensis* (Pickford *et al*. 2008b)

***Diagnosis*:** see Pickford *et al*. (2008b) and Marivaux *et al*. (2011, 2014).

***Holotype*:** GSN BC Tc 1'08, right upper molar.

Type locality: Black Crow, Namibia.

Description

The holotype of *Zegdoumys namibiensis* (Pickford *et al*. 2008b) is illustrated for ease of comparison with teeth of *Tsaukhaebmys calcareus* (Fig. 10). Note the broad, strong lophs and the enlarged protoconule, metaconule and mesostyle of the *Zegdoumys* upper molar, all of which decrease the dimensions of the trigon basin compared with the much more capacious basins in the teeth of *Tsaukhaebmys*.

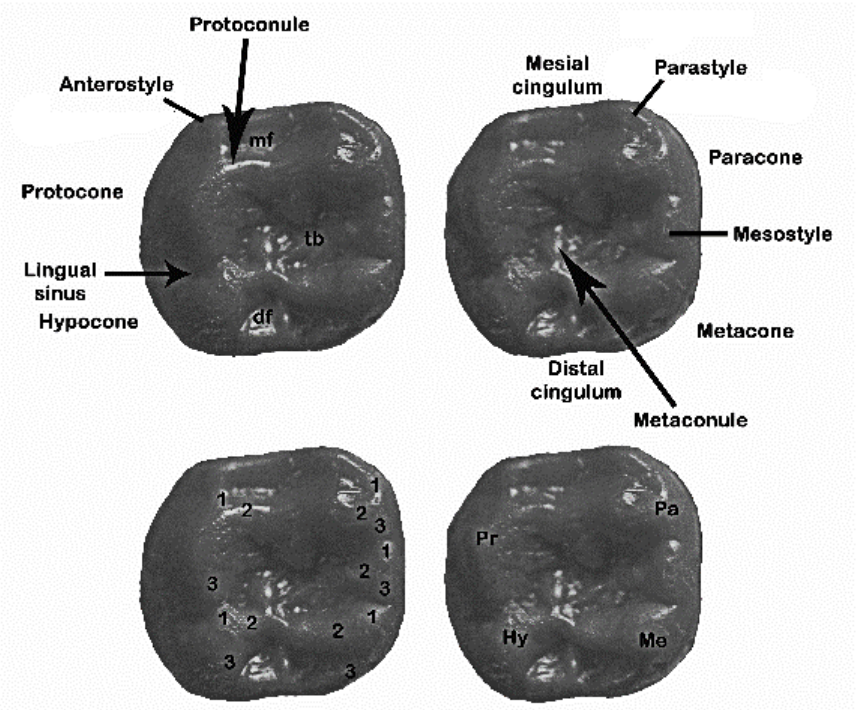

Figure 10. GSN BC 1'08, holotype upper right molar (reversed) of *Zegdoumys namibiensis* from Black Crow. Stereo views of cast with nomenclature (df : distal fovea, mf : mesial fovea, tb : trigon basin, Hy : hypocone, Me : metacone, Pa : paracone, Pr : protocone ; 1, 2, 3, = pre-, endo- and post-crista of respective cusps) The tooth is 2.5 mm long x 2.5 mm broad.

Post-cranial skeleton of *Tsaukhaebmys*

Phalanges

Several phalanges of rodent type were found in the same blocks of limestone as the teeth of *Tsaukhaebmys calcareus*, and we assume that they to belong to this species (Fig. 11, 12).

