

Mandible of *Namahyrax corvus* from the Eocene Black Crow Limestone, Namibia

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Abstract: In 2019 an adult mandible of *Namahyrax corvus* was discovered during acid treatment of limestone blocks from Site A at Black Crow (Ypresian/Lutetian) Namibia. The specimen confirms the peculiar morphology of the symphysis already observed in a juvenile specimen from the same site and it reveals a reduced dental formula (tendency to suppress $i/3$, suppression of the permanent lower canine) and the presence of elongated diastemata between the $i/2$ and the $p/1$. The long gap between the incisors and the anterior cheek tooth indicates that food acquisition was distinct from mastication. The symphysis is weakly fused posteriorly despite the fact that in this individual the $m/3$ is fully erupted and in light wear.

Key words: Hyracoidea, Mandible, Palaeogene, Namibia, Dental morphology.

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Introduction

In May-June 2019, the Namibia Palaeontology Expedition processed 150 kg of limestone from Black Crow in the hope of obtaining additional fossils from these Eocene deposits.

The exercise was successful, with the discovery of several mandibles, a maxilla, isolated teeth and postcranial bones of tiny mammals, over 110 crocodile teeth, abundant scincid jaws and vertebrae and some bird bones, snail steinkerns and fruits of *Celtis*.

Among the larger fossils recovered is an adult mandible of *Namahyrax corvus*. The

specimen shows several features which indicate that the genus is remote from most other described hyracoids, showing several characters in the symphyseal parts which are unique in the order, and which in some ways suggest morphofunctional convergence towards sirenians. Among these is the presence of several prominent mental foramina with anterior grooves, a down-bending of the symphysis, retarded fusion of the symphysis, and the tendency to lose the $i/3$ and suppression of the permanent lower canine.

Geological and faunal contexts

The geological context of the Black Crow Limestone was described by Pickford *et al.* (2008a) and Pickford (2015a). The deposits comprise almost pure calcium carbonate : after acid attack of 150 kg of limestone the insoluble residue, including fossils, weighs less than 1 kg. This sample was collected at site A (Pickford, 2018a, fig. 1).

The abundance of crocodile teeth (112 specimens in 150 kg of raw material) and the presence of silicified plant root systems

indicates deposition in a freshwater swamp or a low energy fluvial backwater.

The associated fauna consists of freshwater fishes and crocodiles (Pickford, 2018b), land snails (Pickford, 2018a) squamates, birds and mammals (Pickford *et al.* 2008b; Pickford, 2015b, 2015c, 2015d, 2015d, 2018c).

The limestones are considered to date from the late Ypresian or early Lutetian (Pickford, 2018a, 2018b, 2018c).

Material and methods

150 kg of limestone were collected at Site A, Black Crow (Pickford, 2018a, fig. 1). Blocks were selected at random, and none of them showed evidence of fossils exposed on the surface.

After transport to Paris, the blocks were dissolved in formic acid (7%) without buffer (addition of calcium triphosphate buffer results in the formation of an insoluble residue that

greatly complicates subsequent search for fossils).

Once treated the insoluble residue was washed in freshwater for 24 hours and then dried. Fossils were then picked out using a low power stereo microscope and consolidated in

plexigum dissolved in acetone. Broken fossils were fixed with cyano-acrylate.

Images were obtained with a Sony Cybershot camera and treated with Photoshop Elements15 in order to improve contrast and eliminate unwanted background. Scales were added during treatment.

Dental nomenclature

Nomenclature of the lower cheek teeth of Hyracoidea is based on Rasmussen & Simons (1988) (Fig. 1).

The anterior premolars possess reduced trigonids, but many of the same morphological features that occur in the molars can be recognised, but are in vestigial states.

