

# Tufamyidae, a new family of hystricognath rodents from the Palaeogene and Neogene of the Sperrgebiet, Namibia

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**Abstract:** The Palaeogene tufa deposits at Eocliff are a rich source of micromammals, probably the richest such site in Africa, having yielded thousands of specimens, including complete skulls, mandibles and associated post-cranial elements, with perhaps millions of specimens remaining in the field. Rodents are well-represented but are of relatively low diversity, comprising six common species and a rare one. We here describe an early hystricognath, hystricomorph rodent from the site, based on a complete skull associated with post-cranial elements, and many maxillae, mandibles, isolated teeth and post-cranial bones. This is currently the earliest known member of the superfamily Thryonomyoidea, possible earlier records being based on isolated teeth or fragmentary maxillae and mandibles which do not provide solid evidence for their superfamilial status. The originality of the morphology of the incisors, the simplicity of the molars and other features indicate that this thryonomyoid represents a hitherto unknown family of rodents, herein named Tufamyidae.

**Key words:** Eocene; Biogeography; Evolution; Taxonomy; Systematics, Rodentia.

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## Introduction

The tufa deposits at Eocliff and Eoridge in the Sperrgebiet, Namibia, have yielded an impressive diversity of micromammals of Late Eocene age, among which rodents are particularly well represented, even though low in diversity (7 taxa).

Fossils from Silica North previously attributed to *Apodecter* cf *stromeri* and cf *Bathyergoides* sp. (Pickford *et al.* 2008) belong instead to *Tufamys woodi*, a new genus and species defined herein, the three teeth matching specimens from Eocliff. These re-allocations modify some of the discussions concerning the age of the Silica North deposits.

There has been debate about the age of the tufas but herein they are considered to be Late Eocene, probably Bartonian, but possibly Priabonian. Estimates of a Chattian correlation (Sallam & Seiffert, 2016) or a Miocene correlation (Marivaux *et al.* 2014) were based on preliminary identifications of the rodents and other mammals, without first-hand knowledge of the fossils themselves.

Most of the fossils found at Eocliff are evidently the remains of disaggregated owl pellets, but a few pellets have remained complete.

This article focusses on one of the common rodent species at Eocliff, being the first of a series of papers treating each of the genera occurring at the site. Given its importance in the fauna, the first form treated will be a thryonomyoid which shows many of the classic osteological and dental traits of this group of rodents (*sensu stricto*) which differentiate it from other rodent families with superficially similar cheek teeth such as the Gaudeamuridae the Bathyergidae and Renefossoridae.

It is pertinent to mention that prior to the discovery of *Tufamys*, the oldest described skull of a hystricognathous rodent was *Tsaganomys* from the early Oligocene of Mongolia (Briant & McKenna, 1995; Hautier *et al.* 2011; Wang, 2001). For this reason, particular interest attaches to the Namibian fossil which is not only appreciably older than the Mongolian one, but in addition is represented by a more complete skull with mandibles associated with much of the post-cranial skeleton.

An important point about the Eocliff rodent collection is that many of the specimens are juveniles with unworn teeth, meaning that detailed cusp morphology can be studied. There are also many sub-adult, adult and senile individuals. Some tooth positions are

represented by dozens of specimens, which allows the range of morphological and metric variation to be accessed.

The range of metric variation in the incisors of *Tufamys woodi*, for example, suggests that this species was sexually bimodal.

### Geological and faunal contexts

The freshwater limestone deposit at Eocliff in the Sperrgebiet, Namibia (now the Tsaukhamb National Park) is a rich source of information about vertebrates of Late Eocene age (Mourer-

Chauviré *et al.* 2014, 2018; Pickford, 2015b, 2015c, 2015d, 2015e). For a recent summary of the geological and faunal contexts of the limestone, refer to Pickford (2015a).

**Table 1.** Provisional list of rodent species from Eocliff, modified from Pickford (2008b, 2015b) arranged from largest to smallest (see Fig. 42).

Taxon	Length d/4-m/3	Length D4/-M3/	D3/	Other localities	Reference
Phiomyidae/Diamantomyidae	11.4 mm	10.2 mm	Yes	--	This paper
<i>Prepomonomys bogenfelsi</i>	10.2 mm	8.6 mm	Yes	Silica North, Eoridge	Pickford <i>et al.</i> 2008b
<i>Prepomonomys</i> small sp.	9.2 mm	7.9 mm	Yes	--	This paper
<i>Tufamys woodi</i>	7.4 mm	6.5 mm	No	Silica North	<i>nomen nudum</i> in Pickford, 2015b
<i>Silicamys cingulatus</i>	--	--	--	Silica North	Pickford <i>et al.</i> 2008b
Undetermined genus A	5.2 mm	5.3 mm	Yes	--	This paper
Undetermined genus B	4.5 mm	4.6 mm	No	--	<i>Namaphiomys</i> in Pickford, 2015b

### Material and methods

The fossils described herein are curated at the Geological Survey of Namibia (GSN) and have the prefix EC (for Eocliff, the locality where they were collected). There are several concentrations of fossils at Eocliff, each one given a separate number, even though preliminary analyses indicate that all the occurrences contain similar faunas, implying deposition over a relatively short span of geological time.

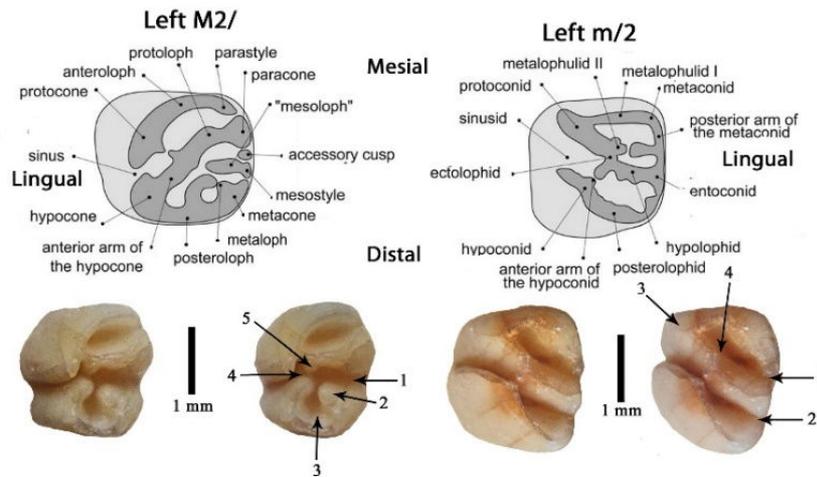
Fossils were released from their limestone matrix using a 7% solution of formic acid buffered with calcium triphosphate. After acid treatment, the fossils were washed in cool flowing water for 24 hours, dried and consolidated with glyptol dissolved in acetone. Delicate fossils which broke were repaired with cyanoacrylate using a needle point to position tiny droplets of the glue to the surfaces to be joined together.

The fossils from Eocliff were photographed with a Sony Cybershot camera with its lens

placed over the eyepieces of a binocular microscope, thereby obtaining stereo pairs of images. Scans of the holotype were taken and treated by M. Mason at the Cambridge Biotomography Centre (UK).

Cheek tooth nomenclature follows the system of Marivaux *et al.* 2004, and Sallam *et al.* 2011 (Fig. 1). Nomenclature of the ankle bones is modified from Ginot *et al.* (2016).

Measurements of larger specimens were taken with sliding calipers to the nearest tenth of a mm. In mesial and distal views, cheek teeth of *Tufamys woodi* are curved from root to crown (concave lingually in lower teeth, concave buccally in upper teeth) and the molars have concavo-convex mesial and distal surfaces. The D4/ and d/4 have prominent mesial extensions which overhang the cervix. Because of this morphology the dimensions of the occlusal surfaces of the teeth continually change through life. For this reason, in this paper measurements are given to one significant figure.



**Figure 1.** Top row : cheek tooth nomenclature of hystricognath rodents employed in this paper, based on the schemes of Marivaux *et al.* 2004 and Sallam *et al.* 2011. Lower row : stereo images of molars of *Tufamys woodi* with comments (scale : 1 mm). Upper molars of *Tufamys* show 1) absence of accessory cusp and mesostyle between the paracone and metacone, 2) presence of a distinct cusplet at the mesial end of the metaloph joined to the metacone by a short low endocrista, 3) no mesial crest on the posteroloph, 4) clear separation by a deep slit between the anterior arm of the hypocone and the protoloph, 5) presence of a short distally directed crest from the lingual end of the protoloph separated from the anterior arm of the hypocone by a deep slit, and a strong join between the lingual end of the protoloph and the protocone. Lower molars show 1) weak posterior arm of metaconid and no cristid extending buccally from it, 2) low sill at the end of the postero-lingual fossettid, 3) weak antero-buccal projection of the pre-protocristid, 4) absence of, or much reduced, metalophulid II.

### Taphonomy

The holotype specimen was enclosed in a block of limestone with the skull and mandibles in anatomical connection but slightly displaced from each other, and with various bones of the post-cranial skeleton inside the oral cavity and surrounding the skull, especially on its ventral side.

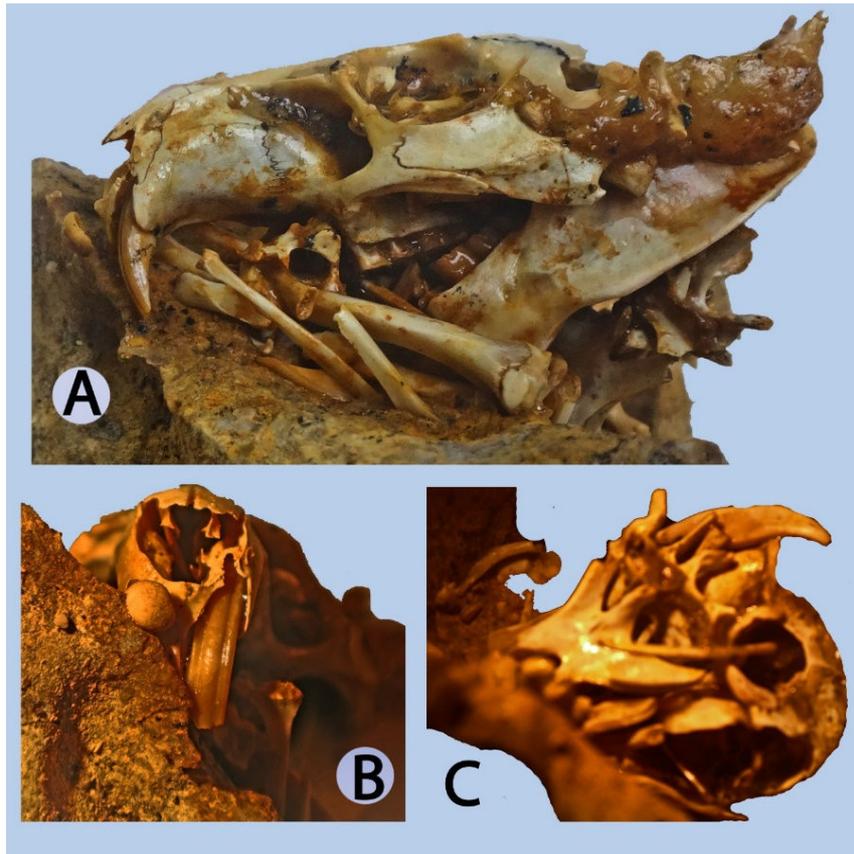
The only other fossils in direct association with the skull were an edentulous mandible fragment of a macroselidid, an isolated molar of a small phiomyid and several small vertebrae that could belong to the phiomyid.

The arrangement of the bones in this fossil concentration (mandible in anatomical connection with the cranium, vertebrae close to the foramen magnum and between the mandibular rami, the tibia, fibula, radius and manual and pedal phalanges and metapodials inside the diastemal space, several ribs preserved (Figs 2, 3) strongly indicate that this assemblage represents a pellet, probably a regurgitation pellet of an owl, that has suffered little or no post-regurgitation disturbance.

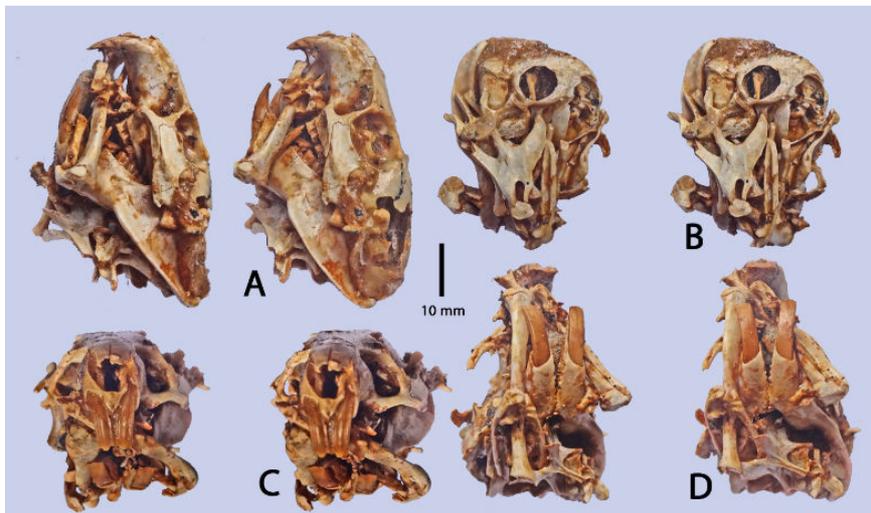
The left d/4 was not *in situ* in the mandible (Fig. 2A) but was inside the oral cavity and could be fitted back in its proper place once the specimen had been fully cleaned. This fact attests to the absence of post-depositional disturbance.

In dorsal view the skull has a small circular depression in the left parietal, close to where the rest of the parietal is broken away (the broken piece is preserved separately). This damage accords with the kind of injury caused by the claws of a bird of prey when the animal is seized abruptly from above, the claw penetrating the cranial cavity thereby ensuring rapid death of the prey. The left parietal was ripped open, and this damage permitted some small phalanges to enter the brain case during digestion.

From all this evidence, it is concluded that the skeleton and skull from EC 10 represent a single individual which is herein selected as the holotype of the new genus and species, *Tufamys woodi*.



**Figure 2.** The holotype specimen of *Tufamys woodi* gen. et sp. nov. from EC 10, Namibia, partly freed from its limestone matrix. A) left lateral view, B) anterior view (humeral head obscuring the right di2/), C) ventro-posterior view. Note the paucity of fossils in the limestone surrounding the specimen contrasting with the high concentration of bones close to the ventral side of the skull and inside the oral cavity, all of which indicates that this was a pellet. Lack of duplication of elements indicates that a single individual is represented in the pellet.



**Figure 3.** Stereo views of the holotype of *Tufamys woodi*, gen. et sp. nov. from EC 10, at a more advanced stage of preparation than in Fig. 2. A) left lateral view, B) ventro-posterior view showing some fore limb elements lying parallel to the tooth rows, C) anterior view, D) ventro-anterior view. Note the postcranial bones in the oral cavity and on the ventral side of the skull. Note also the presence of vertebrae and ribs close to the foramen magnum and in the space between the mandibular rami and the left and right tibiae either side of the mandible, one crossing through the diastemal gap (scale : 10 mm).

## Systematic Palaeontology

### Order Rodentia Bowdich, 1821

#### Suborder Ctenohystrica Huchon, Catzefflis & Douzery, 2000

#### Infraorder Hystricognathi Tullberg, 1899

#### Family Tufamyidae nov.

**Type genus:** *Tufamys* gen. nov.

**Included genera:** *Efeldomys* Mein & Pickford, 2008

**Diagnosis:** Family of hystricomorph, hystricognath rodents in which the upper incisors are orthodont, labially have an open channel either side of a prominent central ridge, alveolar capsule of upper incisors terminate above the roots of D4/; D4/ and d/4 not replaced by a permanent counterpart, mesio-distally broad lower incisors with flat labial section, cheek teeth thryonomyid-like, upper cheek teeth with lingual part much taller than buccal part, lower cheek teeth with buccal part taller than lingual part, small post-orbital process of frontal with no posterior constriction, fibula complete and unfused to tibia.

Tufamyidae differs from Thryonomyidae in the style, position and quantity of channels in the upper incisors : single open channels either

side of a prominent central ridge in *Tufamys* and *Efeldomys*, three slit-like channels crowded into the mesial half of the crown in *Thryonomys*. Dentine enamel junction in DI2/ undulating.

Tufamyidae differs from Renefossoridae Mein & Pickford (2008) by the presence of channelled upper incisors, less pro-odont incisors, posterior choanae positioned further forwards and elongated cranium, but it shares some characters with the latter genus including large infra-orbital foramen and lower incisors mesio-distally broad with a flat labial section.

Tufamyidae differs from Phiomyidae by the W-shaped section of the pulp cavity in the upper incisor, contrasting with the unbranched labiolingually oriented slit in Phiomyidae (Wood, 1968).

#### Genus *Tufamys* nov.

**Type species:** *Tufamys woodi* sp. nov.

**Diagnosis:** Small thryonomyoid with channelled upper incisors (two open grooves either side of a prominent central ridge) undulating dentine-enamel junction (dej) and mesio-distally broad lower incisors with flat labial surface in section. Upper incisor capsule (radicular apex) occupies the space immediately above the D4/. Post-orbital process of the frontal bone present but small and frontal not

narrower behind the post-orbital process than in front of it. Molars trilophed. Angular process of mandible elongated distally well beyond articular condyle, coronoid process low (about the same level as the mandibular condyle) and relatively rounded in profile. Dental formula (1).0.(1).3 / (1).0.(1).3 (brackets denote retained deciduous teeth). Fibula complete, unfused to tibia.