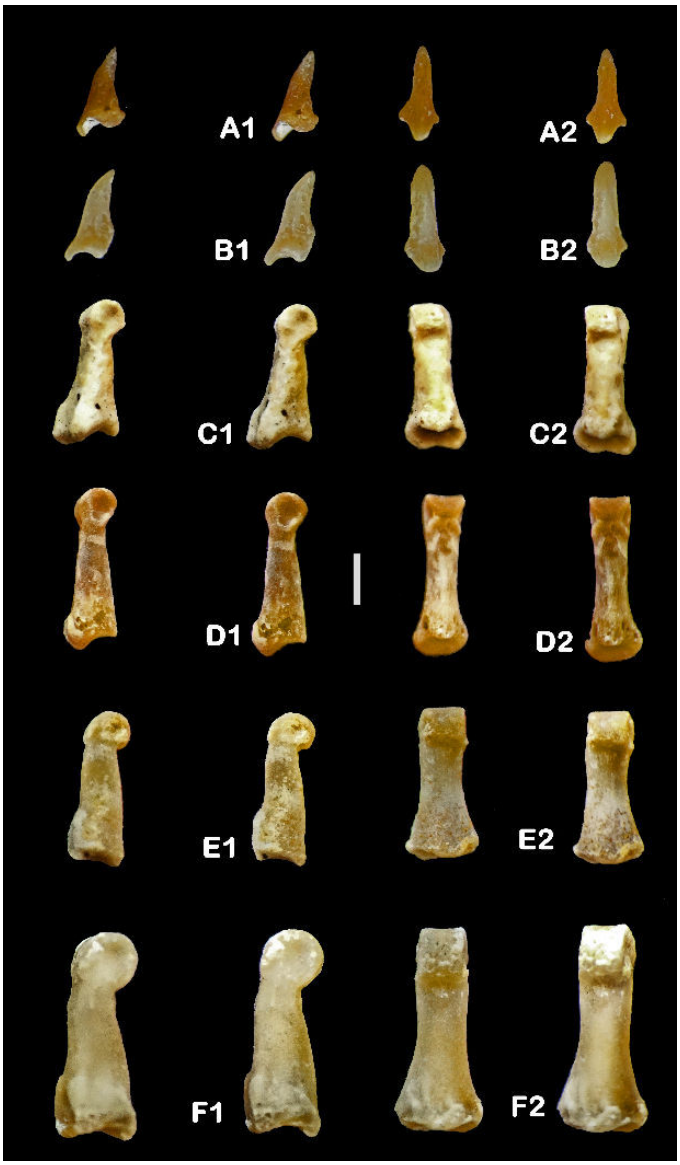

Figure 11. Stereo images (1 - side views, 2 - dorsal views) of phalanges from Black Crow provisionally attributed to *Tsaukhaebmys calcareus.* A-B) BC Tc 12'17 & BC Tc 13'17, third phalanges, C-F) BC Tc 8'17 - Tc 11'17, second phalanges (scale : 1 mm).

The second phalanges from Black Crow, attributed to *Tsaukhaebmys calcareus* are characterised by their dorsally raised distal epiphyses with almost cylindrical articular facets for the third phalanges. This morphology is comparable to that observed in *Nonanomalurus soniae* from the Eary Miocene of Uganda (Pickford *et al*. 2013).

Figure 12. GSN BC Tc 14'17, third phalanx from Black Crow provisionally attributed to *Tsaukhaebmys calcareus*. A) stereo lateral view, B) stereo dorsal view, C) stereo medial view (scale : 1 mm).

Two of the third phalanges attributed to *Tsaukhaebmys* are small and short with a broad proximal articulation and a pointed apex. A third specimen is larger, is compressed medio-laterally and is tall, with a well-developed ungual insertion. It is possible that the large compressed specimen comes from the first digit, and the other two specimens are from digits 2, 3 or 4.

Discussion

The new zegdoumyid specimens from Black Crow show sufficient morphological differences from other genera of the family that they are here attributed to a new genus *Tsaukhaebmys*. The new fossils differ from a previously described zegdoumyid from Black Crow, identified as *Glibia namibiensis* Pickford *et al*. (2008b) by the more slender lophs traversing the crowns of the teeth, and the smaller, more finely constructed mesostyle and mesocone. Marivaux *et al*. (2014, 2017) attributed the holotype of *Glibia namibiensis* to the genus *Zegdoumys*, partly on the basis of its supposedly youthful age, and partly on the basis of its morphology and large size.

The mandible of *Tsaukhaebmys calcareus* is sciurognath, and in addition it has a low mandibular condyle only marginally above the occlusal plane, and a weak, low coronoid process not rising above the condyle. The diastemal ridge is not depressed beneath the level of the alveoli of the lower cheek teeth, unlike anomalurids and pedetids which have a deeply depressed diastemal ridge in the lower jaw. In this feature *Tsaukhaebmys* is close to *Nonanomalurus* (Pickford *et al*. 2013). The mandible of *Tsaukhaebmys* differs markedly from those of Pedetidae (MacInnes 1957) which have the mandibular condyle far above the occlusal plane of the cheek teeth, and a difference from Anomaluridae concerns the greater development and projection of the coronoid process above the condyle in anomalurids. The coronoid process of *Tsaukhaebmys* is weakly developed and low, quite similar to that of *Nonanomalurus*.