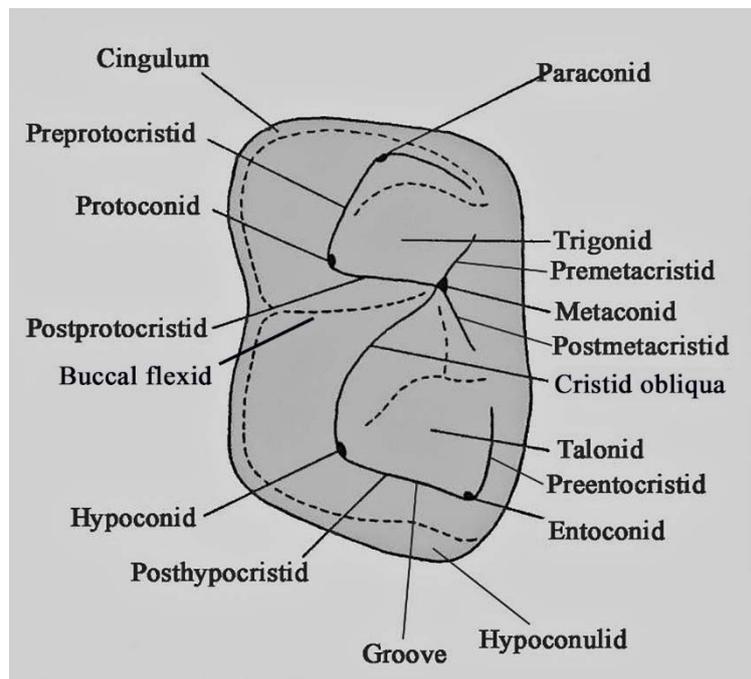


Figure 1. Nomenclature of hyracoid left lower molar modified from Rasmussen & Simons (1988).

Systematic Palaeontology

Order Hyracoidea Huxley, 1869

Genus *Namahyrax* Pickford *et al*, 2008b

Species *Namahyrax corvus* Pickford *et al*, 2008b

Description

GSN BC 1'19 is the symphysis and left mandible of a hyracoid slightly larger than that of extant *Procavia capensis* (the Rock Hyrax) (Figs 2-6). It contains the left p/1-m/3.

The specimen was broken in the matrix but has been successfully reconstructed and preserves the complete symphysis and the left body as far back as the base of the ascending

ramus. The jaw beneath the posterior molars is missing but from the m/1 anteriorly it is complete.

In lateral view four mental foramina are observed forming a linear group. The posterior one is beneath the junction between p/3 and p/4 at about mid-height of the ramus. The next one is beneath the p/1, the third is beneath the

diastema between the p/1 and the alveolus of i/3, whilst the fourth foramen lies in an elongated gutter beneath the i/3 alveolus. On the right side, the two anterior foramina are preserved, but there is no alveolus for the i/3.

Behind the m/3 the coronoid foramen is conspicuous and it passes backwards and downwards into the mandibular canal. The ascending ramus does not hide the rear of the m/3 in lateral view.

The symphysis is elongated and bends slightly downwards anteriorly such that the incisors would have emerged almost horizontally. The symphysis is compressed in the dorso-volar direction (only 4 mm thick) but deepens beneath the p/1 (ramus 16 mm deep). The ramus is 20.5 mm deep at the rear of m/1, indicating that the jaw as a whole deepens posteriorly.

In superior and ventral views the symphysis is observed to be solidly fused in its anterior

three quarters, but the posterior quarter is weakly fused or unfused. On the left side of the symphysis the alveolar margin between the alveoli for the i/2 and i/3 forms a long diastema, and there is a second diastema between the i/3 alveolus and the p/1. On the right side, in contrast, there is no sign of an alveolus for the i/3, so the diastema is continuous from i/2 to p/1 (the latter tooth is missing on this side). The gap measures 22.5 mm in length on the right and left sides.

There is no sign of mandibular swelling in this specimen, but it is noted that the mandibular canal is well-developed and there is cancellous bone above it between the roots of the lower molars.

The alveoli of the i/1s are smaller (l x b : 2.2 x 3.5 mm) and not as deep as those for the i/2s (l x b : 3.0 x 3.8 mm). The single alveolus for the left i/3 is steeply inclined and measures 2.5 x 1.7 mm.