**Differential diagnosis:** *Tufamys* cheek teeth superficially resemble those of Gaudeamuridae, save for their less-developed hypsodonty and lack of supplementary cusplets (mesostyle, accessory cuplet) and ridges in the fossettes, but the genus differs fundamentally from the members of this family by the presence of mesio-distally broad incisors, the upper incisors being channelled, the radicular capsule of the

upper incisors lying close above the roots of the D4/, the section of the lower incisors having a flat labial part, the coronoid process of the mandible being lower than the articular process, and the angular process of the mandible being much elongated distally, extending well to the rear of the mandibular condyle. The posterior choanae invade the palate as far anteriorly as the middle of M2/ (at the front of M3/ in

*Gaudeamus*), the palatine foramina are at the level of the front of M1/, and the less developed post-orbital process of the frontal without the narrowing behind the post-orbital process. Furthermore, D4/ and d/4 are not replaced by a permanent tooth.

*Tufamys* differs from *Thryonomys* by its smaller dimensions and by the presence of two grooves in the upper incisor rather than three, the two grooves being either side of a prominent central ridge, unlike the three grooves in *Thryonomys swinderianus* which are squeezed into the mesial half of the tooth. Furthermore, the dentine-enamel junction in the upper incisor of *Tufamys* is strongly undulating and the enamel thickness is constant from mesial to distal edges, whereas in *Thryonomys* the dentine-enamel junction is considerably less undulating, almost straight, and the grooves are incised into the enamel.

*Tufamys* resembles *Efeldomys* by its incisor morphology and dimensions as well as by

several features of the skull such as the orthodont upper incisors, the radicular termination of the upper incisor above the D4/, the forward position of the posterior choanae invaginating between the M2/ and M3/ and the low coronoid process of the mandible. The molars of *Efeldomys* however, have converged on those of bathyergids, with relative reduction of the occlusal dimensions of the P4/, M1/ and M3/ leaving the M2/ as the largest cheek tooth (Mein & Pickford, 2008). Furthermore, the cheek teeth in *Efeldomys* are relatively taller than those of *Tufamys* and the D4/ narrows more towards its cervix. But overall *Efeldomys* is close to *Tufamys* and is probably descended from it.

*Tufamys* differs from Oligocene South American *Changquin* by its smaller dimensions and less hypsodont cheek teeth but a relationship between these two genera can be imagined.

**Etymology:** *Tufa* is a soft, generally porous, superficial limestone deposit commonly formed around hardwater springs, the likely

depositional environment of the Eocliff Limestone from which this genus of rodent was first collected; *mys* is Greek for mouse.

**Species *Tufamys woodi* nov.**

**Diagnosis:** As for the genus. Length D4/-M3/ : 6.5 mm, length d/4-m/3 : 7.3 mm.

**Holotype:** GSN EC 10 Tw 1, skull with articulated mandibles and associated post-

cranial elements from fossil concentration EC 10 at Eocliff.

**Synonymy:** 2008, Pickford *et al.* *Apodecter cf stromeri* from Silica North (SN 9'08).  
2008, Pickford *et al.* *cf Bathyergoides* sp. from Silica North (SN 20'08).

**Type locality:** Eocliff, Namibia (fossil concentration EC 10).

**Other locality:** Silica North (Pickford *et al.* 2008).

**Other material from Eocliff:**

**Table 1.** *Tufamys woodi* material studied for this paper.

Locality	Maxillae	Mandibles	Isolated upper incisors	Isolated lower incisors	Isolated cheek teeth
EC 1	-	1	-	-	-
EC 4	6	3	14	4	74
EC 6	11	14	19	10	61
EC 7	14	48	36	8	194
EC 8	9	4	3	3	35
EC 9	19	23	47	12	63
EC 10	8	14	21	7	92

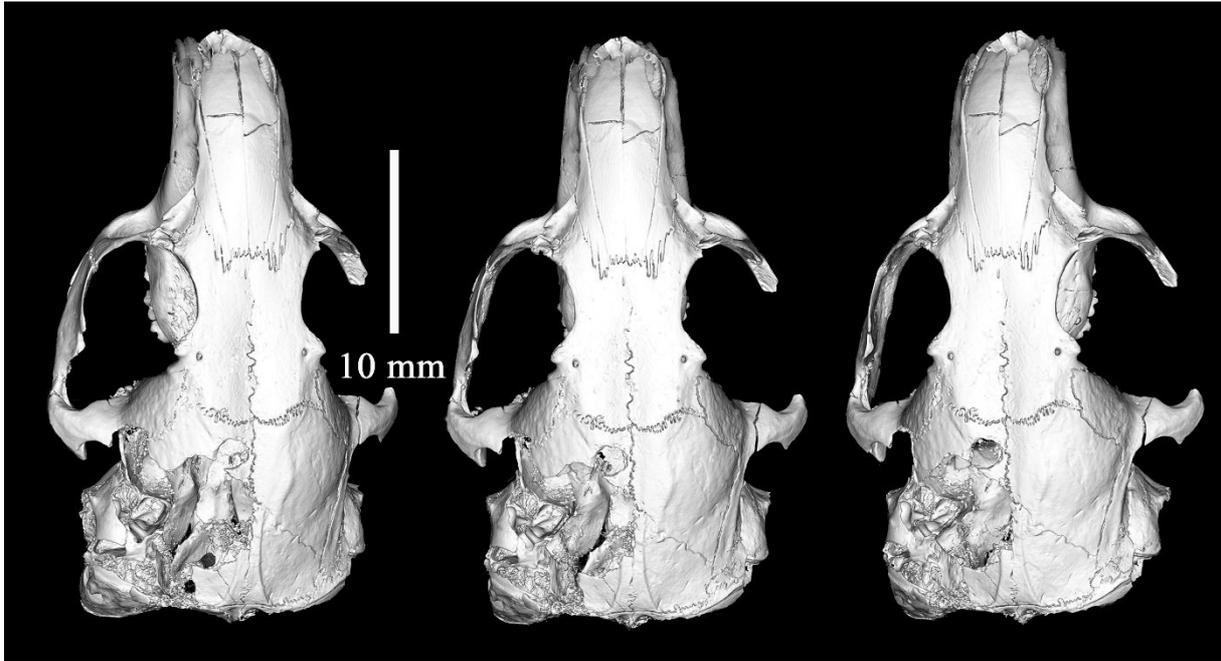
**Age:** Bartonian (possibly Priabonian) (Eocene).

**Etymology:** The species name is in honour of the pioneer student of African Palaeogene rodents, Albert E. Wood. Note that the name

was published as a *nomen nudum* by Pickford 2015d. This paper validates the name.

## Description

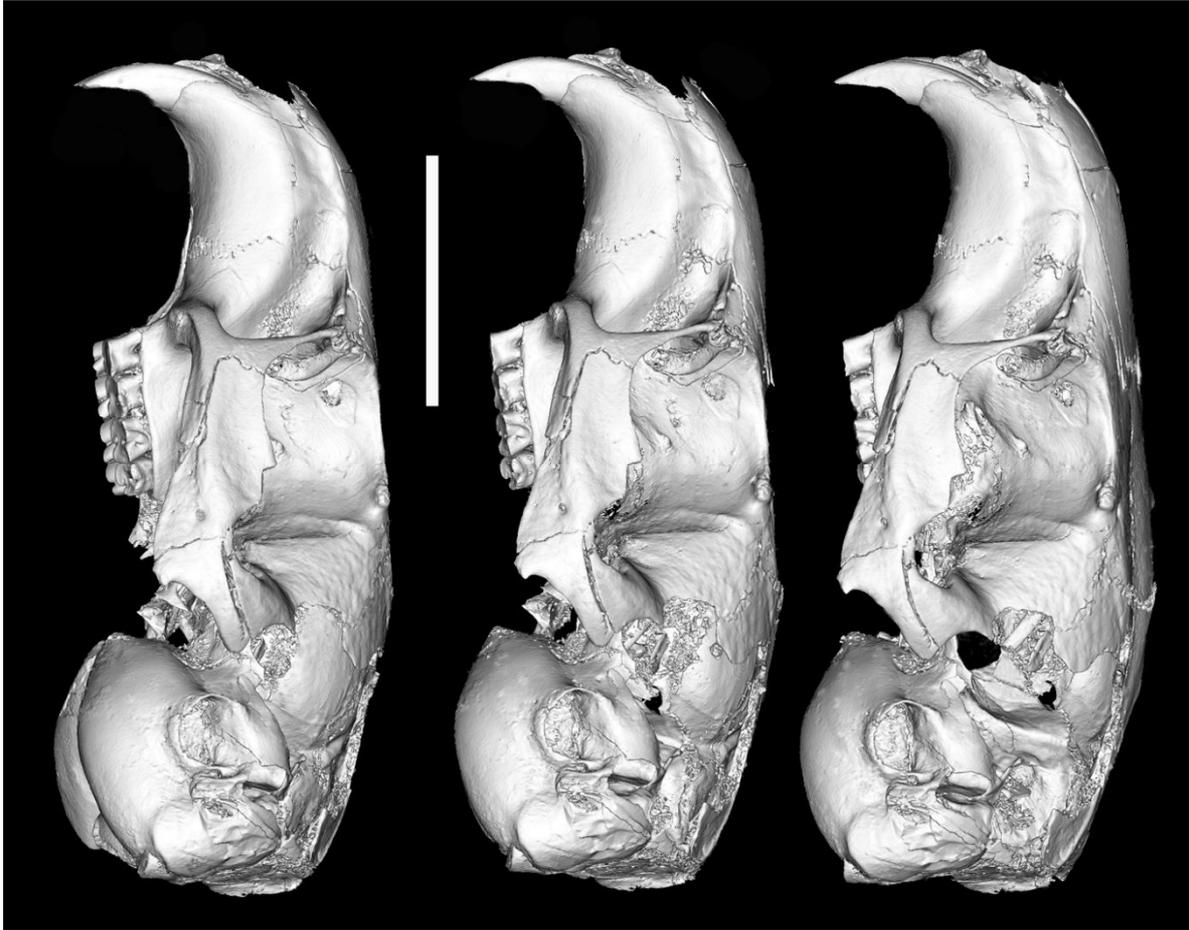
### *Skull and mandible*



**Figure 4.** Stereo dorsal views of the holotype cranium of *Tufamys woodi* from locality EC 10, Sperrgebiet, Namibia (scale : 10 mm).

In dorsal view (Fig. 4), the skull of *Tufamys* shows a disposition of the bones which is basically similar to that of the rat (*Rattus*) (Schaub, 1958). The nasals are elongated, the suture with the frontals being slightly behind the leading edge of the orbits, and their anterior extremities do not extend beyond the premaxilla beneath. The premaxilla contacts the frontal distally, the premaxillo-frontal suture extending slightly further to the rear than the naso-frontal suture. The lacrymal bone is located behind a small shelf-like process of the maxilla which roofs over the vast infra-orbital foramen. The zygomatic process of the maxilla sweeps steeply laterally at an angle of about 70°, before turning towards the rear. The jugal terminates anteriorly in a very anterior position, above the front of the M1/ and is disposed such that its distal end is slightly further from the sagittal plane than its proximal end. The frontal bones are broadest at the post-orbital processes which

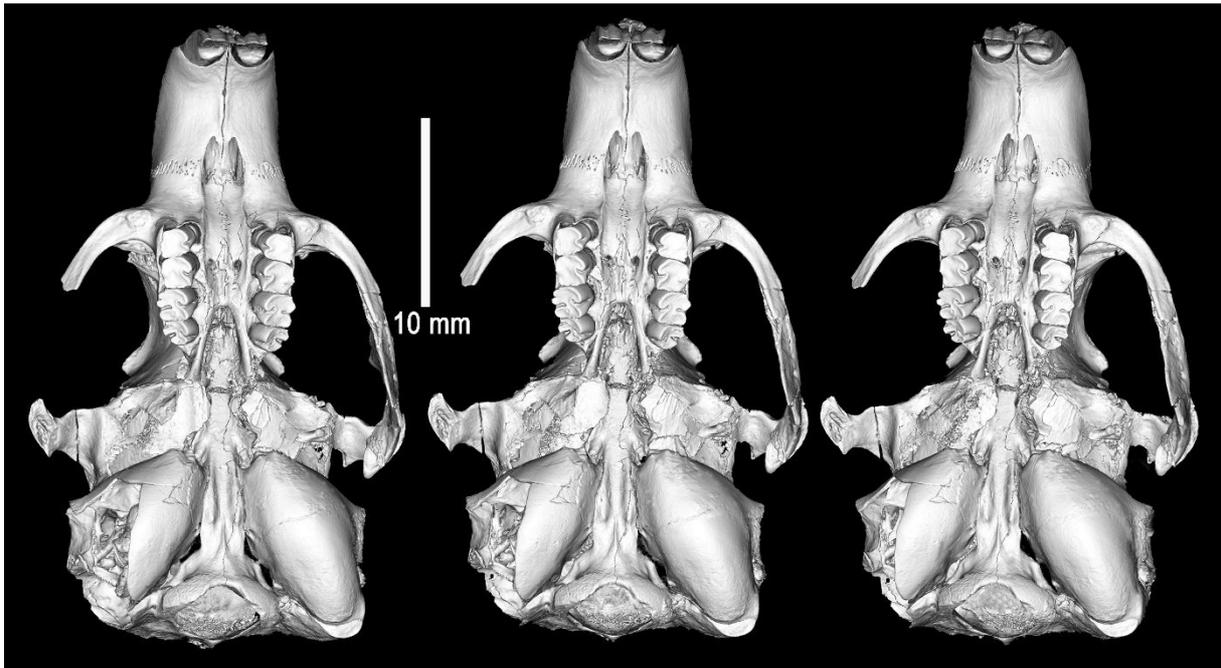
are slightly swollen but medio-laterally short. The post-orbital constriction is weak, the frontal bones being slightly narrower in front of the post-orbital processes than behind them. Each post-orbital process is accompanied by a prominent foramen on the roof of the skull. The skull is broadest at the temporal bone where it forms the distal portion of the zygomatic arch. The parietals are prominent, the suture with the frontals being in line with the rear of the temporal fossa a short distance behind the post-orbital processes and at right angles with the sagittal suture. The parietal bone is large and its anterior margin extends between the parietal bones to form a V-shaped suture. Low but sharp-edged ridges mark its dorsal surface close to the sagittal plane, but they do not form a sagittal crest. These ridges diverge gently distally before blending into the occipital crests which form the rear of the dorsal part of the skull.



**Figure 5.** Stereo left lateral views of the holotype cranium of *Tufamys woodi* from locality EC 10, Sperrgebiet, Namibia (scale : 10 mm).

In lateral view (Fig. 5) the nasals form the roof of the snout but they stop short anteriorly, slightly behind the ends of the premaxillae. Laterally the premaxilla has an almost vertical suture where it contacts the maxilla, but it turns distally near the dorsal surface of the skull to terminate behind the leading edge of the orbit where it contacts the frontals. The upper incisors are orthodont, the wear facet with the lower incisor being located vertically beneath the anterior ends of the nasals. The lacrymal lies immediately behind a prominent shelf-like process of the maxilla above the infra-orbital foramen. The zygomatic process of the maxilla sweeps laterally where it joins the jugal bone whereupon it subdivides into two parts, the lower branch with a ventral expansion extending distally beneath the jugal, the other ascending vertically to wall off the lateral side of the infra-orbital foramen. The upper half of the latter process is extremely slender where it contacts the lacrymal. The jugal has a triangular extension in the middle of its dorsal edge, which

forms a short post-orbital process. The palatal process of the maxilla is robust and carries four cheek teeth. The incisor alveolus forms a low curved jugum on the lateral side of the premaxilla and the front of the maxilla, its radicular end terminating above the anterior cheek tooth, in line with the root of the zygomatic process of the maxilla. There is a curved depression paralleling the upper edge of the incisor jugum where the medial division of the masseter inserts after passing through the infra-orbital foramen (Marcin, 2000). The post-orbital processes project slightly laterally without bending ventrally or dorsally. The bullae dominate the rear of the skull, each with a large ovoid external auditory meatus in the upper half of the bulla opening dorso-posteriorly. The bulla is quite inflated and has a pointed anterior end which terminates in line with the most distal parts of the zygomatic arches. The posterior apophysis of the temporal is hidden by the upper parts of the bulla.