Dental eruption sequence

The young adult mandible from Black Crow contains the incisor, the lightly worn p/4, the empty alveoli of the m/1 and m/2, and the m/3 in its crypt. During acid treatment, the jaw broke into two fragments at the rear of the p/4. There was no sign of a replacement tooth beneath the alveoli of the p/4, nor is there any sign that there was a p/3, the diastemal ridge extending distally until it abuts against the mesial alveolus of the p/4. The mandible was repaired and the p/4 was replaced in the jaw, its two large, pillar-like roots fitting snugly into the alveoli.

On the basis of the Black Crow mandible, it is deduced that the p/4 erupts and is in wear before the m/3 is fully formed and well before it has erupted.

There has been a long-lasting debate in the literature concerning the deciduous teeth of rodents. In forms which do not replace the anterior cheek tooth, there are two opinions – one, that the tooth is a retained deciduous tooth, the other, that it is a permanent tooth that does not have a deciduous precursor. Wood (1965) for example, was unable to decide whether the anterior cheek tooth in *Pedetes*, the Spring Hare, was a deciduous tooth or a permanent one.

In mammals in general, the morphology of the fourth deciduous cheek tooth (both upper and lower) resembles that of the permanent first molars, but is usually somewhat smaller and often of slightly different occlusal outline. In many mammals, the permanent premolars that replace the D4/ and d/4 are usually unlike the permanent first molars, the crown being simpler «premolariform» (there are exceptions such as perissodactyls and hyracoids in which the permanent premolars, and in the latter Order even the canines, are fully molariform). There are a few mammals (carnivorans) that possess a permanent fourth premolar which has a more simplified crown morphology than the deciduous tooth that it replaces. It is concluded that zegdoumyids followed the general mammalian «pattern», and that the D4/ and d/4 were more «molariform» than the P4/ and p/4. In this, zegdoumyids resemble *Notoparamys costilloi* from the Early Eocene Willwood Formation, Wyoming, USA (Rose & Von Koenigswald 2007).

Marivaux *et al*. (2011, 2014) illustrated isolated teeth of zegdoumyids from Chambi, Tunisia, and Gour Lazib (Glib Zegdou) in Algeria. These authors reconstructed upper and lower tooth rows from isolated teeth, including the D4/ and d/4. The supposed d/4s of *Zegdoumys lavocati* and *Glibia pentalopha* have occlusal outlines similar to that of the p/4 in the mandible of *Tsaukhaebmys calcareus*. As interpreted by these authors the supposed permanent 4th premolars of the *Z. lavocati* and *G. pentalopha* have a more molariform occlusal outline than the supposed deciduous teeth which preceded them. It is deduced from this that the authors have misinterpreted the d/4 as the p/4 and the D4/ as the P4/. That the serial position of the p/4 is not sure was realised by Vianey-Liaud *et al*. 1994, who identified a tooth of *Zegdoumys lavocati* from Glib Zegdou as d/4(?). The diphyodont nature of the zegdoumyid dentition seems secure, but what have previously been interpreted as the permanent premolars are in fact the deciduous ones, and vice versa.

Dental formula

There are four lower cheek teeth in the Black Crow mandible with no sign of a p/3 or even of a small alveolar scar on the diastemal ridge in front of the p/4, from which the lower dental formula of *Tsaukhaebmys calcareus* is deduced to be 1/0/1/3. The P4/ has a contact facet mesially caused by pressure against the P3/, on the basis of which it is concluded that the upper dental formula was 1/0/2/3. Marivaux *et al*. (2011) had no information about the presence of P3/ in the zegdoumyids that they studied, so in the matrix they scored this character as (?). No deciduous teeth of rodents have been found at Black Crow, but North African zegdoumyids are reported to possess D4/ and d/4 (Marivaux *et al*. 2011), although, as explained above, these authors inverted the P4/ and D4/, and the p/4 and d/4, a transposition which impacts on the phylogenetic analysis.

Locomotion

The second phalanges attributed to *Tsaukhaebmys calcareus* show a dorsally rotated distal articulation with an almost cylindrical articular surface. This is similar to *Nonanomalurus* (Pickford *et al*. 2013) and suggests the possibility of hyper-extension of the third phalanx, possibly an adaptation to climbing where the substrate is three-dimensional with abundant infractuosities. One of the third phalanges (probably of the first digit) attributed to *Tsaukhaebmys* indicates that it was endowed with a strong, medio-laterally compressed, sharp claw, again like *Nonanomalurus*. The other third phalanges from Black Crow are smaller and more pointed, conical in shape, probably from digits 2, 3 or 4.