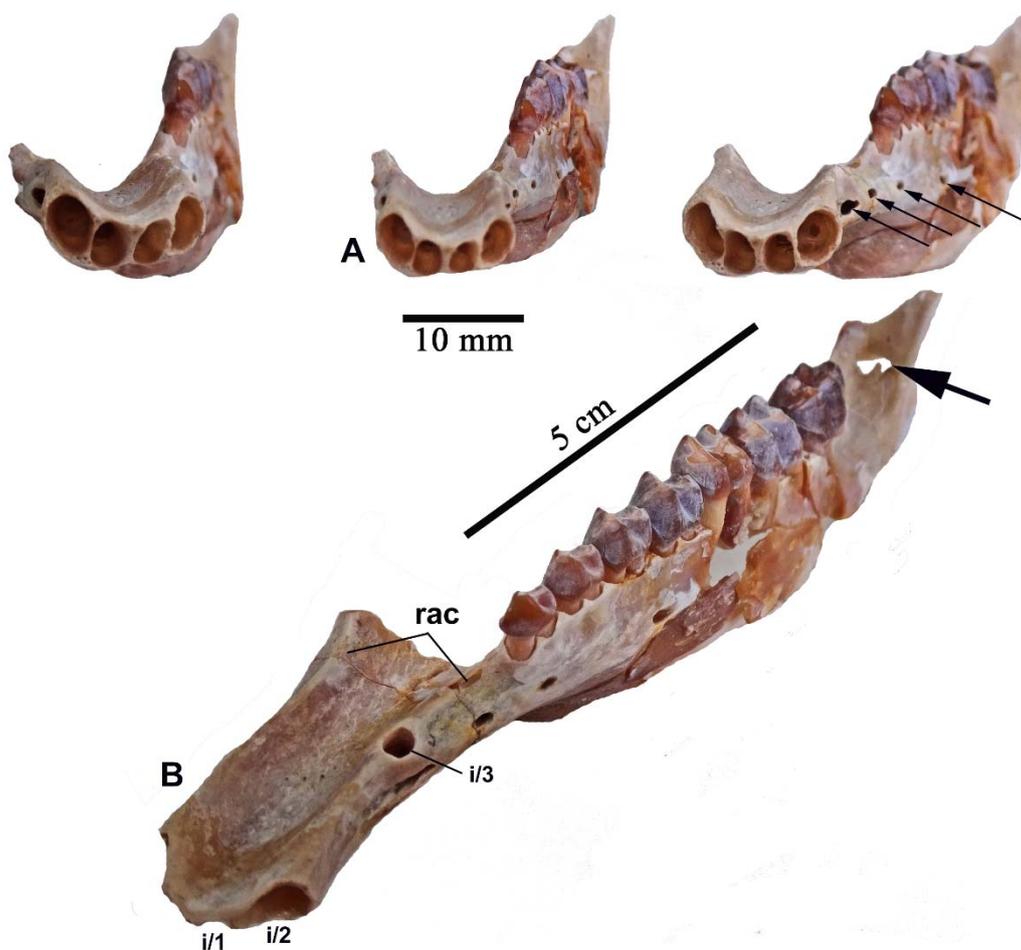


Figure 2. GSN BC 1'19, adult mandible of *Namahyrax corvus* from Black Crow, Namibia. A) stereo anterior views and B) an oblique lateral-occlusal view. Note in particular the alignment of four enlarged mental foramina (thin arrows in 'A'), the large coronoid foramen (thick arrow in 'B') and the absence of i/3 on the right side and the complete suppression of the lower canines (rac : resorbed alveoli of the lower canines).