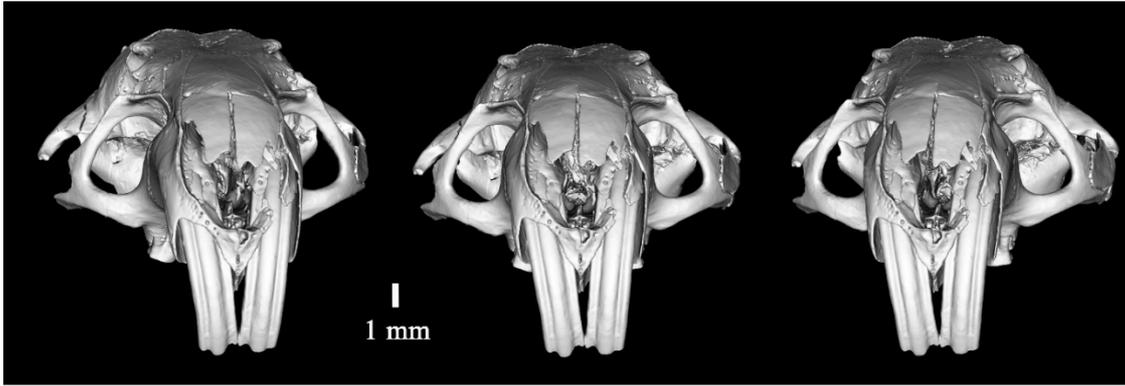
**Figure 6.** Stereo palatal views of the holotype cranium of *Tufamys woodi* from locality EC 10, Sperrgebiet, Namibia (scale : 10 mm).

In palatal view (Fig. 6), the cranium of *Tufamys* shows the presence of large temporal fossae which broaden posteriorly. The premaxillo-maxillary suture is at the rear of the incisive foramina which form two elongated oval depressions in the ventral surface of the diastema. The outer edges of the incisive foramina extend rearwards onto the maxilla, and continue as low ridges as far as the palatine bone between the distal edges of the M1/. This forms a long, narrow, but shallow depression in the sagittal quarter of the maxilla which bends ventrally towards the alveolar part of the maxilla and then extends horizontally between the anterior cheek teeth almost reaching the posterior choanae. The palatine foramina are prominent in the floor of this depression near its distal end, being located opposite the contact between the D4/ and M1/. The root of the zygomatic process of the maxilla shows a

tubercle close to the D4/ after which there is a shallow fossa extending distally where the lateral division of the masseter inserts. The posterior choanae invaginate between the posterior cheek teeth as far as the middle of the M2/. The external pterygoid apophyses are long and straight with a rounded ventral margin, and are slightly divergent towards the rear. The glenoid fossa is in a very lateral position and is comprised of a broad but short valley with a rounded roof with open anterior and posterior ends. The otic bullae (Figs 6, 7) dominate the posterior third of the skull, comprising two large ovoid bones oriented obliquely such that their front ends are closer to the sagittal plane than the rear ends. The basisphenoid intervenes between the two bullae. The occipital condyles are located in between the posterior ends of the bullae.



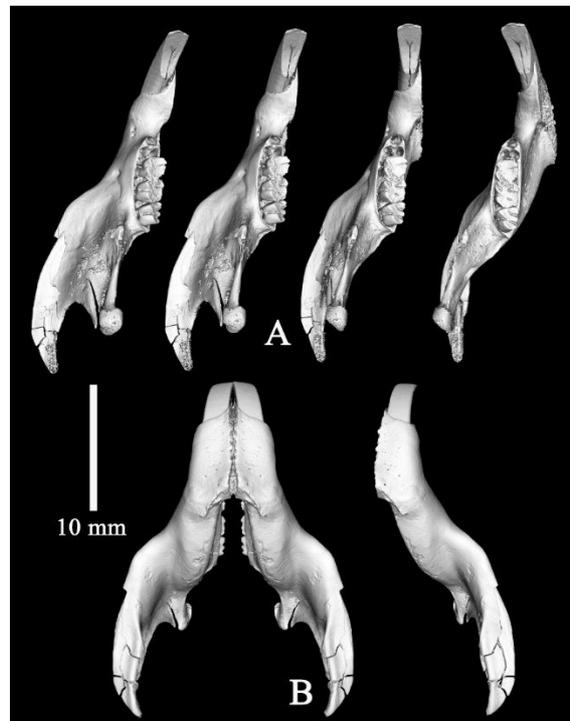
**Figure 7.** Stereo view into the interior of the right otic bulla to show some of the internal morphology and part of the external auditory meatus (scale : 2 mm).



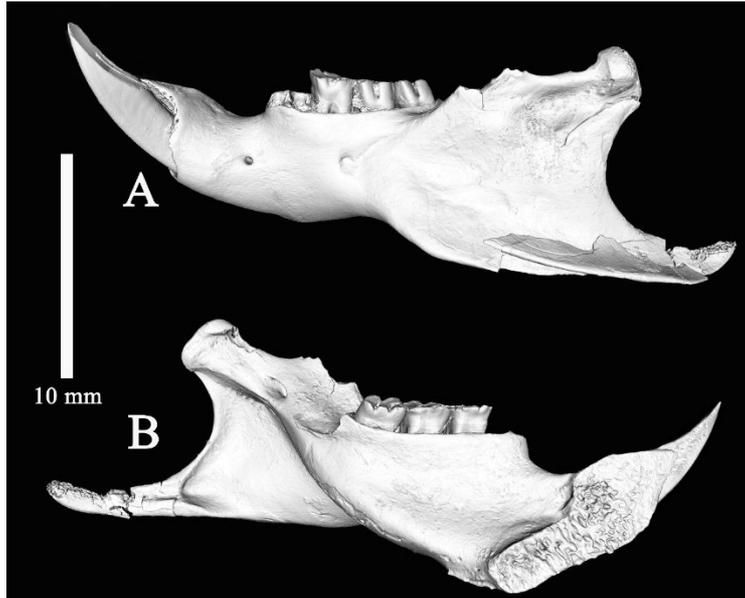
**Figure 8.** Stereo anterior views of the cranium of the holotype of *Tufamys woodi* (EC 10'13) to show the large infra-orbital foramen and the channeled morphology of the upper incisors, with a prominent central ridge and lower mesial and distal ridges separated from the central one by broad channels (scale at level of incisors : 1 mm).

In anterior view (Fig. 8), *Tufamys* shows a characteristic hystricomorphous condition with a vast infra-orbital foramen roofed over by a shelf-like process of the maxilla which projects slightly anteriorly. The nasals show a gently curved dorsal profile but there is no depression between them, unlike the situation in *Thryonomys* in which a valley is formed between the two nasal bones. The nasal bones also bend slightly ventrally towards their anterior extremities, unlike the nasals of *Thryonomys* which are horizontal throughout their length. The anterior end of the left nasal

has an encoche, but on the other nasal it is broken off. *Thryonomys* has an encoche but it is considerably larger and is located on the side of the nasal where the lateral half of the bone bends ventrally. The nasal margins of the premaxilla in *Tufamys* are sharp, and where the premaxillae meet anteriorly in the midline they form a triangular wedge of bone between the incisors. The outer edges of the premaxilla are not ridged but show a rounded profile, unlike the strong ridge that is present in *Thryonomys*, and which forms the dorsal margins of the masseteric fossa on the rostrum.



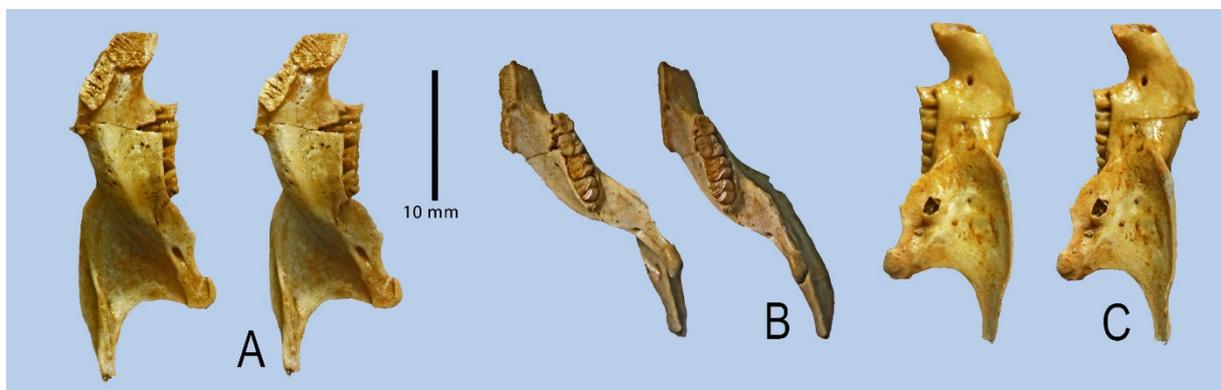
**Figure 9.** Stereo views of the holotype left mandible of *Tufamys woodi* from locality EC 10, Sperrgebiet, Namibia. A) occlusal view, B) stereo ventral view of left mandible with mirror image (scale : 10 mm).



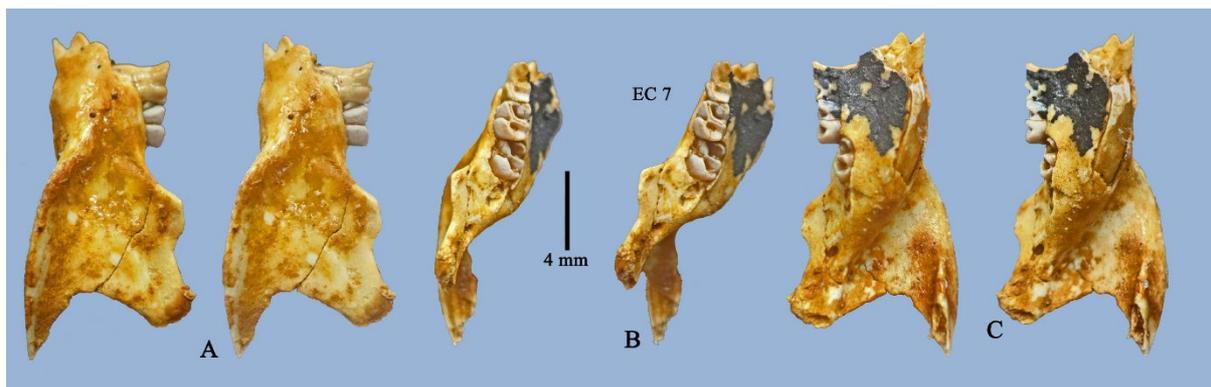
**Figure 10.** Views of the left mandible of the holotype of *Tufamys woodi* from locality EC 10, Sperrgebiet, Namibia. A) buccal view, B) lingual view (scale : 10 mm).

The mandible of *Tufamys* is hystricognath (Figs 9-12). The mental foramen is at mid-height of the jaw in the middle of the diastema, somewhat in advance of the d/4. The ventral margin of the masseteric fossa extends anteriorly as far as the level of the m/1 and posteriorly it forms an elongated angular process that terminates well behind the condyle. The coronoid process is low and rounded, not projecting above the condyle, and not having a posteriorly pointing process. The condyle is slightly above the occlusal surface of the cheek teeth. The ascending ramus is retired slightly such that, in lateral view, its root does not obscure the m/3. In lingual view, the

mandibular foramen enters the ramus well behind the tooth row at about the level of the occlusal surface. There is a large sublingual fossa behind the incisor alveolus which extends distally as far as the angular process. The incisor alveolus terminates distally behind and slightly lateral to the m/3. The symphysis is thicker superiorly than ventrally and its rear profile shows a vertical part close to the diastema, and a sloping part ventrally. The rear of the symphysis does not thin down to any great extent but shows a rectangular termination with rounded corners, and as such it develops a shallow genial fossa.



**Figure 11.** Stereo views of right mandible of *Tufamys woodi* from EC 9. A) lingual view, B) occlusal view, C) buccal view. Note the laterally flaring flange of the masseter fossa and the posteriorly elongated angular process (scale : 10 mm).



**Figure 12.** Stereo views of juvenile left mandible of *Tufamys woodi* from fossil concentration EC 7. A) buccal view, B) occlusal view, C) lingual view. Note the complete coronoid process which is exceptionally low and rounded, the low condyle, the laterally flaring flange of the masseter fossa, the posteriorly elongated angular process which curves sagittally towards the rear and the flat labial surface of the lower incisor (scale : 4 mm).

### **Dentition**

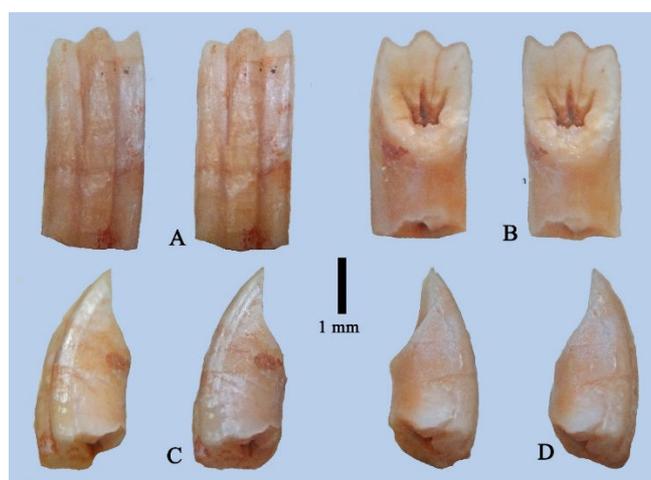
The upper dental formula of *Tufamys woodi* is (1)-0-(1)-3, the only antemolar cheek tooth being a retained D4/. There is no alveolus for a P3/ in any of the specimens examined (over 40 maxillae) and there is no sign that the D4/ is replaced by a permanent counterpart. A few individuals failed to develop the M3/ (Fig. 19b).

The upper incisors of *Tufamys woodi* are orthodont and the labial surface has three ridges separated by two broad channels, the central ridge being the most prominent (Figs 8, 13). The thickness of enamel is constant from mesial to distal sides, unlike the enamel in the incisors of *Thryonomys* in which the enamel is thick on the ridges and thin at the grooves. The pulp cavity in the upper incisor of *Tufamys* has a complex

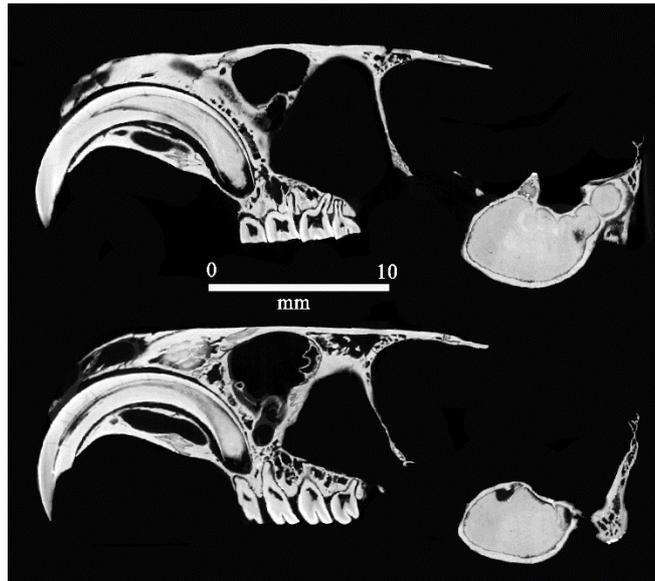
outline comprised of three slits pointing labially and a rounded profile lingually.

The lingual side of the crown is enamel-free with a rounded profile. The enamel covering the labial side extends a short way onto the mesial and distal edges of the tooth. In lateral view the capsule of the alveolus of the upper incisor is observed to terminate in the space immediately above the roots of the D4/ (Fig. 14), and it therefore encroaches on the mesial part of the alveolar process of the cheek teeth. This is perhaps the main reason why the D4/ is not replaced in this rodent.

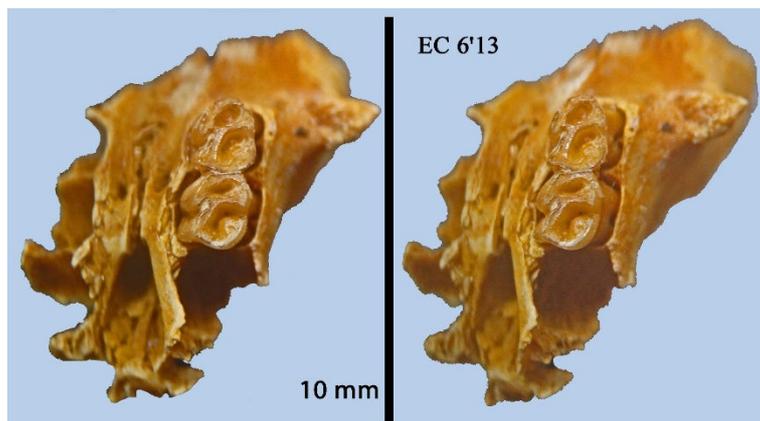
The wear facet at the apex of the incisor shows a change in slope from vertical near the apex to about 150° lingually, unlike the right-angled wear facet that occurs in *Thryonomys*.



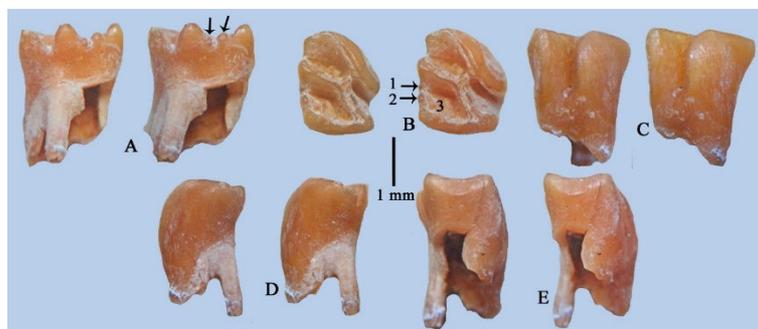
**Figure 13.** Stereo views of upper incisor of *Tufamys woodi* from EC 9, Eocliff, Namibia. A) labial, B) lingual, C) and D) side views (scale : 1 mm).