From this it is inferred that *Tsaukhaebmys calcareus* was likely an arboreal rodent of squirrel-like locomotor repertoire.

Phylogenetic implications

The new zegdoumyid from Black Crow seems to be more primitive in some features of its dentition than other members of the family (low sharp lophs and lophids, relatively unadorned floors of the trigon basin and talonid basin, mammalian tribosphenic molar «grundplan»), but in other respects it seems more derived (tiny hypocone in M3/). The mandible of *Tsaukhaebmys* is sciurognath, and the lower incisor is rather like that of *Nonanomalurus*. The coronoid process of the mandible is low and weakly developed, barely surpassing the height of the mandibular condyle and the form of the diastemal ridge is like that of *Nonanomalurus*. This is different from the situation in Anomaluridae in which the coronoid process is taller and curves upwards and backwards towards the condyle. In *Tsaukhaebmys* the mandibular condyle is low, only marginally above the level of the occlusal plane, whereas in Pedetidae it is far above the occlusal plane (MacInnes 1957).

Previous phylogenetic analyses of zegdoumyids were based almost exclusively on dental features (Marivaux *et al*. 2011, 2014) and suggested that Zegdoumyidae were the sister

group of Nonanomaluridae, which was next to Nementchamyidae, and then Anomaluridae. Marivaux *et al*. (2014, fig. 5) did not include Pedetidae in their analysis.

Conclusions

New remains of rodents are described from Black Crow, Namibia, previously correlated to the Lutetian but possibly of Late Ypresian age. The fossils include the first known mandible of the family Zegdoumyidae, and some post-cranial elements were found in the same blocks of limestone. The remains are attributed to the family Zegdoumyidae, but dental differences from established genera and species indicates that we are in the presence of a new genus and species, herein named *Tsaukhaebmys calcareus*. Although the zegdoumyid affinities of the new Black Crow rodent are clear, the presence of both primitive and derived features in the cheek teeth make it difficult to decide whether it is a basal member of the group, or whether it is rather derived, as its previous stratigraphic correlation would imply. This is the second species of zegdoumyid to be described from Black Crow, the other taxon being based on an isolated upper molar initially identified as *Glibia namibiensis* (Pickford *et al*. 2008b) but in recent literature attributed to the genus *Zegdoumys* (Marivaux *et al*. 2011, 2014). The upper molar of this species differs from those of *Tsaukhaebmys* by the possession of strongly developed and thick lophs traversing the occlusal surface of the crown, which contrasts with the low, fine and discontinuous lophs(ids) in the teeth of *Tsaukhaebmys*. As a result of the thickness of the transverse lophs in *Zegdoumys namibiensis*, the trigon basin is small and crowded, contrasting with the capacious and relatively unencumbered basins in *Tsaukhaebmys*.

The new rodent fossils from Black Crow, both the mandible and the post-cranial elements, indicate that the closest relatives of zegdoumyids are the nonanomalurids, and that the phylogenetic relationships to anomalurids (Coster *et al*. 2015) and pedetids (MacInnes 1957; Wood 1965) are remote.

Acknowledgements

Thanks to the Geological Survey of Namibia, the Ministry of Mines and Energy (Gloria Simubali, Anna Nguno, Vicky Do Cabo, Ute Schreiber, Helke Mocke), the Ministry of Environment and Tourism, the Namibian National Heritage Council (Mr Karipi, Erica Ndalikokule, Helvi Elago), and Namdeb (Mike Lain, Bob Burrell, Jürgen Jacob, John Ward, Renato Spaggiari, Hester Fourie) for facilitating and supporting the research programme in the Sperrgebiet which has been undertaken every year since 1992. Thanks to Namdeb for making its unpublished archives available for consultation (Gloudina Brand). I thank the French Embassy in Namibia (M. J.-L. Zoël, Mme J. Bassa-Mazzoni), the Cooperation Service of the French Embassy in Windhoek (M. J.-P. Martin, M. P. Portes-Gagnol), the Sorbonne Universités (Muséum National d'Histoire Naturelle, Paris, UMR 7207 and CR2P (CNRS, MNHN)) (Sylvie Crasquin).

Funding for field surveys was supplied by French government agencies (Sorbonne Universités, CNRS, MNHN, Collège de France and the University of Rennes) and by Namdeb. I am anxious to acknowledge the long term collaboration that I have enjoyed with my colleagues Brigitte Senut and Helke Mocke.

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