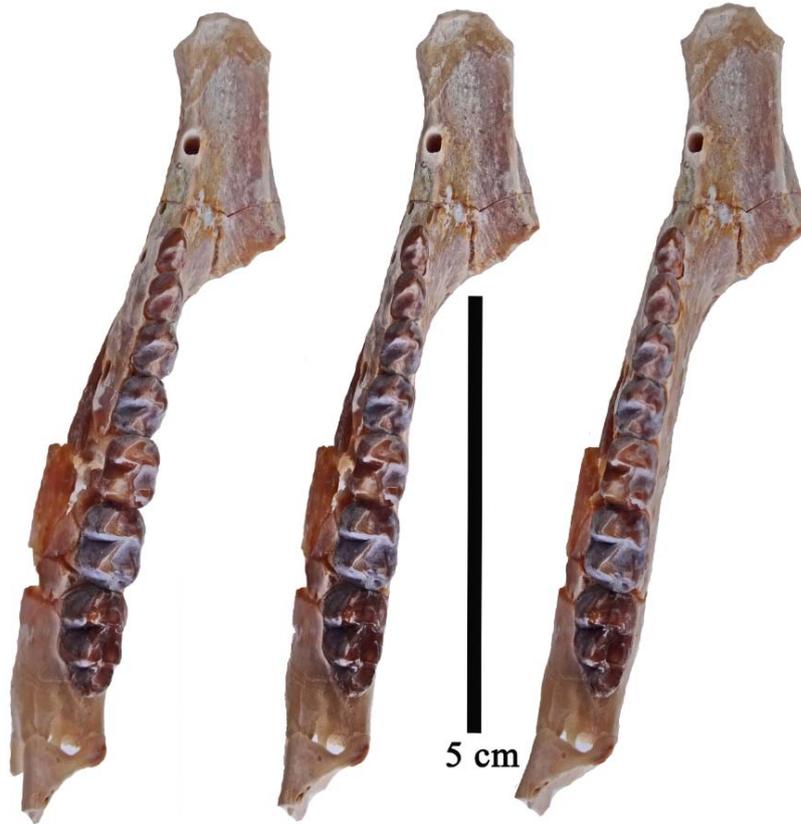


Figure 3. Stereo occlusal views of adult mandible, GSN BC 1'19, of *Namahyrax corvus* from Black Crow, Namibia.

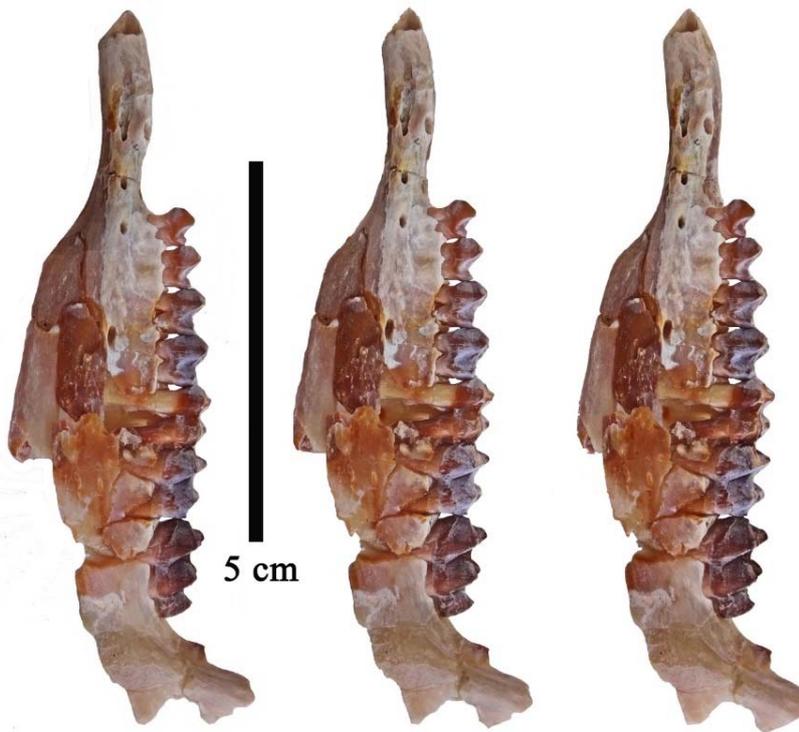


Figure 4. Stereo lateral views of GSN BC 1'19, mandible of *Namahyrax corvus* from Black Crow, Namibia.