**Figure 14.** Parasagittal sections along the upper incisor in the holotype skull of *Tufamys woodi* to show the morphology of the incisor alveolar capsule and its relation to the alveolar process of the cheek teeth. In the lower frame note how the capsule extends as far as the roots of D4/ and therefore takes over the space that would have been occupied by the mesial part of the cheek tooth alveolar process had the capsule been positioned more anteriorly, as it is, for instance, in *Gaudeamus*. The cheek tooth alveolar process is well-developed above the M1/-M3/.



**Figure 15.** Oblique stereo view of a damaged palate of *Tufamys woodi* (EC 6'13) showing the occlusal surfaces of the lightly worn left D4/ and M1/ (scale : 10 mm).



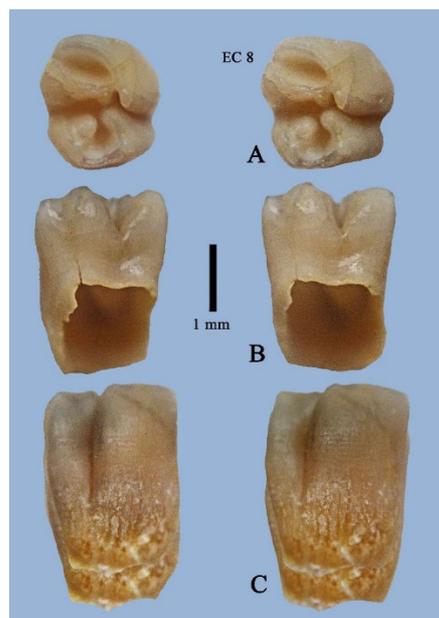
**Figure 16.** Stereo views of lightly worn right D4/ of *Tufamys woodi* from fossil concentration EC 6, Eocliff, Namibia. A) buccal, B) occlusal, C) lingual, D) mesial, E) distal views. 1 : small cusplet at base of post-paracrista (= accessory cusp in Fig. 1), 2 : small cusp at base of pre-metacrista (= mesostyle in Fig. 1), 3 : swelling in mesial face of metacone (scale : 1 mm).

The D4/ is comprised of four main cusps; protocone, paracone, hypocone and metacone positioned near the corners of the tooth, the ensemble forming an ovoid crown slightly narrower anteriorly than posteriorly (Figs 15, 16, 18-20). The protocone is linked to the parastyle via a well-developed anteroloph, the paracone is linked to the hypocone via a strongly developed protoloph while the hypocone is linked to the metacone via a weakly expressed transverse posteroloph.

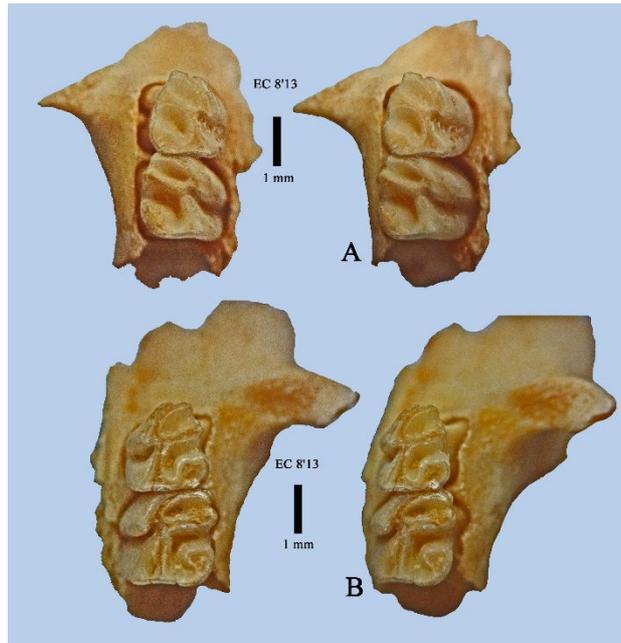
The anteroloph is obliquely oriented, extending from the midline of the tooth mesially towards the middle of the lingual side of the tooth. It is strongly linked to the protoloph via the endo-protocrista which courses disto-buccally to join a crest running mesio-lingually from the middle of the protoloph. The protoloph extends obliquely right across the crown from the mesio-buccal corner of the tooth to the hypocone on the disto-lingual corner of the tooth. The posteroloph is orthogonal to the long

axis of the crown, and walls off the rear of the tooth.

There are short cristae running from the rear of the parastyle and the front of the paracone (pre-paracrista) which meet low down, thereby walling off a shallow mesio-buccal fovea. The v-shaped sinus between the protocone and hypocone is angled such that it opens disto-lingually and there is no hint of a pre-hypocrista interrupting its rear wall. The occlusal basin located between the paracone and the metacone is open buccally except near its floor, where weak post-paracrista and pre-metacrista meet each other low down near the buccal edge of the crown. The ends of these cristae are developed into small low cusplets, best seen in unworn specimens (Fig. 16). This basin shows no sign of an accessory cusplet, mesostyle or mesoloph and there is no indication of a crest leading anteriorly into this basin from the posteroloph, but there is a low swelling in the mesial face of the metacone (Fig. 16).



**Figure 17.** Stereo views of germ of right M2/ of *Tufamys woodi* (EC 8). A) occlusal view, B) buccal view, C) lingual view (scale : 1 mm).

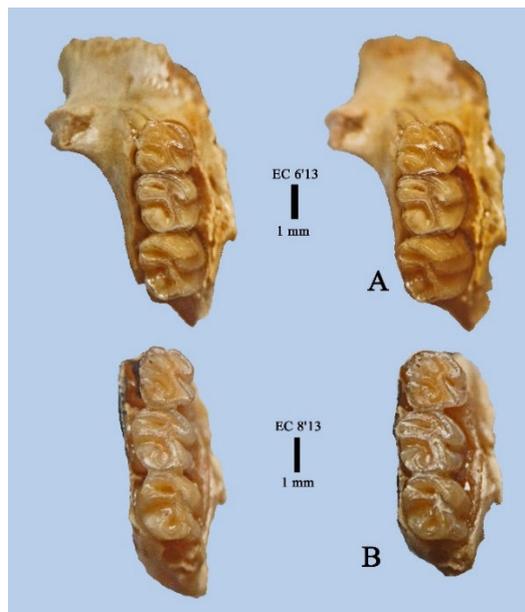


**Figure 18.** Stereo occlusal views of two maxillae of *Tufamys woodi* (EC 8'13) with lightly worn D4/ and M1/. A) right maxilla, B) left maxilla (scales : 1 mm).

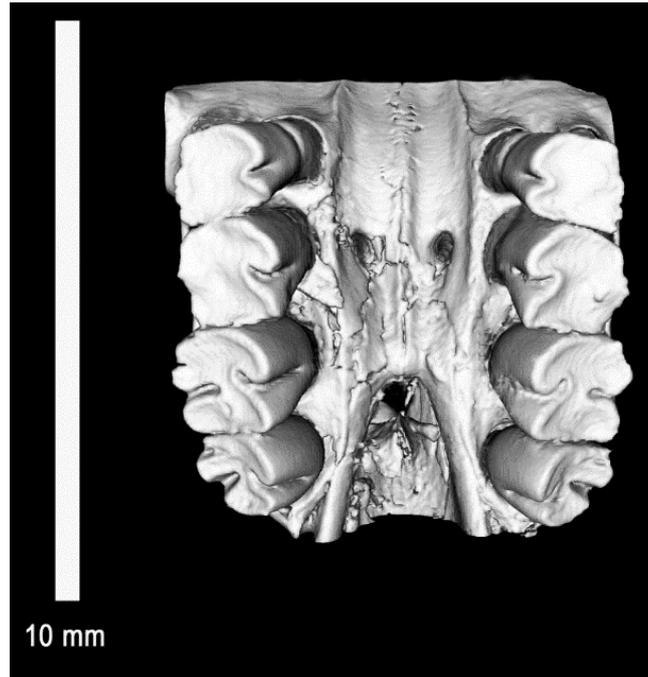
The M1/ is in many ways an enlarged copy of the D4/ (Figs 15, 18-20). The only significant morphological difference is the weaker development of the post-paracrista and the pre-metacrista, which means that the occlusal basin between the paracone and metacone is more open buccally with only a low sill at its buccal edge, although the height of the sill seems to be slightly variable in the available sample. The

metacone is large, and this contributes to shaping the basin into a right-angled L-shape, with a transverse buccal half and a distally directed central half. In addition the crown is slightly taller than that of the D4/.

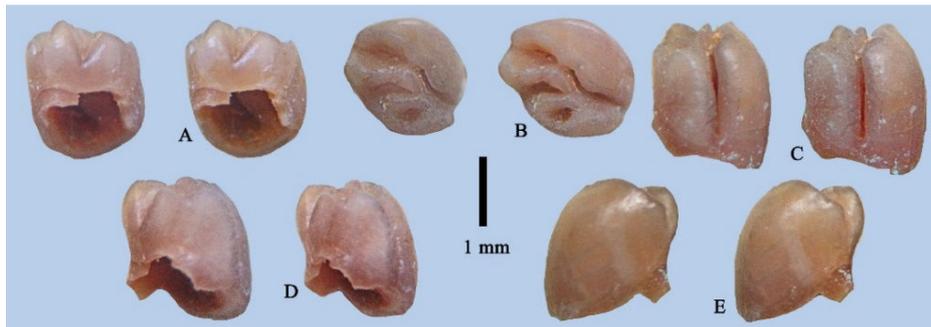
The M2/ is of similar construction to the M1/ and is of almost the same dimensions as it (Figs 17, 19-20).



**Figure 19.** Right maxillae of *Tufamys woodi*. A) EC 6'13, containing medium worn D4/ to lightly worn M2/ and B) EC 8'13, an aberrant individual containing D4/-M2/ and no development of the M3/, the alveolar process is the usual pattern in front of the D4/ but it terminates immediately behind the M2/ (scale bars : 1 mm).



**Figure 20.** Scan of the palate of the holotype of *Tufamys woodi* from EC 10, showing the heavily worn teeth, and the relative reduction of the M3/ compared to M2/ and M1/ (scale : 10 mm).



**Figure 21.** Stereo views of an unworn right M3/ of *Tufamys woodi* from fossil concentration EC 7, Namibia. A) buccal, B) occlusal, C) lingual, D) distal, E) mesial (scale : 1 mm).



**Figure 22.** Stereo occlusal views of three unworn left M3/s of *Tufamys woodi* from EC 6 to show some of the variation in cusp layout and dimensions in this tooth (scale : 1 mm).

The M3/ of *Tufamys woodi* is tri-lophed as in the M1/ and M2/, but the crown is shorter and

narrower and its distal half is much reduced in breadth relative to the mesial half (Figs 21-23).

**Table 1.** Measurements (in mm) of upper cheek teeth of *Tufamys woodi*. All specimens are in maxillae. N.B. deeply worn D4/s are shorter than unworn specimens. Measurements of the teeth of the type specimen are not given because they are heavily worn (lt – left, rt – right).

Catalogue	Tooth	Mesio-distal length	Bucco-lingual breadth
EC 7'14	D4/ lt	1.3	1.8
EC 8'13	D4/ lt	2.0	1.9
EC 6'13	D4/ lt	1.5	1.5
EC 10	D4/ lt	1.8	1.6
EC 4'13	D4/ rt	1.6	1.7
EC 8'14	D4/ rt	1.9	1.8
EC 6'13	D4/ rt	1.4	1.8
EC 7'14	M1/ lt	1.6	1.9
EC 8'13	M1/ lt	1.8	1.8
EC 6'13	M1/ lt	1.9	1.7
EC 10	M1/ lt	1.7	1.6
EC 10	M1/ lt	1.7	2.0
EC 4'13	M1/ rt	1.8	1.9
EC 8'14	M1/ rt	2.0	1.9
EC 6'13	M1/ rt	1.7	1.9
EC 7'14	M2/ lt	1.8	1.9
EC 4'13	M2/ rt	2.0	1.9
EC 6'13	M2/ rt	1.8	1.7
EC 7'14	M3/ lt	1.6	1.5
EC 9'14	M3/ lt	1.8	1.6
EC 9'14	M3/ lt	1.5	1.4
EC 7'14	M3/ rt	1.6	1.6



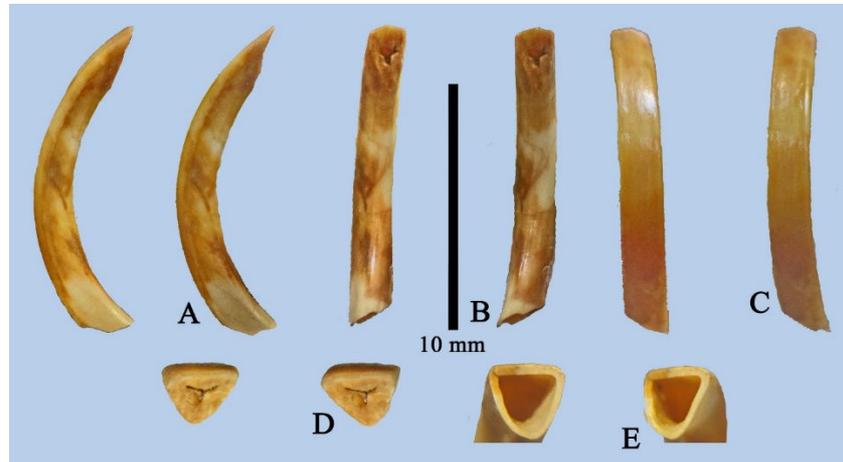
**Figure 23.** Stereo palatal view of EC 7'13, palate of *Tufamys woodi*. Note the palatine foramina in line with the middle of M1/ and the deep invagination of the posterior choanae to the level of the middle of M2/ (scale : 1 mm).

### Lower dentition

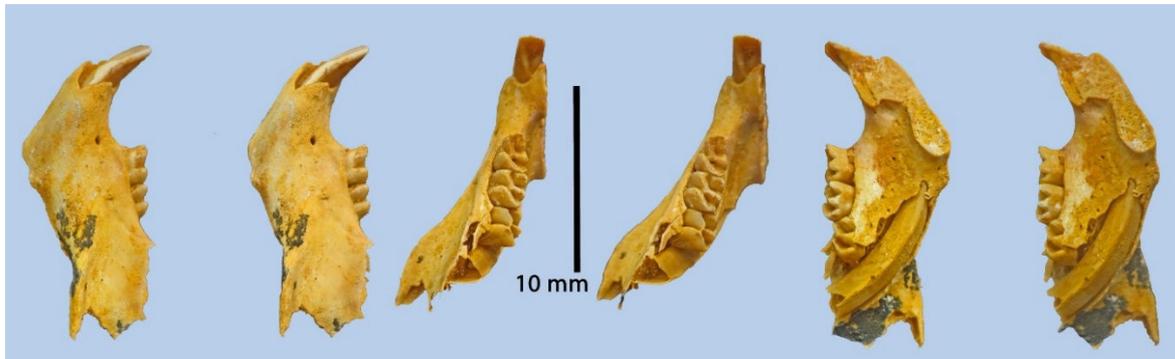
The lower dental formula is (1)-0-(1)-3. The d/4 is not replaced by a permanent counterpart.

The lower incisor (Figs 24, 25) is broad with a flat, enamel-covered labial side, and a rounded enamel-free lingual side as in other rodents, and the enamel extends only slightly onto the mesial

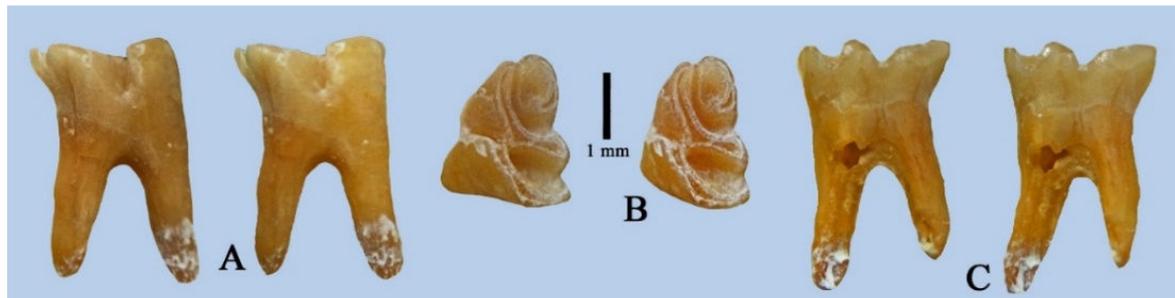
and distal sides of the tooth. Its radicular apex extends backwards beyond the cheek teeth, terminating immediately behind and buccal to the m/3 and slightly higher than it. The exposed part of the incisor is quite low (Fig. 25).