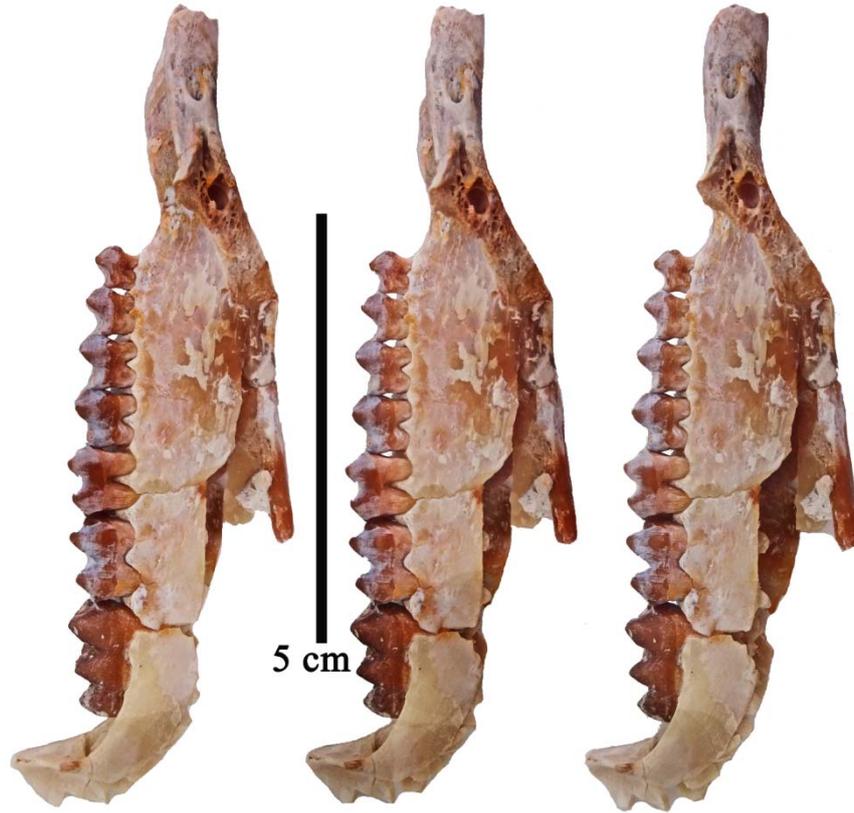


Figure 5. Stereo lingual views of left mandible, GSN BC 1'19, *Namahyrax corvus* from Black Crow, Namibia.



Figure 6. Stereo ventral view of GSN BC 1'19, mandible of *Namahyrax corvus*, from Black Crow, Namibia.

Table 1. Measurements (in mm) of the cheek teeth of GSN BC 1'19, *Namahyrax corvus*, from Black Crow, Namibia. In brackets are measurements of the corresponding teeth in GSN BC 10'08 (m/1 and m/2, paratype of *Namahyrax corvus*) and GSN NC 2'17 (p/2).

Tooth	Mesio-distal length	Bucco-lingual breadth
p/1 lt	5.0	3.1
p/2 lt	5.6 (5.6)	3.7 (3.4)
p/3 lt	6.1	4.5
p/4 lt	6.7	5.3
m/1 lt	8.2 (8.9)	6.1 (6.2)
m/2 lt	9.6 (9.8)	7.2
m/3 lt	13.0	7.3

The four premolars in the mandible each have two roots, the anterior molars have four and the m/3 has five. The p/1 is weakly molariform, the trigonid being reduced anteriorly and the talonid is low and narrow. The main cusp is comprised of coalescent protoconid and metaconid, with low relief postprotocristid and postmetacristid, a stronger preprotocristid and an almost obsolete premetacristid. The hypoconid is nearly in the centre-line of the crown, and shows a low cristid obliqua (prehypocristid) and a short, transverse posthypocristid. There is no hypoconulid and no sign of a buccal cingulum.

The p/2 is similar in morphology to the p/1 but is larger, and the cristids are more in evidence. There is no hypoconulid.

The p/3 is larger than the p/2 and is more molariform, having a better developed preprotocristid leading to the paraconid, the protoconid and metaconid are distinct from each other (even if still closely applied to each other) and the hypoconid, cristid obliqua and posthypocristid form a crescentic cusp.

The p/4 is even more molariform and is larger than the p/3 and the hypoconid is relatively taller, being about $\frac{3}{4}$ the height of the protoconid. The protoconid and metaconid are well-separated from each other apically, but are fused to each other over most of their height. The cristid obliqua rises anteriorly ending close to the apex of the metaconid. There is a low entoconid adjacent to the termination of the posthypocristid.

The m/1 is heavily worn, but shows classic hyracoid cusp layout, with distinct protoconid, metaconid, hypoconid and entoconid and a

small hypoconulid. There is a tiny remnant of a buccal cingulum in the buccal flexid.

The m/2 is less worn than the m/1 and serves as a model for interpreting the first lower molar. The protoconid has a preprotocristid that runs towards the midline of the crown anteriorly, where it ends in a low, weak paraconid. The postprotocristid is transversely oriented and joins the metaconid near its apex. The metaconid is smaller than the protoconid but is slightly taller than it. The premetacristid is subtle, the postmetacristid stronger. The hypoconid is the largest cusp, and has a well-formed cristid obliqua leading upwards towards the metaconid, and a low-relief posthypocristid leading backwards towards the hypoconulid. There is a weak buccal cingulum, and a distal cingulum either side of the hypoconulid.

The m/3 is like the m/2 but the hypoconulid and distal cingular complex are enlarged to form a distinct cusp at the rear of the tooth slightly to the lingual side of the midline. This extra cusp is supported by a fifth root which is coalescent with the root beneath the entoconid.

The entire lower cheek tooth row in GSN BC 1'19 is 54 mm long (premolars : 23 mm, molars : 31 mm), which compares with ca 60 mm for the length of the upper tooth row in the holotype of the species (P2/-M3/ ca 53.6 plus the length of the P1/ which is missing in the holotype). The difference in lengths of the upper and lower cheek tooth rows is probably not taxonomically significant, but it is noted that the upper tooth row in hyracoids is usually slightly shorter than the lower one.

Discussion

In 2008, the only mandible of *Namahyrax* available for study corresponded to a juvenile individual with the deciduous anterior cheek teeth and two permanent molars. The peculiar

shape of the symphysis, its lack of fusion and the presence of four mental foramina were pointed out as being unusual in a hyracoid context (Pickford *et al.* 2008b).

The new adult mandible underlines those observations and it shows the presence of other peculiar features such as the suppression of the canines and the absence of the right $i/3$ whereas the tooth was present on the left as shown by the deep single-rooted alveolus. The diastemata are elongated, as was already visible in the previously available specimen, and this feature reveals that there was probably a clear separation between food acquisition and food mastication. The presence of four well-developed mental foramina arranged in linear fashion along the side of the jaw from the $p/3$ forwards indicates the possibility of enhanced vascularisation and innervation of the lips and other soft tissues surrounding the symphysis.

An isolated hyracoid tooth from Black Crow was interpreted to be a $p/1$ by Pickford (2018c) but the newly available jaw indicates that the tooth in question is in fact a $p/2$. The height of the paraconid and the dimensions are revelatory.

The combined evidence suggests that *Namahyrax corvus* should indeed be included in Geniohyidae as thought by Pickford (2018c) even though there are some differences in mandibular morphology and dimensions between *Namahyrax* and *Geniohyus*. Both taxa show a slender mandibular symphysis which slopes anteriorly, and the presence of long diastemata between the incisors and the cheek teeth. Unlike *Namahyrax*, *Geniohyus* retains the $i/3$ and canines (Matsumoto, 1926) and it has a large lateral swelling of the lower jaw and a capacious mandibular chamber which is lacking in *Namahyrax*. But overall the similarities in the dentitions of the two genera indicate reasonably close phylogenetic affinities.

Conclusions

An adult mandible of *Namahyrax corvus* from Black Crow underlines the peculiar morphology of the symphysis and peri-symphyseal osteology of this buno-selenodont hyracoid. The presence of four prominent mental foramina and the great separation of the incisor battery from the cheek teeth suggest that facial elongation has occurred, with enhanced vascularisation and innervation of the lips and neighbouring soft tissues. All this suggests that food acquisition and mastication were separated from each other, and that mobile lips probably played an important role in food acquisition.

The lower permanent dental formula of *Namahyrax corvus* is now known to comprise 2-3 incisors ($i/3$ sometimes present sometimes absent) 0 canines, 4 premolars, 3 molars.

It is pointed out that some of the modifications in the symphyseal area and the tardy fusion of the symphysis observed in *Namahyrax* occur in sirenians such as *Metaxytherium*, a genus which also has rather buno-selenodont lower cheek teeth. *Metaxytherium* has taken recurving of the symphysis to extremes, whereas in *Namahyrax* the tendency is present but relatively weak when compared to *Metaxytherium*. Both genera also appear to have possessed well vascularised labial and surrounding soft tissues.

Whether these similarities denote phylogenetic proximity, or whether they point towards functional convergence remains to be examined.

Comparisons with the mandible of the brachyodont early Priabonian hyracoid *Dimatherium patnaiki* Barrow *et al.* (2010) from the Fayum, Egypt, are limited due the fact that the symphysis of that species is not preserved. The molars of *Dimatherium* are more elongated than those of *Namahyrax*, the hypoconulid of the $m/3$ is more buccally aligned than in the Namibian genus and the buccal cingulids are more strongly developed, confirming that they are distinct genera, despite being similar in overall dimensions ($m/3$ in *Dimatherium patnaiki* ranges in length from 12.3 to 14.8 mm and in breadth from 6.6 to 7.8 mm, whereas the same tooth in *Namahyrax corvus* measures 13.0 x 7.3 mm).

The symphysis of *Namahyrax* is peculiar in that it shows tardy fusion in this fully adult individual : the rear quarter of the symphysis is still not fully fused. It is noted that some of these features, such as ventrally recurved symphysis with late fusion and well-vascularised lips and peri-labial tissues occur in the Sirenia, but in this group they have been taken to extreme. Whether there is phylogenetic proximity between *Namahyrax* and sirenians seems doubtful, but the possibility of some degree of convergent evolution seems to be present.

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