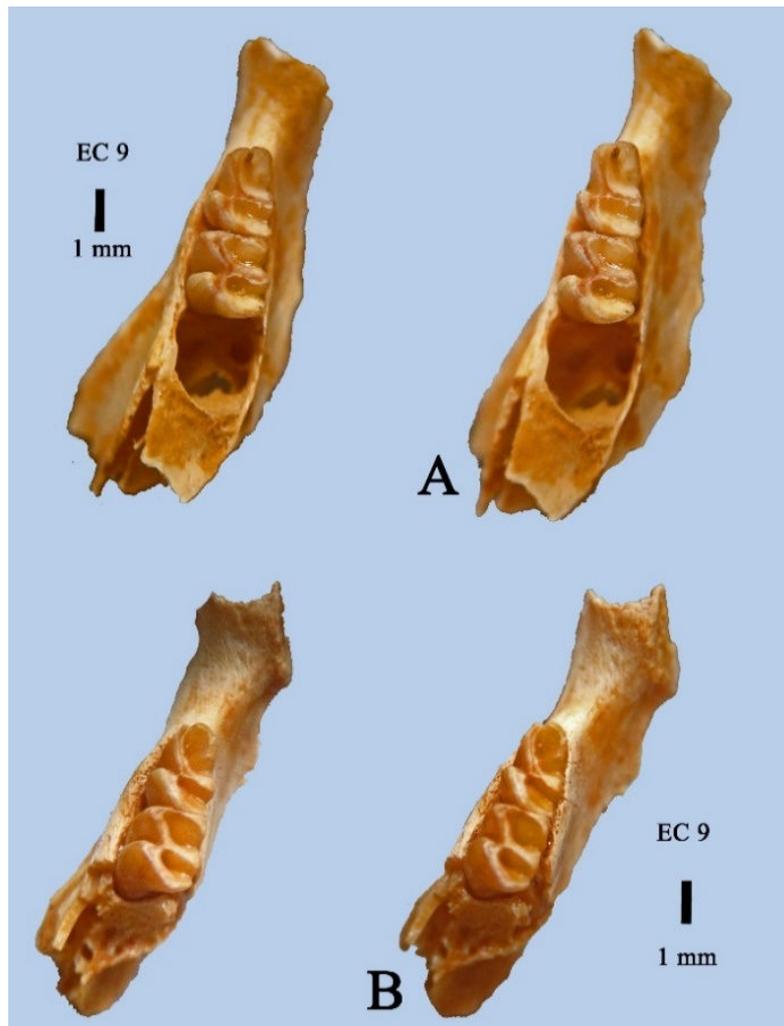
**Figure 24.** Stereo images of left lower incisor of *Tufamys woodi* from Eocliff, EC 9, Namibia. A) buccal, B) lingual, C) labial, D) apical, E) radicular views (scale : A-C - 10 mm, D-E - 5 mm).



**Figure 25.** Stereo images of juvenile left mandible of *Tufamys woodi* from Eocliff, EC 7, containing the incisor d/4 and m/1-m/2. A) buccal, B) occlusal, C) lingual views (scale : 10 mm).



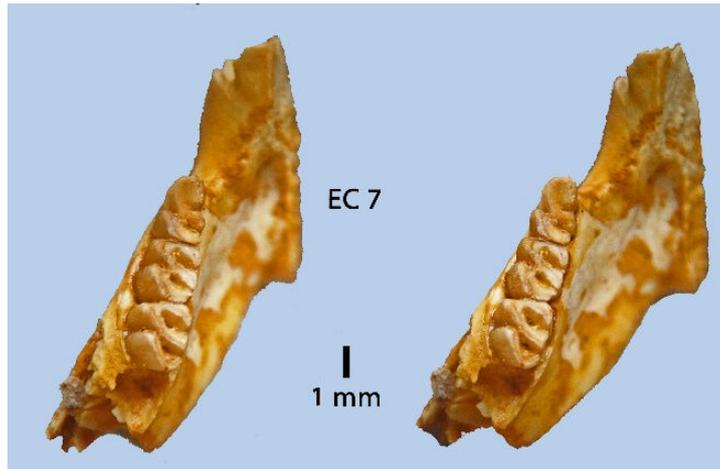
**Figure 26.** Stereo views of lightly worn left d/4 of *Tufamys woodi* from fossil concentration EC 6, Namibia. A) buccal, B) occlusal, C) lingual views (scale : 1 mm).



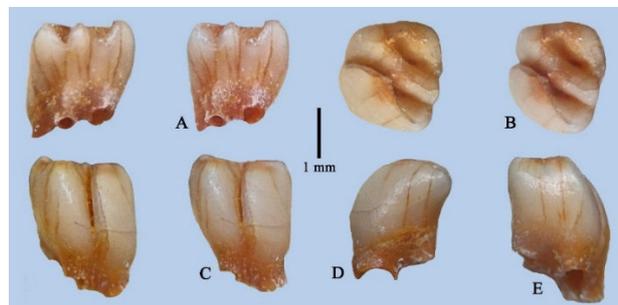
**Figure 27.** Stereo occlusal views of two juvenile left mandibles of *Tufamys woodi* from locality EC 9, to highlight the crown morphology of the d/4 and m/1. Note that the floor of the capsule of the unerupted m/2 in (A) shows alveoli for four roots (scales : 1 mm).

The anterior lower cheek tooth is the d/4, which appears not to be replaced in this species (Figs 25-28, 30). Its occlusal outline is ovoid with the mesial end narrower than the distal end. Its occlusal surface is comprised of three oblique lophids, a short anterior one comprised of the angled metaconid in a mesio-lingual position which sends a narrow cristid (metalophulid I) buccally towards the protoconid. The middle oblique lophid joins the protoconid to the entoconid via the ectolophid and hypolophid, and the distal oblique lophid is comprised of the hypoconid and the long posterolophid which terminates in the disto-lingual corner of the tooth. There is a low link

between the middle and distal oblique lophids near the centre of the crown where the anterior arm of the hypoconid extends mesially to join the end of the ectolophid. The sinusid is v-shaped in occlusal outline and is oriented obliquely in the tooth row, opening mesio-buccally. The sills between the metaconid and the entoconid and between the entoconid and the buccal end of the posterolophid are quite low, such that the two lingual basins are open lingually until the crown is quite deeply worn. The d/4 has three sub-equal roots which are circular in section, one in the midline anteriorly and two arranged side-by-side posteriorly.



**Figure 28.** Stereo occlusal view of a left mandible of *Tufamys woodi* from locality EC 7 containing d/4-m/2 and the empty alveolar capsule of m/3 (scale : 1 mm).



**Figure 29.** Unworn left lower molar of *Tufamys woodi* from fossil concentration EC 10, Namibia. A) stereo lingual view, B) stereo occlusal view, C) stereo buccal view, D) distal view, E) mesial view (scale : 1 mm).

The m/1 has a more rectangular occlusal outline than the d/4 and it is somewhat higher crowned (Figs 25, 27-30). The metaconid is isolated, with a weak metalophulid I, and there is a slit between it and the protoconid. The layout of the protoconid, entoconid, hypoconid and the associated lophids is similar to than seen in the d/4. The v-shaped sinusid is like that in the d/4, and because the posterior arm of the

metaconid is weakly developed and the pre-entocristid and post-entocristid are poorly expressed, the mesial and distal basins are wide open lingually, even in moderately worn teeth. The anterior arm of the hypoconid crosses towards the ectolophid thereby linking the distal oblique lophid to the middle oblique lophid in the centre of the crown.



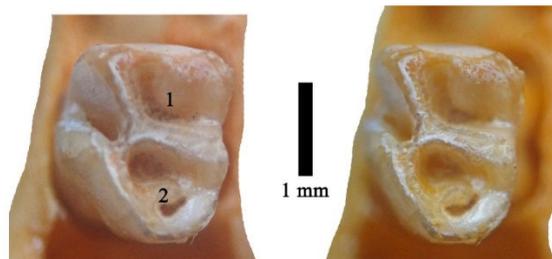
**Figure 30.** Stereo occlusal views of left mandibles of *Tufamys woodi* from localities EC 7 (A) and EC 6 (B). A) fully adult individual with deeply worn d/4 and m/1, heavily worn m/2 and moderately worn m/3; B) juvenile individual with lightly worn d/4 and m/1 (scales : 1 mm).

The m/2 is similar in dimensions and construction to the m/1 but is slightly taller than it (Figs 25, 28, 30, 31).

The m/3 is on average slightly shorter than the m/2 and the distal half of the crown is appreciably narrower than the mesial half (Figs 30, 32), but the height of the crown is similar to that of the m/2, although the buccal side is not as high-crowned as that of m/2. Overall, the basic morphology of the tooth is like that of the m/2 with comparable layout of the main cusps (protoconid etc.) and lophids.

The toothrow as a whole has a straight lingual edge, but the buccal edge is convex.

A juvenile mandible from EC 7 has an incisor alveolar section with a broad flat labial surface characteristic of *Tufamys woodi*, but it possesses a lightly worn m/2 which shows some unusual features. In other respects the specimen is typical of the species. The posterior part of the protoconid is swollen to a greater extent than is usually the case in the species, and there is a distinct cusplet in the disto-lingual basin linked to the posterolophid by an isthmus (Fig. 31).

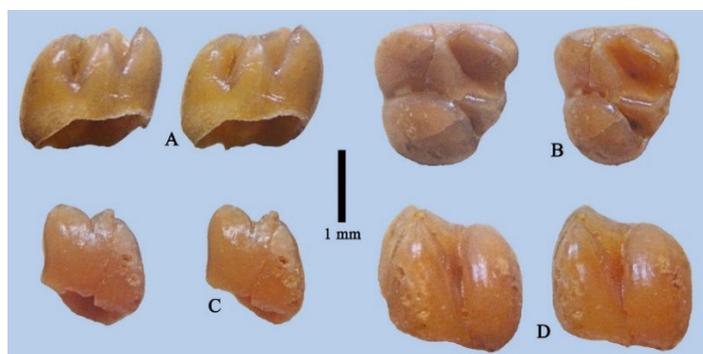


**Figure 31.** Stereo occlusal image of left m/2 in mandible EC 7 of *Tufamys woodi*, showing unusual morphology of the lingual cusps. 1) swollen distal face of the metaconid, 2) accessory cusplet in the postero-lingual basin emanating from the posterolophid (scale : 1 mm).

**Table 2.** Measurements (in mm) of lower cheek teeth of *Tufamys woodi*. All teeth are in mandibles. N.B. Heavily worn d/4s are very short. Measurements of the teeth of the type specimen are not given because they are heavily worn (lt – left, rt – right).

Catalogue	Tooth	Mesio-distal length	Bucco-lingual breadth
EC 6'13	d/4 lt	1.8	1.5
EC 7'14	d/4 lt	2.1	1.6
EC 9	d/4 lt	2.1	1.5
EC 7	d/4 lt	1.7	1.3
EC 7	d/4 lt	2.1	1.5
EC 9	d/4 lt	2.0	1.7
EC 10'14	d/4 lt	2.0	1.5
EC 9	d/4 rt	2.0	1.5
EC 7	d/4 rt	1.8	1.5
EC 10'14	d/4 rt	2.5	1.5
EC 6'13	m/1 lt	2.1	1.8
EC 7'14	m/1 lt	2.0	1.8
EC 9	m/1 lt	1.9	1.7
EC 7	m/1 lt	1.6	1.8
EC 7	m/1 lt	1.9	1.7
EC 9	m/1 lt	2.0	1.7
EC 10'13	m/1 lt	2.0	1.8
EC 10'14	m/1 lt	1.8	1.7
EC 10'14	m/1 lt	2.1	1.8
EC 9	m/1 rt	1.9	1.9

EC 7	m/1 rt	1.8	1.7
EC 7'14	m/2 lt	2.0	1.8
EC 7	m/2 lt	1.9	1.9
EC 7	m/2 lt	2.1	1.8
EC 9'14	m/2 lt	1.8	2.0
EC 9'14	m/2 rt	1.8	2.1
EC 9	m/2 rt	1.8	1.9
EC 7	m/2 lt	2.1	1.7
EC 7	m/2 rt	1.8	2.1
EC 7	m/3 lt	1.8	1.8
EC 9'14	m/3 lt	2.0	1.8
EC 9'14	m/3 rt	1.8	1.9
EC 9	m/3 rt	2.0	1.8
EC 7	m/3 rt	1.8	1.8



**Figure 32.** Stereo views of unworn left m/3 of *Tufamys woodi* from EC 9, Namibia. A) lingual, B) occlusal, C) mesial, D) buccal views (scale 1 mm).

### ***Post-cranial skeleton***

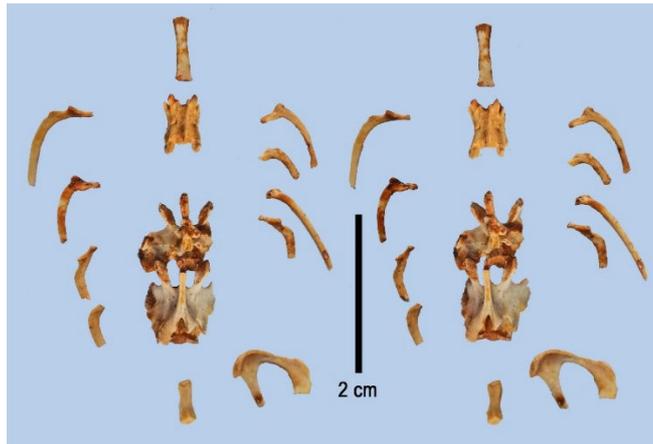
The descriptions which follow are of the bones associated closely with the holotype skull and considered to represent the same individual. Some of the bones were missing one or other end, and these missing parts are described on the basis of more complete specimens found at Eocliff which have the same morphology and dimensions as the broken specimens, as is pointed out in the figure captions. Associated with the skull there are several vertebrae,

including one caudal vertebra, a lot of ribs, part of a pelvis, and forelimb and hindlimb bones. The long bones and the calcaneum and talus are described in detail, because there is a higher degree of confidence that they belong to the holotype. The bones of the carpus, manus and pes are mentioned briefly. Two terminal phalanges are illustrated to complete the description, even though there is slight doubt about their attribution to *Tufamys*.

### ***Axial skeleton***

Several vertebrae and ribs, as well as a possible manubrium and part of a pelvis were found packed around the holotype cranium and even inside the oral cavity (Fig. 33). From a morphometric aspect there is nothing extraordinary about these bones, but they yield some information about the dimensions of the

rib cage, and the caudal vertebra indicates that *Tufamys* probably had a tail. The lumbar vertebrae are appreciably larger than the thoracic one, but this seems to be a primitive characteristic of rodents, found in *Paramys delicatus* for example (Wood, 1962).

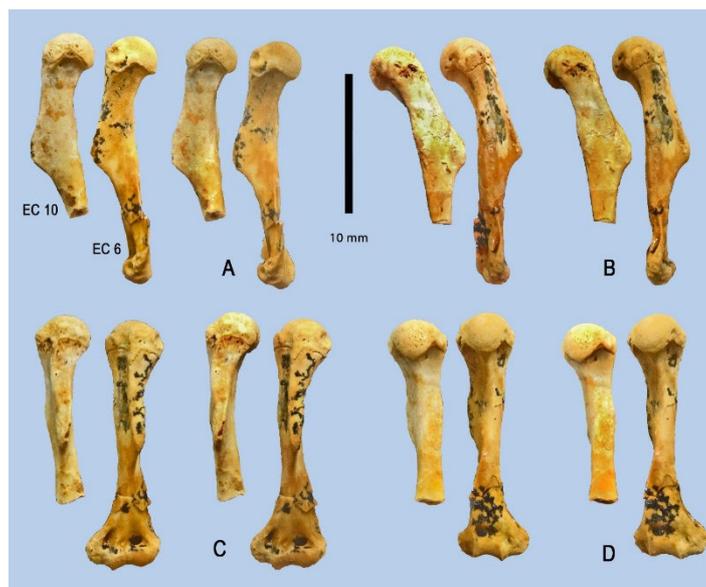


**Figure 33.** Stereo dorsal views of elements of the axial skeleton, rib cage and pelvis recovered packed around the oral cavity of the holotype cranium of *Tufamys woodi* from EC 10, Namibia. Top row is a possible manubrial bone, down the centre are a thoracic vertebra, two lumbar vertebrae and a caudal vertebra, ribs are arranged either side and at bottom right there is a fragment of the os coxa preserving part of the obturator foramen (scale : 2 cm).

### Humerus

There is a humerus associated with the holotype but it is missing the distal third of the bone (Fig. 34). To realise the description a complete specimen from EC 6 was selected which matches the holotype in its proximal parts. The humerus is a relatively short, robust bone with spherical head which leans posteriorly, thereby overhanging the diaphysis to a marked extent. There are prominent medial and lateral tuberosities at the level of the proximal epiphyseal suture which is closed but still discernible as a line surrounding the base of the head. The deltoid ridge is prominent and projects strongly anteriorly just above the

middle of the bone and is tallest at the deltoid tuberosity which has a concave lateral profile. The distal end is moderately expanded medio-laterally and there is an entepicondylar foramen. There are depressions above the distal epiphysis anteriorly (olecranon fossa) and posteriorly (coronoid fossa) with fenestration between them. There is a prominent lateral condyloid crest for the brachio-radialis muscle which extends up the diaphysis almost as far as the deltoid tuberosity. The cranial profile of the bone is rectilinear except where it bends anteriorly just beneath the head.

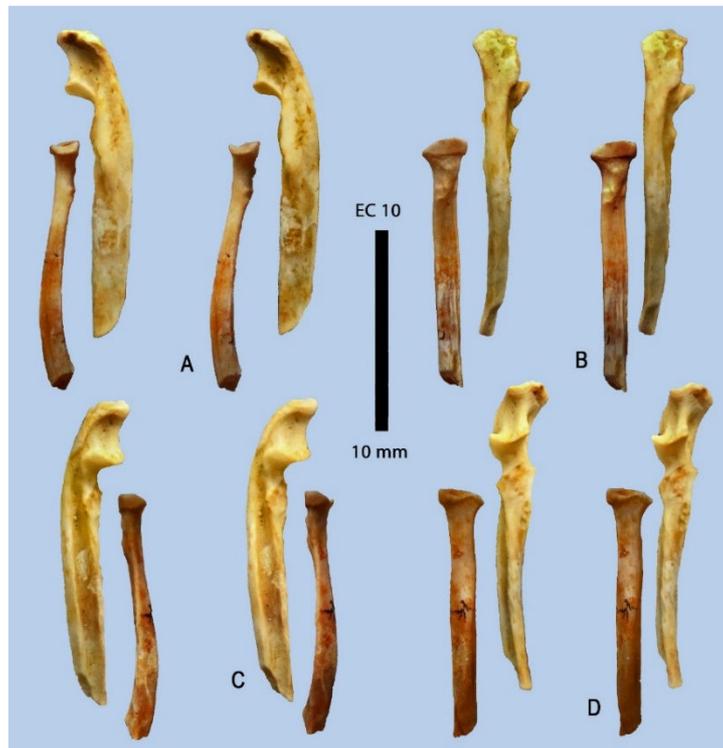


**Figure 34.** Stereo images of left humerus of *Tufamys woodi* from EC 10 (holotype) and EC 6. A) lateral view, B) medial view, C) cranial view, D) caudal view (scale : 10 mm).

### Radius and ulna

The ulna has a short, robust olecranon process, the caudal profile of which is bent over anteriorly towards its proximal apex (Fig. 35). Both the lateral and medial sides of the olecranon process are concave, the medial side more so than the lateral one. The sigmoid notch is deep proximally with a prominent anconeal

process, but distally there is almost no beak at the base of the notch, only a broad facet for the proximal end of the ulna. The shaft of the ulna is concave on its lateral side from the olecranon process down to the broken distal part and its surface is convex medially.



**Figure 35.** Stereo images of right ulna and radius of *Tufamys woodi* from Eocliff, Namibia, part of the holotype. A) medial view, B) caudal view, C) lateral view, D) cranial view. Both bones lack the distal ends (scale : 10 mm).

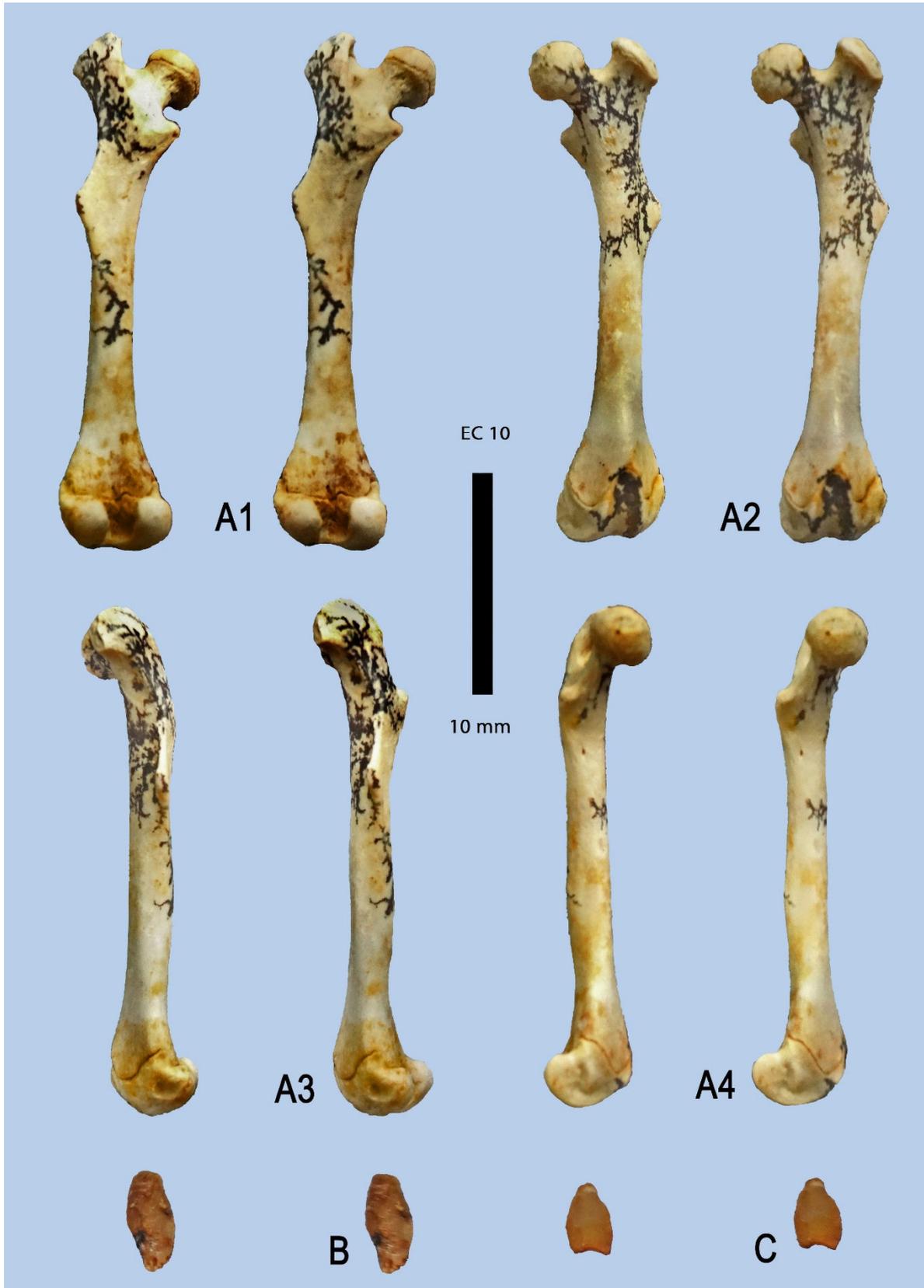
The radius is a delicate bone with an ovoid proximal articulation flattened internally where it contacts the ulna (Fig. 35). On the caudal aspect of the bone immediately beneath the proximal end there is a roughened raised

promontory of bone where the interosseous ligaments inserted. The bone is straight proximally but bends caudally towards the distal end.

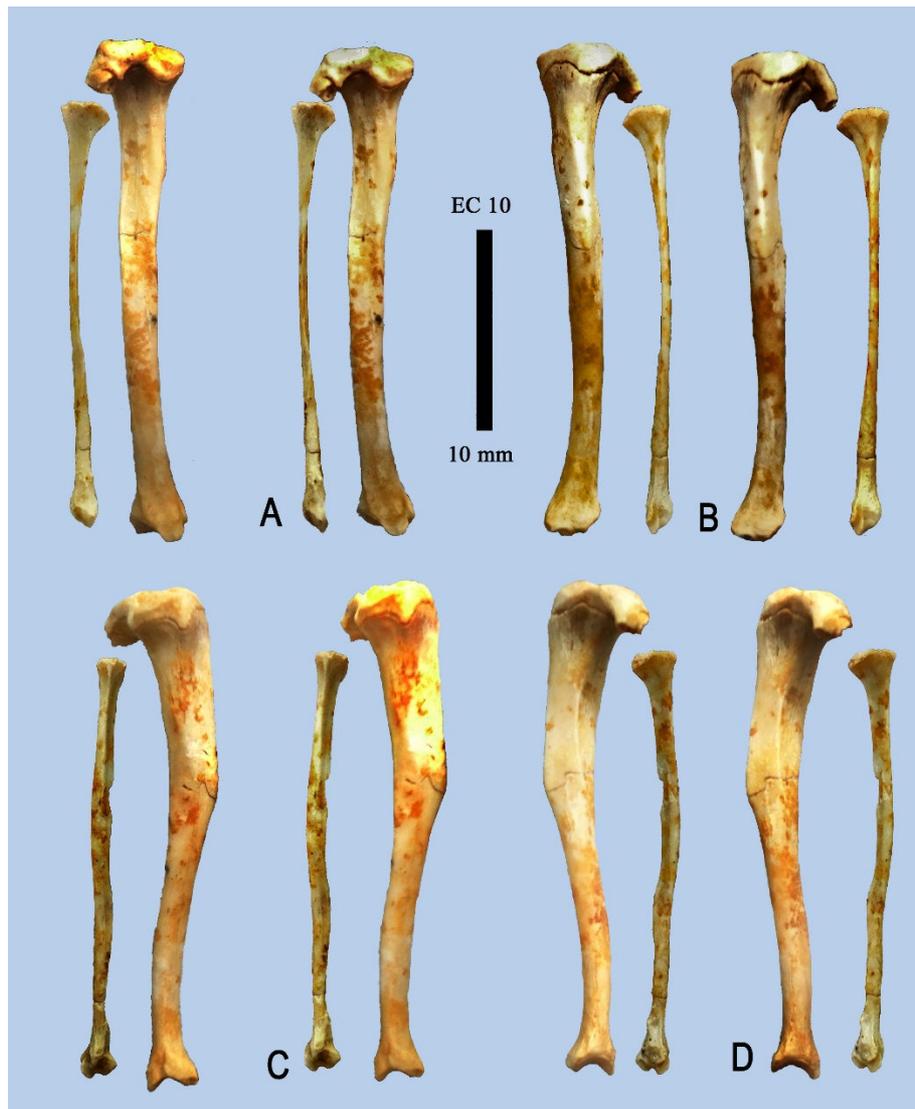
### Femur

The femur (Fig. 36) is substantially longer than the humerus (22.7 mm versus 17.9 mm). The greater trochanter is low, terminating proximally very slightly above the top of the head. The head is spherical with a prominent ligamentary fossette medially, the neck is short and robust, the digital fossa is short proximodistally and at its base it curves medially towards the lesser trochanter. The third trochanter forms a crest with the most elevated part about one third of the way down the

diaphysis. The distal epiphysis is relatively narrow and low cranially, the patellar groove being narrow and encroaching only a short way up the diaphysis. In caudal view, the two condyles are seen to be well separated from each other with a deep, broad intercondylar fossa between them. The distal epiphysis is unfused even in this relatively aged individual (M3/ heavily worn) and medially and laterally it has prominent ligamentary attachment fossettes.



**Figure 36.** Stereo images of A) left femur and B-C) two patellae from EC 10, Namibia, of the holotype specimen of *Tufamys woodi*. A1) caudal view, A2) cranial view, A3) lateral view, A4) medial view, B-C) articular views (scale : 10 mm).

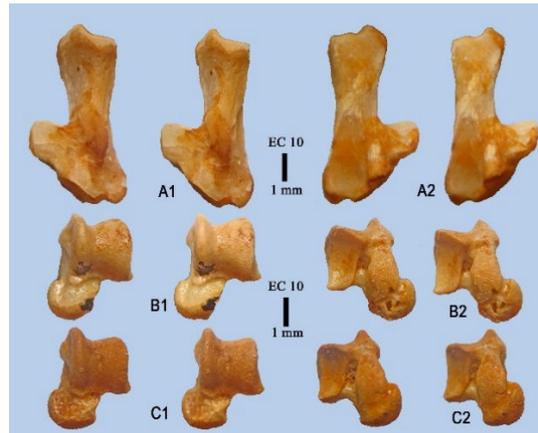


**Figure 37.** Stereo images of left tibia and right fibula (reversed) of the holotype individual of *Tufamys woodi* from Eocliff, Namibia. A) caudal view, B) cranial view, C) medial view, D) lateral view (scale : 10 mm).

### Tibio-fibula

In *Tufamys woodi* the tibia is the longest of the limb bones (24.3 mm versus 22.7 mm for the femur) and two fifths of the way down the shaft it is slightly bent towards the caudal side (Fig. 37). The bone is robust proximally and thins towards the distal epiphysis. The tibial plateau has low relief proximally, and caudally it overhangs the diaphysis to a large extent. The proximal end of the fibula articulates with the base of the lateral part of the tibial plateau. In most individuals the fibula is not fused to the tibia proximally, but in the aged holotype, it is attached on the left side but is free on the right. The distal epiphysis is gracile with weak beaks for the talar trochlea.

The fibula is a long delicate bone with prominent expansions proximally and distally (Fig. 37). It is unfused to the tibia except proximally in a few old individuals. Due to the curvature of the tibia and fibula diaphyses, there results an elongate, capacious interosseus space between them. The distal epiphysis (lateral malleolus) which contacts the talus and calcaneum is relatively robust, with clearly defined articular facets. It evidently played an important role in retaining the ankle joint in a stable configuration in extension as well as flexion.



**Figure 38.** Stereo images of left calcaneum (A) and left tali (B, C) of *Tufamys woodi* from Eocliff 10, Namibia. The calcaneum is part of the holotype individual. A1) dorsal view, A2) plantar view, B1), C1) dorsal views, B2), C2) plantar views (scale bars : 1 mm).

### Calcaneum

The calcaneum of *Tufamys woodi* is a robust bone with a short neck and low tuber (Fig. 38). The sustentaculum is angled, pointing medially and caudally at an angle of about 60° to the neck. The peroneal process is distally positioned and lies in line with the base of the sustentaculum, and with it, the cuboid facet faces cranio-medially at an angle of about 60° to the long axis of the neck. The ectal facet is sharp and extends to the mid-height of the neck. In dorsal view, there is a prominent but short ridge of bone in line with the medial edge of the neck, ending at the cuboid facet. The part of the bone distal to the base of the ectal facet is short.

### Talus

The talus has a somewhat dorso-plantarly flattened head with a short flat neck joining it to the trochlea (Fig. 38). The cranial ends of the two ridges of the trochlea are in line with each other, but the caudal ends are offset to a small degree, with the medial one projecting further caudally than the lateral one. This is the opposite of the situation in *Marmota* (Ginot *et al.* 2016). In plantar view, there is a large offset in height of the ectal facet from the sustentacular facet with a deep groove between them where the achilles tendon inserts. The ectal facet is separated from the articular surface of the head by a shallow groove and there is a short depressed area between the ectal facet and the base of the medial ridge of the trochlea.

**Table 3.** Measurements (in mm) of the long bones of *Tufamys woodi* from Eocliff, Namibia. Measurements are of the holotype unless indicated otherwise.

Bone	Anatomical part	Measurement	Comment
Humerus	Length	17.9	EC 6
	Proximal medio-lateral breadth	4.2	
	Proximal cranio-caudal diameter	3.6	
	Midshaft medio-lateral diameter	2.1	
	Midshaft cranio-caudal diameter	1.7	
	Distal medio-lateral breadth	5.4	EC 6
	Distal functional breadth	3.5	EC 6
Radius	Proximal cranio-caudal diameter	1.4	
	Proximal medio-lateral diameter	2.2	
	Midshaft cranio-caudal diameter	1.1	
	Midshaft medio-lateral diameter	1.3	
Ulna	Height of olecranon process on cranial side	2.7	
	Maximal breadth of sigmoid notch	2.0	
	Midshaft cranio-caudal diameter	1.8	
	Midshaft medio-lateral diameter	1.1	
Femur	Length from head to distal articulation	22.7	
	Cranio-caudal diameter of head	2.8	
	Medio-lateral breadth of distal epiphysis	4.8	
	Cranio-caudal height of distal epiphysis	4.0	
	Midshaft cranio-caudal diameter	2.0	
	Midshaft medio-lateral diameter	2.0	

Tibia	Total length	24.3	
	Proximal medio-lateral diameter	4.8	
	Proximal cranio-caudal diameter	4.0	
	Midshaft cranio-caudal diameter	1.5	
	Midshaft medio-lateral diameter	1.7	
	Distal cranio-caudal diameter	2.5	
Fibula	Distal medio-lateral diameter	2.7	
	Total length	21.3	
	Proximal cranio-caudal diameter	2.4	
	Distal cranio-caudal diameter	1.7	

**Table 4.** Measurements (in mm) of the calcaneum and talus of *Tufamys woodi* from Eocliff, Namibia. Measurements are of the holotype unless indicated otherwise.

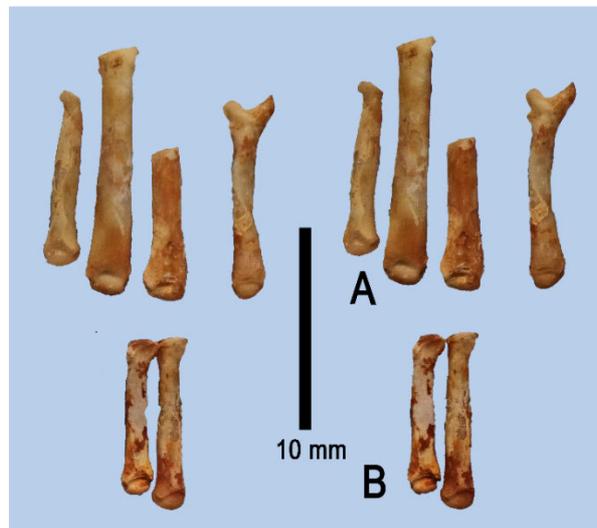
Bone	Anatomical part	Measurement	Comment
Calcaneum	Total length	6.1	
	Height of tuber, cranial part above the talar facet	2.8	
	Tuber shaft least medio-lateral diameter	1.5	
	Tuber shaft least cranio-caudal diameter	1.7	
	Greatest medio-lateral breadth of articular surface	3.5	
Talus	Total medio-lateral breadth	2.2	EC 10 Not directly associated with holotype
	Total proximo-distal length	3.6	EC 10 Not directly associated with holotype
	Medio-lateral diameter of head	1.8	EC 10 Not directly associated with holotype

### Metapodials and phalanges

There are eight metacarpals and six metatarsals associated with the holotype skull, and there are six first phalanges, ten second phalanges, and two third phalanges (Figs 39, 40). These fossils are tentatively attributed to the species on the basis of their dimensions and because they were found inside or close to the

oral cavity of the holotype. However, there are other rodent taxa at EC 10 to which these bones could belong, so we do not insist on their association with each other.

The first metacarpal is short and robust. The axial metacarpals are twice as long as the first one, and are also quite robust.

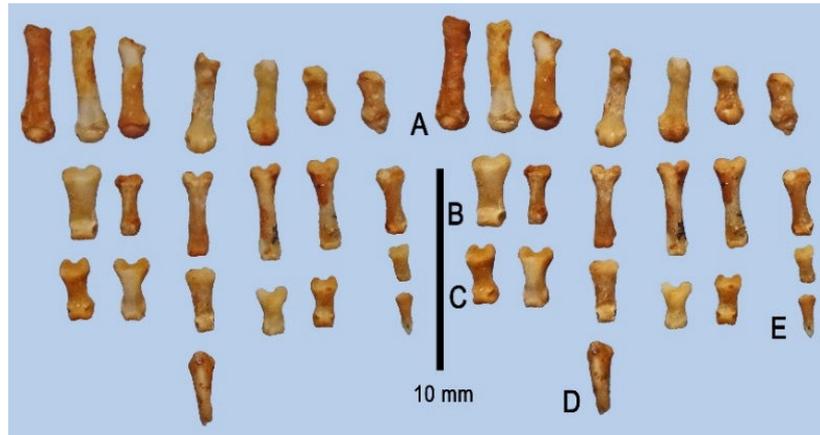


**Figure 39.** Stereo dorsal views of metatarsals found inside the oral cavity and packed close to the palate of the holotype of *Tufamys woodi* from EC 10, Namibia. A) 1st, 2nd, part of 3rd and 5th metatarsal, B) two metapodials of uncertain position (scale : 10 mm).

The 5th metatarsal has a projection extending proximo-laterally beyond the articular facet for the 4th metatarsal, much as in the paramyids *Paramys delicatus* and *Pseudotomus robustus* (Wood, 1962). The metatarsals are appreciably

longer than the metacarpals, as is generally the case in rodents.

The first and second phalanges are unremarkable in a primitive rodent context, resembling their counterparts in Paramyidae, for example (Wood, 1962).

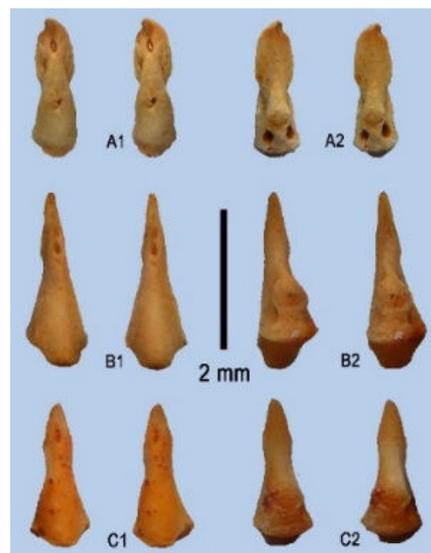


**Figure 40.** Stereo dorsal views of metacarpals and phalanges found packed around and inside the holotype cranium of *Tufamys woodi* from EC 10, Namibia. A) five axial metacarpals and two first metacarpals, B) six first phalanges, C) six second phalanges, D) large terminal phalanx, E) small spatulate terminal phalanx (scale 10 mm).

The third phalanges (Fig. 41) however differ from those of paramyids by the possession of a deep depression (or several depressions) on the dorsal ridge located towards the distal end of the bone and they show variable development of lateral flanges which impart a more or less spatulate form to the distal half to the bone. The development of depressions in the dorsal ridge and the splaying apart of the flanges could represent a nascent stage in the evolution of bifurcate phalanges as exemplified by the third phalanges of the extant cane rat, *Thryonomys swinderianus* (Onwuama *et al.* 2015).

A third phalanx from Eocliff found close to the skull of the holotype has a spatulate distal half with a prominent central dorsal depression separating two ridges which extend towards the distal end. Other specimens are more claw-like but show slight development of flanges with depressions along the dorsal ridge. It is likely that these phalanges come from different digits, of both the manus and pes.

The spatulate morphology of the terminal phalanges is suggestive of a digging behaviour.



**Figure 41.** Terminal phalanges from Eocliff EC 7 (top row) EC 10 (middle and bottom rows), Namibia, attributed to *Tufamys woodi*. A) has a spatulate distal half with a central dorsal depression, B) is longer and has a hint of a distal flange and a series of four dorsal depressions, C) is slightly spatulate with a dorsal depression. In all three types of phalanx the plantar tubercle is well developed and it overhangs large and deep medial and lateral fossae (scale : 2 mm).

### Tooth succession in *Tufamys woodi*

The Eocliff sample of *Tufamys woodi* is comprehensive enough to reveal that the anterior cheek tooth is not replaced during the life of the individual. There is a spectrum of maxillae and mandibles available which represent several different ontogenetic phases, from specimens with the first and second tooth in wear, but not the third, up to aged individuals in which the most distal cheek teeth (M3/, m/3) are deeply worn. In none of the specimens does the anterior cheek tooth show signs of replacement, it being the most deeply worn cheek tooth in all individuals examined in which the D4/ and d/4 were *in situ* (25 maxillae, 27 mandibles).

The extant cane rat, *Thryonomys swinderianus*, shows the same retention of the deciduous incisors and D4/-d/4 throughout life, and it shows the same relationship between the position of the radicular alveolar termination (capsule) of the upper incisors as that present in *Tufamys*, with this capsule lying above the D4/, thereby occupying the space that is, in other rodents which replace the D4/ with a P4/, occupied by the anterior quarter of the cheek tooth alveolar process. It is here postulated that the presence of the upper incisor alveolar capsule at the front of the cheek tooth alveolar process occupies the space where the P4/ would develop, and thereby prevents the P4/ from forming, although it does not affect the

development of the M1/-M3/ in the more posterior part of the cheek tooth alveolar process.

The termination of the incisor alveolus occurs above the D4/ in *Efeldomys* from the Early Miocene of Elisabethfeld, Namibia (Mein & Pickford, 2008) and the anterior cheek tooth is the most deeply worn in all the available material. Mein & Pickford (2008) reported replacement of the anterior cheek tooth, but a second look at the question indicates that this is probably not the case.

Van der Merwe (2000) described the situation clearly, employing a growth series of cane rat individuals that were scanned on a regular basis during ontogeny. It would thus appear that in the thryonomyids, the retention of the D4/ and d/4 into adulthood and senility has an enormously long geological history (at least 37 million years).

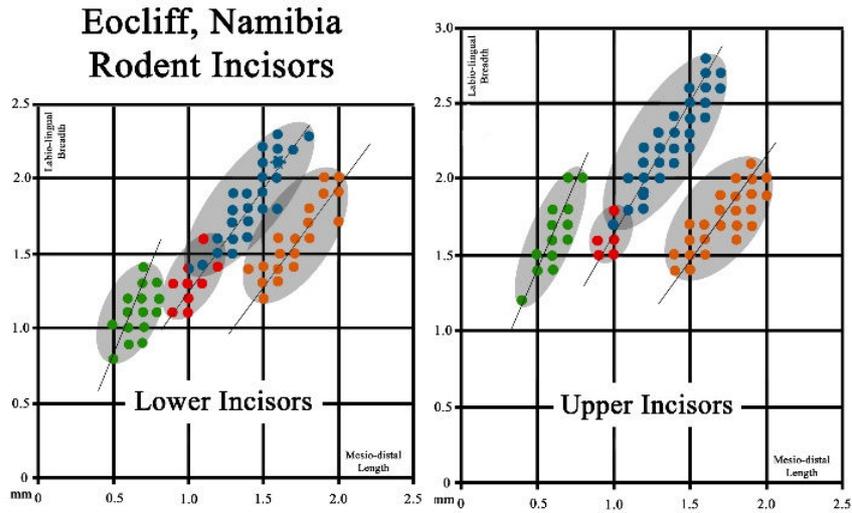
In other rodent families with cheek teeth that recall those of thryonomyids, such as Gaudeamuridae (Sallam *et al.* 2011) the D4/ and d/4 are replaced by a P4/ and p/4 respectively, but in this family the upper incisor capsule terminates in front of the cheek tooth alveolar process, and therefore does not interfere with the usual mammalian development pattern in which the posterior deciduous tooth is replaced by a permanent premolar.

### Bimodality in *Tufamys woodi*

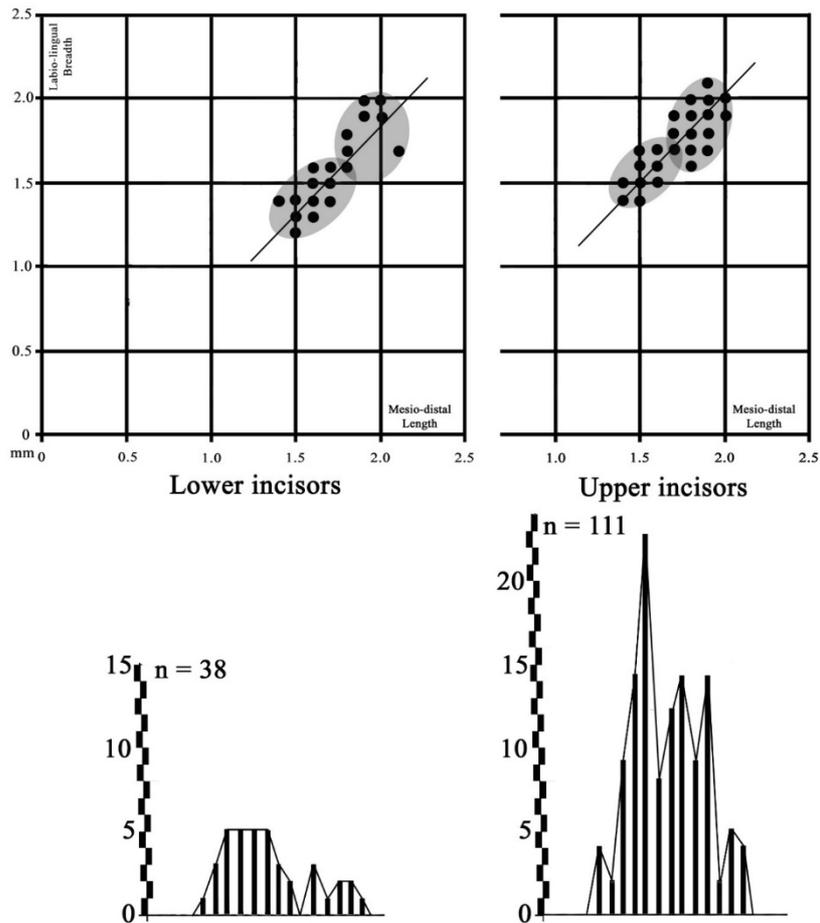
Bivariate plots of all the rodent incisors (n = 145 lower and 235 upper) from Eocliff indicate the presence of at least five groups (no incisors known for *Silicamys*), varying in dimensions and length-breadth proportions (Fig. 42). *Tufamys* incisors plot well off the regression lines for the other incisors, reflecting their mesio-distally broader dimensions. Lower incisors of three taxa of phiomysids plot along a

separate regression line, and there is a third group of tiny rodents with mesio-distally slender but labio-lingually broad incisors.

Mesio-distal length and labio-lingual breadth measurements were taken of 111 upper incisors and 38 lower incisors of *Tufamys woodi* in order to document metric variation in the incisors of the species (Figs 43-44).



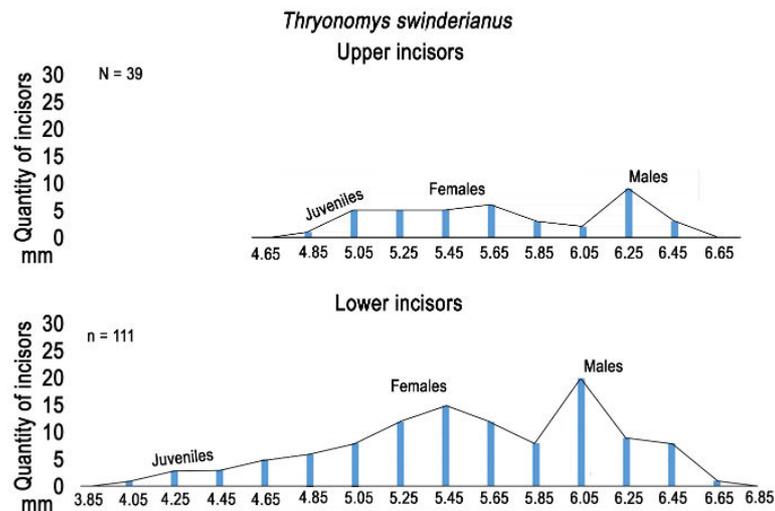
**Figure 42.** Bivariate (length-breadth) plots of 145 lower incisors and 235 upper incisors of rodents from Eocliff, Namibia. Orange dots - *Tufamys*; blue dots - *Prepomonmys* spp. and large phiomyid/diamantomyid (blue star is GSN SN 8'08, the type specimen of *P. bogenfelsi*); red dots - small phiomyid (A in Table 1); green dots - tiny rodent (B in Table 1). There is some overlap in dimensions between some of the groups. No incisors of *Silicamys* have been recognised in the collections.



**Figure 43.** Bivariate plots of mesio-distal lengths and labio-lingual breadths of lower and upper incisors of *Tufamys woodi* from Eocliff, Namibia. Both show an overlapping bimodal distribution suggestive of sexual bimodality in the species (many of the smaller specimen are juveniles). The lower histograms show the number of incisors at points along the regression lines.

Measurements of the mesio-distal length and labio-lingual breadth of the upper and lower incisors of *Tufamys woodi* yield a bimodal distribution for both teeth. It is likely that this could be due to a combination of two factors :- 1) the inclusion of sub-adults in the sample (teeth of sub-adults are smaller than those of fully adult individuals), and 2) the presence of sexual bimodality, with females having, on average, slightly narrower and shorter incisors than males. This is why the peak of smaller

individuals (the left part of the histograms in Fig. 43) is taller and the spread is broader than the peaks for the larger individuals. There are no morphological differences between the smaller and larger incisors and there is evidently slight overlap in the range of measurements of the two groups. No morphometric differences were observed in the rest of the dento-gnathic system of *Tufamys*. The variation of the incisors in *Tufamys* is compared with that in an extant species, *Thryonomys swinderianus* (Fig. 44).



**Figure 44.** Histogram of mesio-distal length measurements of upper and lower incisors of extant *Thryonomys swinderianus* from Iriri, Napak, Uganda, showing bimodal distribution and a narrow tail, interpreted in terms of sexual bimodality with a contribution from the inclusion of juveniles in the sample.

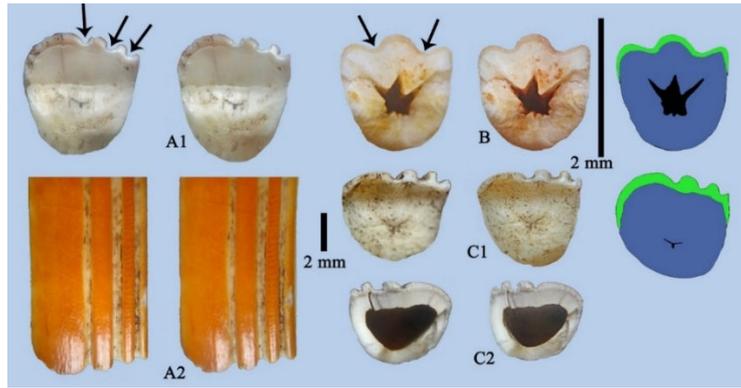
Some other rodents such as *Thryonomys swinderianus* (the extant Cane Rat) have bimodal distribution of their upper and lower incisor measurements (personal observation of 39 upper incisors and 111 lower incisors of cane rats from Iriri, Napak, Uganda, obtained in one field season from local children who hunt them

for food) (Fig. 44). There are some differences in mandibular dimensions of cane rats, females being smaller than males, and there are some morphological differences, notably in the position of the mental foramen which is more caudally positioned in the female than the male (Parés-Casanova *et al.* 2015).

### Incisor morphology in *Tufamys* and *Thryonomys*

The presence of grooves in the upper incisors of *Tufamys* and *Thryonomys* warrants closer examination in order to determine whether the structural basis is homologous in the two taxa or

not (Fig. 45). Given that Tufamyidae seems to be the sister-group of Thryonomyidae, a closer look at the incisor morphology is necessary to see what the possibilities are.



**Figure 45.** Comparison of upper incisors of *Thryonomys swinderianus* (A and C) and *Tufamys woodi* (B). A1) apical view of right DI2/ of *Thryonomys*, A2) labial view of same tooth (apex pointing downwards), B) naturally broken surface of an upper incisor of *Tufamys*, C1) apical view of right DI2/ of *Thryonomys*, C2) pulp cavity in the same specimen. The dentine-enamel junction (dej) in *Thryonomys* is evenly curved with very slight undulations, that of *Tufamys* is strongly undulating. The dej morphology is reflected through to the pulp cavity, which has a single anterior process in *Thryonomys*, the ensemble being Y-shaped (best seen in the apical views) whereas in *Tufamys* it is doubled, producing a W-shaped cavity. At the right there are sketches of the dej in *Tufamys* above, and *Thryonomys* below (green - enamel, dark blue - dentine, black - pulp cavity) (scales : 2 mm).

The differences between the incisors of *Thryonomys* and *Tufamys* are striking. In the Cane Rat, the grooves in the labial surface of the DI2/ are incised into the enamel, meaning that the enamel thickness at the grooves is much less than it is between the grooves. In *Tufamys* in contrast, the enamel thickness remains the same throughout the mesio-distal extent of the tooth. The dentine-enamel junction (dej) is almost straight in *Thryonomys*, with very slight undulations near the grooves, but in *Tufamys* the dej undulates markedly. Thus the underlying nature of the grooves or channelling in the upper incisors is radically different in *Thryonomys* and *Tufamys*: incision into the enamel in the Cane Rat, and undulations of the dej in *Tufamys*.

From this it is concluded that incisor channelling in *Thryonomys* and *Tufamys* are not homologous structures, but evolved by separate pathways.

### Behavioural implications of the *Tufamys* remains

The cranial, dental and post-cranial skeleton of *Tufamys woodi* is complete enough to indicate some aspects of its behaviour, including locomotion and diet. Study of the inner ear is under way with Dr Matt Mason, Cambridge University, so it will not be discussed herein, except to note that the otic bullae are large and inflated, dominating the posterior part of the skull. An interesting point about the cranium is that the occipital condyles are positioned in between the distal ends of the

These differences in dej are carried through into the dentine as shown by the different outlines of the pulp cavities (Y-shaped in *Thryonomys* : W-shaped in *Tufamys*).

Kraatz *et al.* (2013) described a thryonomyid from Late Miocene deposits of the Arabian Peninsula, *Protohummus dango*. The upper incisor has two grooves arranged either side of a central ridge much as in *Tufamys*, the main difference being the less undulating dej. The lower molars have similar basic morphology as those of *Tufamys*, but the species is considerably larger.

Similar upper incisor morphology is reported for *Paraulacodus indicus* from Chinji levels (Late Middle Miocene) of Pakistan (Black, 1972) but the available information does not indicate whether the dej undulates as in *Tufamys*, or not, as in *Thryonomys*.

bullae. In other primitive rodents such as *Paramys*, the condyles are behind the rear of the bullae (Wood, 1962). This suggests either that the rear of the skull in *Tufamys* was in the process of bending forwards, implying shortening of the back of the skull and its twisting ventrally, or that the bullae were getting larger and projecting further to the rear than is the case in *Paramys*.

The incisors of *Tufamys woodi* catch our attention. The lower ones are broad with a flat

labial section and the upper ones are mesio-distally broad and have a central ridge bordered by longitudinal channels. Broad incisors occur in many rodents that burrow in the ground, such as *Bathyergoides* Stromer (1922), *Renefossor* Mein & Pickford (2008), bathyergids in general (Lavocat, 1973), geomyids (Coues, 1875), *Thryonomys* (Woods, 1984) and hystricids (Woods & Kilpatrick, 2005) among others.

The post-cranial skeleton of *Tufamys* appears to be rather generalised and overall quite primitive in proportions, much as that of *Paramys* (Wood, 1962) yet, if the association of bones is correct, its terminal phalanges show indications of developing a robust spatulate distal half as in many burrowing mammals. In

addition, the dorsal ridge is marked by a central depression or depressions which suggest that the apex of the bone is in the process of bifurcating, as in the terminal phalanges of *Thryonomys*, for example, but that the splitting process in *Tufamys* is in a nascent phase.

From this it is inferred that *Tufamys* may have been a burrowing rodent, although it had not yet developed the highly specialised post-cranial and cranial adaptations of dedicated fossorial rodents such as bathyergids, but was more like the situation in marmots (Svendsen, 1976) and other rodents that burrow in soft soils but which also spend much time foraging on the land surface.

### Links to South America

The Eocene rodents from Eocliff invite comparisons with South American taxa. For example, the species *Changquin woodi* Vucetich *et al.* 2014, from the Late Oligocene of Patagonia, has lower molar cusp layout that resembles that of *Tufamys*, but its cheek teeth are considerably more hypsodont. The upper incisor of *Changquin* has not been described.

The species *Canaanimys maquiensis* Antoine *et al.* 2011, has lower molars that recall those of *Tufamys* in general but the d/4 has a liaison between the metalophulid II and the anterior

pair of cuspids, which is absent in *Tufamys*, and the lower molars have a well-formed metalophulid II, also absent in the Namibian form.

The possibility therefore exists of phylogenetic relationships between the Eocene rodents of Namibia and the Palaeogene and Neogene ctenohystricans of South America.

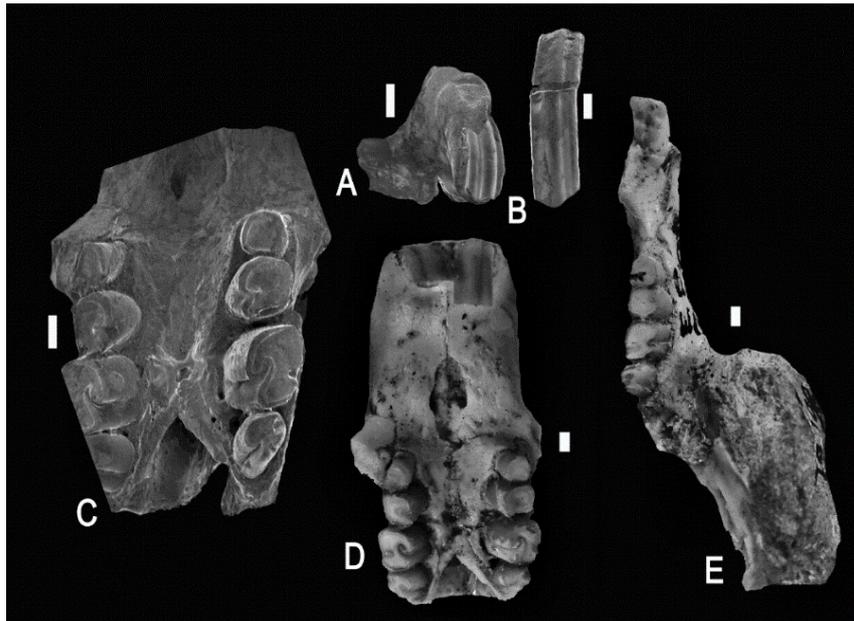
When all the rodents from Eocliff have been studied, a general comparison with South American rodents would be desirable.

### Discussion

*Tufamys* provides an interesting challenge to rodent systematics and phylogenetics. It shares some dental and cranial features with genera attributed to Gaudeamuridae (Sallam *et al.* 2011), Thryonomyidae (this paper) and fossils previously misattributed to Bathyergidae (*Efeldomys* in Mein & Pickford, 2008). It also has some dental resemblances to Renefossoridae (Mein & Pickford, 2008) but is cranially very divergent from Bathyergidae *sensu stricto*.

*Tufamys* is close to *Thryonomys* in several cranio-dental features, notably the low coronoid

process of the mandible, the posteriorly prolonged angular process of the lower jaw, the flat labial section of the lower incisor, the presence of channels in the upper incisors (albeit arranged differently in the two genera), the orthodont upper incisor with the radicular capsule located immediately above the roots of the D4/, the morphology of the cheek teeth, the form and position of the incisive foramina, the anteriorly invaginating posterior choanae, and the vast infra-orbital foramina among others.



**Figure 46.** Cranio-dental remains of *Efeldomys loliae* from the Early Miocene of Elisabethfeld, Namibia, showing the channelled morphology of the upper incisors (A, B, D), the broad, flat labial surface of the lower incisor (E) and the posterior choanae extending anteriorly as far as the rear of M2/ (C, D) all of which are features found in *Tufamys woodi* from the Eocene of Eocliff. The cheek teeth of *Efeldomys* are much simplified, have different interdental proportions and are more hypsodont than those of *Tufamys* (images from Mein & Pickford, 2008) (scales : 1 mm).

*Tufamys* resembles *Efeldomys* in that the orthodont upper incisors are almost morphologically identical in the two genera (Fig. 46), and they both have large infraorbital foramina and posterior choanae invaginating anteriorly to the level of the M2/. However, interdental proportions of their cheek teeth differ greatly, those of *Efeldomys* resembling the cheek teeth of Bathyergidae in general, which is why Mein & Pickford (2008) included *Efeldomys* in this family despite the presence of channelled upper incisors, large infraorbital foramen and low coronoid process in the mandible, all of which are features unknown in other bathyergids. The discovery of *Tufamys* prompts a revision of this classification, and it is considered to be more likely that *Efeldomys* is not a Bathyergidae, but that it converged in some features towards this family, notably in the cheek tooth morphology. It is here included in a new family of rodents, Tufamyidae.

There are some features shared between *Tufamys* and *Renefossor* including large infraorbital foramina and simple molar morphology but there are significant differences such as the position of the upper incisor alveolar capsule which terminates above the M3/ in *Renefossor* (Mein & Pickford, 2008). The back of the skull is also highly divergent in these two genera.

The lower dentition of *Neosciuromys* from the Early Miocene of Namibia (Mein & Pickford, 2008) recalls that of *Tufamys*, but the upper dentition shows a number of significant differences, such as the presence of a short mesoloph which partly infills the metaflexus. In addition, *Neosciuromys* has more than twice the dimensions of *Tufamys*.

As for the family Gaudeamuridae, the main resemblance to *Tufamys* lies in the morphology of the cheek teeth, although teeth of *Tufamys* are lower crowned and have fewer accessory cusps and crests than those of *Gaudeamus*, but in many other cranio-dental features the genera *Gaudeamus* and *Tufamys* are vastly different. Upper incisors of *Gaudeamus* are mesio-distally narrower than those of *Tufamys*, they show no sign of channelling, their labial profile is rounded rather than flat, and the radicular capsule does not lie immediately above the D4/ but terminates anterior to the alveolar process of the cheek teeth (Sallam *et al.* 2011). The lower incisors of *Gaudeamus* are narrow and their labial profile is rounded, the coronoid process of the mandible is tall and recurved distally, the posterior elongation of the angular process is weak (Fig. 47), and the invagination of the posterior choanae between the upper tooth rows is less advanced anteriorly than in *Tufamys*.

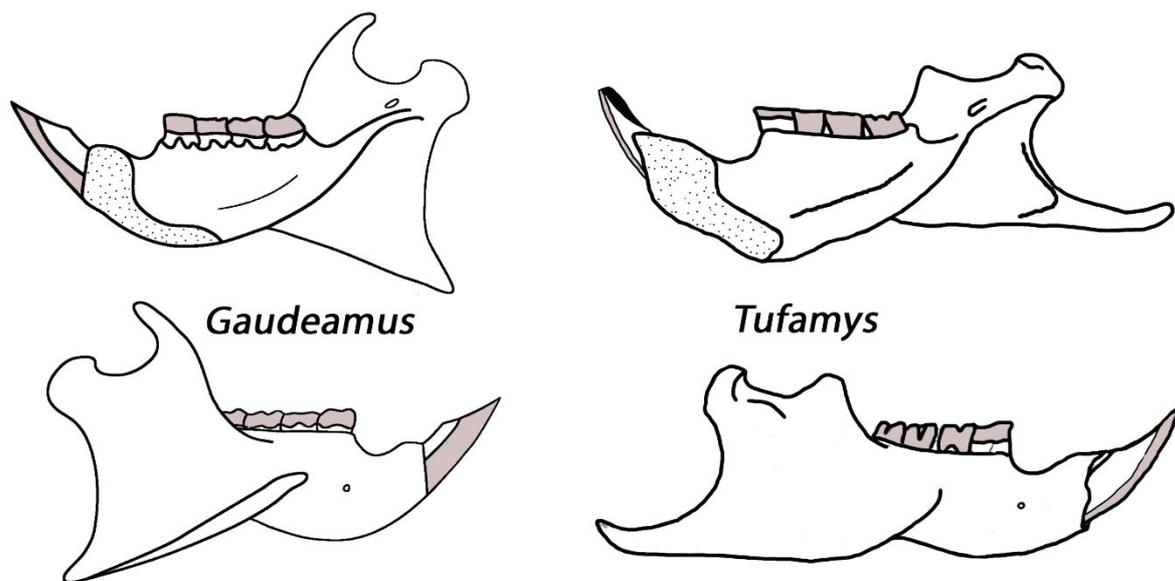
From this it is concluded that *Tufamys* is much more distantly related to Gaudeamuridae than it is to Thryonomyidae, and that resemblances to Bathyergidae are due to convergence rather than to proximally shared evolution.

Despite the overall morphological resemblances between the craniodental and postcranial elements of *Tufamys* and *Thryonomys*, the manifest differences in incisor morphology and body dimensions, suggest that these taxa belong to distinct families. The new family Tufamyidae is accordingly created to include *Tufamys* and *Efeldomys*, this family being in a sister-group relationship to Thryonomyidae, with Gaudeamuridae more distantly related, and Bathyergidae even more remotely positioned.

Judging from its cheek-tooth morphology, *Efeldomys* appears to have had a similar diet to Bathyergidae, which is one of the reasons why Mein & Pickford (2008) included it in

Bathyergidae. However, the discovery of *Tufamys*, which has identical incisor morphology to *Efeldomys* as well as its hystricomorph infra-orbital morphology, the low coronoid process in the mandible, the posteriorly elongated angular process of the ramus, the complete unfused fibula (strongly fused distally in Bathyergidae) indicates that inclusion of *Efeldomys* in Bathyergidae is no longer tenable.

Thus, even if Tufamyidae are quite closely related to Thryonomyidae, it would appear that, by the late Eocene, a member of the family was already engaged on an evolutionary trajectory towards a subterranean lifestyle, only partly so in *Tufamys* as revealed by the general lack of burrowing specialisation in the post-cranial skeleton, but more completely so in Early Miocene *Efeldomys*, but in any case more so than extant members of the Thryonomyidae.



**Figure 47.** Comparison of right mandibles of *Gaudeamus* and *Tufamys*. *Gaudeamus* drawings modified from Sallam *et al.* (2011). Upper row : lingual views, lower row : buccal views. Note the differences in coronoid process development and the posterior elongation of the angular process, as well as the different contribution of enamel to the mesial and distal sides of the incisors. Note also the presence of p/4 in *Gaudeamus* and d/4 in *Tufamys* (not to scale).

### Conclusions

A partial skeleton of a hystricomorph, hystricognath rodent is interpreted to represent a new genus and species in a new family, Tufamyidae, which combines a relatively primitive post-cranial skeleton, akin to those of Paramyidae and Scuridae, with a specialised anterior dentition (channeled, orthodont upper

incisors) and cheek teeth similar in general plan to those of Thryonomyidae and Gaudeamuridae but without accessory cusplets and mesocones. It also shares cheek tooth similarities with Renfossoridae and some South American rodents. The new family contains *Tufamys* of Eocene age, and *Efeldomys* of Early Miocene

age, and it is interpreted to be in a sister-group relationship with Thryonomyidae.

The available fossil sample indicates that, unlike Gaudeamuridae, which replace the deciduous fourth molars with a permanent fourth premolar, tufamyids retained the D4/ and d/4 throughout life. The absence of replacement of the posterior premolar in Tufamyidae is likely to be related to the fact that the upper incisor alveolar capsule terminates immediately above the roots of the D4/, and has therefore occupied the space that, in other rodents such as Gaudeamuridae and Phiomyidae in which the incisor capsule terminates well in front of the alveolar process of the cheek teeth, is left free.

The post-cranial skeleton of *Tufamys* is unspecialised, resembling those of paramyids (Wood, 1962) and sciurids in general (complete fibula unfused to tibia for example) being radically different from those of Bathyergidae

and Pedetidae, for example, in which the distal third of the fibula is intimately fused to the tibia.

The morphology of the cheek teeth of *Tufamys* recalls those of Gaudeamuridae and Thryonomyidae in general, but the teeth lack the accessory cusplets and crests that occur in *Gaudeamus*, for instance (Sallam *et al.* 2011). What this means is that isolated cheek teeth of these three families can be difficult to distinguish from each other, especially when worn, causing difficulties in taxonomic identification analogous to those experienced by early researchers on ruminants when trying to sort out isolated cheek teeth of bovids, giraffids, cervids, tragulids, moschids and even camelids, or of researchers working on bunodont suoid cheek teeth (Pickford, 2016) where for nearly a century and a half, isolated teeth from five families were interpreted as belonging to only two families.

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